

## Mesostigmatid mites (Acari: Mesostigmata) on rainforest tree trunks: arboreal specialists, but substrate generalists?

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**Abstract** Predatory mites (Acari: Mesostigmata) on tree trunks without significant epiphytic growth in a subtropical rainforest in Eastern Australia were assessed for habitat specificity (i.e. whether they are tree trunk specialists or occupying other habitats) and the influence of host tree and bark structure on their abundance, species richness and species composition. The trunks of nine tree species from eight plant families representing smooth, intermediate and rough bark textures were sampled using a knockdown insecticide spray. In total, 12 species or morphospecies of Mesostigmata (excluding Uropodina *sensu stricto*) were collected, most of which are undescribed. Comparison with collections from other habitats indicates that epicorticolous Mesostigmata are mainly represented by suspended soil dwellers (six species), secondarily by generalists (four species) and a bark specialist (one species). A typical ground-dwelling species was also found but was represented only by a single individual. In terms of abundance, 50.5% of individuals were suspended soil dwellers, 40.7% bark specialists, and 8.3% generalists. Host species and bark roughness had no significant effect on abundance or species richness. Furthermore, there was no clear effect on species composition. The distribution of the most frequently encountered species

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suggests that most mesostigmatid mites living on bark use many or most rainforest tree species, independent of bark roughness. These findings support the hypothesis that some epicorticolous Mesostigmata use tree trunks as 'highways' for dispersing between habitat patches, while others use it as a permanent habitat.

**Keywords** Habitat specificity · Host specificity · Bark roughness · Epicorticolous mites · Predators · Subtropical rainforest

## Introduction

Forest canopies support diverse arthropod assemblages, which are largely distinct from those on the forest floor (e.g. ants, Longino and Colwell 1997; mites, Walter and Behan-Pelletier 1999; all arthropods, Majer et al. 2002; spiders, Sørensen 2003). Thus, arthropod species associated with foliage (the primary target of canopy fogging) are generally absent from forest floor soil and litter, and vice versa. The distinction between corticolous—associated with tree bark—and forest floor arthropods is not as clear-cut. Some species may use trunks as 'highways' to travel between the forest floor and arboreal refuges (Wilson 1959; Moeed and Meads 1983; Rodgers and Kitching 1998; Majer et al. 2003), while others may use it as a long-term habitat (Proctor et al. 2002). For example, xylophagous beetles that burrow into subcortical spaces of trees are confined to tree trunks for most of their life cycle (Atkinson and Peck 1994). The same may be true for many of the fungivores, predators and symbionts—including many mites—that live under the bark or that use the galleries of wood-boring beetles as a habitat (Moser and Roton 1971; Lindquist and Wu 1991). The epicorticolous fauna, associated with the bark surface, may not be as specific to tree trunks. A broad diversity of arthropods use the bark surface and cracks and crevices as refugia, as places to rest, or to feed, and many of these arthropods spend most of their time or life cycle (e.g. immature stages) elsewhere, especially in the soil (Moeed and Meads 1983; Nicolai 1986; Majer et al. 2003). Nevertheless, some species of Psocoptera and many oribatid and prostigmatid mites are primarily or exclusively found on tree trunks, while others are mostly or only found in litter, or foliage (André 1984, 1986; Thornton 1985; Norton and Palacios-Vargas 1987; Walter and Behan-Pelletier 1999; Proctor et al. 2002; Karasawa and Hijii 2004). Psocids, oribatids and corticolous Prostigmata feed primarily on fungi, algae and/or lichen (Thornton 1985; Hopkin 1997; Behan-Pelletier and Walter 2000). Broad differences in the microflora growing on trunks versus leaves versus litter (New 1970) might explain, at least in part, why many of these microbivores are habitat specific. Although the majority are microbivore-fungivores, *Collembola* occurring on tree trunks are, in contrast, never restricted to this habitat and often occur on the forest floor litter (Bowden et al. 1976; Ponge 1993).

Many predators occur on bark, and some spiders, pseudoscorpions, adult predatory flies, bugs and possibly some predatory mites primarily or exclusively live on tree trunks (Nicolai 1986; Adis and Mahnert 1990; Manhart 1994; Walter et al. 1998). Non-parasitic mesostigmatid mites (Acari: Mesostigmata) represent the most diverse group of predatory mites in soil and on plants (Walter and Proctor 1999). Mesostigmata tend to be generalist predators, feeding on nematodes, collembolans, other mites and/or immature insects (although some also feed or preferentially feed on fungi or pollen; Walter 1988; McMurtry and Croft 1997), and this also pertains to Australian species (Walter and Proctor 1998;

Beaulieu and Walter unpubl. data). A study in Australian rainforest suggests that some mesostigmatid species are bark-specific while a few also occur in suspended soil or on the forest floor (Walter et al. 1998). In contrast, data from temperate forests of Europe indicate that the mesostigmatid fauna on tree trunks (collected from epicorticolous lichen and underlying bark) are dominated by species that typically inhabit leaves and stems (Phytoseiidae) (André 1986).

While folivorous and xylophagous arthropods show various degree of specificity to the plant hosts on which they feed (Atkinson and Peck 1994; Novotny and Basset 2005), epicorticolous arthropods, predominantly composed of fungivores, predators and herbivores (the latter feeding on the epiphytic flora), may show low host specificity because they are not using the bark as a food source (Menzel et al. 2004). For example, Psocoptera on trunks are generally not host-specific but a few species have broad associations to conifers or broad-leaved trees, which reflect differences in microflora (New 1970). Although historical associations with a tree species might be maintained by chemical attributes of the host for some bark dwellers, the bark structure and the epiphytic cover (algae, lichen, mosses) may be the key factors for most others, as in general, faunal distinctions between tree species can be explained by bark structure and/or epiphyte cover, which largely determine microclimate, shelter and resource availability (André 1985; Nicolai 1986; Menzel et al. 2004). Trees with complex bark (with many fissures or scales) in Europe tend to have richer invertebrate faunas dominated by different species compared to those with smooth bark (Nicolai 1986). Rough-barked rainforest tree trunks in Australia harbored more beetle species and a greater abundance of predatory beetles than smooth bark trunks (Menzel et al. 2004). In a neotropical rainforest, many web-building spiders did not show any preference for a bark type, but several hunting spiders preferred smooth bark trunks (Manhart 1994). The presence and type of lichen (foliose, fruticose or crustose) strongly influenced the community composition of oribatid mites and Collembola on bark, with some species almost restricted to certain lichen type (André 1985; Prinzing and Wirtz 1997; Walter and Behan-Pelletier 1999). Lichen cover was also found to affect the abundance of species of bark-dwelling Mesostigmata (André 1986).

Free-living mesostigmatid mites are especially abundant and diverse in soil and litter, but many species also occur on plant parts, including foliage and tree trunks (André 1986; Walter et al. 1998). Data on Mesostigmata from tree trunks is scant, particularly in Australia. The present study examined the assemblage structure of mesostigmatid mites from trunks of nine rainforest tree species with bark texture ranging from smooth to rough, and compared these assemblages with collections of Mesostigmata from other habitats, to test the following hypotheses:

- (1) Epicorticolous Mesostigmata are bark specialists.
- (2) Total abundance and species richness is related to bark roughness.
- (3) Species composition is related to bark roughness.
- (4) Mite species assemblages vary with host tree species.

## Material and methods

### Study area

All work was carried out within subtropical rainforest (complex notophyll vine forest, sensu Webb 1978) in or adjacent to Lamington National Park (153°07' E, 28°13' S,

750–950 m), approximately 90 km south of Brisbane, Queensland. Sampling of tree trunks was carried out within an area of approximately 25 ha, between March 27 and April 1, 2003. The tree flora of this site has been described in detail in Laidlaw et al. (2000). A previous survey was conducted on tree trunks in the same area in November and December 1992, January 1995 (Walter et al. 1998) and July 1996, and data from this survey was incorporated alongside the results from the present study (see Table 2).

## Design

To test for the influence of host tree and bark structure, a two-way design was used, in which six replicates of each of nine species of trees were sampled. These nine species were grouped into three categories based on visual assessment of their bark roughness, with three species in each grouping. Tree species with exfoliating bark were excluded because the degree of roughness could not be measured (see below). Within each grouping, all species selected belong to different families to minimize potential influences of tree host phylogeny (Table 1). Bark roughness was then assessed using a simple index (RI) based on the comparison of the surface distance (SD—that is a linear distance obtained using a fine cord tracking each irregularity in the bark) and a simple circumferential distance (CD) of 50 cm around the tree, viz.:

$$RI = \frac{SD - CD}{SD} \times 100$$

This measure was made three times on half of the trees sampled and a mean calculated (therefore  $n = 3$  for each tree species) (Table 1). ANOVA shows significant differences among tree species ( $F_{8,19} = 7.4$ ,  $P = 0.0002$ ). Post hoc comparisons (Fisher's PSLD test) of bark roughness between tree species indicate that smooth- and intermediate-barked trees are not significantly different among each other ( $P > 0.05$ ), but they all have significant

**Table 1** Tree species studied listed in increasing order of mean bark roughness index ( $\pm$ Std. dev.) (see text)<sup>A</sup>

Bark type	Species	Family	Mean bark RI <sup>B</sup>	Bark type average RI
Smooth	<i>Orites excelsa</i> R. Br.	Proteaceae	0.55 $\pm$ 0.34a	0.61 $\pm$ 0.08
	<i>Cryptocarya obovata</i> R. Br.	Lauraceae	0.59 $\pm$ 0.42a	
	<i>Geissois benthamii</i> F. Muell.	Cunoniaceae	0.70 $\pm$ 0.47a	
Intermediate	<i>Acradenia euodiiformis</i> (F. Muell.) T. Hartle	Rutaceae	1.30 $\pm$ 0.35a	1.57 $\pm$ 0.28
	<i>Caldcluvia paniculosa</i> (F. Muell.) Hoogl.	Cunoniaceae	1.56 $\pm$ 1.10ab	
	<i>Syzygium crebrinerve</i> (C. T. White) L. Johnson	Myrtaceae	1.85 $\pm$ 0.73ab	
Rough	<i>Argyrodendron actinophyllum</i> (F. M. Bailey) Edlin	Sterculiaceae	4.38 $\pm$ 1.79bc	5.90 $\pm$ 1.44
	<i>Synoum glandulosum</i> (Smith) Adr. Juss.	Meliaceae	6.10 $\pm$ 4.01cd	
	<i>Diospyros pentamera</i> Woods & F. Muell. ex F. Muell	Ebenaceae	7.23 $\pm$ 2.01d	

<sup>A</sup>Modified from Menzel et al. (2004)

<sup>B</sup>Index values are significantly ( $P < 0.05$ ) different if not followed by the same letter

differences with rough-barked trees ( $P < 0.05$ ), except two intermediate bark trees versus the rough-barked *Argyrodendron actinophyllum* (which were only marginally significantly different:  $0.06 < P < 0.09$ ). Despite non-significant differences between them, there is a substantial gap between values of smooth versus intermediate versus rough barked tree species. The non-significant differences between them appear to be due to the low number of replicates ( $n = 3$ ). Indeed, when smooth and intermediate tree species are pooled in two groups ( $n = 9$  for each), ANOVA indicates highly significant difference ( $F_{1,16}=12.6$ ,  $P=0.003$ ).

### Mite sampling

All samples (for the present study, and previous survey) were obtained by chemical knockdown of the arthropods on a section of tree trunk. As far as possible, trunks covered with moss or lichen or with attached vascular epiphytes were avoided. Before spraying, a collecting “apron” made from an opened plastic bag was pinned flush with the trunk beneath the area to be sampled with a collecting vial containing 80% ethanol at its vertex. A commercial pyrethroid insecticide (Slay-Afe<sup>TM</sup> and Mortein<sup>TM</sup>, in pressurised cans) was used to spray a 1×0.5 m area of bark at breast height for about 15 s. About 30 min later, the sprayed area was swept with a soft brush to dislodge remaining arthropods.

All adult and immature (protonymphs or deutonymphs) Mesostigmata, excluding Uropodina sensu stricto, were sorted, cleared in Nesbitt’s solution, mounted in PVA on glass slides and identified under differential-interference contrast microscopy. Specimens were identified to family, genus and species (or to morphospecies) using the literature (mainly: Lee 1970; Halliday et al. 1998; Walter 2001) and previous collections in the University of Queensland Insect Collection (UQIC). Voucher specimens are held at the UQIC, Department of Zoology and Entomology, St. Lucia, Queensland 4072, Australia.

### Habitat specificity of the bark fauna

To test whether species from tree trunks are habitat specific (i.e. bark specialists), we verified whether they were also collected in other habitats (forest floor soil and litter, suspended soil i.e. humus and litter perched in epiphytic ferns, foliage, and fungal sporocarps growing on logs or snags) that were intensively surveyed in the same area (Walter et al. 1998; Beaulieu 2005). Each species collected on tree trunks was assigned an ecological category, primarily based on the relative frequency of occurrence in forest floor versus suspended soil (see Beaulieu 2005): (1) suspended soil dwellers: species for which  $\geq 90\%$  of all occurrences (occurrence = presence in a sample) were in suspended soil (therefore  $< 10\%$  on ground); (2) generalists: species for which  $< 90\%$  of occurrences were in suspended soil and  $< 90\%$  on ground; (3) forest floor dwellers: species for which  $\geq 90\%$  of all occurrences were on ground; (4) bark specialists: species found exclusively on tree trunks; (5) Foliage dwellers: species primarily found on foliage. Mite species also identified from fungal sporocarps growing on dead wood, or from canopy fogging (pyrethrum knockdown, January 1995, Walter et al. 1998) could not be assigned to a habitat category on that basis alone (occurrences on fungi were too low, and canopy is a mixture of habitats), but mite species from tree trunks also identified from fungi or canopy fogging were indicated as such in Table 2.

**Table 2** Number of occurrences and (individuals) of Mesostigmata species collected from sprayed trunks of nine rainforest tree species ranging from smooth to rough bark, and from previous collections from sprayed trunks, canopy fogging and fungal sporocarps from dead wood (=previous survey)

Family	Smooth bark			Intermediate bark			Rough bark			Previous survey			Main habitats other than bark <sup>B</sup>
	<i>O.</i>	<i>Cr.</i>	<i>G.</i>	<i>Ac.</i>	<i>Ca.</i>	<i>Syz.</i>	<i>Ar.</i>	<i>Syn.</i>	<i>D.</i>	Other tree spp.	Canopy fogging	Fungi on dead wood	
<i>Present study</i>													
Celaenopsideae	5(10)	5(19)	6(15)	5(10)	5(15)	4(10)	1	3(8)			1	1	?
Ologamasidae	2(11)	4(8)	3(3)	4(8)	4(23)	3(7)	3(9)	4(10)	4(12)	1	2(2)	1	SS
Sejidae			1	2(5)	1(3)					1	1		SS
Ologamasidae		1		1	1(2)			1	1				FF, SS
Ologamasidae		1		1(2)	1(2)		1	1		1	1	1	SS
Ologamasidae			1				1(4)	1(2)		2(2)			FF, SS
Ologamasidae			1						1				FF, SS
Ascidae					1								SS
Ascidae			1										SS
Ologamasidae												1	FF, SS
Laelapidae												1	SS
Leptolaelapidae							1						FF
<i>Previous survey</i>													
Ologamasidae			1				1(2)			1	1(3)		?
Ologamasidae						1				1	1(3)		?
Ologamasidae							1				2(2)	1	?
Ologamasidae										1	1		FF
Phytoseiidae											3(3)		FOL?

<sup>A</sup>New species codes as per Beaulieu (2005). ? = uncertain taxonomic placement

<sup>B</sup>FF = forest floor, FOL? = presumably foliage, SS = suspended soil, ? = unknown. *Celaenopsis* n. sp. 1 is considered a bark specialist in Figs. 1 and 2. Species having both suspended soil and forest floor as main habitats are grouped as 'generalists' in Figs. 1, 2

## Effect of tree species and bark roughness

In order to test the effect of tree species and bark roughness on the number of species and the number of individuals (abundance data were log-transformed as  $\ln(X+1)$  to achieve normality) per sampled tree, a nested ANOVA with tree species nested within bark category was performed using SAS (SAS Institute 1996).

Finally, species richness was compared between bark type using rarefaction curves based on the number of individuals collected (=sampling effort) on all three species of trees for each bark category. The curves were computed using the software *EstimateS* (Colwell 2000) and each represents the average curve of 100 randomizations of the order in which samples were added.

The effect of tree species and bark roughness on species composition was assessed by comparison of Sørensen's coefficients of similarity among pairs of samples of the same or of different treatment. Sørensen's coefficient is based on the presence/absence of species and is the number of shared species between two samples divided by the average of the total number of species in each sample (Legendre and Legendre 1998). Potential values for the Index range from 1.00 (total co-occurrence) to zero (no overlap). Samples where no mites were found were excluded from the calculation of averages for Sørensen's coefficients. A test incorporating species abundances (e.g. Bray-Curtis) was not employed because abundances were quite low for all species. The influence of tree species was tested statistically by comparing Sørensen's coefficients between samples within tree species versus coefficients among tree species, for each category of bark roughness, using a non-parametric Mann-Whitney test. The effect of bark roughness was tested statistically by comparing species composition between pairs of samples using an Analysis of Similarity (ANOSIM) procedure, based on a matrix of Sørensen distances (1-Sørensen's coefficient of similarity), using the software PATN (Belbin 1995).

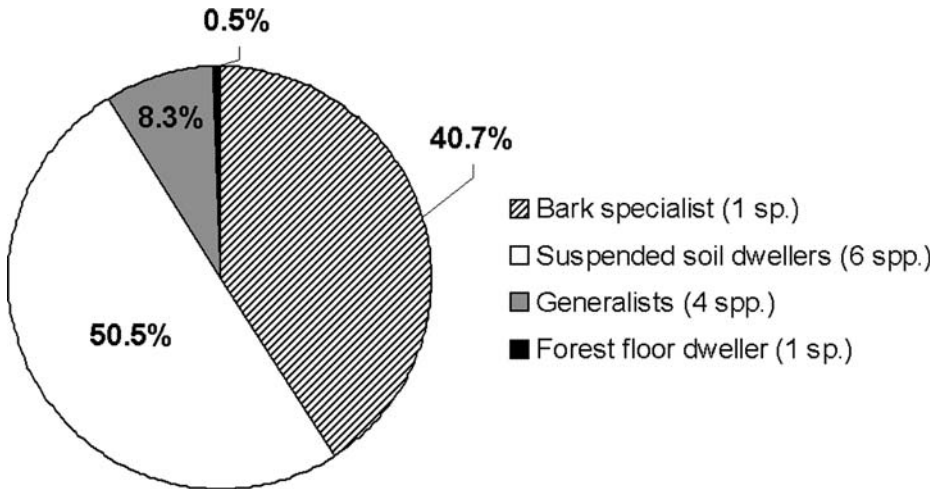
The effect of tree species and bark roughness was also assessed by examining the distribution (abundance and number of occurrences) of individual mite species across tree species and bark categories.

## Results

The 54 tree trunks sampled from nine tree species yielded a total of 216 mesostigmatid mites (including 25 juveniles) or about 8 mesostigmatans per  $m^2$  of bark surface, representing 12 species belonging to six families (Table 2). The juveniles all belonged to suspended soil dwellers or bark specialists: *Celaenopsis* n. sp. 1 ( $n=6$ ), *Caliphis tamborinensis* ( $n=11$ ), *Sejus* n. sp. 1 ( $n=4$ ) and *Caliphis queenslandicus* ( $n=4$ ). From the 12 species list, only four could be confidently assigned to described species. Five additional species were recovered from the previous survey on tree trunks, all apparently undescribed. All are likely predators of nematodes and/or soft-bodied arthropods (Walter and Proctor 1998; Beaulieu and Walter unpubl. data), except *Proctolaelaps pygmaeus/nesbitti* which may be able to feed on fungi as well as invertebrate prey (Halliday et al. 1998).

### Habitat specificity

From the 216 individuals collected, 59.3% belonged to species abundant in other habitats (Fig. 1). Most of these non-bark specialists are primarily associated with suspended soil,



**Fig. 1** Relative abundance of bark specialists, suspended soil dwellers, generalists and forest floor dwellers represented on tree trunks from nine rainforest tree species ( $n = 216$  mite individuals). The number of species represented in each category is shown in parentheses

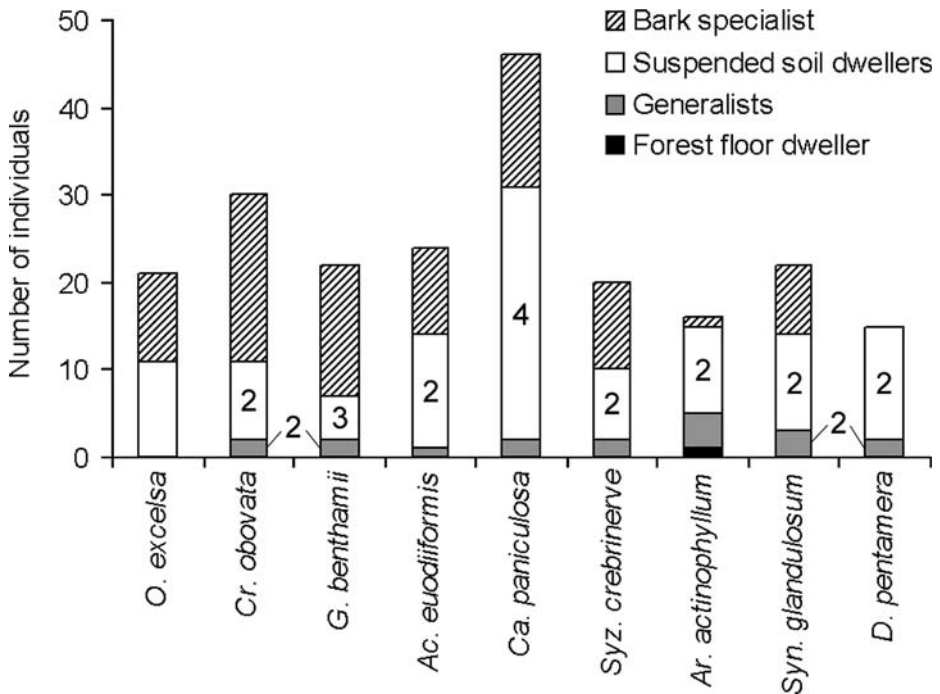
and are largely absent from the forest floor (suspended soil dwellers: 50.5% of individuals). A small portion (8.3%) was represented by generalists, commonly occurring in both suspended soil and forest floor soil and litter. Forest floor dwellers, virtually absent from suspended soil, were a negligible portion of the tree trunk fauna (0.5% of individuals). This leaves 40.7% of individuals to bark specialists, represented by a single species, *Celaenopsis* n. sp. 1 (Fig. 1). This species was never found in non-arboreal habitats except from a decaying fungal sporocarp of a polypore growing on a log (Table 2). In terms of species richness, six out of twelve species are considered suspended soil dwellers, four species are generalists, only one is a bark specialist and another species is a forest floor dweller (Fig. 1 and Table 2). No species were foliage dwellers.

The relative abundance of ecological groups across tree species reflects the overall pattern (Fig. 2). Suspended soil dwellers were usually the most abundant and diverse group, although the bark specialist *Celaenopsis* n. sp. 1 dominated on three host species. The latter is usually abundant and almost ubiquitous on smooth and intermediate bark trees, but was absent or rare on two rough-barked tree species (*Ar. actinophyllum* and *D. pentamera*). The relative abundance of generalists was always low but they occurred on every tree species except one (*O. excelsa*). A single individual of a forest floor dweller occurred on a single host (*Ar. actinophyllum*).

Among the five additional species from the previous survey conducted in the area, one is a forest floor dweller (*Ologamasidae* sp. 1), and another is a species belonging to a family and genus typically associated with foliage (*Neoseiulella* n. sp. nr *cottieri*). Three species (all from the genus *Acugamasus*) have been collected too rarely to establish their habitat distribution.

#### Effect of tree species and bark roughness

Average abundance and species richness of mesostigmatid mites were low, with averages of 2.5–7.7 individuals and 1.2–2.2 species per individual tree (Fig. 3). There was no



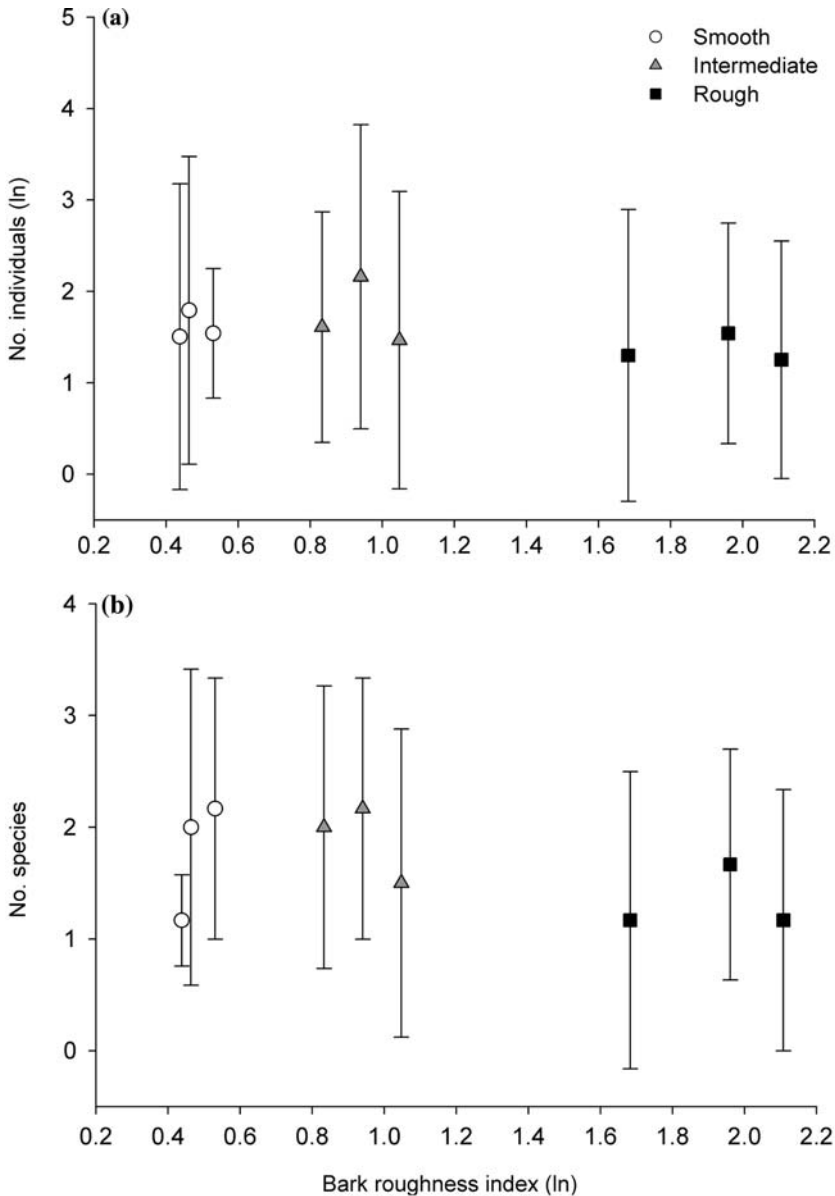
**Fig. 2** Relative abundance of bark specialists, suspended soil dwellers, generalists and forest floor dwellers represented on tree trunks from nine rainforest tree species. For each tree host, the number of species represented in a category is shown in bold. Categories without a number are represented by a single species

significant effect of tree species ( $F_{6,45} = 0.804$ ,  $P=0.74$ ) or bark type ( $F_{2,45} = 2.06$ ,  $P=0.21$ ) on the number of species per individual tree. Nor was there any effect of tree species ( $F_{6,45} = 1.25$ ,  $P=0.30$ ) or bark type ( $F_{2,45} = 1.21$ ,  $P=0.36$ ) on the abundance of mites per individual tree.

The total number of mite species collected per tree species was very similar between bark categories, with  $4.3 \pm 2.1$  (st. dev.),  $4.7 \pm 0.6$  and  $4.7 \pm 1.2$  mite species for smooth, intermediate and rough barked tree species, respectively. Altogether, rough barked trees had fewer individuals, but accumulated species faster than intermediate and smooth barked trees (Fig. 4). However, the steep slope of the line for smooth bark trees suggests that they may have the highest overall diversity. Nevertheless, these differences are negligible when considering the strong overlap between the 95% confidence intervals of the three curves.

For each bark type, Sørensen's coefficients of similarity were not significantly different within and among tree species (SS, II, RR; Fig. 5) (Mann–Whitney test,  $0.3 < P < 0.96$ ). Therefore, even when controlling for a potential effect of bark structure, host species has no apparent effect on species composition of mesostigmatid mites.

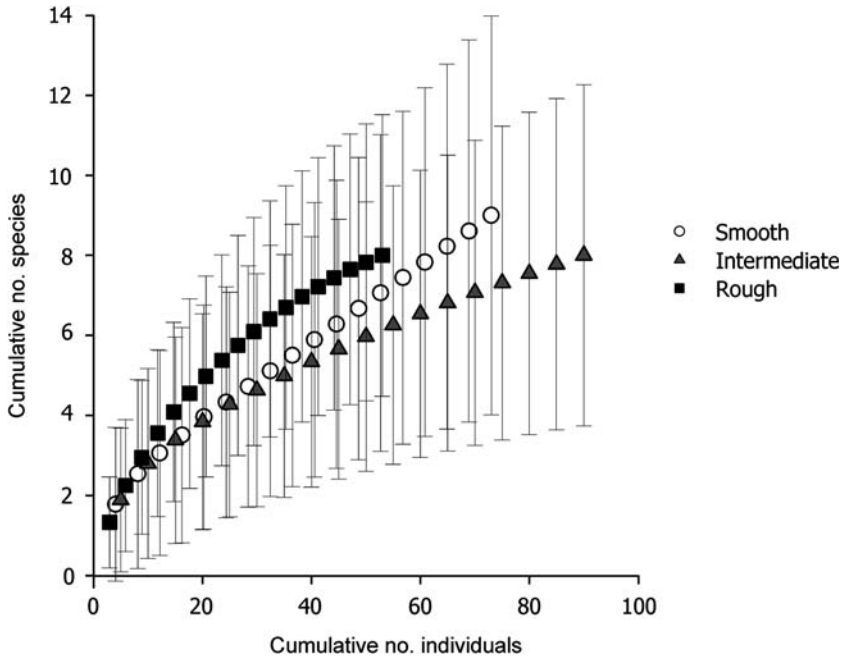
Results of ANOSIM indicate that smooth and intermediate bark samples were not different ( $P=0.38$ ), although rough bark samples were significantly distinct from smooth ( $P=0.002$ ) and intermediate bark samples ( $P=0.006$ ). Accordingly, rough bark samples have lower indices of similarity with smooth or intermediate bark samples (SR and RI lower than SI, Fig. 5). However, the apparently higher distinctiveness of rough bark is due mainly to one mite species: the bark specialist *Celaenopsis* n. sp. 1 (Table 2). When this



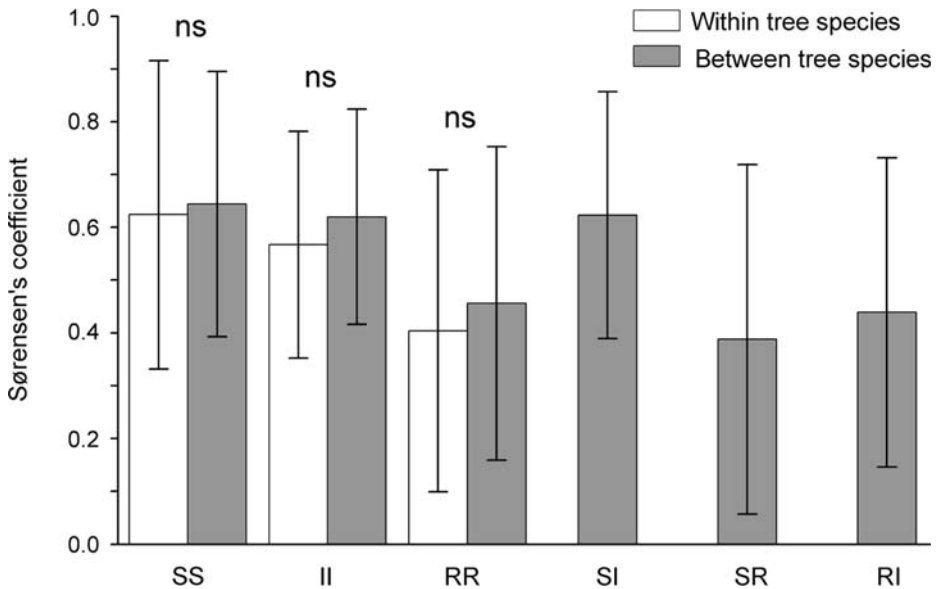
**Fig. 3** Average number of individuals (a) and species (b) ( $\pm$  Std. dev.) collected on the bark of nine rainforest tree species ( $n = 6$ ), ranging from smooth to rough bark. Y axis represents bark roughness index (ln)

species is removed prior to ANOSIM, no significant differences are observed between any bark categories ( $0.12 < P < 0.80$ ).

The distribution of Mesostigmata across tree species appears to be almost random, and seem to have little to do with bark type. Besides *Celaenopsis* n. sp. 1, *Caliphis tambo-rinensis* is another common species on trunks and was found on at least half of all trees sampled ( $\geq 3$  out of 6) for each tree species (except on *O. excelsa*; Table 2). All other



**Fig. 4** Rarefaction curves of species collected from smooth, intermediate and rough barked trees. Each curve represents the average, randomized number of species accumulated for a given number of individuals collected on the three tree species of the same bark type. The 95% confidence intervals are shown



**Fig. 5** Sørensen's coefficient of similarity ( $\pm$ Std. dev.) between pairs of samples of smooth (S), intermediate (I) and rough (R) barked trees. 'ns' indicate non-significant differences between coefficient of similarity within tree species (open bars) and among tree species (solid bars) ( $P > 0.05$ )

species were scattered and rather rare in occurrence and abundance. Nevertheless, four other species (out of the remaining 10) were found on at least one tree species of each bark category (Table 2). Five of the most common species were also collected on tree trunks during the previous survey, and four species were also collected from fungi growing on dead wood (Table 2).

## Discussion

A relatively species-poor collection of mesostigmatid mites was made from the 54 samples of the surface of rainforest tree trunks, even though the samples represented nine species of trees and a broad range of bark roughness. In comparison, a single liter of soil and litter in Australian rainforests commonly contains 15–20 species of Mesostigmata and a liter of suspended soil averages 7–10 species (Beaulieu 2005). The more three-dimensional structure, more favorable microclimate and greater food supply of soil and litter probably explains its denser fauna. A comparative study between litter and the bark of hoop pine (*Araucaria cunninghamii* Aiton ex D. Don) showed a similar pattern for oribatid mites, with many more individuals and species per litter sample than bark sample (Proctor et al. 2002). However, these authors obtained seven times more individuals (not surprising since their target species feed on lichens, fungi and decaying plant matter and ours are mainly predatory) and 3–4 times more species per sample from their bark studies than we encountered.

Our data indicate that the mesostigmatid mite fauna (Uropodina excluded) of tree trunks is mainly a mixed set dominated by suspended soil inhabitants and ‘generalist’ species, with few bark specialists in terms of numbers of species, while the rich ground-dwelling fauna has little to do with tree trunks (partly supporting hypothesis 1). Foliar mites also appear to be nearly completely absent from bark. It may not be the case for bark in the upper canopy where foliar mites may seek refuge in bark crevices from nearby leaves and stems (in contrast to suspended soil which occur as low as 0.5 m high, F.B. pers. obs.). The overlap in species between the forest floor and arboreal habitats appear to be mainly via generalist species co-occurring in ground litter and suspended soil. Hence, tree trunks appear mainly as a small, undifferentiated component of the arboreal realm. These results do not quite agree with the ‘sandwich stratification’ discussed by Prinzing and Woas (2003), which dictates that the canopy soil and forest floor microarthropod faunas (oribatids and collembolans in their case) are similar and divided by a distinct tree bark fauna. For mesostigmatid mites, it appears that the sandwich has considerably different top (suspended soil) and bottom (ground) layers (Walter et al. 1998; Beaulieu 2005), separated by a relatively depauperate middle layer (trunk), which is largely a subset of the top layer. This suggests that tree trunks represent a ‘highway’ for most Mesostigmata using them. The low frequency and abundance of most species collected (except the two most abundant species) support this hypothesis (compared to their frequency in suspended soil). Thus, suspended soil inhabitants may use the trunk to disperse between suspended soil patches, or to re-enter the arboreal stratum after becoming dislodged.

Tree trunks function as links between the ground and the canopy for a diversity of arthropods, including many herbivores which develop or lay their eggs in the soil (Moeed and Meads 1983), canopy nesting ants occasionally foraging on the ground (and vice versa, Wilson 1959), and many typical soil dwellers (e.g. earthworms, springtails, centipedes, amphipods, mites) which may use tree trunks to commute between forest floor and suspended soil, as suggested by their occurrence in trunk traps (Moeed and Meads 1983).

Upward migration on tree trunks appears as the most likely strategy by which canopy soil is colonized by oribatid mites (Behan-Pelletier and Winchester 1998) and collembolans (Bowden et al. 1976; Rodgers and Kitching 1998) although they may also be grazing on epicorticolous algae and fungi.

Tree bark may be a (permanent or transient/seasonal) habitat for some Mesostigmata. The commonness of *Celaenopsis* n. sp. 1 and *Caliphis tamborinensis* (and the presence of juveniles) supports the view that these species actively forage (and develop) on the bark habitat. Although few species were collected in total from tree trunks, other species may be associated with bark habitats. The ecology of *Acugamasus* spp. is unknown but their occurrence on tree trunks and their capture from canopy fogging suggest an association with arboreal or woody habitats. The inspection of epicorticolous epiphytes (lichen, mosses) would likely add several species to the tree trunk fauna. Moreover, inner layers of bark, especially the galleries of bark and wood boring insects may well contain a diverse and specialized acarofauna in Australian forests (see Moser and Roton 1971). *Celaenopsis* species most often occur beneath the bark of dead trees or in the galleries of bark beetles, and are phoretic on the beetles (Kinn 1970). Thus, it is possible that specimens of *Celaenopsis* n. sp. 1 that we collected represent only the tip of the iceberg, with most of the population to be found beneath the bark. In sum, a rich mite fauna may remain cryptic until we explore more cracks and hidden layers on and beneath the surface of tree trunks.

There was no apparent effect of bark structure on mesostigmatid species richness and composition (not supporting hypotheses 2 and 3). More complex bark structures did not favor the maintenance of a richer mesostigmatid fauna. One species, *Celaenopsis* n. sp. 1, even appeared to have some preference for smoother bark as opposed to rough bark. One might suggest that the lower abundance of the species on rough bark samples is due to a bias in sampling efficiency, where most individuals could have been lodged in cracks and crevices. However, we do not believe that a bias occurred as extra caution was paid when brushing the narrow spaces and grooves of rough bark (and this extra caution resulted in some bark pieces being brushed off the trunk). Moreover, the method used has been proven efficient for the sampling of mites on bark (Kitching et al. 2001; Proctor et al. 2002).

Our findings do not concur with those of Nicolai (1986, 1989) and Menzel et al. (2004), who found richer arthropod (including oribatid) and beetle faunas, respectively, on trees with more complex bark. However, the patterns found by Nicolai in Europe and Africa (1986, 1989) were not consistent and some tree species with fissures or scales did not support more individuals or species than smooth bark trees. Majer et al. (2003) found that some arthropod taxa (ants, beetles, bugs, flies) were trapped more abundantly on smooth bark than on rough bark eucalypt trees in Australian woodlands. Although their results have been analyzed, to date, only at higher taxonomic levels (orders), it suggests that at least some species are preferentially distributed on smooth bark. Majer et al. (2003) stated that most invertebrates trapped originate from the canopy or the forest floor (hence using the bark as a dispersal mean or transient habitat) and proposed that the richer fauna on smooth barked eucalypts may be due to a more diverse fauna inhabiting the canopy and forest floor below these trees.

Our study did not show any sign of tree–host specificity of Mesostigmata. Rather, these mite species seem to have a random distribution on tree trunks, irrespective of the tree species (not supporting hypothesis 4). However, it would be premature to draw definitive conclusions on host specificity because the abundance and occurrences of most species were low and quantitative sampling was restricted to a single date. The apparent lack of strict host specificity is not surprising given that most species studied also commonly occur in habitats only loosely associated with the host tree, namely suspended soil and ground

soil-litter. Even Mesostigmata (Phytoseiidae) living on plant leaves generally show little host specificity and occur on many host plants (e.g. Walter 1992; McMurtry and Croft 1997; Chiara and Tsolakis 2001). Some phytoseiid species, however, occur on a narrow range of hosts (e.g. on one plant family, McMurtry and Croft 1997), and some may be host-specific at the plant species level, as suggested by a survey in sclerophyllous woodlands of Eastern Australia (Beard and Walter 2001).

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