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BENEATH BIODIVERSITY: FACTORS INFLUENCING THE DIVERSITY AND ABUNDANCE OF CANOPY MITES

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ABSTRACT. We examined the fauna inhabiting the leaves and small stems that compose the outermost canopy of Australian rainforests, and found them inhabited by an abundant and diverse fauna of mites (Acari), including scavenging-fungivores (especially oribatid mites), predators, and plant-parasites. Foliar mite species diversity and abundance was highest on structurally complex leaves, especially those with leaf domatia or erect tomenta. Tropical rainforest trees with hairs on their leaves averaged nearly three times as many species and five times as many individuals as those with smooth leaves. Some mite species were restricted to each leaf type. Subtropical rainforest trees and lianas with leaf domatia had twice as many species and three times as many mites as those on which domatia were blocked with bitumen paint. Patterns of mite abundance and diversity persisted through time with both foliar and stem-inhabiting mites increasing in abundance from the summer-rainy season through the autumn and winter dry periods. Oribatid mites also dominated the stem fauna, but the species composition on stems differed from that on leaves. Species turnover was high between samples within a tree, between tree species, and among sites for both leaf and stem mites, suggesting that the overall contribution of mites to canopy biodiversity is high.

INTRODUCTION

Mites (Acari) are among the smallest of terrestrial arthropods, so small that until recently their importance to the canopy fauna has been all but ignored (Walter & O'Dowd 1995). Soil and decomposing plant litter have traditionally been considered the centre of abundance of the Acari and the sources of most mite diversity (Krantz 1978, Dindal 1990). A few studies, however, hint that mite diversity and abundance may be high on the surfaces of plants well above the soil. For example, orchard trees and vines are typically infested by a variety of damaging plant-parasitic mites, and when pesticides are not used, predatory mites are often abundant enough to regulate the populations of these pests (Jeppson *et al.* 1975). Further, a relatively rich fauna of oribatid mites (Oribatida) has been collected by insecticide fumigation of a variety of trees (Aoki 1973), from lichens and mosses growing on trunks (André 1984, 1985, Travé 1963, Wunderle 1992), and from leaves (Spain & Harrison 1968, Walter & Behan-Pelletier 1993).

The small size and obscurity of mites could mask a good deal of their diversity in tropical forests (May 1988). Recent surveys in Australia that have reached upward into the rainforest canopy have indicated that mites are the most abundant of the canopy arthropods (Walter *et al.* 1994, Walter & O'Dowd 1995). For example, a small understory tree (*Randia benthamiana* F. Muell., the native gardenia) was estimated to support nearly 400,000 leaf-inhabiting mites. Further, the foliar mite populations on this tree were not especially high compared to those on other trees at the same site or to numerous other estimates from temperate to tropical rainforests in eastern Australia (Walter 1993, Walter & O'Dowd 1995). Thus, the forest canopy promises to be a rich mine of mite diversity. The sheer numbers of these minute arthropods suggest that they may play important, but virtually unexplored, roles in the forest canopy.

How persistent are these populations of foliar mites, and what factors influence their abundance and diversity? Some studies suggest that leaf hairs and other surface structures strongly influence population levels (e.g. Walter 1992, Walter & O'Dowd 1992, 1995). A particularly striking structure on the leaves of many woody dicots is the leaf domatium, a small, enclosed space in vein junctures on the undersides of leaves. Although long considered of only taxonomic interest, leaf domatia clearly house symbiotic mites (see reviews in O'Dowd & Willson 1989, Pemberton & Turner 1989, Walter & O'Dowd 1992a, b). However, mites are unlikely to reside solely on leaves. In the following paper, we take the canopy mite story a step farther by looking at the abundance and diversity of mites

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inhabiting the small stems that subtend the leaves. We determine if foliar and stem abundances and functional group composition persist through time. And, we test the effect of two aspects of leaf surface structure, hairs and domatia, on mite abundance and diversity.

Materials and Methods

Patterns of diversity and abundance of canopy mites. For eight tree species, we sampled mites in each of two upper canopy microhabitats: leaves and small stems. Canopies of these trees were accessible by tower (Mick's Tower) and walkway (O'Reilly's Canopy Walkway) in a subtropical rainforest (complex notophyll vine forest) at O'Reilly's Mountain Resort (28°13'S, 153°07'E) in Queensland, Australia. Shoots (3–5 per species per date) were clipped using extendable pole-pruners, placed in plastic bags, and refrigerated. Leaves on most trees were sampled on an irregular basis, and about 20 cm of small stem (<6 mm diameter) from each shoot was similarly examined for mites. However, leaves and small stems in the upper crown (7–10 m) of a native gardenia at Mick's Tower were sampled on seven and on ten dates, respectively, from November 1993 through October 1994. We compared leaves with different surface structures at similar canopy positions on three dates, by sampling leaves from a furry silkpod liana (*Parsonsia fulva* S.T. Blake, Apocynaceae) and the interspersed leaves of the scrub beefwood tree (*Stenocarpus salignus* R. Br.) that supported it.

Leaves and stems were examined under a stereomicrosope using cool light. Leaves were classified as smooth (lacking hairs on the lamina or veins) or hairy. Mites were then removed from leaves and stems; any structures (domatia, galls, webbing, exuviae, detritus, bark fissures, etc.) or growths (lichens, liverworts, etc.) were dissected with a scalpel. Species identifications were based on mites cleared in Nesbitt's solution and mounted in Hoyer's medium on glass slides (Krantz 1978). Species were assigned to feeding guilds after Walter & O'Dowd (1995). Summary statistics are presented as means (rounded to the nearest whole number where practical) ± one standard error.

Effect of leaf hairs on the diversity and abundance of foliar mites. In April 1993, samples of leaves from 22 species of trees were collected from tropical rainforests at Curtain Fig (17°16'S, 145°34'E) and Wongabel (17°20'S, 145°29'E) near Atherton, Pine Creek (16°59'S, 145°50'E) south of Cairns, and on Mt Lewis (16°32'S, 145°15'E) in north Queensland. At each site, similar amounts of vegetation were collected from each tree species; leaves were classified as either hairy (surface with prominent tomentum) or smooth (leaf surface either glabrous or covered with appressed scales). Eight species of trees had hairs on the leaf surface (*Alstonia muelleriana* Domin, *Cryptocarya mackinnoniana* F. Muell., *Diploglottis diphyllostegia* [F. Muell.] Bailey, *Gardenia ovularis* Bailey, *Rhodamnia blairiana* F. Muell., *Rhodamnia sessiliflora* Benth, *Sarcopteryx* sp., *Tetrasynandra laxiflora* [Benth.] Perkins), including one species with tuft domatia (*G. ovularis*). Fourteen species had smooth leaf surfaces without visible hairs (*Acacia aulacocarpa* Cunn. ex Benth., *Aglaia sapindina* [F. Muell.] Harms, *Aleurites moluccana* [L.] Willd., *Argyrodendron peralatum* [Bailey] Edlin ex I.H. Boas, *Beilschmiedia bancrofti* (Bailey) C. White, *Elaeocarpus sericopetalus* F. Muell., *Euodia haplophylla* F. Muell., *Flindersia pimenteliana* F. Muell., *Polyalthia* sp., *Pullea stutzeri* [F. Muell.] Gibbs, *Rhodomyrtus macrocarpa* Benth., *Syzygium cormiflorum* [F. Muell.] B. Hyland, *Toona ciliata* M. Roemer, Unknown [Myrtaceae?]), including one species with pocket domatia (*T. ciliata*).

Leaves were observed under the microscope as above, mites counted, and the number of mite species per leaf was estimated using recognisable taxonomic units (RTUs) (Rees 1983). This technique probably results in an underestimate of true species diversity, but we were only able to slide-mount predators, and some fungivores and plant-parasites, from these samples for species confirmation. We used mean values for each species in a single-factor (leaves hairy or smooth) analysis of variance in the *Statview* statistical package (Abacus Concepts, 1992) to test for a difference in numbers of mites per leaf (log-transformed), number of mite RTUs per leaf, and total number of mite RTUs per tree.

Effect of leaf domatia on the diversity and abundance of foliar mites. We selected individuals or patches of 12 different species of rainforest trees and lianas with leaf domatia (see Appendix I) at a variety of sites in northern New South Wales and south-eastern Queensland in September 1991. For each species, equal numbers of leaves were randomly assigned to two treatments: domatia blocked with bitumen paint or domatia left open, but dabs of paint placed below the domatia to control for any effects of the paint (Walter & O'Dowd 1992b). After five months (February 1992) we collected the leaves and counted and identified the mites present to species. We used mean values for each species in a single-factor (domatia open or blocked) analysis of variance in the *Statview* statistical package (Abacus Concepts, 1992) to compare log-transformed counts of domatia, mites, and mite species.

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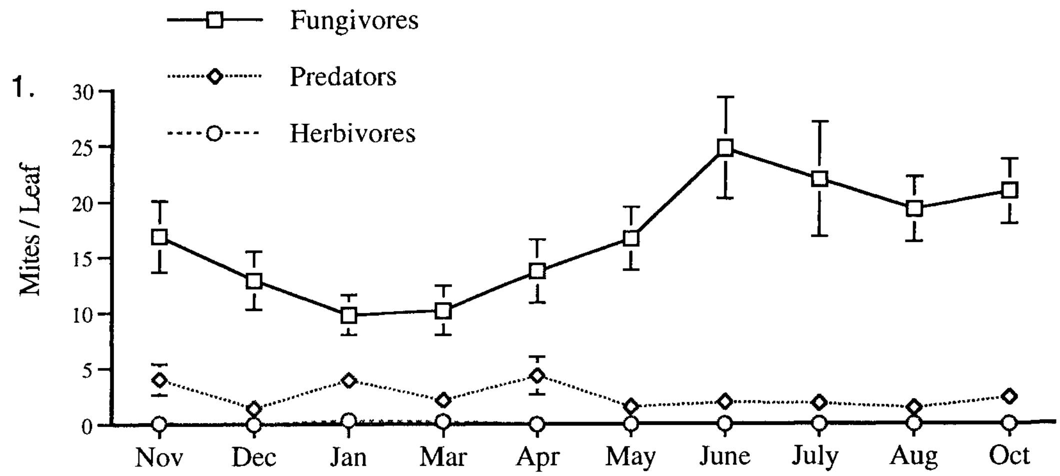

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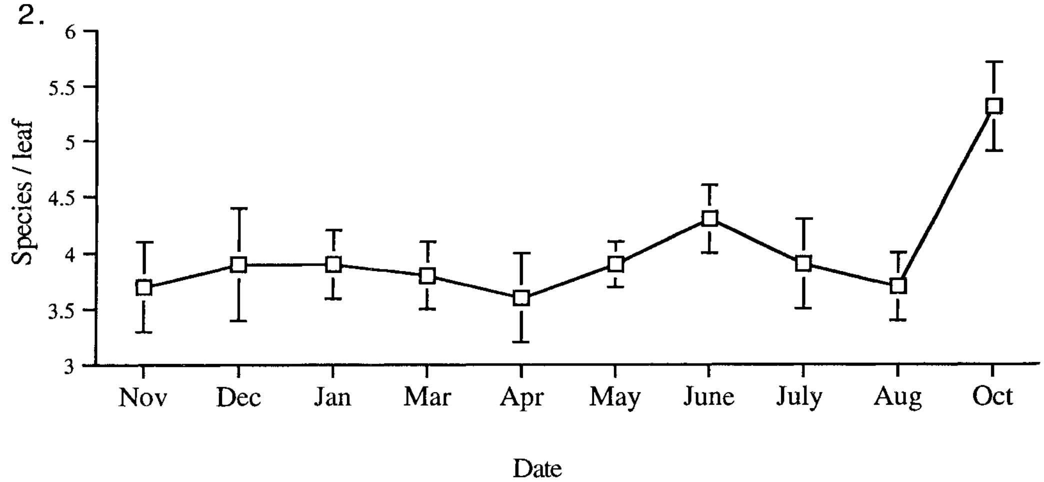

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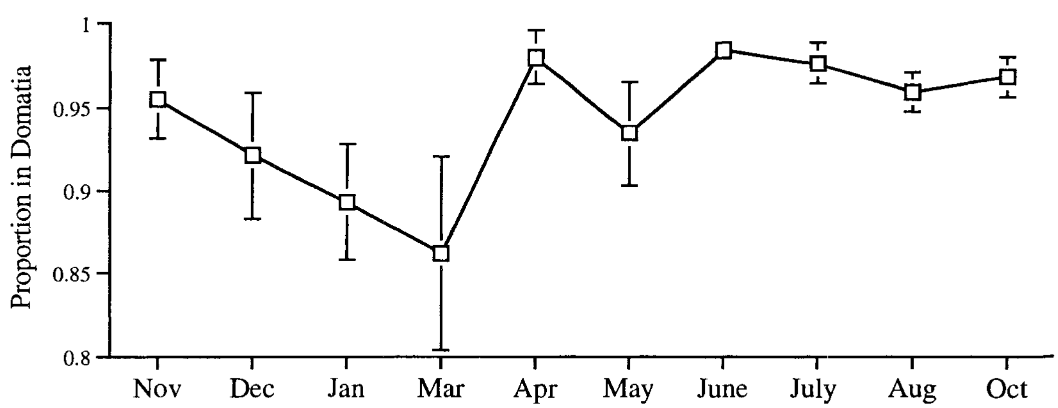


FIGURES 1–3. Mean (± standard error) estimates of foliar mite populations in the upper crown of an understory native gardenia (*Randia benthamiana*) in subtropical rainforest at Lamington, Queensland in 1993–94. 1. Number of scavenger-fungivore, predatory, and plant-parasitic mites per leaf. 2. Number of mite species per leaf. 3. Proportion of all mites collected within leaf domatia.

Results

Diversity and abundance of canopy mites. Leaves in the upper canopy (7–10 m) of a native gardenia (the same tree reported on in Walter 1993) were inhabited by an average of 13 to 26 mites per leaf (range = 0–85, mean overall dates = 17). Most (88%) of these mites were scavenger-fungivores, especially Oribatida (59%). The remainder were primarily predators, with only a few plant-parasitic Eriophyidae collected (Figure 1). High numbers were present on every sampling date; however, mite abundance increased in the winter dry season (Figure 1). A similar pattern was found on a second native gardenia growing along the Canopy Walkway and sampled at 9–10 m on five dates between September 1991 and May 1994. An average leaf of the walkway gardenia was inhabited by 24 mites (range = 0–91), with 85% representing fungivores (50% Oribatida) and 15% predators. Both gardenia trees contained a diverse fauna of foliar mites with up to 11 species on a single leaf, and typically an average of 4–5 species per leaf sampled (e.g. Figure 2). Leaves of native gardenia were smooth and glabrous except for minute pits with hairs in the vein axils on the undersides of the leaves (domatia). The vast majority of mites, 97 ± 1% on the tower gardenia and 81 ± 4% on the walkway gardenia, were consistently found within these domatia (e.g. Figure 3).

Near the terminal buds on native gardenia, the small stems were densely hairy, and often inhabited by large numbers of mites (up to 100 mites on a 10 cm segment). Oribatid mites also dominated the stem fauna (93%); however, there was little overlap in species composition between leaf and stem. Stem mites were relatively rare in the summer-wet season (means = 5–14 per 10 cm segment), but like foliar mites on the same tree, increased to high numbers (averaging 65 per 10 cm segment in August) in the winter-dry season (Figure 4).

Foliar mite abundances and feeding guild composition varied among tree and liana species in the upper canopy. The leaves of a soft corkwood tree (*Caldcluvia paniculosa* (F. Muell.) Engl., Cunoniaceae), with tuft domatia and hairy midribs, had abundant populations of foliar mites (up to 356 mites on a single leaf) on the three dates sampled (averaging 11 mites per leaf in the May to 83 per leaf in the August). Again most mites (85%) were fungivores, especially Tydeidae (57%) and Oribatida (26%). However, the leaves of the six tree species with smooth, glabrous leaves (*Acradenia euodiiformis* [F. Muell.] T. Hartley, *Baloghia lucida* Endl., *Doryphora sassafras* Endl., *Orites excelsa* R.Br., *Pseudoweinmannia lachnocarpa* [F. Muell.] Engl., and scrub beefwood)

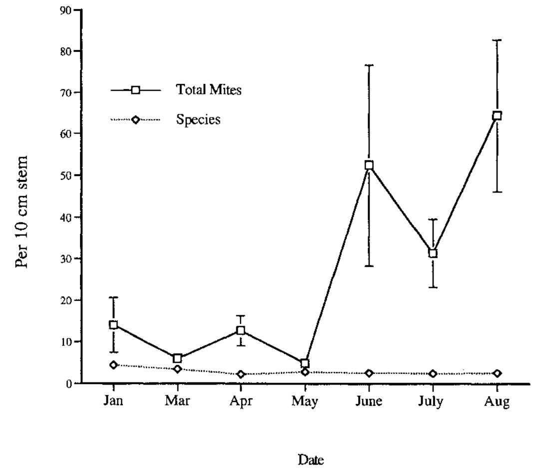


Figure 4. Mean (± standard error) number of mites and mite species per 10 cm of small stem in the upper crown of an understory native gardenia (*Randia benthamiana*) in subtropical rainforest at Lamington, Queensland in 1994.

(Figure 5) rarely had many mites (means = 0.4 ± 0.1 to 12 ± 10), and often included a high proportion of plant-parasites (38% overall six species). An exception was a single leaf of *A. euodiiformis* inhabited by 151 tydeid mites (95% of the total collected from this species).

Even when smooth leaves of the scrub beefwood were interspersed with hairy leaves of the silkpod liana in the canopy, the abundance of foliar mites remained low (Table 1). On all three sampling dates, mites were extremely rare on the smooth leaves of scrub beefwood (only 18 mites were collected from the 82 leaves examined), but very abundant (up to 123 on a single leaf) on silkpod leaves (which have a surface densely coated with hairs and deep pits in the vein axils). Most silkpod mites were fungivores (83%), especially Tydeidae (49%) and Oribatida (25%).

The abundance and diversity of stem-inhabiting mites on these same eight species showed little relation to the patterns on leaves; three of the four highest density populations occurred on trees with few foliar mites (Table 2). The vast majority of stem-inhabiting mites were scavenger-fungivores, especially Oribatida (90%). Most stem-inhabiting mite species were not found on leaves, and only rarely were foliar mites found on stems. Species turnover was high between shoots within a tree and between trees indicating a high absolute diversity of arboreal mites. To date, over 200 species of canopy mites have been identified from the collections around O'Reilly's Mountain Resort and in the adjacent Lamington National Park.

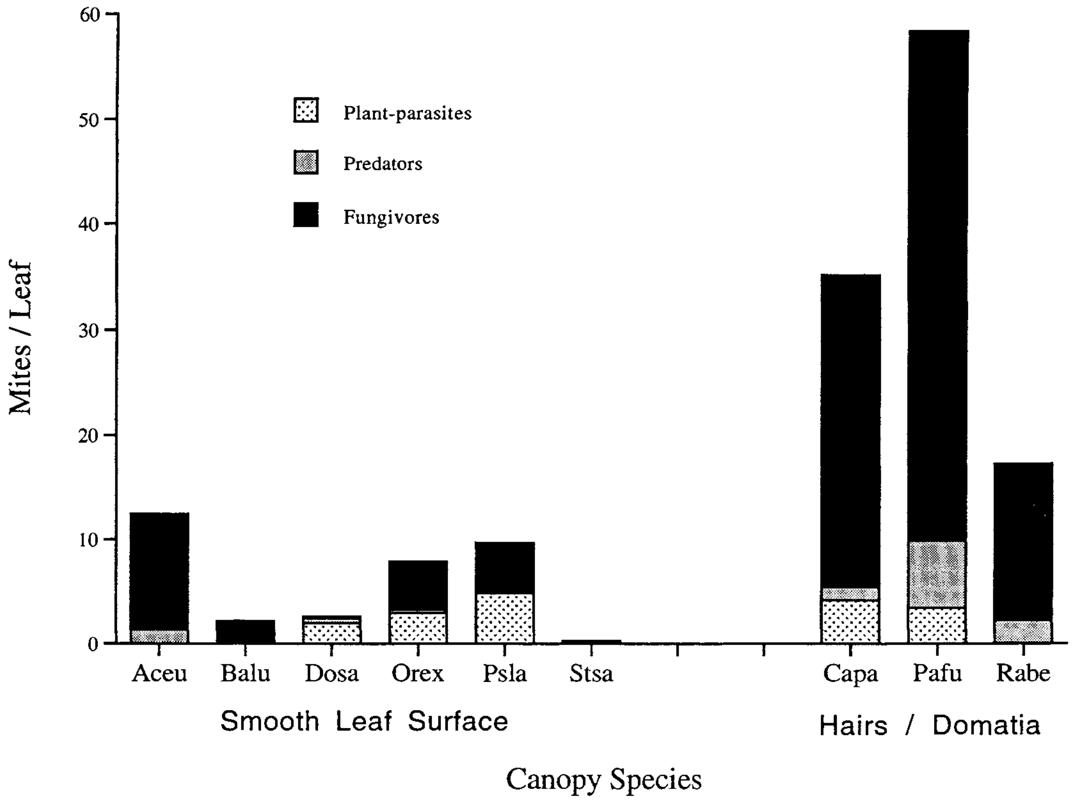


FIGURE 5. Mean numbers of mites in different feeding guilds on leaves of trees with different surface characteristics in subtropical rainforest at Lamington, Queensland in 1993–94. Letter codes of the x-axis refer to the first two letters of the generic and species names of the plants (see TABLE 2).

Effect of leaf hairs on species diversity. A test of the hypothesis that foliar mite density and diversity vary with leaf hairiness was conducted on 22 tropical rainforest trees sampled in April 1993. An average tree had 14 ± 5 mites and 2.4 ± 0.5 RTUs per leaf. The eight trees with hairs on the leaf surface had more than twice as many RTUs per sample as the 14 species with smooth leaves. Total RTUs and total mites were also much higher on trees with hairy leaves (TABLE 3).

Analysis of the species composition of the can-

TABLE 1. Mites respond to leaf structure, not canopy position. Mean (±standard error) number of mites in three feeding guilds, and mean number and range of all mite species per upper crown leaf of a scrub beefwood tree (*Stenocarpus salignus* R. Br., Proteaceae) with smooth leaves and of a furry silkpod liana (*Parsonsia fulva* S. T. Blake, Apocynaceae) with densely hairy leaves growing in its crown.

Date	Mites per leaf			Mite species	Range
	Fungivores	Predators	Plant-parasites		
		Scrub beefwood			
March 1993	0.1 ± 0.1	0	0	0.1 ± 0.1	0–1
May 1994	0	0.1 ± 0.1	0	0.2 ± 0.1	0–1
October 1994	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0–2
		Furry silkpod liana in top of scrub beefwood			
March 1993	32 ± 10	5 ± 1	0	6.6 ± 0.4	5–7
May 1994	72 ± 14	4 ± 2	0.2 ± 0.2	5.6 ± 0.7	4–8
October 1994	42 ± 3	10 ± 1	10 ± 10	4.8 ± 0.5	3–6

TABLE 2. Mites on small stems. Mean (±standard error) number of scavenger-fungivore and predatory mites, and mean number of all mites species, per 10 cm of upper crown small stem for eight species of tree at Lamington, Queensland, sampled on various dates in 1994. Codes refer to FIGURE 5.

Code	Canopy tree species	Fungivores	Predators	Mite species
Aceu	*Acradenia euodiiformis*	1 ± 1	0.3 ± 0.2	0.8 ± 0.7
Balu	*Baloghia lucida*	9 ± 1	0.2 ± 0.1	2.8 ± 0.7
Capa	*Caldcluvia paniculosa*	4 ± 1	1.4 ± 0.5	2.0 ± 0.1
Dosa	*Doryphora sassafras*	1 ± 1	0.3 ± 0.2	1.0 ± 1.0
Orex	*Orites excelsa*	2 ± 1	0.2 ± 0.2	1.3 ± 0.1
Rabe	*Randia benthamiana*	26 ± 6	1.0 ± 0.3	2.9 ± 0.3
Psla	*Pseudoweinmannia lachnocarpa*	11 ± 2	06 ± 0.4	2.9 ± 0.2
Stsa	*Stenocarpus salignus*	7 ± 2	0.5 ± 0.3	4.0 ± 0.3

opy mite fauna in the rainforests of north Queensland is at an early stage; however, some patterns relating to leaf surface structure are already clear. Some predatory mites (e.g. species of the phytoseiid genera *Phytoseius, Paraphytoseius* and of undescribed genera of Stigmaeidae and Cunaxidae) appear to be restricted to hairy leaf surfaces. Similarly, species of *Fungitarsonemus* (Tarsonemidae) that build hideaways for oviposition and molting by gluing detritus to leaves appear to be common only on smooth leaf surfaces. Also, plant-parasitic species of Tetranychidae, Tenuipalpidae, and Eriophyidae appear to be host specific.

Effect of leaf domatia on the diversity and abundance of foliar mites. Blocking of leaf domatia with bitumen paint resulted in a significant (ANOVA, $F_{1,22} = 48.176$, $P < 0.0001$) reduction in the number of domatia available for mite use (0.5 ± 0.1 domatia per leaf vs 6.4 ± 0.4 on controls). Five months after treatment, mean mite species number was reduced by half on leaves with blocked domatia (TABLE 4, FIGURE 6). Numbers of predatory mites were strongly reduced on leaves with domatia blocked (compared to controls) on all 12 plant species treated (FIGURE 7) and fungivorous mites were strongly reduced on the 11 species on which they occurred (FIGURE 8); but, numbers of plant-parasitic mites were not consistently affected (FIGURE 9).

DISCUSSION

Mites are abundant and diverse in the outer canopy of trees and vines in both tropical and subtropical rainforests in Australia. Furthermore, high abundance and high local species richness are maintained seasonally; over one year, average numbers never fell below 13 mites and 3–4 species per leaf on native gardenia. These findings add further substance to previous spot surveys of broad geographic scope in Australian rainforests showing that mite abundance on leaves is high. However, mite abundance changed seasonally, both on leaf and on stem microhabitats. The reduction in mite populations during the rainy season, especially on smooth, rain-shedding leaves, has been noted in other Australian rainforest studies (Walter 1995).

Our results clearly show that leaf surface structures—both general features like erect tomenta that carpet the phylloplane and specialised domatia restricted to vein junctures—appear to be the most important features contributing to the abundance and local diversity of mites on canopy leaves. Leaf surface features had the most pronounced effects on mites with fungivorous and predatory habits. Further, these patterns were even maintained for leaves of the furry silkpod interspersed with the smooth leaves of the scrub beefwood over three sampling dates spread across

TABLE 3. Mites are more abundant and diverse on hairy leaves. In April 1993, 14 tropical rainforest trees in north Queensland with smooth leaf surfaces had far fewer mites and mite recognisable taxonomic uints (RTU's) than 8 tree species with hairy leaf surfaces (see text for species names). Values represent means ± standard errors. All comparisons were significantly different (Bonferroni/Dunn correction for multiple comparisons).

	Smooth	Hairy	$F_{1,20}$	P
Mite RTU's per leaf	1.5 ± 0.5	4.0 ± 0.8	11.550	0.0029
Total RTU's per tree	5.3 ± 1.1	11.6 ± 1.1	13.939	0.0013
Total mites per leaf	4.9 ± 2.1	28.8 ± 12.6	9.073	0.0069

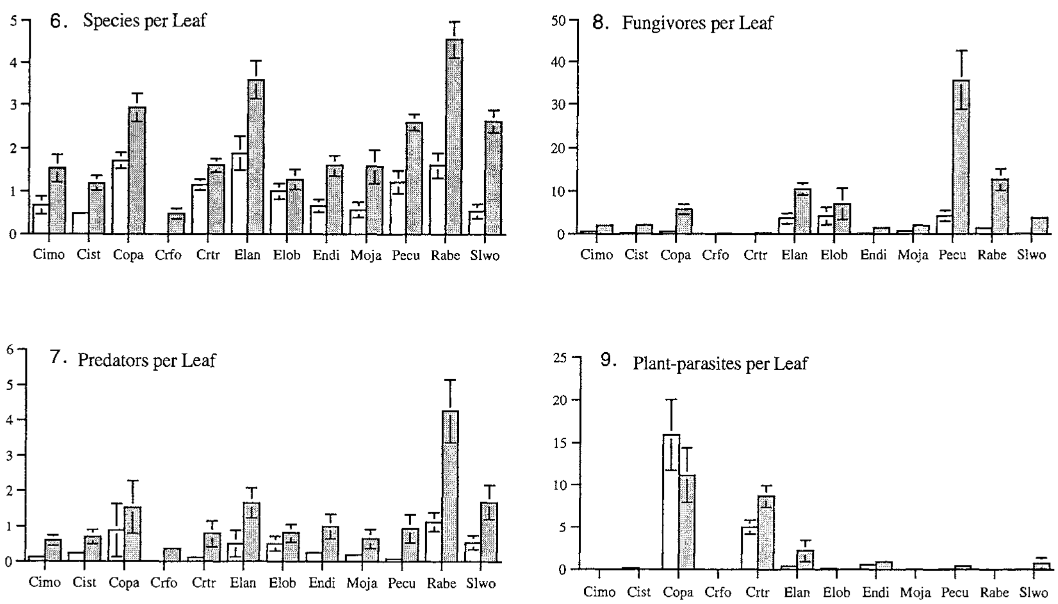
TABLE 4. Blocking domatia reduces number and diversity of mites. Five months after treatment, the number of predatory and scavenger-fungivore mites on leaves with domatia blocked with bitumen paint were significantly lower than those with leaves with paint daubed below the domatia. Values represent means ± standard errors. All comparisons except for plant-parasites were significantly different (Bonferroni/Dunn correction for multiple comparisons).

	Domatia			
	Blocked	Open	$F_{1,22}$	P
Mite species	0.9 ± 0.1	2.0 ± 0.1	10.279	0.0041
Fungivores	1.0 ± 0.2	5.7 ± 0.8	10.279	0.014
Predators	0.3 ± 0.1	1.1 ± 0.1	14.506	0.001
Plant-parasites	1.8 ± 0.4	2.1 ± 0.4	0.204	0.6559

20 months. These local patterns probably contribute to total diversity, because a number of different lineages of mites appear to be found only on hairy leaf surfaces (and a few seem to be restricted to smooth leaves).

On native gardenia, most mite abundance and diversity was found within leaf domatia. Relatively large populations of fungivores and predators inhabited the leaves of this tree, and most of the mites congregated in the small hairy pits at the junctures of the lateral and midveins. Domatia may form the basis of a widespread protective mutualism between woody plants and mites. To date, tests of the effects of domatia on the population sizes of mites have been restricted to just a few species (Walter & O'Dowd 1992a, b, 1995, Grostal & O'Dowd 1994). However, the results of our blocking experiment (FIGURES 6–9, TABLE 5) clearly demonstrate that potentially beneficial mites respond similarly on a dozen haphazardly selected rainforest plants with a variety of types of domatia. In every case, when domatia were blocked, numbers of predators and fungivores were strongly reduced.

A simple hypothesis to explain the enhanced populations and diversity of mites on leaves with well developed tomenta or leaf domatia is that these structures protect the mites from adverse



FIGURES 6–9. Mean (± standard error) number of mite species and mites in three feeding guilds five months after leaves had domatia painted shut (open bars) or untreated (shaded bars) for 12 species of subtropical rainforest trees and lianas. Letter codes of the x-axis refer to the first two letters of the generic and species names of the plants (see Appendix I). 6. Mite species per leaf. 7. Predatory mites per leaf. 8. Fungivorous mites per leaf. 9. Plant-parasitic mites per leaf.

environmental conditions. Animals as small as mites would be easily washed from leaves in storms or desiccated by intense sun or dry winds. Indeed, the leaf surface must represent an extreme habitat for a mite. However, leaves are not the only microhabitats available to mites in the rainforest canopy. The small stems immediately below the outermost canopy leaves, although seemingly an equally extreme habitat, are host to a variety of mites not found on leaves. Other, better protected microhabitats abound in forest canopies, and the few that have been sampled house distinctive assemblages of mite species (Wunderle 1992, Walter 1995). Therefore, it seems clear that May's (1988) supposition is true: mites are a significant component of the canopy fauna. The high abundances and intimate association of predatory and fungivorous mites with leaf domatia, structures that appear to have evolved to shelter tiny arthropods, also suggests that mites are important to the functioning of the canopy system.

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APPENDIX 1. Plant species used in the domatia blocking experiment. And the type and mean (±standard error) number of domatia per leaf.

Code	Domatia bearing species	Domatia Type	Domatia Number
Cimo	*Citronella moorei* [F. Muell. ex Benth.] R. A. Howard	pit	3 ± 0.4
Cist	*Cissus sterculiifolia* [F. Muell.] Planchon	pit	6 ± 0.4
Copa	*Coleospermum paniculatum* F. Muell.	pit	9 ± 0.5
Crfo	*Cryptocarya foveolata* C. T. White & Francis	pit	2 ± 0.1
Crtr	*C. triplinervis* R. Br.	tuft	2 ± 0
Elan	*Elaeocarpus angustifolius* Blume	pit	9 ± 1.0
Elob	*E. obovatus* G. Don	pocket	2 ± 0.4
Endi	*Endiandra discolor* Benth.	pocket	4 ± 0.2
Moja	*Morinda jasminoides* Cunn. ex Hook.	pit	3 ± 0.2
Pecu	*Pennantia cunninghamii* Miers	pit	17 ± 1.3
Rabe	*Randia benthamiana* F. Muell.	pit-tuft	12 ± 0.5
Slwo	*Sloanea woollsii* F. Muell.	pit-tuft	15 ± 0.6