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The Taxonomic Composition of the Arthropod Fauna Associated with an Australian Rainforest Tree

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Abstract

The composition of the arthropod fauna foraging within the canopy of *Argyrodendron actinophyllum* Edlin (Sterculiaceae) in a subtropical rainforest near Brisbane, Australia, was investigated during a 2-year field study. Collecting methods included flight interception traps, restricted canopy fogging, and hand-collecting. Over 50 000 canopy arthropods were collected and about 760 species sorted, from which 660 were identified at least to the generic level by taxonomists. The arthropod fauna of *A. actinophyllum* is characterised by the abundance of Clubionidae, Theridiidae, Psylloidea, Phlaeothripidae, Chrysomelidae, Corylophidae, Curculionidae and Braconidae, and by the scarcity of Empididae, Symphyta, Ichneumonidae and Formicidae. The major determinants of the composition of the arboreal fauna are discussed, including biogeographical and historical constraints, rainforest mesoclimate and host phenology, host architecture and biochemistry, and intrinsic composition of the foliicolous fauna. The faunistic composition of this subtropical rainforest tree species exhibits several features common to both temperate trees (such as the high numbers of homopterans and spiders and the limited populations of arboreal ants) and tropical rainforest trees (such as the large beetle populations and the high orthopteran biomass).

Introduction

The potientially rich and diverse arthropod fauna from Australia remains largely undiscovered and its systematics is still fragmentary (Taylor 1983). This is particularly true of herbivores and of species associated with arboreal habitats (Woinarski and Cullen 1984). Forest entomology in Australia has been focused mainly on pests associated with two genera of trees, dominant in Australian ecosystems: *Eucalyptus* and *Acacia* (e.g. Froggatt 1923; Morrow 1977; Carne and Taylor 1978; New 1979, 1984; Van den Berg 1980; Ohmart *et al.* 1983*b*). Other Australian native trees and their associated fauna have received little attention from entomologists (e.g. Froggatt 1923; Woinarski and Cullen 1984; Andersen and New 1987) and even fewer studies are relevant to canopy arthropods associated with Australian rainforest trees (e.g. Lowman 1985).

The aims of the present study were to record the arthropod fauna foraging within the crowns of the rainforest tree *Argyrodendron actinophyllum* Edlin (i.e. the fauna 'associated with' *A. actinophyllum*) and to assess the ecological features of this arboreal community. This global approach was chosen because Moran and Southwood (1982) showed that trees support a rich arthropod fauna, consisting of species of differing food habits, commonly classified by ecologists into a system of arboreal guilds. Space limitations do not allow presentation of comprehensive checklist of arthropods collected in the crowns of the host tree studied. Such a checklist does, however, exist (Basset 1989) and is available from the author on request. The taxonomic composition of the arboreal fauna is examined here at

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the family level, but the dominant arthropod genera within the collections are, whenever possible, indicated in parentheses in the text. The abundance of component taxa, their host specificity, and the species richness and guild structure of the arboreal community will be discussed elsewhere.

Materials and Methods

Study Area and Host Tree

The research program was carried out in a stand of complex notophyll vine forest (warm subtropical rainforest: see Webb *et al.* 1984). The exact location of the site was in the 'Beauty Spot 54' of Mount Glorious State Forest (27°19′20″S.,152°44′55″E., altitude 700 m), some 30 km north-west of Brisbane, in Queensland. A detailed account of the floristics of the site is given in Young (1985: group 9). *Argyrodendron actinophyllum* (Bailey) Edlin, 1935, the black booyong, is a tall tree from the family Sterculiaceae (Malvales), reaching 50 m high (Boland *et al.* 1984). Detailed accounts of the phenology and distribution of this rainforest species are reported in Boland *et al.* (1984) and Basset (1989). In the Mt Glorious area, the leaf flush of this species is synchronous among individuals and restricted from October to February (Basset 1989).

Collecting Methods

Canopy access was provided by single rope techniques (Perry 1978; see Basset 1989 for further details). Canopy arthropods were collected by three main techniques. Firstly, composite flight interception traps, consisting of malaise and window trap subunits, were set up in five *A. actinophyllum* trees and were run continuously day and night during the consecutive years 1986 and 1987. Secondly, samples of 0·7 m^2 of leaf area were enclosed and arthropods were knocked down with carbon dioxide (hereafter this method is termed 'restricted canopy fogging', in analogy with 'canopy fogging', which involves chemical insecticide knockdown). In all, 240 such samples were obtained from 10 trees in 1987. Both interception traps and restricted canopy fogging are detailed and compared elsewhere (Basset 1988, 1990). To summarise, agreement between sampling methods was good for certain arthropod groups but weak for others; overall, the two methods were considered complementary. Interception traps provided more mobile arthropods, whereas restricted canopy fogging yielded more sedentary, apterous and juvenile specimens. Thirdly, specimens were hand-collected from the foliage during the thousands of hours spent by the author in the canopy. Galls, mines and dead branches were picked up and kept until imagines emerged. Phytophagous species were sometimes collected alive; their feeding records on *A. actinophyllum* saplings in glasshouse were documented. This confirmed that most phytophagous taxa sampled from black booyong crowns also feed upon its saplings (Basset 1989).

Material

The collected specimens were stored in 70% ethanol, with the exception of some dry-pinned reference collections. The keys provided by Waterhouse (1970) were employed for sorting the material into orders and families; nomenclature was followed accordingly, except for a few taxa where updating was necessary. Acari and Collembola (mostly Oribatei and Entomobryidae) were disregarded because the handling of the specimens was too time-consuming and the proper estimation of their abundance would have required washing the inner part of the enclosure after each fogging sample (Hijii 1983; Basset 1990). Imagines of Lepidoptera were simply sorted by 'family habitus', since exact sorting increased the time investment tenfold without increasing the ecological information gained very much. Other arthropod groups were either extensively sorted into recognisable taxonomic units (RTUs: morphospecies), or sorted to family only (e.g. most of Diptera, Hymenoptera and Lepidoptera). Extensive sorting primarily concerned phytophagous species, reference collections of these groups were forwarded to 40 interested taxonomists for checking and finer study (Appendices I, II). The RTU assignment was corrected after examination by specialists, if needed. Furthermore, juveniles could not always be assigned to families with certainty (e.g. heteropterans, psocids) and had to be recorded as different species from adults. Most of the material collected was subsequently lodged at the Queensland Museum, Brisbane, after the completion of the study. Other specimens were donated to the Australian National Insect Collection, Canberra, and to other institutions involved with the sorting of the material.

Table 1. Literature compiled to assess the characteristics of the arthropod community associated with *A. actinophyllum*

Subject	Source	Locality	Host tree
Temperate ecosystems			
Reviews	Dajoz 1980	–	–
	Coulson and Witter 1984	–	–
Conifers	Martin 1966	U.S.A.	*Pinus*
	Klomp and Teerink 1973	Netherlands	*Pinus*
	Ohmart and Voigt 1981, Ohmart 1981	U.S.A.	*Pinus*
	Hijii 1983	Japan	*Chamaecyparis*
	Mouna *et al.* 1985	France; Morocco	*Cedrus*
	Basset 1985*a*, 1985*b*	Switzerland	*Pinus*
Deciduous trees	Couturier 1973	France	*Malus*
	Nielsen 1975	Denmark	*Fagus*
	Moran and Southwood 1982	U.K.	Several species
	Fowler 1985	U.K.	*Betula*
	Hargrove 1986	U.S.A.	*Robinia*
	Bigot *et al.* 1987	France	*Quercus*
Tropical ecosystems	Erwin and Scott 1980	Panama	*Luehea*
Rainforests	Erwin 1983	Brazil	Several species
	Adis *et al.* 1984	Brazil	Several species
	Stork 1987*a*, 1987*b*	Borneo	Several species
	Watanabe and Ruaysoongnern 1989	Thailand	Several sepcies
Other environments	Gagné 1979	Hawaii	*Acacia*, *Metrosideros*
	Moran and Southwood 1982	South Africa	Several species
Australian ecosystems			
Review	New 1983*a*	Australia	–
Eucalypts	Moore 1972	Australia	*Eucalyptus*
	Morrow 1977	Australia	*Eucalyptus*
	Neumann 1978, 1979	Australia	*Eucalyptus*
	Ohmart *et al.* 1983*a*, 1983*b*	Australia	*Eucalyptus*
	Woinarski and Cullen 1984	Australia	*Eucalyptus*
	Majer and Recher 1988	Australia	*Eucalyptus*
	Yen 1989	Australia	*Eucalyptus*
Non-eucalypts	Neumann 1978, 1979	Australia	*Pinus*
	New 1979, 1983*c*, 1984	Australia	*Acacia*
	Woinarski and Cullen 1984	Australia	Several species

Literature Compilation

The authors cited in Table 1 were consulted to assess the characteristics of the arthropod community associated with *A. actinophyllum*. The references listed in Table 1 deal with the whole or a large proportion of the arboreal community associated with the host-plant studied. These data are, however, often difficult to compare, since authors used different sampling techniques.

Results

Some 46 000 specimens distributed in 231 different arthropod families were collected by the five interception traps. The restricted canopy fogging program yielded 5600 individuals and 113 families. Species provided by hand-collecting were common in both the trap and the fogging collections. Appendix I details the number of individuals collected by orders and families, for each sampling method. When available, the number of species sorted (or RTUs) is listed, along with the assignment within the system of arboreal guilds (see Basset

1989). Out of 759 species which were recognised in this material, 439 were named at the generic level and 219 species were identified. Seven genera and 38 species were formally recognised as new and await description. These statistics emphasise the poor taxonomic knowledge of rainforest arthropods in Australia and, particularly, that of canopy arthropods. The taxonomic composition of each arthropod order is briefly outlined below.

Araneae

Spiders were the dominant order on the foliage. Such spider dominance has been reported from several temperate trees (oak: Patocka *et al.* 1962 (cited in Nielsen 1975); beech: Nielsen 1975; pine: Ohmart and Voigt 1981; cork oak: Bigot and Kabakibi 1987). Spiders are an important element of the canopy fauna in Europe (Nielsen 1975). They are well represented on eucalypt species in Australia but are supplanted by ants (Yen 1989; Majer *et al.* 1990). Woinarski and Cullen (1984) observed that spiders are more abundant in non-eucalypt trees than in eucalypts.

Arboreal spiders were well represented among the families Theridiidae (*Synotaxus* Simon, *Thwaitesia* Cambridge, *Euryopsis* Menge, *Achaearanea* Strand), Clubionidae (*Clubiona* Latreille, *Cheiracanthium* Koch), Salticidae (*Helpis* Simon, *Holoplatys* Simon), Araneidae (*Araneus* Clerck, *Dolophones* Walckenaer) and Thomisidae (*Diaea* Thorell, *Sidymella* Strand), as found in other arboreal studies (references in Table 1). However, Linyphiidae (*Bathyphantes* Menge) and Erigoniidae, scarcely obtained from the foliage sampled, represent an important component of the spider fauna on temperate trees (e.g. Renault and Miller 1972; Albert 1976). On the eucalypt species examined by Yen (1989) Salticidae were the dominant family, unlike Theridiidae in the present study. All families cited above are also well represented in the rainforest litter (Davies 1976, 1977) and a good proportion of the genera encountered on the foliage in this study (see Basset 1989) are also found at ground level (Davies 1976, 1977). It is well known that some European spiders migrate seasonally from the litter to the forest canopy and vice versa (Albert 1976); a similar situation may exist in Australian subtropical rain forests. Interestingly, leaf rollers such as *Deliochus* Simon and *Phonognatha* Simon (Araneidae: Main 1981) were not uncommon on black booyong foliage.

Coleoptera

The coleopteran fauna was dominated by the following families: Chrysomelidae (*Rhyparida* Baly, *Longitarsus* Berthold, *Colaspoides* Laporte), Scolytidae (*Cryphalus* Erichson, *Xyleborus* Eichhoff, *Xylosandrus* Reitter), Corylophidae, Staphylinidae (*Paraphloeostiba* Steel, *Sepedophilus* Gistel, *Anotylus* Thomson), Curculionidae (*Perissops* Pascoe, *Enteles* Schoenherr, *Saccolaemus* Kuschel, *Storeus* Schoenherr, ?*Hypera* Germar), Scarabaeidae (*Heteronyx* Guérin-Ménéville, *Neoheteronyx* Blackburn), Phalacridae (*Litochrus* Erichson), Lathridiidae (*Cortinicara* Johnson), Mordellidae, Melandryidae (*Orchesia* Latreille), Cerambycidae (*Mesolita* Pascoe), Elateridae (*Conoderus* Eschsholtz), Carabidae (*Trigonothops* Macleay, *Agonocheila* Chaudoir) and Tenebrionidae (*Amarygmus* Dalman). These families are usually common in arboreal habitats (references in Table 1). However, fewer Anthicidae (*Ictistyngna* Pascoe) were collected here than in other rainforest studies (Erwin and Scott 1980; Stork 1987*a*) or in Australian eucalypts (Yen 1989). In contrast, a higher proportion of Biphyllidae (*Biphyllus* Dejean), Laeomophloidae (?*Leptophloeus* Casey, *Placonotus* Macleay), Anobiidae (*Deltocryptus* Lea, *Dorcatoma* Paykull) and Cleridae (*Stigmatium* Gray, *Metademius* Schenkling, *Lemidia* Spinola) were found. These two last groups are well represented in temperate trees. Anobiid beetles are commonly associated with myrtaceous capsules and exhibit a certain ecological radiation in Australia (Andersen and New 1987). Foliage-dwelling Cleridae, such as *Lemidia* spp., were not uncommon and may be psyllid predators, as was reported for *Lemidia subaenea* Mulsant foraging on acacia trees (New 1978). As for the rainforest tree *Luehea seemanii* Triana & Planch (Erwin and Scott 1980),

very few Coccinellidae (*Rhyzobius* Stephens) were discovered in the samples. This family is usually well represented in temperate ecosystems, particularly on conifers (references in Table 1). No Bruchidae were recorded from the collections, but the study was carried out in absence of a large seed yield. New (1983*b*) reported that curculionid species of the genus *Melanterius* Erichson have apparently replaced the Bruchidae in their role of seed-eaters in Australian acacias.

Representatives of the family Lathridiidae appear to be regularly sampled in arboreal surveys (Klomp and Teerink 1973; Gagné 1979; Ohmart 1981; Basset 1985*b*). Some species are considered to be ecological indicators of the stability of forested ecosystems in Europe (Dajoz 1980). Interestingly, three Australian studies mentioned that a lathridiid was the most common beetle on the foliage (New 1979: *Lathridius* sp. on acacias; Ohmart *et al.* 1983*b*: *Corticaria adelaidae* Blackburn on eucalypts; Yen 1989: not specified, on eucalypts). In the present study *Cortinicara* sp. was the most abundant beetle species on the foliage with the exception of two chrysomelid species. This foliicolous fungal-feeder may be associated, among others, with moulds produced by psyllid honeydew (see below).

Diptera

Brachycera were represented by families including typical arboreal representatives (references in Table 1), such as Phoridae, Chloropidae, Empididae, Lauxaniidae, Dolichopodidae and Muscidae. However, dipteran predators, Empididae (*Drapetis* Meigen) and Dolichopodidae (*Amblypsilobus* Bigot, *Chrysotimus* Loew, *Diaphorus* Meigen), were slightly under-represented, especially the former family, in comparison with their occurrence in other arboreal habitats (see Martin 1966; Couturier 1973; Basset 1985*a*). Empididae are most numerous in boreal, temperate or mountainous regions (Collin 1961) and most of those collected here belong to the subfamily Tachydromiinae, whose tiny members rarely fly and usually run actively on the trunk and branches (D. J. Bickel, personal communication). Syrphidae were rarely collected; this family is poorly represented in Australia (Paramonov 1959). Agromyzidae, which were not recorded, are apparently absent from Australian acacias (New 1983*a*). Leaf mining on *A. actinophyllum* appears to be restricted to cecidomyiid and lepidopteran species (Basset 1989).

The Lauxaniidae (*Minettia* Robineau-Desvoidy, *Sapromyza* Fallén), on the contrary, were remarkedly well represented in the collections, making up the fourth most abundant brachyceran family. Broadhead (1984) showed that most of the lauxaniid flies present adaptations of the mouthparts for fungal grazing on the surface of leaves. This habit is apparently well developed in rainforest species, and Broadhead (1984) reported large numbers of these flies in the forest canopy of Panama. An examination of a sample of lauxaniids collected in interception traps showed that their guts were full of fungal hyphae and spores (Basset 1989). There is little doubt that these flies are actively grazing the microepiphyte cover on the foliage. Sciaridae, Cecidomyiidae and Chironomidae represented most of nematoceran collections.

Hemiptera

Psylloidea were by far the dominant insect group (in individuals) collected from the foliage. Of the psyllid specimens, 80% consisted of two undescribed species closely associated with *A. actinophyllum* (K. L. Taylor, personal communication; Y. Basset, personal observation). These species belong to the genera *Aconopsylla* Tuthill & Taylor (Psyllidae) and *Protyora* Kieffer (Carsidaridae). Psyllids are remarkedly diverse in Australia, in contrast with aphids (Eastop 1978) and exhibit major radiations on *Eucalyptus* and on *Acacia* (New 1983*a*). Black booyong psyllids do not produce lerps, although *Protyora* nymphs bear waxy filaments. This free-living mode may promote the coexistence of spider predators on the foliage (Theridiidae, Araneidae, Thomisidae and Salticidae: Watmough 1968). Other psyllid predators or psyllid parasitoids were also relatively abundant on the

foliage: Anthocoridae, Miridae (Coccinellidae), Coniopterygidae, Encyrtidae, Eulophidae, Ceraphronidae, Platygasteridae (Watmough 1968; Hodkinson 1974).

Cicadellidae (*Xestocephalus* Van Duzee, *Tharra* Kirkaldy, *Austrotartessus* Evans), Achilidae (genera near *Callinesia* Kirkaldy and *Francesca* Kirkaldy), Flatidae (*Siphanta* Stål) and Issidae (*Chlamydopteryx* Kirkaldy) were also abundant on *A. actinophyllum*. A striking feature of the homopteran fauna was the absence of both Membracidae and Eurymelidae, which in Australia feed mostly on *Acacia* and *Eucalyptus*, respectively, and are often ant-attended (Woodward *et al.* 1970). Most of the heteropteran species collected consisted of Miridae, Lygaeidae (*Botocudo* Kirkaldy) and Isometopidae.

Hymenoptera

One of the most obvious differences between the arboreal fauna examined and the equivalent fauna of other rainforest trees was the paucity of arboreal ants (*Camponotus* Mayr, *Crematogaster* Lund, *Iridomyrmex* Mayr). In this sense, *A. actinophyllum* is probably closer to temperate trees, which usually support fewer ants, than tropical trees or Australian eucalypts [temperate trees: ant = 0·2–3·0% of individuals collected (Moran and Southwood 1982; Basset 1985*a*); tropical trees: 18–53% (Moran and Southwood 1982; Erwin 1983; Adis *et al.* 1984; Stork 1987*a*); eucalypts: 11–69% (Majer and Recher 1988; Yen 1989)]. The low occurrence of ants in the collections (interception traps, 3%; restricted canopy fogging, 2%) confirms the more general examination by Majer (1990) of the status of arboreal ants in Australian rainforests. This author, sampling both with sticky traps and canopy fogging, showed that the abundance and the diversity of arboreal ants are generally lower in Australian rainforests than in eucalypt woodlands or in other rainforests.

This study failed to record any Symphyta associated with *A. actinophyllum*, with the exception of one Xiphydriidae (*Rhysacephala* Benson), a wood-borer. A few Tenthredinidae were obtained from the interception traps but they belonged to species equally abundant in the field layer (Basset 1989). The family Tenthredinidae is poorly represented in Australia and is replaced by the Pergidae, feeding mostly on eucalypts (Riek 1970). Several surveys in forested ecosystems recorded high ratios of Ichneumonidae to Braconidae, especially at ground level (Martin 1966; Geijskes 1968; Wolf *et al.* 1968). Gauld (1986) showed that certain subfamilies of Ichneumonidae are less diverse in Australian tropics than elsewhere as a consequence of the lack of appropriate sawfly hosts. In the present study Braconidae were collected three times more abundantly than Ichneumonidae. Other well represented large hymenopterans included Apidae (*Apis* Linnaeus) and Halictidae (*Lasioglossum* Curtis).

Sutton and Hudson (1980) gathered high numbers of Agaonidae from the canopy of a rainforest in Zaïre, no fig trees being close to their traps. Despite a similar situation in the present study, agaonids were rarely collected. High proportions of Pteromalidae and Bethylidae were found in the collections. Cynipoidea are poorly represented in Australia and are replaced by flower-bud galling Pteromalidae, particularly on *Eucalyptus* and *Acacia* (New 1983*a*, 1984). However, it is believed that most pteromalids collected in the crowns of *A. actinophyllum* are parasitoid species. The importance of families of Hymenoptera Parasitica, as judged by the number of individuals collected, seems to conform to what has been previously observed in the tropics, particularly the high proportion of egg parasites (Scelionidae, Mymaridae) (Noyes 1989). The high abundance of aleyrodid and coccoid parasites (E. C. Dahms, personal communication), particularly species of Aphelinidae (*Eutrichosomella* Girault) and Encyrtidae (*Cheiloneurus* Westwood), already documented from other rainforest surveys (Noyes 1989), was, however, intriging, since their hosts were not extremely abundant on *A. actinophyllum*.

Thysanoptera

The family Phlaeothripidae (?*Podothrips* Hood, *Teuchothrips* Hood, *Xylaplothrips* Priesner) seemed strikingly abundant on the foliage sampled. Leaf-feeding and leaf-rolling

Phlaeothripidae are particularly common in the high-rainfall areas of eastern Australia, where they form a complex of genera and species related to *Teuchothrips* (Mound 1971), which was abundant on *A. actinophyllum* foliage. It is not certain whether the presence of pouch domatia on black booyong leaves may promote thrip populations. O'Dowd and Willson (1989) reported that 91% of arthropods observed in domatia of 37 Australasian plants are mites, particularly predaceous and fungivorous types. The results of these authors support the existence of plant–mite mutualism, rather than a benefit to thrips.

Other Arthropod Orders

Neuroptera were characterised by a high proportion of Coniopterygidae (*Coniopteryx* Curtis) and a low proportion of Chrysopidae (*Chrysopa* Leach). The former family tend to be more abundant in New Guinean, Indonesian and Malaysian forest canopies, by comparison with the latter family, which, along with Hemerobiidae (*Micromus* Rambur), is more common in Australia (T. R. New, personal communication). Psocid samples were dominated by foliage-dwelling species, particularly Caeciliidae (*Caecilius* Curtis), Stenopsocidae and Ectopsocidae (*Ectopsocus* McLachlan), because the sampling methods had focused on the crown fauna rather than on the bark fauna. Lepidoptera were uncommon on the foliage, with the exception of fungal-feeding Arctiidae (Lithosiinae), and foliage-feeding Lymantriidae, Geometridae and Noctuidae. Most of Orthoptera consisted of Gryllidae (*Ornebius* Guérin-Ménéville), Tettigoniidae (*Austrosalomona* Rentz) and Gryllacrididae. Phasmatodea were rare on the foliage: one single juvenile and unidentified specimen was sighted and neither trapping nor fogging yielded any others. Opiliones were also scarce in the collections, as were Pseudoscorpiones. This last order is abundant on the foliage of pine trees in the U.S.A. (Ohmart and Voigt 1981) and is well represented on the trunk of Brazilian rainforest trees (Adis 1981).

Discussion

Strong *et al.* (1984) review the major determinants of herbivorous insect diversity on their host plants in terms of three hypotheses: the habitat-heterogeneity hypothesis, the encounter-frequency hypothesis and the equilibrium theory of island biogeography. Similarly, the relative occurrence of arboreal taxa (herbivores and others) in the crowns of *A. actinophyllum* seems to be determined by some broad biogeographical and historical constraints, by some ecological determinants resulting from rainforest mesoclimate and host phenology, by some more local effects originating from host architecture (Lawton 1978) and host biochemistry, and from the composition of the arboreal fauna itself. These factors are all interrelated and cannot be isolated from each other with ease. Lawton (1984), for example, showed that non-convergence in community structure of herbivorous insects on same host plants in differing geographic locations is prevented, among others, by climatic differences. The determinants of the arboreal fauna of *A. actinophyllum* are therefore tentatively summarised as follows.

Biogeographical and Historical Constraints

First, the association between black booyong and its specialist herbivores is probably influenced by historical and taxonomic factors. Carsidaridae, for example, appear to feed exclusively on Malvales (Hodkinson 1984), and the association between *Protyora* sp. and *A. actinophyllum* is therefore understandable. Rainforest hosts belonging to plant orders other than Malvales may support other specialised psyllids or none at all. Second, the relative abundance in the collections of certain groups was conform to broad biogeographical expectations concerning Australian arthropods. Psyllids, particularly, are more prevalent than aphids in Australia (Eastop 1978) and were overall well represented on black booyong, whereas aphids included only a few individuals, most of them associated with orchids. The Tenthredinidae, rarely collected, are under-represented in Australia, and their scarcity

may particularly decrease the diversity of certain Ichneumonidae in Australian tropics (Gauld 1986). Braconidae, indeed, outnumbered Ichneumonidae in the samples. Other groups which followed biogeographical expectations included Syrphidae, Agromyzidae and Bruchidae, which appear to be under-represented in Australia, and Anobiidae and Pteromalidae, which exhibit a certain radiation on this continent.

Rainforest Mesoclimate and Host Phenology

Majer (1990) proposed that aboreal ants may be limited in Australian rainforests by the strong seasonal climate and the resulting seasonal productivity, which is less during winter. The present data tend to support this hypothesis. The productivity of foliage arthropods followed closely the host phenology, being 60% lower in winter than during summer, and the contribution that ants made to the biomass of foliage arthropods was far lower in winter than during summer (Basset 1989). Opposing this observation, spiders represented about 85% and 65% of individuals and biomass, respectively, of foliicolous arthropod predators within black booyong crowns. Spiders may feed successfully on the relatively large populations of non-lerp-forming psyllids, psocids, thrips and nematocerans (Turner 1984; Nentwig 1987) present on the foliage during summer. Nentwig (1987) showed that small prey such as thrips may indeed be an important source of food for web-builders, which eat and recycle the silk of their web. In winter spiders can resist long periods of starvation (Riechert and Harp 1987), and therefore may be more competitive than ants during periods of low prey availability in the canopy. This is suggested by the high populations all the year round of both juvenile and adult spiders (Basset 1989). The web-builders can also feed upon the flying Nematocera (Chironomidae, Sciaridae) during winter, since these are important prey of these spiders (Nentwig 1987), particularly arboreal species (Renault and Miller 1972). Nematoceran flyers are abundant all the year round, and relatively active during winter (Basset 1989). Conversely, ants do not prey much upon spiders and usually prefer soft-bodied insects such as aphids and caterpillars (Stradling 1987). Overall, the available information strongly suggests that spiders have taken the predatory role of arboreal ants within *A. actinophyllum* crowns. Beetles may be relatively less sensitive than other groups to a large buildup of spider population on the foliage, since spiders usually avoid strongly sclerotised prey (Nentwig 1987).

Host Architecture and Biochemistry

A structurally rich type of bark, such as the thick and scaly bark of *A. actinophyllum*, may enhance the abundance and diversity of certain spiders (Nicolai 1986) and possibly of some fungal-feeding beetles (e.g. Laemophloidae, Phalacridae, Biphyllidae, Corylophidae, Lathridiidae) and some scavenging taxa (e.g. Gryllidae, some Staphylinidae and Tenebrionidae). A thick bark may also be an appreciable refuge during unfavourable conditions for certain insects such as Carabidae (Stork 1987*c*). Moreover, the compound leaves of this rainforest host, increasing the complexity of the mature foliage, may promote the occurrence of web-building spiders by favouring web establishment, particularly because most spiders respond positively to denser vegetational supports (Robinson 1981). For example, Stratton *et al.* (1979) showed that space-web builders, such as Theridiidae, dominated on the denser and architecturally most complex host of three coniferous species examined in northern Minnesota. Furthermore, the composition of the phytophagous fauna, particularly that of mono- and oligophagous species, is probably influenced by the food quality and the chemical defences of *A. actinophyllum*. Particularly, mucilage cells and canals are numerous in black booyong leaves. In Sterculiaceae (Hegnauer 1973) these structures contain complex sugar polymers (often with a core of galacturonic acid), which may, to a certain extent, 'gum up' insects or reduce their digestibility. The abundance of these cells and canals may limit grazing damage by generalist feeders and may partly explain the relatively low numbers of some orthopteran, phasmatodean and lepidopteran species chewing black booyong foliage.

Sap-sucking species, on the other hand, are probably less restrained by such defences, since they appear to be able to insert their stylets tortuously between cells and rarely pierce any until they reach the phloem elements (Dixon 1975). Investigations on the effect of black booyong chemical defences on associated herbivores were, however, beyond the scope of this work.

Intrinsic Composition of the Fauna

Relatively large numbers of psyllids on the foliage may through their honeydew secretions locally increase the occurrence of moulds on the leaves and may benefit fungal feeding taxa such as Lauxaniidae and Lathridiidae, particularly in absence of ants to regularly remove honeydew. Psyllid predators such as spiders and coniopterygids, and different psyllid parasitoids, may also benefit from large non-lerp-forming psyllid populations. The apparent lack of Membracidae and Eurymelidae, well represented in other Australian trees, may be attributed to the lower occurrence of arboreal ants, since these homopteran families are usually ant-attended.

In summary, the arboreal fauna of *A. actinophyllum* is characterised on one hand by high numbers of homopterans and spiders and limited populations of arboreal ants, a type of faunistic composition close to that on certain temperate trees, and on the other hand, by large beetle populations (e.g. Chrysomelidae, Corylophidae, Curculionidae) and high orthopteran biomass, a type of faunistic composition closer to rainforest trees (references in Table 1). Thus the faunistic composition of this subtropical rainforest species apparently exhibits several features common to temperate and tropical rainforest trees. More comparative arboreal surveys of other tree species are, however, needed to compare adequately arboreal faunas from differing environments.

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References

Adis, J. (1981). Comparative ecological studies of the terrestrial arthropod fauna in Central Amazonian Inundation Forests. *Amazonia* **7**, 87–173.

Adis, J., Lubin, Y. D., and Montgomery, G. G. (1984). Arthropods from the canopy of inundated and Terra firme forest near Manaus, Brazil, with critical considerations on the Pyrethrum-fogging technique. *Studies on Neotropical Fauna and Environment* **19**, 223–36.

Albert, R. (1976). Zusammensetzung und Vertikalverteilung der Spinnenfauna in Buchwenwäldern des Solling. *Faunistisch-Ökologische Mitteilungen* **5**, 65–80.

Andersen, A. N., and New, T. R. (1987). Insect inhabitants of fruits of *Leptospermum*, *Eucalyptus* and *Casuarina* in South-Eastern Australia. *Australian Journal of Zoology* **35**, 327–36.

Basset, Y. (1985*a*). Comparaison de quelques méthodes de piégeage de la faune dendrobie. *Bulletin Romand d'Entomologie* **3**, 1–14.

Basset, Y. (1985*b*). Les peuplements d'arthropodes sur *Pinus mugo* Turra dans les tourbières du Haut-Jura neuchâtelois. *Bulletin de la Société Neuchâteloise de Sciences Naturelles* **108**, 63–76.

Basset, Y. (1988). A composite interception trap for sampling arthropods in tree canopies. *Journal of the Australian Entomological Society* **27**, 213–19.

Basset, Y. (1989). The temporal and spatial distribution of arboreal arthropods associated with the rainforest tree *Argyrodendron actinophyllum*. Ph.D. Thesis, Griffith University, Brisbane.

Basset, Y. (1990). The arboreal fauna of the rainforest tree *Argyrodendron actinophyllum* as sampled with restricted canopy fogging: Composition of the fauna. *The Entomologist* **109**, 173–83.

Bigot, L., and Kabakibi, M. (1987). Evolution spatio-temporelle de la composition et de la structure du peuplement frondicole sur chêne-liège dans le Massif des Maures (Var). *Bulletin d'Ecologie* **18**, 157–68.

Bigot, L., Kabakibi, M., and Loisel, R. (1987). Effet spécifique du débrousaillement sur le peuplement des arthropodes frondicoles d'une chênaie à chêne liège des Maures (Var). *Ecologia Mediterranea* **13**, 21–8.

Boland, D. J., Brooker, M. I. H., Chippendale, G. M., Hyland, B. P. M., Johnston, R. D., Kleining, D. A., and Turner, J. D. (1984). 'Forest Trees of Australia.' (Nelson and CSIRO: Canberra.)

Broadhead, E. C. (1984). Adaptations for fungal grazing in lauxaniid flies. *Journal of Natural History* **18**, 639–49.

Carne, P. B., and Taylor, K. L. (1978). Insect pests. In 'Eucalypts for Wood Production'. (Eds W. E. Hillis and A. G. Brown.) pp. 155–68. (CSIRO: Canberra.)

Collin, J. E. (1961). 'British Flies. Vol. VI: Empididae.' (Cambridge University Press.)

Coulson, R. N., and Witter, J. A. (1984). 'Forest Entomology: Ecology and Management.' (John Wiley: New York.)

Couturier, G. (1973). Etude éthologique et biocénotique du peuplement d'insectes dans un verger naturel. *Travaux et Documents de l'O.R.S.T.O.M.* **22**, 1–96.

Dajoz, R. (1980). 'Ecologie des Insectes forestiers.' (Gauthier-Vilars: Paris.)

Davies, V. T. (1976). Spiders. In 'Fauna of Eastern Australian Rainforests I'. (Ed. J. Covacevich.) pp. 11–12. (Queensland Museum: Brisbane.)

Davies, V. T. (1977). Spiders. In 'Fauna of Eastern Australian Rainforests II'. (Ed. J. Covacevich.) pp. 25–7. (Queensland Museum: Brisbane.)

Dixon, A. F. G. (1975). Aphids and translocation. In 'Encyclopedia of Plant Physiology. Vol. 1: Phloem Transport'. (Eds M. H. Zimmerman and J. A. Milburn.) pp. 154–70. (Springer: Berlin.)

Eastop, V. F. (1978). Diversity of the Sternorrhyncha within major climatic zones. In 'Diversity of Insect Faunas'. (Eds L. A. Mound and N. Waloff.) pp. 71–88. (Blackwell: Oxford.)

Erwin, T. L. (1983). Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. In 'Tropical Rain Forest: Ecology and Management'. (Eds S. L. Sutton, T. C. Whitmore and A. C. Chadwick.) pp. 59–76. (Blackwell: Oxford.)

Erwin, T. L., and Scott, J. C. (1980). Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemanii* Triana and Planch in the Canal Zone of Panama. *Coleopterists' Bulletin* **34**, 305–22.

Fowler, S. V. (1985). Differences in insect species richness and faunal composition of birch seedlings, saplings and trees: the importance of plant architecture. *Ecological Entomology* **10**, 159–69.

Froggatt, W. W. (1923). 'Forest Insects of Australia.' (Australian Government Printer: Sydney.)

Gagné, W. C. (1979). Canopy-associated arthropods in *Acacia koa* and *Metrosideros* trees communities along an altitudinal transect on Hawaï Island. *Pacific Insects* **21**, 56–82.

Gauld, I. D. (1986). Latitudinal gradients in ichneumonid species-richness in Australia. *Ecological Entomology* **11**, 155–61.

Geijskes, D. C. (1968). Insect collecting in Surinam with the help of 'Malaise' traps. *Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen* **48**, 101–9.

Hargrove, W. W. (1986). An annotated species list of insect herbivores commonly associated with black locust, *Robinia pseudoacacia*, in the Southern Appalachians. *Entomological News* **97**, 36–40.

Hegnauer, R. (1973). 'Chemataxonomie der Pflanzen. Bd. 6. Rafflesiaceae–Zygophyllaceae.' (Birkhäuser: Basel.)

Hijii, N. (1983). Arboreal fauna in a forest. I. Preliminary observation on seasonal fluctuations in density, biomass and faunal composition in a *Chamaecyparis obtusa* plantation. *Japanese Journal of Ecology* **33**, 435–44.

Hodkinson, I. D. (1974). The biology of the Psylloidea (Homoptera): a review. *Bulletin of Entomological Research* **64**, 325–39.

Hodkinson, I. D. (1984). Co-evolution between psyllids (Homoptera : Psylloidea) and rain-forest trees: the first 120 million years. In 'Tropical Rain-Forest: The Leeds Symposium'. (Eds A. C. Chadwick and S. L. Sutton.) pp. 187–94. (Leeds Philosophical and Literary Society: Leeds.)

Klomp, H., and Teerink, B. J. (1973). The density of the invertebrate summer fauna on the crowns of pine trees, *Pinus sylvestris*, in the central part of the Netherlands. *Beiträge zur Entomologie* **23**, 325–40.

Lawton, J. H. (1978). Host plant influences on insect diversity: the effect of space and time. In 'Diversity of Insect Faunas'. (Eds L. A. Mould and N. Waloff.) pp. 105–25. (Blackwell: Oxford.)

Lawton, J. H. (1984). Non-competitive populations, non-convergent communities, and vacant niches: the herbivores of bracken. In 'Ecological Communities. Conceptual Issues and The Evidence'. (Eds D. R. Strong, D. Simberloff, L. G. Abele and A. B. Thistle.) pp. 329–52. (Princeton University Press: Princeton.)

Lowman, M. D. (1985). Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Australian Journal of Ecology* **10**, 7–24.

Main, B. Y. (1981). Australian spiders: diversity, distribution and ecology. In 'Ecological Biogeography of Australia'. (Ed. A. J. Keast.) pp. 807–52. (W. Junk: The Hague.)

Majer, J. D. (1990). The abundance and diversity of arboreal ants in Northern Australian. *Biotropica* **22**, 191–9.

Majer, J. D., and Recher, H. F. (1988). Invertebrate communities on western Australian eucalypts: a comparison of branch clipping and chemical knockdown procedures. *Australian Journal of Ecology* **13**, 269–78.

Majer, J. D., Recher, H. F., Perriman, W. S., and Achutan, N. (1990). Spatial variation of invertebrate abundance within the canopies of Australian eucalypt forests. In 'Food Exploitation by Terrestrial Birds'. (Eds M. L. Morrison, C. J. Ralph and J. V. Cooper.) (Ornithological Society: Santa Clara.)

Martin, J. L. (1966). The insect ecology of red pine plantations in Central Ontario. IV. The crown fauna. *Canadian Entomologist* **98**, 10–27.

Moore, K. M. (1972). Observations on some Australian forest insects. 26. Some insects attacking three important tree species. *Australian Zoologist* **17**, 30–9.

Moran, C. V., and Southwood, T. R. E. (1982). The guild composition of arthropod communities in trees. *Journal of Animal Ecology* **51**, 289–306.

Morrow, P. A. (1977). Host specificity of insects in a community of three co-dominant *Eucalyptus* species. *Australian Journal of Ecology* **2**, 89–106.

Mouna, M., Bigot, L., and Fabre, J. P. (1985). Comparaison des communautés frondicoles des Coléoptères du Cèdre (*Cedrus atlantica* Massetti) en France (Provence) et au Maroc (Moyen-Atlas). *Vie et Milieu* **35**, 99–106.

Mound, L. A. (1971). Gall-forming thrips and allied species (Thysanoptera : Phlaeothripinae) from *Acacia* trees in Australia. *Bulletin of the British Museum (Natural History), Entomology* **25**, 387–466.

Nentwig, W. (1987). The prey of spiders. In 'Ecophysiology of Spiders'. (Ed. W. Nentwig.) pp. 249–63. (Springer-Verlag: Berlin.)

Neumann, F. G. (1978). Insect populations in eucalypt and pine forests in north-eastern Victoria. *Australian Forest Research* **8**, 13–24.

Neumann, F. G. (1979). Beetle communities in eucalypt and pine forests in north-eastern Victoria. *Australian Forest Research* **9**, 277–93.

New, T. R. (1978). Notes on the biology of *Lemidea subaenea* (Coleoptera : Cleridae) of *Acacia* in Victoria. *Australian Entomological Magazine* **5**, 21–2.

New, T. R. (1979). Phenology and relative abundance of Coleoptera on some Australian acacias. *Australian Journal of Zoology* **27**, 9–16.

New, T. R. (1983*a*). Systematics and ecology: reflections from the interface. In 'Australian Systematic Entomology: A Bicentennary Perspective'. (Eds E. Highley and R. W. Taylor.) pp. 50–79. (CSIRO: Canberra.)

New, T. R. (1983*b*). Seed predation of some Australian acacias by weevils (Coleoptera : Curculionidae). *Australian Journal of Zoology* **35**, 327–36.

New, T. R., (1983*c*). Colonisation of seedling acacias by arthropods in Southern Victoria. *Australian Entomological Magazine* **10**, 13–18.

New, T. R. (1984). 'A Biology of Acacias.' (Oxford University Press: Melbourne.)

Nicolai, V. (1986). The bark of trees: thermal properties, microclimate and fauna. *Oecologia* **69**, 148–60.

Nielsen, B. O. (1975). The species composition and community structure of the beech canopy fauna in Denmark. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* **138**, 137–70.

Noyes, J. S. (1989). The diversity of Hymenoptera in the tropics with special reference to Parasitics in Sulawesi. *Ecological Entomology* **14**, 197–207.

O'Dowd, D. J., and Willson, M. F. (1989). Leaf domatia and mites on Australasian plants: ecological and evolutionary implications. *Biological Journal of the Linnean Society* **37**, 191–236.

Ohmart, C. P. (1981). An annotated list of insects associated with *Pinus radiata* D.Don. in California. CSIRO Division of Forest Research Divisional Report No. 8.

Ohmart, C. P., Stewart, L. G., and Thomas, J. R. (1983*a*). Leaf consumption by insects in three *Eucalyptus* forest types in South-eastern Australia and their role in short-term nutrient cycling. *Oecologia* **59**, 322–30.

Ohmart, C. P., Stewart, L. G., and Thomas, J. R. (1983*b*). Phytophagous insect communities in the canopies of three *Eucalyptus* forest types in south-eastern Australia. *Australian Journal of Ecology* **8**, 395–403.

Ohmart, C. P., and Voigt, W. G. (1981). Arthropod communities in the crown of the natural and planted stands of *Pinus radiata* (Monterey pine) in California. *Canadian Entomologist* **113**, 673–84.

Paramonov, S. J. (1959). Zoogeographical aspects of the Australian dipterofauna. In 'Biogeography and Ecology in Australia'. (Eds A. Keast, R. L. Crocker and C. S. Christian.) pp. 164–91. (W. Junk: The Hague.)

Perry, D. R. (1978). A method of access into the crowns of emergent and canopy trees. *Biotropica* **10**, 155–7.

Renault, T. R., and Miller, C. A. (1972). Spiders in a fir-spruce biotype: abundance, diversity, and influence on spruce budworm densities. *Canadian Journal of Zoology* **50**, 1039–46.

Riechert, S. E., and Harp, J. M. (1987). Nutritional ecology of spiders. In 'Nutritional Ecology of Insects, Mites, Spiders and related Invertebrates'. (Eds F. Slansky Jr and J. G. Rodriguez.) pp. 645–72. (John Wiley: New York.)

Riek, E. F. (1970). Hymenoptera (Wasps, bees, ants). In 'The Insects of Australia'. (Ed. D. F. Waterhouse.) pp. 867–959. (Melbourne University Press: Melbourne.)

Robinson, J. V. (1981). The effect of architectural variation in habitat on a spider community: an experimental field study. *Ecology* **62**, 73–80.

Stork, N. E. (1987*a*). Guild structure of arthropods from Bornean rain forest trees. *Ecological Entomology* **12**, 69–80.

Stork, N. E. (1987*b*). Arthropod faunal similarity of Bornean rain forest trees. *Ecological Entomology* **12**, 219–26.

Stork, N. E. (1987*c*). Adaptations of arboreal carabids to life in trees. *Acta Phytopathologica et Entomologica Hungarica* **22**, 273–91.

Stradling, D. J. (1987). Nutritional ecology of ants. In 'Nutritional Ecology of Insects, Mites, Spiders, and related Invertebrates'. (Eds F. Slansky Jr and J. G. Rodriguez.) pp. 927–69. (John Wiley: New York.)

Stratton, G. E., Uetz, G. W., and Dillery, D. G. (1979). A comparison of the spiders of three coniferous tree species. *Journal of Arachnology* **6**, 219–26.

Strong, D. R., Lawton, J. H., and Southwood, T. R. E. (1984). 'Insects on Plants. Community Patterns and Mechanisms.' (Blackwell: Oxford.)

Sutton, S. L., and Hudson, P. J. (1980). The vertical distribution of small flying insects in the lowland rain forest Zaire. *Zoological Journal of the Linnean Society* **68**, 111–23.

Taylor, R. W. (1983). Descriptive taxonomy: past, present, and future. In 'Australian Systematic Entomology: A Bicentenary Perspective'. (Eds E. Highley and R. W. Taylor.) pp. 93–134. (CSIRO: Melbourne.)

Turner, B. D. (1984). Predation pressure on the arboreal epiphytic herbivores of larch trees in southern England. *Ecological Entomology* **9**, 91–100.

Van den Berg, M. A. (1980). Natural enemies of *Acacia cyclops* A. Cunn. ex G. Don and *Acacia saligna* (Labill.) Wendl. in Western Australia. I. Lepidoptera. II. Coleoptera. III. Hemiptera. *Phytophylactica* **12**, 165–7; 169–71; 223–6.

Watanabe, H., and Ruaysoongnern, S. (1989). Estimation of arboreal arthropod density in a dry evergreen forest in Northeastern Thailand. *Journal of Tropical Ecology* **5**, 151–8.

Waterhouse, D. F. (Ed.) (1970). 'The Insects of Australia.' (Melbourne University Press: Melbourne.)

Watmough, R. H. (1968). Population studies on two species of Psyllidae (Homoptera, Sternorhyncha) on broom (*Sarothamnus scoparius* (L.) Wimmer). *Journal of Animal Ecology* **37**, 283–314.

Webb, L. J., Tracey, G., and Williams, W. T. (1984). An ecological framework of Australian rainforest. II. Floristic classification. *Australian Journal of Ecology* **9**, 169–98.

Woinarski, J. C. Z., and Cullen, J. M. (1984). Distribution of invertebrates on foliage in forests of south-eastern Australia. *Australian Journal of Ecology* **9**, 207–32.

Wolf, F., Gaspar, C., and Verstraeten, C. (1968). Recherches sur l'écosystème forêt. La Chênaie à *Galeobdolon* et à *Oxalis* de Mesnil-Eglise (Ferage). Hyménoptères récoltés dans des bacs d'eau. *Bulletin de Recherches Agronomiques de Gembloux* **3**, 566–79.

Woodward, T. E., Evans, J. W., and Eastop, V. F. (1970). Hemiptera (Bugs, leafhoppers, etc.). In 'The Insects of Australia'. (Ed. D. F. Waterhouse.) pp. 387–457. (Melbourne University Press: Melbourne.)

Yen, A. L. (1989). Overstorey invertebrates in the Big Desert, Victoria. In 'Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management'. (Eds J. C. Noble and R. A. Bradstock.) pp. 285–99. (CSIRO: Canberra.)

Young, P. A. R. (1985). 'Vegetation and Flora. Brisbane Forest Park.' (Brisbane Forest Park Administration Authority.)

Appendix I. Arthropod collections obtained from the crowns of *Argyrodendron actinophyllum*

Total number of individuals collected by five interception traps during two years of continuous trapping and by 240 samples of restricted canopy fogging. Key: *W*, individuals collected by window trap subunits in interception traps; *M*, individuals collected by malaise trap subunits in interception traps; *IT*, total number of individuals collected by interception traps; *S1*, number of species sorted from interception trap collections; *F*, total number of individuals collected by restricted canopy fogging; *S2*, number of species sorted from fogging collections; *G*, guild assignment [*a*, ants; *c*, chewers; *e*, epiphyte grazers; *f*, fungal-feeders; *g*, gall makers; *h*, phloem-feeders; *i*, incidentals; *m*, mesophyll-feeders; *p*, predators; *r*, parasitoids; *s*, scavengers; *t*, tourists; *u*, uncertains; *w*, wood-eaters; *x*, xylem-feeders]; *I*, *J*, imagines, juveniles; *conservative estimates (number of RTUs)

Taxon	*W*	*M*	*IT*	*S1*	*F*	*S2*	*G*	Taxon	*W*	*M*	*IT*	*S1*	*F*	*S2*	*G*
Araneae	709	1012	1721	117	1408	72	*p*								
Amaurobiidae	1	10	11	6	2	2	*p*	Oonopidae	19	46	65	4	8	2	*p*
Araneidae	25	14	39	8	102	12	*p*	Orsolobidae	1	2	3	3	0	0	*p*
Clubionidae	190	415	605	22	255	5	*p*	Pholcidae	0	0	0	0	2	1	*p*
Ctenidae	0	1	1	1	0	0	*p*	Pisauridae	0	0	0	0	2	1	*p*
Cyatholipidae	3	0	3	1	2	1	*p*	Salticidae	46	70	116	7	97	10	*p*
Cycloctenidae	1	0	1	1	0	0	*p*	Segestriidae	0	1	1	1	0	0	*p*
Gnaphosidae	74	206	280	10	11	3	*p*	Sparassidae	0	2	2	2	0	0	*p*
Hahnidae	1	7	8	1	13	2	*p*	Tetragnathidae	0	2	2	1	1	1	*p*
Hersiliidae	1	1	2	1	1	1	*p*	Theridiidae	160	51	211	21	439	14	*p*
Heteropodidae	1	9	10	3	2	1	*p*	Thomisidae	77	14	91	8	40	8	*p*
Linyphiidae	14	58	72	7	3	2	*p*	Toxopidae	2	0	2	2	5	2	*p*
Micropholcommatidae	1	2	3	3	0	0	*p*	Zodariidae	0	0	0	0	1	1	*p*
Mimetidae	0	1	1	1	0	0	*p*	Unknown (*I*, *J*)	92	99	191	–	422	–	*p*
Mysmenidae	0	0	0	0	1	1	*p*								
Blattodea	330	657	987	7*	69	2*	*s*								
Blaberidae	4	4	8	2*	0	0	*s*	Unknown (*J*)	273	443	716	–	56	–	*s*
Blattellidae	53	210	263	4*	13	1	*s*								
Brachycera	1261	1410	2671	–	42	–	–								
Anthomyiidae	2	67	69	–	0	0	*t*	Muscidae	54	107	161	–	0	0	*t*
Asilidae	2	27	29	3	0	0	*p*	Phoridae	297	234	531	–	4	–	*t*
Asteiidae	1	0	1	1	0	0	*t*	Pipinculidae	0	7	7	1	0	0	*r*
Calliphoridae	3	4	7	–	0	0	*t*	Rhagionidae	2	27	29	2	0	0	*t*
Chamaemyiidae	0	1	1	1	0	0	*p*	Sepsidae	0	4	4	1	0	0	*t*

Chloropidae	296	134	430	—	18	—	*t*
Clusiidae	0	6	6	—	0	0	*t*
Cryptochetidae	3	13	16	—	0	0	*r*
Dolichopodidae	32	153	185	15	1	1	*p*
Drosophilidae	131	14	145	13	0	0	*t*
Empididae	61	348	409	10	3	2	*p*
Ephydridae	4	0	4	—	0	0	*t*
Heleomyzidae	23	51	74	—	0	0	*t*
Lauxaniidae	205	40	245	18	1	1	*e*
Lonchaeidae	1	0	1	1	0	0	*t*
Coleoptera	8863	2669	11532	331	863	68	—
Aderidae	16	2	18	3	0	0	*u*
Anobiidae	147	18	165	4	2	1	*ws*
Anthicidae	4	10	14	2	0	0	*us*
Anthribidae	48	41	89	9	1	1	*w*
Apionidae	1	6	7	1	0	0	*i*
Attelabidae	1	0	1	1	1	1	*c*
Biphyllidae	712	21	733	2	0	0	*f*
Bostrychidae	10	0	10	5	0	0	*w*
Bothrideridae	5	0	5	1	0	0	*r*
Brenthidae	3	0	3	2	0	0	*w*
Buprestidae	17	1	18	7	0	0	*w*
Callirihipidae	1	0	1	1	0	0	*w*
Cantharidae	13	17	30	2	7	2	*p*
Carabidae	84	18	102	10	0	0	*p*
Cerambycidae	38	105	143	26	2	2	*w*
Chrysomelidae	529	1516	2045	17	313	10	*cu*
Cleridae	59	113	172	9	1	1	*p*
Coccinellidae	26	55	81	11	17	4	*p*
Colydiidae	16	3	19	3	0	0	*f*
Corylophidae	1412	44	1456	2*	280	2*	*f*
Curculionidae	270	327	598	70	123	18	*wc*
Elateridae	105	18	123	11	2	2	*t*
Erolytidae	1	0	1	1	0	0	*f*
Eucnemidae	3	0	3	1	0	0	*w*

Simuliidae	0	1	1	1	0	0	*t*
Sphaeroceridae	1	2	3	—	0	0	*t*
Stratiomyiidae	43	41	84	10	0	0	*t*
Syrphidae	8	15	23	9	0	0	*t*
Tabanidae	11	6	17	—	0	0	*t*
Tachinidae	18	72	90	—	0	0	*r*
Tephritidae	6	2	8	5	0	0	*t*
Teratomyzidae	1	0	1	1	0	0	*t*
Therevidae	2	4	6	1	0	0	*p*
Unknown (*I*, *J*)	54	30	84	—	15	—	*u*
Lathridiidae	362	26	388	4	35	2	*f*
Leiodidae	0	0	0	0	1	1	*s*
Limnichidae	24	5	29	1	11	1	*u*
Lucanidae	1	0	1	1	0	0	*w*
Melandryidae	93	25	118	2	5	1	*wf*
Melyridae	30	5	35	5	15	4	*p*
Mordellidae	70	150	220	2	1	1	*w*
Mycetophagidae	30	0	30	1	0	0	*f*
Nitidulidae	59	1	60	3	6	3	*fs*
Phalacridae	1066	20	1086	5*	9	2*	*f*
Platypodidae	7	0	7	2	0	0	*w*
Pselaphidae	47	0	47	19	0	0	*p*
Ptilodactylidae	2	0	2	2	0	0	*t*
Pythidae	1	1	2	1	0	0	*w*
Rhipiphoridae	7	7	14	1	0	0	*r*
Salpingidae	217	2	219	4	0	0	*f*
Scarabaeidae	431	1	432	7	0	0	*ct*
Scolytidae	1632	30	1662	19	0	0	*w*
Scraptiidae	8	1	9	1	0	0	*t*
Scydmaenidae	65	3	68	2*	0	0	*p*
Silvanidae	0	0	0	0	1	1	*f*
Staphylinidae	589	9	598	31	8	5	*ps*
Tenebrionidae	88	19	107	14	0	0	*sc*
Throscidae	9	13	22	1	0	0	*w*

Appendix I (*continued*)

Taxon	*W*	*M*	*IT*	*S1*	*F*	*S2*	*G*
Histeridae	57	0	57	2	0	0	*p*
Laemophloidae	257	2	259	5	0	0	*f*
Languriidae	6	0	6	1	0	0	*s*
Chilopoda	0	0	0	0	1	1	*p*
Unknown	0	0	0	0	1	1	*p*
Diplopoda	4	0	4	–	10	–	*s*
Unknown	4	0	4	–	10	–	*s*
Heteroptera	353	177	530	65	170	16	–
Acanthosomatidae	2	0	2	1	4	2	*m*
Anthocoridae	15	4	19	6	2	1	*p*
Aradidae	15	0	15	3	0	0	*f*
Ceratocombidae	3	0	3	1	0	0	*p*
Cydnidae	4	0	4	1	0	0	*t*
Enicocephalidae	14	0	14	3	0	0	*p*
Isometopidae	63	1	64	2	3	1	*p*
Lygaeidae	58	11	69	12	0	0	*mp*
Miridae	104	46	150	22	22	5	*up*
Homoptera	1170	4713	5883	86	1319	26	–
Achilidae	320	573	892	7	2	1	*h*
Aleyrodidae	21	195	216	2*	15	2*	*h*
Aphididae	74	27	101	5	1	1	*i*
Carsidaridae	68	153	221	1	66	1	*h*
Cicadellidae	277	2781	3058	33	253	9	*hm*
Cicadidae	3	0	3	3	0	0	*x*
Cixiidae	9	40	49	6	0	0	*h*
Coccoidea†	17	8	25	2*	14	2*	*h*
Delphacidae	2	4	6	3	0	0	*h*
Derbidae	4	7	11	3	0	0	*f*

Taxon	*W*	*M*	*IT*	*S1*	*F*	*S2*	*G*
Trogidae	1	0	1	1	0	0	*t*
Trogossitidae	11	0	11	2	0	0	*fp*
Unknown (*I*, *J*)	166	30	196	–	32	–	*u*
Dermaptera	4	2	6	1	3	1	*p*
Forficulidae	4	2	6	1	3	1	*p*
Nabidae	0	1	1	1	0	0	*p*
Pentatomidae	4	9	13	3	5	2	*m*
Piesmidae	0	0	0	0	1	1	*m*
Reduviidae	6	0	6	2	0	0	*p*
Schizopteridae	0	3	3	1	0	0	*p*
Thaumastocoridae	0	0	0	0	3	1	*m*
Tingidae	8	2	10	4	3	1	*m*
Veliidae	2	0	2	1	0	0	*t*
Unknown (*J*)	55	100	155	–	127	–	*u*
Flatidae	11	86	97	2	3	1	*h*
Fulgoridae	0	1	1	1	0	0	*h*
Homotomidae	4	1	5	1	0	0	*i*
Issidae	5	55	60	4	2	2	*h*
Psyllidae	264	281	545	5	440	2	*hi*
Psylloidea (*J*)	54	88	142	2	461	2	*h*
Ricaniidae	2	1	3	1	0	0	*h*
Triozidae	0	0	0	0	1	1	*i*
Tropiduchidae	1	5	6	1	2	1	*h*
Unid. Psylloidea (*I*)	14	13	27	–	8	–	*hi*
Unknown (*I*, *J*)	4	36	40	–	0	0	*h*

Hymenoptera	2705	2030	4735	–	432	–	–
Agaonidae	21	3	24	–	1	1	*i*
Aphelinidae	18	54	72	–	85	–	*r*
Apidae	152	12	164	2	0	0	*t*
Bethylidae	205	26	231	–	3	–	*r*
Braconidae	102	143	245	>22	28	–	*r*
Ceraphronidae	14	61	75	–	22	–	*r*
Chalcididae	2	0	2	–	0	0	*r*
Colletidae	8	1	9	6	0	0	*t*
Cynipidae	6	5	11	–	1	1	*i*
Diapriidae	33	43	76	–	4	–	*r*
Dryinidae	0	1	1	1	0	0	*r*
Encyrtidae	22	89	111	18*	22	3*	*r*
Eulophidae	26	14	40	–	26	–	*r*
Eupelmidae	6	93	99	–	2	–	*r*
Eurytomidae	2	2	4	–	1	1	*r*
Formicidae	603	655	1258	9*	125	8*	*at*
Isopoda	0	0	0	0	1	1	*s*
Unknown	0	0	0	0	1	1	*s*
Isoptera	212	8	220	5	0	0	*t*
Kalotermitidae	1	1	2	1	0	0	*t*
Rhinotermitidae	201	7	208	2	0	0	*t*
Lepidoptera	588	1146	1734	–	98	–	*tc*
Eriocraniidae (*I*)	1	0	1	1	0	0	*t*
'Gelechiidae' (*I*)	207	327	534	–	0	0	*t*
'Geometridae' (*I*)	4	1	5	–	0	0	*t*
'Lymantriidae' (*I*)	6	1	7	–	0	0	*t*
Micropterygidae (*I*)	0	1	1	1	0	0	*t*
'Noctuidae' (*I*)	7	7	14	–	0	0	*t*
'Oecophoridae' (*I*)	46	39	85	–	0	0	*t*
'Stathmopodidae' (*I*)	4	10	14	–	0	0	*t*
'Yponomeutidae' (*I*)	152	502	654	–	0	0	*t*
Unknown (*I*)	83	69	152	–	0	0	*t*

Gasteruptiidae	1	0	1	1	0	0	*r*
Halictidae	141	4	145	7	0	0	*t*
Ichneumonidae	13	70	83	–	0	0	*r*
Mutillidae	2	9	11	–	0	0	*t*
Mymaridae	12	118	130	–	4	–	*r*
Platygasteridae	20	112	132	–	28	–	*r*
Pompilidae	2	24	26	–	0	0	*p*
Pteromalidae	1178	170	1348	–	36	–	*rg*
Scelionidae	56	231	287	–	29	–	*r*
Sphecidae	7	17	24	–	0	0	*p*
Tenthredinidae	8	42	50	4	0	0	*t*
Torymidae	17	13	30	6	5	2	*gr*
Trichogrammatidae	1	1	2	–	0	0	*r*
Typhiidae	0	1	1	1	0	0	*r*
Xiphydriidae	8	1	9	1	0	0	*w*
Unknown (*J*)	19	15	34	–	12	–	*u*
Termitidae	6	0	6	1	0	0	*t*
Termopsidae	4	0	4	1	0	0	*t*
Arctiidae (*J*)	38	114	152	4*	32	2*	*e*
Gelechiidae (*J*)	0	0	0	0	1	1	*c*
Geometridae (*J*)	9	9	18	4*	19	4*	*c*
Lymantriidae (*J*)	8	28	36	9*	1	1	*c*
Noctuidae (*J*)	1	3	4	3*	5	3*	*c*
Plutellidae (*J*)	0	2	2	1	0	0	*c*
Tineidae (*J*)	0	0	0	0	1	1	*c*
Yponomeutidae (*J*)	2	3	5	2*	8	2*	*c*
Unknown (*J*)	20	30	50	–	31	–	*c*

Appendix 1 (*continued*)

Taxon	*W*	*M*	*IT*	*S1*	*F*	*S2*	*G*
Mantodea	0	2	2	1	0	0	*p*
Mantidae	0	2	2	1	0	0	*p*
Nematocera	2070	12543	14613	–	86	–	–
Anisopodidae	7	4	11	–	0	0	*t*
Bibionidae	48	5	53	–	0	–	*t*
Cecidomyiidae	315	3206	3521	–	17	–	*tu*
Ceratopogonidae	176	188	364	–	25	–	*t*
Chironomidae	439	2487	2926	–	20	–	*t*
Culicidae	0	1	1	1	0	0	*t*
Limoniidae	59	841	900	–	3	–	*t*
Neuroptera	208	46	254	13	33	5	*p*
Chrysopidae	2	6	8	4	0	0	*p*
Coniopterygidae	166	21	187	3	17	2	*p*
Hemerobiidae	39	19	58	5	2	2	*p*
Opiliones	1	9	10	–	0	0	*p*
Unknown	1	9	10	–	0	0	*p*
Orthoptera	71	208	279	12	57	3	–
Gryllacrididae	12	18	30	2	0	0	*p*
Gryllidae	38	89	127	4*	46	2*	*s*
Tertrigidae	1	0	1	1	0	0	*s*
Plecoptera	3	1	4	1	0	0	*t*
Eustheniidae	3	1	4	1	0	0	*t*
Pseudoscorpiones	3	2	5	–	0	0	*p*
Chernetidae	3	2	5	–	0	0	*p*
Mycetophilidae	36	96	132	–	0	0	*t*
Psychodidae	74	974	1048	–	0	0	*t*
Scatopsidae	11	2	13	5	1	1	*t*
Sciaridae	900	4721	5621	–	20	–	*t*
Tipulidae	5	2	7	–	0	0	*t*
Unknown (*J*)	0	16	16	–	0	0	*u*
Osmylidae	1	0	1	1	0	0	*p*
Unknown (*J*)	0	0	0	0	14	–	*p*
Tettigoniidae	9	50	59	4	0	0	*pc*
Unknown (*J*)	11	51	62	–	11	–	*p*

Psocoptera	400	288	688	36*	463	25*	*e*								
Archipsocidae	2	0	2	1	0	0	*e*	Peripsocidae	16	13	29	4*	5	4*	*e*
Caeciliidae	31	36	67	6*	17	6*	*e*	Philotarsidae	2	1	3	1	1	1	*e*
Ectopsocidae	11	1	12	6*	12	6*	*e*	Pseudocaeciliidae	7	7	14	6*	15	6*	*e*
Elipsocidae	10	1	11	2*	0	0	*e*	Psocidae	5	1	6	1	0	0	*e*
Lepidopsocidae	26	36	62	4*	3	1	*e*	Stenopsocidae	5	15	20	3*	15	1	*e*
Myopsocidae	4	0	4	2*	0	0	*e*	Unknown (*I*, *J*)	282	176	458	–	395	–	*e*
Thysanoptera	100	35	135	23	536	18	–								
Aelothripidae	3	5	8	3	1	1	*p*	Thripidae	30	8	38	10	53	5	*u*
Phlaeothripidae	63	20	83	9	456	10	*pmfu*	Unknown (*I*, *J*)	4	2	6	–	26	–	*u*

† Pseudococcidae + Margarodidae.

Appendix II. Names of taxonomists (with groups studied) who examined the material collected in the crowns of *A. actinophyllum*

R. A. Beaver (Platypodidae; Scolytidae); C. Besuchet (Pselaphidae); D. J. Bickel (Empidoidea); I. R. Bock (Drosophilidae); E. B. Britton (Scarabaeidae); A. A. Calder (Elateridae); M. Carver (Aphididae); E. C. Dahms (Aphelinidae; Encyrtidae); G. Daniels (Asiloidea; Syrphoidea; Tabanoidea); J. F. Donaldson (Delphacidae); M. J. Fletcher (Cicadelloidea; Fulgoroidea); P. J. Gullan (Coccoidea); J.-P. Haenni (Scatopsidae); T. Heard (Apidae); A. Hiller (Cetonidae); R. de Keyzer (Cerambycidae); J. F. Lawrence (Bostrychoidea; Cantharoidea; Cucujoidea [part]; Dryopodiea); B. Levey (Buprestidae); V. Mahnert (Pseudoscorpiones); L. R. Miller (Isoptera); G. B. Monteith (Heteroptera); B. P. Moore (Carabidae); M. Moulds (Cicadidae); L. A. Mound (Thysanoptera); T. R. New (Neuroptera; Psocoptera); A. F. Newton (Staphylinidae); J. Palmer (Thysanoptera); R. Raven (Araneae); C. A. M. Reid (Chrysomelidae [part]; D. C. F. Rentz (Orthoptera; Mantodea); G. A. Samuelson (Chrys. Alticinae); D. J. Scambler (Cerambycidae); M. Schneider (Lauxaniidae; Heleomyzidae); N. D. Springate (Braconidae; Xiphydriidae); K. L. Taylor (Psylloidea); R. W. Taylor (Formicidae); M. Thayer (Staph. Omalinii); T. A. Weir (Cleroidea, Cucujoidea [part], Histeroidea; Staphylinoidea [part]); K. Walker (Colletidae; Halictidae); E. C. Zimmerman (Curculionoidea).

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