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Aggregation and synecology of arboreal arthropods associated with an overstorey rain forest tree in Australia

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ABSTRACT. The cohesion of the arthropod community associated with the rain forest tree *Argyrodendron actinophyllum* was studied in a warm subtropical rain forest in Australia. The distribution of most arthropods was contagious on the foliage of *A. actinophyllum*. Chewers and phloem-feeders were more clumped than epiphyte grazers and parasitoids. Arthropod predator-prey ratios were high and relatively constant over time, as revealed by measures of their activity. However, similar ratios in abundance and species-richness of arthropods foraging on foliage showed high variability in space and no consistent trends. Species associations on the foliage were difficult to predict and did not constitute either a single, well-united community or well-delimited subcommunities. Most of the data suggest that on the foliage of *A. actinophyllum*, the cohesion of the arthropod community is not extremely strong. Apart from methodological constraints, possible reasons for this include the influence of host-tree phenology, and the high arthropod-diversity of the rain forest environment.

KEY WORDS: arboreal arthropods, aggregation, *Argyrodendron actinophyllum*, Australia, community structure, predator-prey ratios, synecology.

INTRODUCTION

During the last decade there has been growing interest in arthropod communities associated with rain forest trees. Most studies have investigated, with various degrees of precision, the abundance, seasonality and taxonomic composition of arboreal arthropod faunas (e.g. Adis *et al.* 1984, Basset 1991a & 1991b, Erwin 1983, Erwin & Scott 1980, Stork 1991, Stork & Brendell 1990, Watanabe & Ruaysoongnern 1989). Other studies have documented inter-tree differences in taxonomic composition of arthropod populations (e.g. Farrell & Erwin 1988, Stork 1987a), relationships between arthropod abundance, species-richness and body size (Basset & Kitching 1991, Morse *et al.* 1988) and the trophic structure of arthropod communities (e.g. Basset & Arthington 1992, Stork 1987b). However, to date, information about species interactions within arboreal communities is lacking. In particular, the ‘cohesion’ of such communities, i.e. the stability and

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predictability of species associations on the host foliage, is poorly known. The present contribution examines the predictability of arthropod-species associations in an Australian overstorey rain forest tree, *Argyrodendron actinophyllum* (Bailey) Edlin 1935. Three aspects of the cohesion of the arthropod community were studied: (a) aggregation patterns of arthropod populations on foliage; (b) consistency of arthropod predator-prey ratios; and (c) synecology of arthropod species foraging on foliage.

METHODS

Study site, host-tree and arthropod sampling

The study was performed in a stand of complex notophyll vine forest (warm subtropical rain forest) in the Mount Glorious State Forest (27° 19' 20" S, 152° 44' 55" E, altitude 700 m), some 30 km NW of Brisbane, Queensland, Australia, *Argyrodendron actinophyllum* Edlin ('Black Booyong') is a tall member of the Sterculiaceae, up to 50 m high. Description of the study site and host-tree are summarized by Basset (1991b).

Arthropod sampling was performed using two main techniques that were developed to study specifically either the seasonal or spatial distributions of arboreal arthropods. First, five composite interception traps consisting of malaise and window trap sub-units were set up in the crowns of five mature Black Booyong trees. Arthropods were collected continuously, day and night, with these traps, which were monitored weekly during 1986 and 1987. Second, 240 samples each including 0.7 m² of leaf area were fogged with CO₂ ('restricted canopy gassing', also termed 'restricted canopy fogging' in other papers). The samples were obtained during day-time, at different heights and orientations from ten mature trees, and in four discrete sampling periods during 1987 and 1988. Sampling procedures are detailed, compared and discussed elsewhere (Basset 1988, 1990). Collected specimens were stored in 70% ethanol, sorted to morphospecies, which were examined subsequently by numerous taxonomists, and assigned to arboreal guilds (Basset 1991a, Basset & Arthington 1992). Acari and Collembola were disregarded for technical reasons and some arthropod families, particularly most Hymenoptera Parasitica, could not be sorted to species (see details in Basset 1990, 1991a). Both immature and adult stages were considered in the analyses and the level of sorting was identical for trap and gassing data.

Statistical methods

Two different aggregation indices were determined for different arthropod species and also for different arthropod families and guilds. First, Taylor's power law and its index of aggregation b , which is considered to be constant for a particular species (Taylor 1984), were regressed as $\log s^2 = \log a + b(\log m)$, where s^2 = variance, a = a sampling factor and m = mean. Second, Iwao's patchiness index was computed as mean crowding = $mc = m + (s^2/m) - 1$ and

regressed as $mc = \alpha + \beta m$ (Iwao 1968). The index α represents the number of individuals that can be expected to be found with one other individual in the sample, when density is infinitesimally small (index of basic contagion), whereas β is the density-contagiousness coefficient (Iwao 1968). For both α and β , values greater than 1 indicate an aggregated distribution; values equal to 1, a random distribution and values less than 1, a regular distribution. Thirty gassing data sets of eight samples each were considered. The mean, variance and mean crowding values of these data sets, which represent different situations (e.g. different sampling dates, different trees, etc.), were determined. Samples included in a data set were obtained from the same tree and crown level (see Basset 1990). For each arthropod taxon or guild examined, values of the different data sets were regressed to obtain the aggregation indices of Taylor and Iwao. Both statistics were calculated because Taylor (1984) indicated that Iwao's method may lead to erroneous interpretation in some instances, despite the regressions being highly significant.

Predator-prey ratios were obtained by regressing number of individuals or species of predators against prey, by means of Bartlett's three-group method (Sokal & Rohlf 1981). Bartlett's regression represents a safer approximation of predator-prey ratios than simple ratios or ordinary least squares regression, because it allows determination of the relationship between two variables that are both subject to error (i.e. it does not assume that sampling results are unaffected by both prey and predator behaviour) (Lockwood *et al.* 1990). Predators, as here considered, included all entomophagous arthropods (predators and parasitoids), and prey and predator categories were considered to be mutually exclusive. Trap data consisted of the mean number of individuals collected per trap per week, and the pooled number of species collected during one week. Gassing data consisted of the total number of individuals and species collected and sorted in one set of eight samples (about 5.6 m² of leaf area), to ensure sufficient arthropod numbers for analyses.

Species associations are difficult to study when insect population levels are low, as is the case on the foliage of *A. actinophyllum* (Basset & Arthington 1992, Basset & Kitching 1991). In such cases, most association coefficients are biased when numerous double zeros occur and, therefore, quantitative data should be analyzed by detrended correspondence analysis (DCA) (Legendre & Legendre 1984). A DCA was performed on the raw abundance of the 32 most common species (i.e. present in at least 5% of samples) ordered by the 240 gassing samples. In addition, the minimum spanning tree (Digby & Kempton 1987) was drawn when computing Kulczynski's coefficient between each species. This coefficient is defined for absence/presence data and excludes double zeros (Legendre & Legendre 1984). The spanning tree allowed the estimation of relationships between species on a presence/absence basis, and also assisted in the delimitation of species groups.

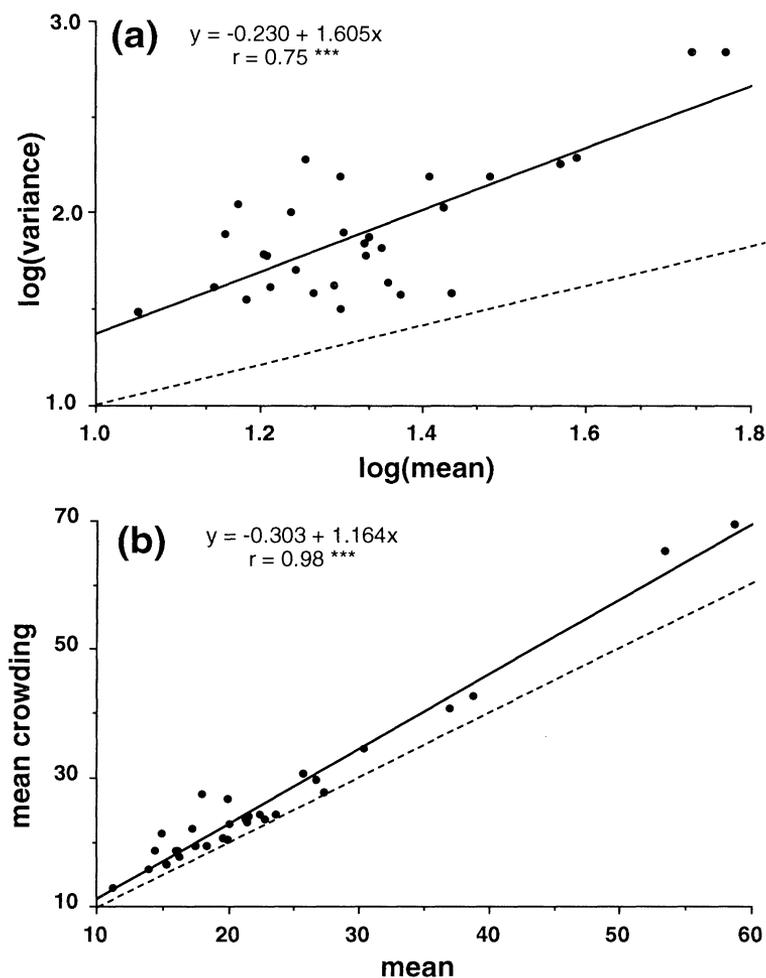


Figure 1. Relationships established for all arthropod individuals in gassing samples (a) between $\log(\text{mean})$ and $\log(\text{variance})$, according to Taylor's method; and (b) between mean and mean crowding, according to Iwao's method. Broken lines denote a slope of 1. For further explanation see methods.

RESULTS

Aggregation of foliage arthropods

Figure 1 displays the regressions computed by Taylor's and Iwao's methods when all arthropod individuals are considered. The slopes of both regression lines are significantly higher than 1 (power law: $t = 18.58$, $P < 0.001$, $df = 28$; mean crowding: $t = 9.43$, $P < 0.001$, $df = 28$), indicating that arthropods are clumped on *A. actinophyllum* foliage. Interestingly, both α and β are negative (Figure 1). Table 1 lists the intercepts and slopes of the regressions computed by the power law and the mean crowding index for selected insect taxa and guilds. Setting aside those instances where the results of the two analyses do not correspond (six out of 33 instances), four groups of distributions can be seen: first, most

Table 1. Aggregation indices computed for several taxa and guilds from 30 groups of 8 gassing samples, according to Taylor's and Iwao's methods (see text).

Taxa/Guild	POWER LAW				MEAN CROWDING				df
	Intercept a	Slope b	Corr. coeff. r	t-test slope ≠1	Intercept α	Slope β	Corr. coeff. r	t-test slope ≠1	
Araneae	-0.395	1.761	0.719 ***	10.57 ***	-2.441	1.578	0.924 ***	13.14 ***	28
Clubionidae	-0.114	0.867	0.622 ***	0.65 NS	-0.347	1.283	0.693 ***	2.48 *	28
<i>Clubiona</i> sp.	-0.092	0.887	0.675 ***	0.68 NS	-0.333	1.452	0.598 ***	2.61 *	28
Salicidae	-0.168	0.853	0.925 ***	3.80 ***	-0.047	0.731	0.765 ***	-3.56 **	26
Theridiidae	-0.044	1.118	0.720 ***	0.93 NS	-0.003	1.036	0.831 ***	0.76 NS	28
<i>Synotaxus</i> sp.	0.107	1.189	0.949 ***	3.94 ***	-0.219	1.728	0.861 ***	5.55 ***	25
<i>Thaletesia argentiopunctata</i>	-0.023	1.064	0.898 ***	1.17 NS	-0.146	1.219	0.681 ***	1.42 NS	24
Thomisidae	-0.123	0.924	0.858 ***	2.25 *	-0.103	0.921	0.351 *	0.34 NS	20
Blattodea	0.124	1.238	0.932 ***	5.71 ***	-0.428	2.489	0.758 ***	5.80 ***	25
Coleoptera									
Chrysomelidae	0.154	1.415	0.931 ***	3.77 ***	0.014	1.499	0.864 ***	5.09 ***	25
<i>Rhyarida</i> sp.	0.095	1.287	0.989 ***	5.30 ***	-0.307	1.450	0.985 ***	6.76 ***	8
<i>Longitarsus</i> sp.	0.236	1.329	0.954 ***	3.85 *	-0.020	1.758	0.837 ***	6.03 ***	23
Corylophidae	0.392	1.851	0.933 ***	5.86 ***	-1.199	3.923	0.887 ***	10.49 ***	24
Curculionidae	0.108	1.219	0.821 ***	2.01 NS	-0.919	3.468	0.742 ***	6.46 ***	26
Homoptera									
Cicadellidae	0.050	1.271	0.803 ***	1.55 NS	0.118	1.171	0.678 ***	1.39 NS	28
Psyllloidea	0.085	1.481	0.972 ***	7.36 ***	-0.546	1.459	0.986 ***	10.85 ***	25
<i>Acanopsylla</i> sp.	0.143	1.267	0.987 ***	4.27 **	-0.117	1.277	0.991 ***	6.82 ***	11
<i>Probyra</i> sp.	0.118	1.167	0.898 ***	2.28 *	-0.060	1.649	0.610 **	2.27 *	18
Hymenoptera									
Aphelinidae	0.041	1.169	0.922 ***	2.60 *	-0.283	1.603	0.888 ***	4.58 ***	20
Formicidae	0.191	1.352	0.951 ***	5.18 ***	-0.216	1.822	0.935 ***	7.88 ***	22
Lepidoptera - chewers	0.034	1.150	0.871 ***	2.81 **	-0.372	2.189	0.615 ***	3.45 **	25
Lepidoptera - epiphyte grazers	0.056	1.118	0.931 ***	2.30 *	-0.164	1.574	0.723 ***	2.32 *	12
Orthoptera	-0.146	0.910	0.821 ***	1.48 NS	-0.166	1.056	0.459 **	0.26 NS	19
Psocoptera	0.169	1.378	0.911 ***	3.23 **	0.602	1.323	0.717 ***	1.85 NS	27
Thysanoptera	0.123	1.329	0.849 ***	2.80 **	0.111	1.346	0.879 ***	4.89 ***	28
? <i>Podothrips</i> sp.	0.233	1.480	0.935 ***	5.51 ***	-0.222	2.018	0.823 ***	6.15 ***	26
<i>Teuchothrips</i> sp.	0.140	1.281	0.889 ***	3.23 **	-0.217	1.823	0.763 ***	4.99 ***	26
All chewers	0.103	1.413	0.875 ***	2.93 **	-0.100	1.557	0.800 ***	4.36 ***	28
All phloem-feeders	0.006	1.489	0.948 ***	6.99 ***	-0.531	1.373	0.988 ***	11.42 ***	28
All epiphyte grazers	0.190	1.325	0.890 ***	2.64 *	0.756	1.287	0.706 ***	1.71 NS	27
All fungal-feeders	0.291	1.759	0.940 ***	6.27 ***	-1.925	3.739	0.910 ***	13.55 ***	28
All parasitoids	-0.015	1.117	0.856 ***	0.91 NS	0.013	1.068	0.822 ***	0.86 NS	28
All predators	-0.346	1.710	0.621 ***	12.55 ***	-2.123	1.450	0.911 ***	13.26 ***	28

* P < 0.05. ** P < 0.01. *** P < 0.001. NS = not significant.

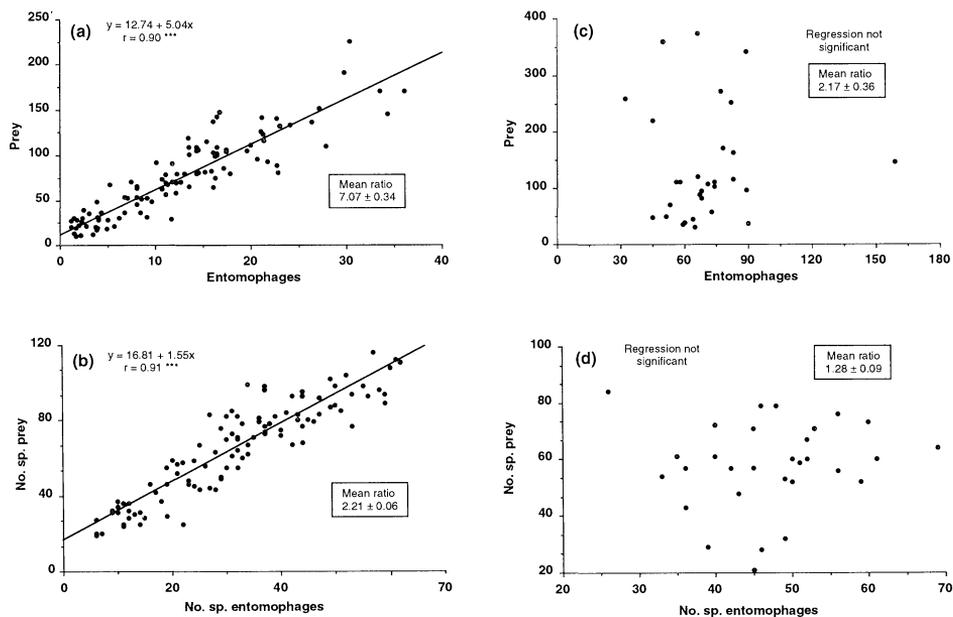
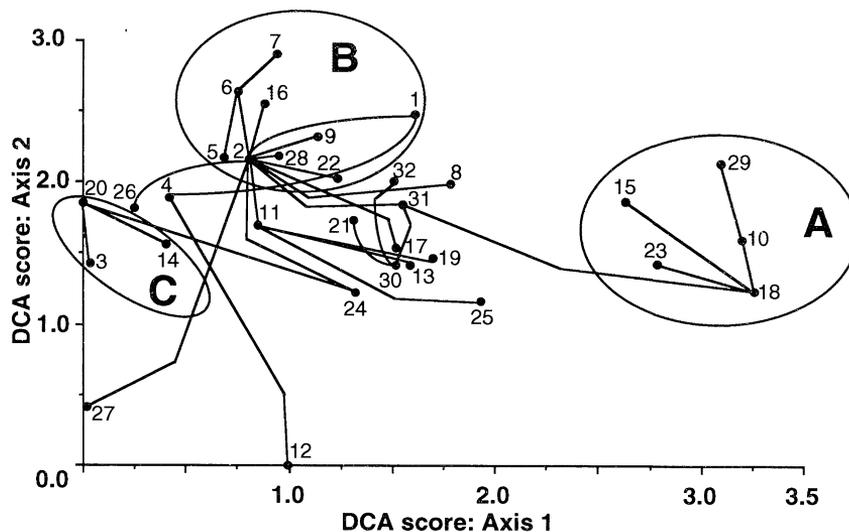


Figure 2. Bartlett's regression of entomophagous arthropods against arthropod prey for individuals (a) and species (b) collected by interception traps, and for individuals (c) and species (d) collected by restricted canopy gassing. Mean ratios of entomophagous arthropods to arthropod prey are indicated in boxes.

phytophagous taxa (chewers, phloem-feeders, chrysomelids, psyllids, etc.) and corylophid beetles are aggregated; second, epiphyte grazers (psocids), thrips and ants are less clumped; third, some spider groups (particularly theridiids), all parasitoids considered together, orthopterans and cicadellids are randomly distributed; and fourth, salticid spiders exhibit a uniform distribution.

Arthropod predator-prey ratios

Interception trap data indicate that the seasonal activity of predators is highly correlated with that of potential arthropod prey (Figure 2). In this case, the predator-prey ratios determined by the slopes of Bartlett's regression (Lockwood *et al.* 1990) are high: 5.0 for individuals and 1.6 for species (slopes significantly different from zero: $t = 19.5$ and $t = 61.2$ for individuals and species, respectively, $P < 0.001$ in both cases). Mean ratios are notably higher than slopes determined by regressions: 7.1 (range 2.5–13.0) and 2.2 (range 1.5–3.6) for individuals and species, respectively. However, when the abundance and species richness of foliage arthropods are analyzed, regressions for predator-prey ratios are not significant (gassing data, Figure 2; $t = 0.84$ and $t = 1.03$ for individuals and species, respectively, $P > 0.05$). In this case mean ratios are 2.2 for individuals (range 0.4–8.1) and 1.3 for species (range 0.5–3.2). Furthermore, when herbivores only are considered as potential prey, the regressions remain non-significant ($t = 0.30$ and $t = 0.18$ for individuals and species, respectively).



- | | | |
|--|---------------------------------------|--|
| 1 Clu <i>Cheiracanthium</i> sp. | 12 Cor Undetermined sp. | 23 For <i>Crematogaster</i> sp. |
| 2 Clu <i>Clubiona</i> sp. | 13 Cur <i>Saccolaemus</i> sp. | 24 For <i>Camponotus</i> sp. |
| 3 Clu <i>Matidia</i> sp. | 14 Cur Undetermined sp. | 25 For <i>Iridomyrmex</i> sp. |
| 4 The <i>Euryopsis</i> sp. | 15 Cur ? <i>Hypera</i> sp. | 26 Arc Lithosiinae sp. |
| 5 The <i>Synotaxus</i> sp. | 16 Cur <i>Storeus</i> sp. | 27 Grl <i>Ornebius</i> sp. |
| 6 The <i>Thwaitesia argentiopunctata</i> | 17 Lat <i>Cortinicara</i> sp. | 28 Ste Undetermined sp. |
| 7 The <i>Theridion</i> sp. | 18 Psy <i>Aconopsylla</i> sp. | 29 Thr <i>Megalurothrips kellyanus</i> |
| 8 Ara <i>Araneus</i> sp. | 19 Psy <i>Protyora</i> sp. | 30 Phl ? <i>Podothrips</i> sp. |
| 9 Bla Undetermined sp. | 20 Psy <i>Ctenarytaina longicauda</i> | 31 Phl <i>Teuchothrips</i> sp. |
| 10 Chr <i>Rhyparida</i> sp. | 21 Cic Undetermined sp. | 32 Phl <i>Xylaplothrips ?clavipes</i> |
| 11 Chr <i>Longitarsus</i> sp. | 22 Coe <i>Icerya</i> sp. | |

Figure 3. Detrended correspondence analysis of 32 species ordered by 240 gassing samples. Plot of the species in the space formed by the first two axes of the ordination. The minimum spanning tree, as obtained with Kulczynski's coefficient, is superimposed. Taxa codes as follows: Clu = Clubionidae; The = Therediidae; Ara = Araneidae; Bla = Blatellidae; Chr = Chrysomelidae; Cor = Corylophidae; Cur = Curculionidae; Lat = Lathridiidae; Psy = Psylloidea; Cic = Cicadellidae; Coe = Coccoidea; For = Formicidae; Arc = Arctiidae; Grl = Gryllidae; Ste = Stenoposocidae; Thr = Thripidae; Phl = Phlaeothripidae.

Synecology of foliage arthropods

The first two axes of the detrended correspondence analysis account for a high proportion (68%) of the variance (44.4% and 23.5% for Axes 1 and 2, respectively) and thus allow appraisal of the strength of the associations between species (Figure 3). Axis 1 is interpreted as a gradient of foliage age and its suitability for arthropods, with taxa situated on the right of the ordination plot being usually restricted to young foliage. Interpretation of Axis 2 remains obscure. There are few conspicuous trends in the grouping of the species. However, based on the ordination scores and the minimum spanning tree, three 'groups' (the word 'sub-community' may be too categorical in this context) are recognized (Groups A, B, and C in Figure 3). The species of Group A are restricted to young foliage (four herbivores and one ant). Species of Group B exhibit a ubiquitous spatial distribution, which is nearly random (five spiders, one coccoid, one cockroach, one weevil and one psocid). Lastly, species associations in Group

C (one spider, one psyllid and one weevil) remain unexplained, but may be related to temporal segregation.

DISCUSSION

A negative value for α theoretically suggests a repulsive interaction between individuals, related for example to territoriality (Iwao 1968). In practice, it suggests that the gassing technique may have been less efficient at lower densities. Furthermore, Taylor (1984) warned that small samples, including a single individual, cannot enable distinction between true and pseudo-randomness. However, the general low arthropod densities prevented the exclusion of these samples, which accounted for a substantial part of the data set, particularly when taxa were considered at higher taxonomic resolution. In fact, both Taylor's and Iwao's indices were originally developed for studying the aggregation of unispecific populations.

Most insect herbivores associated with *A. actinophyllum* showed contagious distributions. Since they appear to be highly dependent on the presence of young foliage, which is scattered throughout tree crowns during leaf-flush periods (Basset 1991c, d, e), their distribution probably reflects that of their food items. Epiphyte grazers appeared less clumped on the foliage than herbivores, presumably because epiphyll load was more evenly distributed on the foliage than suitable patches of young leaves. For example, leaf-feeding caterpillars were slightly more aggregated in the samples than epiphyll-feeding caterpillars. Other arthropod groups, particularly parasitoids, showed an apparently random distribution on the foliage, but, until more is known about their behaviour in the rain forest canopy, the interpretation of these limited data will remain difficult.

Predator-prey ratios, as determined by arthropod activity, were high, particularly when computed for individuals. This was because numerous insects (such as Sciaridae), emerging from the forest litter and swarming into the tree crowns, were not readily collected by gassing (Basset 1990, 1991a). The corresponding ratio for species-richness was much lower, and similar to those determined in other studies (e.g. Evans & Murdoch 1968, Lockwood *et al.* 1990). However, it may have been even lower if the Hymenoptera Parasitica had been sorted and included. The good correlation between the activity of arthropod predators and prey suggests that predator-prey ratios may be relatively constant over time, as in most terrestrial habitats (Lockwood *et al.* 1990). Conversely, no consistent trends were evident in space, particularly when arthropods were sampled on trees displaying different magnitudes of foliage turnover (see Basset 1991b). In fact, arthropod predators did not appear to respond to increased densities of herbivore prey in samples which included numerous young leaves (Basset 1992).

Although insect taxa were aggregated on the foliage, few trends in species association were evident. In the ordination plot, species were neither grouped into a single large, well-united group, nor into well-defined sub-communities. This suggests that, when interspecific aggregation occurs on the foliage of *A.*

actinophyllum, the groups so delimited are not consistently composed of the same species. However, certain species were relatively closely associated and this probably originated from specific predator-prey interactions. Among possible associations of this type, note the spider *Clubiona* sp. and one undetermined species of stenopsocid (nos. 2 and 28 in Figure 3), and the ant *Crematogaster* sp., which may collect honeydew from or prey upon the psyllid *Aconopsylla* sp. (nos. 23 and 18). Few such examples occurred, supporting the opinion that many arboreal predators are polyphagous (Jermy 1988). In contrast to interspecific associations, arthropod intraspecific aggregation generated clusters of samples which were quite distinct from others, as exemplified by one undetermined species of corylophid (no. 12), which was isolated in the ordination plot.

To summarize, the data suggest that the cohesion of the arboreal community associated with *A. actinophyllum* is not extremely strong. This observation may be explained in at least three ways.

First, since arthropod sampling in, and regular access in, the rain forest canopy are not straightforward, methodological problems cannot be excluded. However, most arthropods collected by either sampling method were regularly seen on and collected from the foliage, and only a few species that were commonly seen on the foliage, were not collected by either sampling methods (Basset 1991a). Exclusion of species of Collembola, Acari and of most of the Hymenoptera Parasitica from the analyses may have resulted in poorly-defined species interactions and in very variable predator-prey ratios. However, it is not clear why the level of sorting should influence gassing data and not interception trap data. Perhaps this is because arthropod sampling was during day-time only with gassing, whereas interception traps provided continuous sampling, day and night. Probably more crucial is the problem of defining the boundaries of the arboreal community associated with *A. actinophyllum*. Many species may be rare and may be foraging only occasionally within the crowns of this tree. Inclusion of these species in the analyses may result in a perception of the arthropod community as a rather 'open' system (see Basset & Kitching 1991).

Second, *A. actinophyllum* cannot be considered as a 'highly-apparent' tree for herbivores (*sensu* Feeny 1976), in comparison with, for example, eucalypt trees growing in nearby forests. Arthropod communities on *Eucalyptus* spp. are relatively well structured and distinct from those of other Australian trees (Woinarski & Cullen 1984); predators, such as ants, are abundant on their foliage (e.g. Majer & Recher 1988), and many eucalypt insects are highly host-specific (Morrow 1977). This is presumably because (a) shoot growth in *Eucalyptus* is indeterminate, and new, highly-suitable leaves for herbivores are produced in response to leaf-damage; and/or (b) this genus is represented by many species in Australia which are broadly similar in chemistry, phenology and morphology (Fox & Morrow 1986). Although the biochemistry of *A. actinophyllum* and *Eucalyptus* leaves certainly differ, their water and nitrogen content are similar (Basset 1991d). However, both the high botanical diversity of the rain forest habitat of *A. actinophyllum* and the temporal heterogeneity of leaf production of this tree, crucial to its associated

herbivores (Basset 1991e), may prevent or restrain the formation of predictable assemblages of herbivores. In being relatively unapparent to its herbivores, *A. actinophyllum* may also, to a certain extent, be unapparent to predators and parasitoids of herbivores, thus limiting the strength of species associations within the arthropod community to a few species. In support of this argument, both spiders and ants were scarce on young foliage, where most herbivores aggregated.

Third, arboreal guilds such as wood-eaters, tourists, epiphyte grazers and scavengers appear to depend more for trophic requirements on the overall rain forest community than on *A. actinophyllum* (Basset & Arthington 1992). Strong associations between arthropod species may be difficult for us to detect, or difficult for the insects to achieve, within a highly complex and species-rich ecosystem such as a rain forest. For example, May (1973) showed that theoretically the more species in the food-web, the greater the intensity of trophic interactions, and this in turn decreases the stability of the system.

Studies of other arboreal arthropod communities and manipulative field experiments in rain forests are needed for verification of the trends presented here. Such studies may establish whether the trends reported here for *A. actinophyllum* are characteristic or not of rain forest trees and of their associated arthropod communities.

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