

Aspects of the reproductive ecology of a south-east Australian *Avicennia marina* mangrove community — flower visitors and potential pollinators

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Abstract: Sampling of day-active invertebrates visiting the flowers of Grey Mangrove *Avicennia marina* subsp. *australasica* (Walp.) J.Everett (family Acanthaceae) was undertaken at a study site on the Harrington estuary, northern New South Wales, Australia. The study extended over a 4 season period (from 2016 to 2020), with more than 170 anthophilous species being recorded. Nearly all were observed contacting flower stigmas and/or anthers during foraging episodes. At least 113 of the approximately 168 species examined for pollen loads, carried *Avicennia* pollen. None carried mixed pollen loads, indicating foraging constancy/fidelity. Although pollen carriage does not automatically assign the status of pollinator, nevertheless, the findings indicate *Avicennia marina* is pollinated by a taxonomically diverse suite of native invertebrates which sit within an assemblage of flower visitors that may include non-pollinating species.

Although the invasive honeybee *Apis mellifera* was seasonally common during most days of observation, it was uncommon or absent on some days. The occurrence of native flower-visiting species was often found to be episodic, with many species being abundant during one day or season of observation, but then absent or rarely encountered at other times. Such behavioral events highlight the need for extended periods of field investigation to illuminate more fully the pollination ecology of individual plant species. Comparison with additional anthophilous insect records from a previous 1990 – 1994 study in an adjacent littoral rainforest community, indicated that this community may furnish a pool of native insects from which *Avicennia marina* can seasonally recruit a dynamic pollinator network.

Keywords: *Avicennia marina*, Grey mangrove, maritime rainforest, littoral rainforest, pollination, flower visitors, *Apis mellifera*, invertebrates, conservation management.

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Introduction

Despite the diversity and distribution of mangroves world-wide we know relatively little about the biotic agents that facilitate their pollination. Pollination, as distinct from fertilisation, is the transfer of pollen from an anther to a stigmatic surface and is an essential process in the life cycle of the majority of flowering plants (angiosperms). Interactions between successfully placed pollen grains and the stigma and style of the receptive flower are crucial intermediary processes between pollination and fertilisation (Willmer 2011). Pollen transfer can be achieved by passive ‘abiotic’ agents of wind, water or gravity, or by active ‘biotic’ vectors such as invertebrates, birds, mammals and reptiles (Williams & Adam 2010). *Transfer* of pollen is a necessary precursor to fertilisation in most angiosperms, but *transport* by an abiotic or biotic agent relates only to that vector’s ability to carry or move pollen, and unless this is deposited on the surface of the flower’s stigma, of itself pollen carriage plays no role in plant pollination and subsequent reproduction. This distinction is fundamental when considering putative pollinator roles (Williams & Adam 2010).

World-wide (i.e. across all latitudes) ~87% of extant flowering plants are now estimated to be pollinated by animals, and this rises to 94% in tropical communities (Ollerton *et al.* 2011). Although there is evidence for the role of wind in the pollination of mangroves (Nadia & Machado 2014), globally biotic vectors dominate in those species that have been studied (see Discussion). But as with mangrove species elsewhere, there are remarkably few studies of the pollination ecology, or of attendant anthophilous animals in general, of Australian species. One species that has been the subject of investigation is the ‘Grey mangrove’ *Avicennia marina* subsp. *australasica* (e.g. Clarke 1992; Clarke & Myerscough 1991; Homer 2009; Hermansen *et al.* 2014a, 2014b, 2015), the most widespread of Australian mangroves (see Appendix 1 for description). However, existing studies, while expanding our understanding of the reproductive dynamics of Australian *Avicennia marina* populations, nevertheless have raised further questions as to the nature, function and recruitment of flower visitor assemblages. These questions include the impact of alien honeybees (*Apis mellifera*) on native animals within *Avicennia* pollination networks, the composition of pollination networks throughout the range of *Avicennia marina* and the extent to which stands are able to recruit potential pollinators from adjacent terrestrial habitats. Knowledge of the biotic agents that facilitate pollination, and the ability of *Avicennia marina* (indeed all mangrove species) to recruit pollinators from terrestrial habitats, is important in the undertaking of successful conservation/restoration management strategies for isolated stands. But studies undertaken to date in Australian *Avicennia* populations have either been limited in duration, or the composition of the anthophilous fauna has not been the study focus, or have largely considered select visitor suites (due to sampling restraints) within more taxonomically-diverse flower visitor–potential pollinator assemblages.

An overview of mangrove ecosystems

Mangrove ecosystems are valuable for their role in conserving biodiverse plant and animal communities (Hutchings and Recher 1981, Adam 1992), and world-wide are recognised for their capacity in contributing to the stabilization of shorelines, their role in sustaining food webs and ecosystem function, and as fish nursery areas (Clough 1982, Dahdouh-Guebas *et al.* 2005, Kathiresan and Rajendran 2005, Laurance *et al.* 2011, Luther and Greenberg 2009, Robertson and Duke 1987, Saenger 2002, Wolff *et al.* 2000). In addition, they have been utilised as a source of fish, timber (including as charcoal, and ash for soap manufacture), salt, and honey production for humans (Bird 1981, Birtchnell and Gibson 2008, Liebezeit and Rau 2006, Yap 2000). Although mangroves can colonise sites (often at the expense of saltmarsh) where suitable sediment and nutrient conditions exist (Adam 1990, McLoughlin 1987, Mitchell and Adam 1989a, 1989b), nevertheless, there have been dramatic reductions in the extent of mangrove habitat world-wide through clearing, infilling and unregulated harvesting (Adam 1992, Ali 2012, Ong 1995, Thu and Populus 2007, Valiela *et al.* 2001, Warne 2011, Wee *et al.* 2014). These threats continue, with a world-wide loss since 1980 of approximately 3.6 million hectares (Ashbridge *et al.* 2016); in Australia there has been a reduction in mangrove cover to -11,142 (+/- 57) km² in 2017, from a recorded 2010 maxima of -11,500 km², (see Lymburner *et al.* 2020). Such on-going losses will have significant environmental and social impacts.

Mangrove communities can be considered a distinctive salt-tolerant maritime rainforest formation (Adam 1992, Warne 2011, Whitmore 1984, Williams 2020) and are essentially tropical and subtropical in distribution. In Australia mangroves are widely distributed along the eastern and northern coasts. They vary structurally from that of a closed-canopy forest to open woodland (Adam 1992), being floristically diverse at lower latitudes and most extensively developed in sheltered estuary zones. Regional variation in estuary length and size, temperature, salinity, groundwater, tidal amplitude, patterns of inundation, and possibly rainfall, influence species richness (Reef and Lovelock 2014, Saenger and Moverley 1985, Smith and Duke 1987). Some mangrove stands may represent a transitional community, but exposed shores and hypersalinity can act as a barrier to colonisation (Adam 1992, Mitchell and Adam 1989a). In northern Australia, where species richness is greater (Duke 2006, Hutchings and Recher 1981), different mangrove species sometimes exhibit apparent zonation responses; though these cannot be simplistically characterised, instead showing complex patterns that may be attributed to specific estuary attributes. In New South Wales mangrove forests can be extensive (e.g., Port Stephens, Hunter River, Hawkesbury River [West *et al.* 1985]), comprising in total about 100 sq. km (West *et al.* 1984), and often form seaward zonation with landward saltmarsh communities (Adam 1990, Mitchell and Adam 1989a, Saintilan 1997). Narrow bands of mangrove trees and colonizing seedlings extend inland to the tidal limit where conditions may be brackish or almost fresh.

Structurally mangroves possess a dense terrestrial canopy established above a dynamic daily-inundated soft-sediment marine layer, however, in the south-east region of Australia where mangrove stands often have a park-like appearance, the canopy at the community scale is open (P. Adam pers. comm.). Although mangrove forests are generally restricted to the intertidal zone, some individual plants may establish on elevated rock platforms with minimal tidal influence. Seasonal tidal movements may result in inundation of lower and mid level branches and foliage. Individual mangrove species may reach heights of 30 m or more, though in subtropical and temperate Australia canopy heights are usually much lower (<5–12 m). Although the Australian mangrove flora comprises over 40 species (Duke 2006, 2013) only three reach the mid-north coast of subtropical New South Wales; *Avicennia marina* (Acanthaceae; previously in Avicenniaceae), *Aegiceras corniculatum* (L.) Blanco (Primulaceae/Myrsinaceae) and *Excoecaria agallocha* L. (Euphorbiaceae). *Avicennia marina* and *Aegiceras corniculatum* are common in the Harrington Inlet, mid north coast NSW, the study site (Fig. 1), with *Avicennia marina* often forming dense fringing forests and *Aegiceras corniculatum* as an associated species in the understory but more commonly along sheltered landward margins. *Excoecaria agallocha* is rarely encountered (e.g., at Cattai Creek, a northern tributary of the Manning River estuary), and here is about at its southern-most point of distribution. This floristically-impoverished woody mangrove flora can be compared with that of the Mary River of south-east Queensland where eleven mangrove species have been recorded (Saintilan 1996), illustrating the relatively rapid northward increase in species richness.



Figure 1: Study site, Harrington Inlet, mid north coast NSW, with *Avicennia marina* often forming dense fringing forests and *Aegiceras corniculatum* in the understory but more commonly along sheltered landward margins.

Aims and Methods

The study aim was to ascertain the diversity of flower-visiting diurnal invertebrates and vertebrates to *Avicennia marina*, to determine foraging behaviour and pollen carriage potential of

invertebrate visitors and their possible function as pollinators, and to compare this assemblage to the anthophilous invertebrate fauna in an adjacent littoral rainforest previously studied in 1990–1994 (Williams 1995) to gauge potential recruitment to *Avicennia* of pollinators from contiguous terrestrial littoral rainforests not subject to tidal inundation. Such information could assist habitat restoration strategies for mangrove communities more widely, providing a degree of assurance that a pool of pollinators was likely available. However, during the *Avicennia marina* study it was not possible to simultaneously investigate insect assemblages and individual species, concurrently present in other regional vegetation communities (not just littoral rainforests).

The mangrove study site is less than 10 ha in size, is subject to an austral subtropical-warm temperate climate, and is located on the northern shore of Harrington Lagoon, (31°52'13" S, 152°41'53" E), on the northern edge of the Harrington - Manning River Inlet/Estuary (Birrell 1987, Oxley 1820). West *et al.* (1984) give the total area of mangroves in the Manning River at about 3.5 sq. km. Harrington Lagoon was a consequence of a stone ocean retaining wall built in the late 19th Century to facilitate ship movements in and out of the northern opening of the Manning River (Linton 1998). This wall constitutes a continuous barrier that impedes entry of water-borne seeds from mangroves elsewhere in the estuary. In 1980 *Avicennia marina* at the study site was only represented by several small shrub-like plants within a *Juncus*-dominated rush swamp – saltmarsh matrix (G. Williams pers. obs.) but there are now more than 40 mature trees (~3–6 m in height with multiple large, lateral branches), > 300 saplings greater than 2 m in height, and some thousands of smaller seedlings of varying age and size at the site. Occasional shrubs of *Aegiceras corniculatum* are scattered throughout the stand and a narrow band of *Casuarina glauca*/*Banksia integrifolia*-dominated woodland in part separates the mangrove study site from a large stand of littoral rainforest to the immediate north. Near-adjacent mangrove community sites comprise three stands to the south; (1) a small stand of saplings located on the southern face of the breakwall that has progressively established from dispersing propagules over the last twenty years, (2) a larger mature stand aged at greater than 100 years established on artificial islands formed by dredging spoil from the mouth of the Manning River, and (3) a narrow band that fringes the banks of the Manning River along the foreshore of Harrington village.

At the study site 20 mature trees (4–6 m in height) extending as a narrow, almost continuous band were observed throughout their flowering period (January – April) in 2016, 2017, 2019 and 2020. The same trees were investigated each year of study and this constant transect was casually walked back and forth on each day of observation. Tidal movements did not restrict field visits. Field observations were carried out during daylight at least twice a week and for a minimum of 2–3 hours on each occasion; this collectively representing more than 120 hours of investigation during daylight. Although there might be several night-visiting contenders to flowers (e.g. various moths, possums, bats) no night observations were undertaken. Individual plants were observed (across the full height spectrum of flowering

trees, at times using binoculars to view higher flowers) for a minimum of 5-15 minutes at a time before moving to the next plant. Diurnal observations were largely restricted to sunny, warm days (>25° C.) owing to insects ceasing to forage, or greatly reduced, during cool, overcast weather and during rain. Wind also affected insect activity, with foraging by most large insects concentrated in sheltered positions of each tree crown. Over each season visitation was spread casually throughout the day, such that sampling events individually occurred within a time span from early morning (~0900 hrs) to late afternoon (~1700 hrs). Insects were generally less abundant when temperatures exceeded 30-35° Celsius, and as a consequence observations in excessively hot periods, usually midday, were less frequent. The 2020 sampling followed extreme and prolonged drought conditions, but coincided with a later period of heavy rainfall and moderate flooding of the Manning delta.

Feeding behaviour (on nectar, and possibly floral parts) and flight behaviour were observed (Tables 1.1, 1.2, 1.3); these observations facilitated by the spatially-constrained movements of many species and the positioning of flowers from crown to almost ground level which gave repeated opportunities for observation. However, it was not always possible to observe the behaviour of small-sized (<5 mm) individuals, but from a standing position it was often possible to visually track the flight behaviour of large-sized individuals over many metres (e.g. that of butterflies and conspicuous wasps and beetles, over distances up to 15 m or more). The movements of birds and large butterflies could be tracked for even greater distances. Records of pollen feeding were more opportunistic as it was not always possible to differentiate this activity from that of nectar feeding. Interactions between species were observed but generally these are not reported here. Importantly, individually prolonged field observations allowed flower visitors (i.e. all species present) to be categorised as either potential pollinators (those that contacted stigmas and/or anthers and moved between individual flowers, flower clusters or trees) or simply visitors (those that from either behaviour or size did not contact stigmas or anthers and so were unlikely to acquire pollen loads, transfer pollen or were known pollen consumers). The latter includes colletid bees that are known to eat pollen but nevertheless can also carry small residual loads on their bodies (see Williams & Adam 1997, 2010 for a discussion of the pollination role of native bees). Duration of feeding bouts at individual flowers were assigned to one of three classes, <10 seconds, >10-<30 seconds, >30 seconds; as field observations indicated these periods of time reflected natural behavioural patterns for species. Finer feeding bout time scales were deemed to have little practical application. Frequency of visitation is widely reported as highly variable for anthophilous insects, their occurrence subject to weather patterns, daily and weekly variation in resource availability, chance disturbance events, changes to the population size and foraging patterns of individual animals, competing co-flowering plant species, and the nature of the vegetation matrix from which flower visitors are recruited. Consequently scoring was only intended to give a general indication of activity.

Although some species (e.g., large wasps) apparently preferred visiting inflorescences positioned high in individual tree crowns, all large species appeared to forage throughout the height of each tree, enabling close visual observation at lower flower clusters. Examples of insect visitors were collected either by hand netting (species >5mm in length) or by aspirator (minute individuals). Thus large, fast flying, and uncommon species, that are difficult to collect by passive sticky traps were effectively targeted; though some butterflies were identified only by visual observation and were not collected. Examples of each collected taxon were placed in separate plastic vials, the underside of their lids having been pre-sprayed with pyrethrin-based 'knock down' insecticide, and later inspected by microscope for the presence of pollen (Table 1.1). Integument sculpture, vestiture, and pollen deposition on individual insects were noted (Table 1.1). Pollen was imbedded in glycerine gel and saffranin stain and mounted on microscope slides, stored for 24 hours to maximise localization and uptake of saffranin stain, and then viewed with a light microscope (at 40x) so as to determine whether insects were carrying only 'home' (i.e. *Avicennia marina* pollen only) or mixed pollen loads. Owing to limitations of time and resources detailed counts of individual numbers of grains on particular body parts were not made, rather pollen loads principally are given as summarised totals or densities (Table 1.1). Specimens were identified either by available keys, by comparison with material in the Australian Museum, Sydney, or in several cases with the assistance of colleagues. Where identifications are uncertain a '?' immediately precedes the first (genus) or second (species) name of the binomial, or follows undetermined species that are assigned a distinguishing number. Voucher specimens of all invertebrates are deposited in the Australian Museum, and a smaller series is held by the author for reference. Owing to restraints of expertise, numerous small Diptera (< 5 mm) could not be identified. Examples of these were placed in alcohol-charged vials and deposited with the Australian Museum for future reference. Field and laboratory notes remain with the author.

Results

Flowering across all *Avicennia* trees in the population was highly synchronous (though no formal assessment was undertaken) with flowering extending from January to late March, and occasionally by a small number of trees into early April, in the first three seasons of field observations. In 2020 all plants ceased flowering by mid March. Most plants flowered each season, but flower abundance varied. Details of flowering patterns of individual trees were not recorded.

Insects were the primary flower visitors, both in abundance and species richness, with the majority of species foraging at individual flowers or individual clusters for 10 to about 30 seconds per event (Tables 1.1., 1.3). Diptera, Hemiptera, bees and day-active moths generally foraged within the same flower cluster or same tree with few or no observed movements to other trees (Table 1.3). Observations indicated all species were able to contact anthers and/or

stigmas so may potentially function as pollinators even if pollen transfer is inefficient, infrequent or pollen loads on individuals are small (see Williams & Adam 2010). In all 173 species, representing 54 families were identified and recorded (Appendix 2). A subset of 168 species (51 families) was examined for pollen carriage (see Tables 1.1, 1.2 and pollen results presented later). The sample base for the examined subset varies, with species often represented by a single specimen only. Consequently, the results for pollen carriage are only an indication of potential. The overall total does not include some minute Diptera species that were not determined to any lower taxon rank, and thus are excluded from Appendix 2. Thus the number of species cited, for total species and species from which pollen was isolated, is an underestimation of the suite of insects that may visit flowers, and transport pollen.

With the exception of the predatory reduviid bug *Pristhesancus plagipennis*, all observed insect species appeared to feed on nectar (being the likely reason most, even predatory wasps, were attracted to flowers), though in some instances pollen was also eaten (e.g. by Colletidae, *Syrhitta luteinervis* and Syrphini generally, *Rutilla lepida*, *Amenia* spp., and possibly *Calopompilus defensor* and *Saralba* sp. 1); this was determined by direct observation but pollen feeding was most reliably suggested by the presence of pollen clusters associated with mouthparts (see Table 1.1). Only bees actively harvested pollen. No instances of feeding on floral parts were observed. None of the recorded insects are known to be host plant-specific for floral food resources during their adult life stages. Owing to the size, similar appearance and/or flight speed of some species (e.g., Tachinidae, small Pompilidae – Pompilinae, Colletinae, Halictidae) it was not always possible to track individual behaviour beyond immediate or adjacent flower clusters. Consequently, observations given in Table 1.1 are only tentative, or indicative at the level of family or genus.

In addition to observed apparent daily variation in species abundance and diversity the seasonal occurrence of some species varied substantially throughout the seasons 2016, 2017 and 2019. There was also a dramatic reduction in overall abundance and diversity in 2020; this following a prolonged extreme drought event. This exceptional seasonal event aside, individual species could be prolific for several days within a single season, then apparently absent (or nearly so) in all others. Examples of such ‘episodic’ occurrences include *Aedes vigilax* (in 2020), *Tropocalymna dimidatum*, *Glycyphana brunnipes*, *Catopsilia pomona* and various Thynnidae.

The following comments relate mainly to observations during 2016, 2017 and 2019; most species observed in those years were generally rare or absent in 2020.

Coleoptera

Overall beetles tended to have the longest feeding bouts of all orders at individual flowers and clusters (Tables 1.1, 1.3) with individual feeding bouts usually being >30 seconds. Twenty

species and 11 families were recorded on flowers (Appendix 2). Despite being numerous in adjacent forest (Williams 1993, 1995, Williams & Adam 2019) Buprestidae were solely represented by *Castiarina neglecta* (Fig. 2), this species being only occasionally observed in two of the four seasons of the study. Large beetles (e.g., Cetoniinae, Cerambycidae) were usually absent in late phase flowering when available flowers had diminished. Large species were normally associated with upper strata and undertook flights to distant trees, rather than to near-neighbours, when disturbed. *Tropocalymna dimidatum* (Cerambycidae) (Fig. 3) was frequently observed in the early to peak stages of flowering in 2019 but was otherwise apparently absent during the study. Cetoniinae were represented by *Eupoecila australasiae*, *Glycyphana brunnipes* (Fig. 4), and *Neorrhina punctata*. All are common species known to occur in diverse forest and woodland communities. Their overall occurrence at *Avicennia marina* flowers was infrequent, however, during peak phase flowering in 2019 *Glycyphana brunnipes* was commonly found resting or feeding at flower clusters, often for periods exceeding 30 minutes, but was absent thereafter. *Eupoecila australasiae* was usually only observed at upper strata and when disturbed flew to distant, rather than adjacent, flowering trees. Other larger-sized Coleoptera, such as *Aridaeus thoracicus* (Cerambycidae), *Tanychilus dubius* (Tenebrionidae) and *Palaestria ?rubripennis* (Meloidae), were rarely observed. Melyridae were frequently encountered, including in 2020, their feeding activities confined for periods longer than 1 minute at individual flowers, before moving to adjacent open flowers in the same cluster.

Diptera

The majority of species observed foraged at individual flowers and clusters for periods extending from between 10 to about 30 seconds, before moving to other clusters (Tables 1.1, 1.3). Approximately 65 species (20 families) were recorded (Appendix 2). Most, such as various Bombyliidae, Stratiomyidae, Tabanidae and Therevidae (Fig. 5) were generally not commonly observed. Of the common species observed in 2016, 2017 and 2019 *Saralba* sp. 1 (Tachinidae), *Ceriana macleayi* and *Syrhitta luteinervis* (Syrphidae) were absent in 2020. Various Tachinidae were frequently observed but owing to the similarity of most taxa field identification was generally not possible. *Mesembrius hilaris*, *Ceriana macleayi* and *Syrhitta luteinervis* (Syrphidae) were common visitors but Syrphini – Syrphidae and Calliphoridae¹ are likely to be pollen feeders (see Table 1.1); though may still facilitate pollen transport owing to the presence of isolated grains scattered on the body. Although Dolichopodidae were common on leaves they were not observed at flowers.

An outstanding episodic occurrence was that of thousands of male and female mosquitoes of *Aedes vigilax* (Culicidae) (Fig. 6) feeding on nectar on the 19th February 2020. Individuals were especially prolific during the morning (conditions hot, humid, sunny, light breeze) but reduced in abundance approaching midday. This phenomenon was not

1: Including species previously in Calliphoridae–Rhiniinae (ie. Stomorhina) but now in Rhiniidae.

previously observed, nor during following days of field study. Few other insects were observed on flowers while mosquitoes were present; *Apis mellifera* was conspicuously absent, and few native bees were observed. Although the contribution of Culcidae to pollination of *Avicennia marina* was not further explored, it is noted that their role as pollinators (e.g. of Asteraceae, Caryophyllaceae, Orchidaceae) has been reported elsewhere (Brantjes & Leemans 1976, Lahondère *et al.* 2020, Peach & Gries 2016, 2020).

Hymenoptera

A high proportion of Hymenoptera sampled were found to carry pollen loads (Tables 1.1, 1.3). Of the overall 14 Hymenoptera families and approximately 75 species recorded, ~12 species were bees (Table 1.1, Appendix 2), the majority of which tended to forage at individual flowers and flower clusters for between 10 to about 30 seconds (Tables 1.1, 1.3). Halictidae were the most abundant native bees observed, with *Lasioglossum carbonarium*, *Homalictus ?findersi* and *Lipotriches* sp. being relatively common visitors. These generally carried large pollen loads (Table 1.1) and were observed on most days, but largely ceased foraging during cool or overcast weather. Native Apidae were represented by *Amegilla pulchra*, *Exoneura* sp. and *Braunsapis* sp.. These are 'longue-tongued' bees and all were rare, or infrequently observed. The native apid *Tetragonula carbonaria* was absent, as well as being apparently absent from adjacent rainforest (Appendix 2, Williams 1995), but is otherwise commonly encountered throughout the region on a floristically diverse spectrum of native and introduced trees, shrubs and herbs (Williams & Adam 1997, Williams 2020, G. Williams unpubl. records). The exotic honeybee *Apis mellifera* (Apidae) was frequently seen throughout each sampling visit in the years 2016, 2017 and 2019, and was especially common during peak phase flowering; but often infrequent or absent in late phase flowering in those years. Only on rare occasions during 2016, 2017 and 2019 was *Apis* not observed during peak phase flowering. In 2020 *Apis mellifera* was uncommon throughout the mangrove stand, and frequently absent on most trees during most days of observation. No commercial hives were known from the area and so all *Apis* individuals were considered to emanate from feral colonies. Colletidae were dominated by the subfamily Colletinae, with Euryglossinae and Hylaeinae being poorly represented. A previously unknown *Leioproctus* was collected (M. Batley pers. comm.) and this is deposited in the Australian Museum collection.

During 2020 native bees were uncommon or apparently absent during each daily visit.

Ants (Formicidae) were entirely absent during the 2016, 2017, 2019 sampling seasons but very small numbers of two species (of uncertain identity, see Table 1.1) were present on low-positioned flower clusters on a single (same) tree during two days of sampling (19 February, 4 March) in 2020; following which they were again absent.

Wasps (excepting microhymenoptera) were diverse (~62 spp., 10 families), with the majority observed foraging for periods <10 seconds (19 spp.) to periods ranging from between 10 to

about 30 seconds (28 spp.) (Tables 1.1, 1.3). Those foraging for very short times (<10s) were primarily represented by Crabronidae, and large Scoliidae and Sphecidae, with species of Evaniidae, Gasteruptiidae, Pompilidae and Thynnidae tending to forage over slightly longer periods (>10-<30s). Few species were abundant, with a suite of large-sized species (*Bembix* spp., *Heterodontonyx* spp., *Sceliphron laetum*, *Sphex* spp., *Austroscolia* sp., *Abispa splendida*, *Pseudabispa confusa*, *Rhynchium ?mirabile*) making only infrequent or fleeting visits to flowers (Table 1.1) during the overall study. Exceptions were *Bidentodynerus bicolor*, which was a frequent flower visitor in most seasons, and *Polistes humilis* (Fig. 9) – this being common and observed on all trees during each study visit. During cloudy, cool days *Polistes humilis*, in concert with *Apis mellifera*, was often the only insect seen. Thynnidae, collectively, were often encountered (rarely seen or absent in 2020), though only *Rhagigaster ?mutatus* and *Rhagigaster* sp. near *kiandrensis* were common in the preceding three seasons. The occurrence of *Rhagigaster ?mutatus* was often episodic, with individuals being commonly observed on some days, but apparently few or absent on others. Individual *Rhagigaster ?mutatus* would sometimes forage until late in the afternoon (i.e., 1700hrs). Male and female-coupled *Rhagigaster* sp. near *kiandrensis* (Fig. 10) displayed a distinctive feeding behaviour in which transporting males positioned themselves on flower clusters in such a way that their partnered flightless females could feed on nectar and whose feeding bouts often extended longer than 30 seconds.

Very few microhymenoptera were observed. These are not recorded. However, numerous microhymenopteran species have been recorded from flowering plants in the adjacent rainforest (Appendix 2).

Miscellaneous invertebrates

Oncopeltus sordidus (Lygaeidae) (Fig. 8) was usually commonly seen during most days of observation, and remained common in 2020. However, individuals were 'patchy' in occurrence being absent or infrequent on some trees, yet abundant on others. The only other Hemipteran frequently encountered in 2016, 2017, and 2019 was the ambush hunter *Pristhesancus plagipennis* (Reduviidae), but again this species was not observed in 2020. Individual *Pristhesancus plagipennis* remained motionless on flower clusters for long periods and were not observed moving to adjacent clusters.

Day-active Lepidoptera were generally rare or infrequent visitors to flowers. Only two day-active moths were observed (*Pollanisus* sp. 1 - Zygaenidae, *Amata* sp. – Erebidae); both were rarely seen. Butterflies were infrequent visitors (8 spp., 4 families; Appendix 2), except for 2020 (contrary to the apparent impoverished nature of other insect taxa in that study season) when *Danaus affinis affinis*, *D. chrysippus* (Nymphalidae) and *Catopsilia pomona* (Pieridae) were often conspicuous visitors (during particular days of observation), to flowers. *Danaus affinis affinis* occasionally exhibited short feeding bouts, but swiftly moved to distant flowering *Avicennia marina* trees, or to adjacent rainforest margins or

patches of *Casuarina/Banksia* woodland. *Tirumala hamata hamata* and *Danaus chrysippus*, respectively, were rare or infrequent visitors in 2016, 2017 and 2019, though the latter was commonly observed during 13th February 2020. *Catopsilia pomona* was absent in 2016, 2017 and 2019, and only commonly seen in mid February 2020 (otherwise infrequent in that season) but individuals rarely landed on flowers. Their presence coincided with an episodic mass emergence elsewhere at coastal localities (e.g. Lake Cathie, Lansdowne) within the region. Lycaenidae (e.g., *Hypochrysops cyane*) and Hesperidae (>1 undetermined species) were infrequent visitors.

Spiders (e.g. *?Lehtinelagia* sp. — Thomisidae) were rarely seen on flowers, and these were sedentary in habit (Fig. 3). Specimens stored in ethyl alcohol were deposited with the Australian Museum.

Vertebrate visitors

Birds were generally absent, though my observations may have been timed each day such that early morning (<0900 hr) foraging was missed. Observed birds were nearly always solitary individuals. Their visits were infrequent and episodic, but with occasional mixed species groups tending to move rapidly from the subcanopy strata of individual trees to that of adjacent trees. Visitors observed included Brown honeyeater *Lichmera indistincta*, White-cheeked honeyeater *Phylidonyris nigra*, *Gerygone* spp., Red wattlebird *Anthochaera carunculata*, Willie wagtail *Rhipidura leucophrys*, Superb blue wren *Malurus cyaneus*, Varied triller *Lalage leucomela* and one unidentified species of flycatcher *Myiagra* sp.. All species restricted their behaviour to foraging in the subcanopy, and only rarely were observed flowers; flower visits being no more than several seconds on a few at flower clusters, or a single cluster, per tree. No mammals, reptiles or amphibians were observed.

Pollen records

With the exception of bees (which actively collect pollen) insects visiting flowers acquire pollen loads incidental to feeding on or searching for nectar. *Avicennia marina* 'home' pollen was isolated from ~113 species (36 families) of the ~168 species (51 families) collected for examination (Table 1.1); but the total is likely an underestimate within the examined subset given that the absence of pollen from many of the species investigated for pollen loads may reflect insufficient foraging effort or time for pollen to adhere to their bodies. For example, of the 10 individual *Lipotriches* sp. 1 (Halictidae) bees overall collected in 2020 to investigate pollen loads, none carried pollen; all individuals being collected as soon as they landed on flowers. Significantly, however, no examined insect species carried mixed pollen loads, indicating temporal foraging constancy/fidelity (this behavioural trait is discussed in Williams & Adam 2010).

Of the individual orders examined for pollen loads, Hymenoptera were the most diverse (78 spp.) of which 62 species carried pollen, followed by Diptera (~64/36 spp.), Coleoptera (20/14 spp.) and Hemiptera (3/1 spp.) (Tables 1.1,

1.2). Although this suggests Hemiptera are inconsequential in their contribution to pollination the lygaeid *Oncopeltus sordidus* (Fig. 8) was present in significant numbers in all seasons, with pollen being isolated from the majority of individuals that were examined. Equally, small Diptera (Figs. 5, 7) often carried significant pollen loads (Table 1.1). Few Lepidoptera were examined, and as a consequence their contribution to out-crossing is unknown.

There was considerable variation in body topography, with all examined species possessing body structures, surface sculpture or setae capable of snaring and carrying pollen (Table 1.1). For example, Diptera are generally clothed with dense, often erect setae and bristles that facilitate the capture of pollen grains, and their transport to other flowers. But not all examined individuals carried pollen, and there was considerable variation in the loads that were carried by species. Thus Table 1.1 gives only an indication, not an absolute identifier, of the capacity of a species to transport particular loads.



Figure 2: *Castiarina neglecta* (Buprestidae)



Figure 3: *Tropocalymma dimidatum* (Cerambycidae) and cryptic thomisid spider



Figure 4: *Glycyphana brunnipes* (Scarabaeidae)



Figure 7: *Bibio imitator* (Bibionidae)



Figure 5: *Anabarhynchus* sp. (Therevidae)

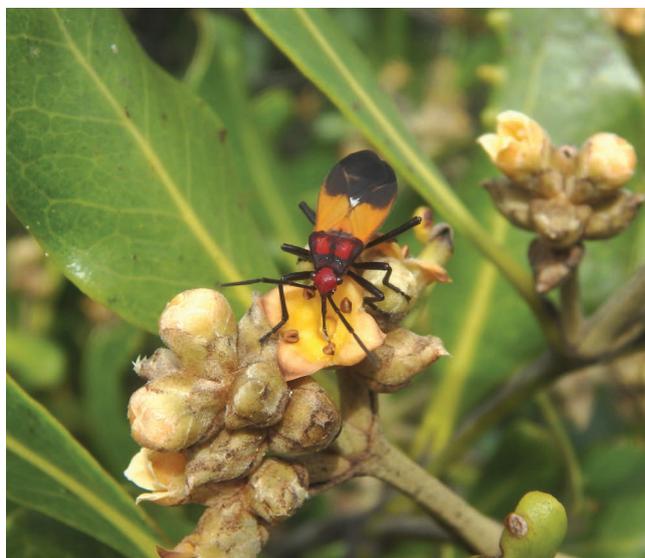


Figure 8: *Oncopeltus sordidus* (Lygaeidae)

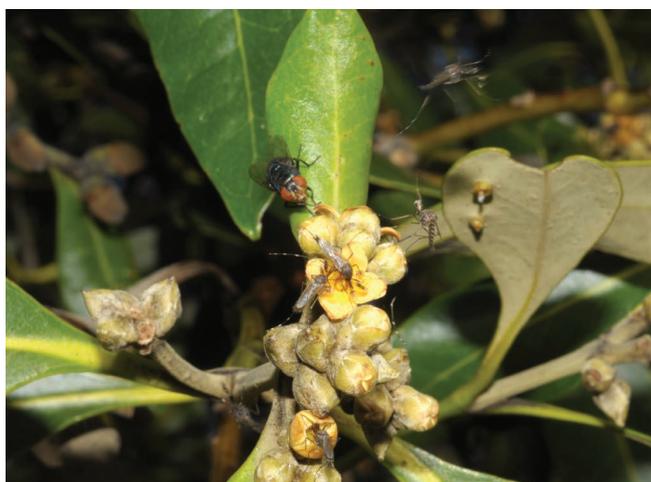


Figure 6: *Aedes vigilax* (Culicidae) feeding on floral exudate



Figure 9: *Polistes humilis* (Vespidae)



Figure 10: *Rhagigaster* sp. near *kiandrensis* (Thynnidae)

Table 1.1. Indication of pollen carriage, feeding behaviour and foraging duration of insects visiting flowering *Avicennia marina*.

Does not include species observed but not collected and examined for pollen loads.

Key: Families listed alphabetically under order. ‘?’ in Taxa column placed before genera or species, or following numbered species indicates identification of taxon uncertain. Indication of integument sculpture and presence of setae (cited with individual ‘Taxa’) denoted as a potential to facilitate pollen carriage. Number of individuals examined (‘n =’/ pollen frequency) for pollen loads cited as number with pollen versus total number examined. Pollen placement and feeding behaviour given as a general overview (range) within the examined series. Approximate duration of feeding bouts at single flowers in parentheses and cited as seconds (s) in three classes; <10s, >10-<30s, >30s. Behaviour and duration of feeding not recorded for all species. Behaviour comments relate to characteristics displayed by all individuals recognizably observed of that species.

See Naumann (1991) for a description of body terms used.

Taxa	n =	pollen placement	feeding behaviour	duration
Coleoptera				
Anthicidae				
? <i>Anthicus</i> sp. 1 integument clothed with moderately dense long setae on pronotum, elytra and head	0/11		mainly within same flower or flower cluster	>30s
Buprestidae				
<i>Castiarina neglecta</i> (Carter) numerous long setae on ventral surface	2/2	large pollen masses (>100 grains each) on gular region, numerous scattered grains between prosternum and mesosternum, foretibiae and elsewhere	prolonged feeding bouts at individual flowers (activity usually at higher levels within crown) followed by long interplant flights	>30s
Cantharidae				
<i>Chauliognathus flavipennis</i> Macleay integument densely clothed with both erect and adpressed setae	1/3	several scattered grains on vertex, frons, pronotum, mid leg, numerous clusters on epipleural margin of elytra	movements mainly to adjacent flowers and flower clusters	>30s
Cerambycidae				
<i>Aridaeus thoracicus</i> (Don.) with dense short curved setae	2/2	large clusters on mouthparts and clypeus, small clusters on forefemur, mid trochanter ; few scattered grains on gular region, forelegs and prosternum	forages at individual clusters for long periods then moves to adjacent or distant trees	>30s
<i>Hesthesis variegata</i> (Fab.) with dense adpressed short setae	1/1	pollen mass and scattered single grains and small clusters on gular region	infrequent movements within same tree, foraging at individual flowers and clusters prolonged	>30s
<i>Tropocalymma dimidatum</i> Newman integument smooth	1/2	single grains on foretibia and eyes	long feeding bouts at individual flowers and clusters followed by flight to distant trees	>30s
Chrysomelidae				
<i>Aulacophora</i> sp. 1 integument generally smooth	0/2		movements restricted to flowers in same cluster	>30
<i>Monolepta australis</i> (Jacoby) upper body generally smooth but legs with stout, short, erect setae	1/4	several grain clusters and scattered single grains on hypomeron, pronotum, elytra	movements mainly to flowers in same cluster and adjacent clusters	>30s
<i>Monolepta</i> sp. near <i>modesta</i> Blackburn dorsal surface of integument smooth, ventral surface sparsely clothed with moderately long setae	2/2	numerous small clusters or single grains on pronotum, epipleurae, elytra, mid femur	remained mainly at same flower, then to adjacent flowers in same cluster	>30s

Taxa	n =	pollen placement	feeding behaviour	duration
undetermined sp. 1 integument with very short dense setae	0/1		behaviour not recorded	
Meloidae				
<i>Palaestria ?rubripennis</i> Laporte integument densely clothed with short, adpressed setae	0/1		movements mainly to adjacent flowers and clusters	>30s
Melyridae				
<i>Carphurus</i> sp. near <i>azureipennis</i> Macleay integument covered with numerous erect, stout setae	6/9	scattered grains and small clusters on head, pronotum, hypomeron, forecoxae, elytral humeri, fore and mid legs	movements mainly to flowers in same cluster	>30s
<i>Dicranolaius cinctus</i> Redtenbacher integument densely clothed with long, erect setae	2/2	scattered single grains and small clusters on head, mouthparts, pronotum, ventral surface of forebody - >100 grains on pronotum, scattered grains elsewhere	movements to adjacent flowers in same cluster	>30s
Phalacridae				
undetermined sp. 1 integument generally smooth	0/1		behaviour not recorded	
Scarabaeidae				
<i>Eupoecila australasiae</i> (Don.) integument generally smooth	2/3	>100 grains on forecoxae, prosternal process and lodged among long setae on ventral surface, otherwise small cluster on fore femur, scattered single grains on clypeus and mouthparts	long interplant flights following individual flower feeding bouts	>30s
<i>Glycyphana brunnipes</i> (Kirby) setae almost scale-like, dense long setae on prosternum and prosternal lobe	3/4	pollen masses (>200 grains) associated with mouthparts, smaller pollen clusters and individual grains scattered on ventral surfaces, foretibiae	long interplant flights following individually long flower feeding bouts; individuals commonly rest motionless in flowers for many minutes	>30s.
<i>Neorrhina punctata</i> (Don.) ventral surface of forebody with dense long setae	2/2	>200 and >300 grains associated with mouthparts as small clusters and larger masses, scattered grains elsewhere on forelegs and ventral surface generally	long feeding bouts followed by long interplant flights	>30s
Scirtidae				
<i>Pseudomicrocara</i> sp. 1 integument densely clothed with fine, short, adpressed setae	1/2	scattered grains on pronotum, humerus of elytra	movement behaviour not recorded	>30s
undetermined sp. 1 integument with short setae on pronotum, elytra and head	0/1		behaviour not recorded	
Tenebrionidae				
<i>Tanychilus dubius</i> Newman integument generally smooth, but mesosternum and metasternum with widely separated, shallow punctures	1/1	few grains on metasternum, pronotum	behaviour not recorded	
Diptera				
Bibionidae				
<i>Bibio imitator</i> Walker (females only) integument densely clothed with short, erect setae	2/3	scattered single grains on forebody, fore and mid legs - >300 grains over whole body especially ventral surface	movements to adjacent flowers in same cluster	>30s
Bombyliidae				
<i>Geron</i> sp. 1 integument with moderately long setae	0/3		movements to nearest clusters	>10-<30s

Taxa	n =	pollen placement	feeding behaviour	duration
<i>Geron</i> sp. 2? integument moderately to densely clothed in long upright setae	0/1		movements to nearest clusters	not recorded
<i>Ligyra bombyliformis</i> Macleay ventral surface and anterior 3 rd of scutum with dense long setae	0/1		frequent movements to adjacent trees	not recorded
<i>Villa fuscicostata</i> (Macquart) integument with numerous long setae, especially on ventral surfaces	1/5	small cluster on propleuron	frequent movements to adjacent trees	<10s
<i>Villa</i> sp.1 integument with dense setae, especially on ventral surfaces	0/1		movement behaviour not recorded	<10s
Calliphoridae				
<i>Amenia chrysame</i> (Walker) integument with numerous long stout setae on dorsal and ventral surfaces	1/2	>20 grains on mouthparts	movement behaviour not recorded	>30s
<i>Amenia</i> sp. near <i>dubitalis</i> Malloch integument with numerous long stout setae on dorsal and ventral surfaces	2/6	>100 grains on mouthparts, >10 grains on forefemur	frequent movements to adjacent clusters and trees	>10-<30s
<i>Stomorhina xanthogaster</i> (Weidemann) integument clothed with stout curved setae on dorsal surface, long dense setae on cheeks, part ventral surface of forebody, ventrites 1, 2	2/3	few scattered grains on mouthparts, legs and ventral surface generally, expelled pollen mass near apex of abdomen	few observable interplant movements, feeding bouts at individual clusters	<10s
<i>Stomorhina</i> sp. 1 integument with numerous long setae on dorsal and ventral surfaces	0/2		observed movements within single cluster	>10-<30s
genus near <i>Stomorhina</i> sp. 1 upper surface with stout, moderately dense short to long bristles, face with dense moderately long setae, ventral surface with short to moderately long setae and bristles	6/8	grain clusters (<10 - <50) on proboscis and face	movements mainly with same cluster	>10-<30s
<i>Chrysomya ?megacephala</i> Fab. scutum and ventral surfaces clothed with dense erect setae	2/2	numerous grains on cheeks, mouthparts, mesopleuron, forelegs, ventral surface generally	movement behaviour not recorded	>10-<30s
<i>Chrysomya</i> sp. 1 integument clothed with moderately dense, erect, stout setae	1/1	>50 grains scattered on sternopleuron, propleuron, mesopleuron	movement behaviour not recorded	>10-<30s
undetermined sp. 1 integument clothed with moderately dense, erect, stout setae	3/4	>10 - >100 grains scattered on sternopleuron, propleuron, mesopleuron, all legs, 2 large masses on proboscis	movement behaviour not recorded	>10-<30s
undetermined sp. 2 integument clothed with scattered long and short stout setae	0/1		behaviour not recorded	
Chloropidae				
<i>Pemphigonotus mirabilis</i> Lamb	0/1		movements mainly on same cluster	>30s
Conopidae				
<i>Microconops</i> sp. 1 integument with moderately long erect setae on scutum	1/1	scattered grains (12) on face and mouthparts	behaviour not recorded	
Culicidae				
<i>Aedes vigilax</i> (Skuse) integument with dense adpressed scales and small setae, antennae plumose, long erect setae on abdomen	0/9		movements mainly within same flower cluster	>10-<30s

Taxa	n =	pollen placement	feeding behaviour	duration
Empididae				
<i>Tachydromia</i> sp. 1 integument clothed with moderately long, curved setae	1/4	2 large clusters (each >10 grains) and 2 single grains on scutum	movement behaviour not recorded	>10-<30s
Ephyrididae				
undetermined sp. 1 integument with scattered long stout curved setae, plus densely clothed with short curved setae	0/2		movement behaviour not recorded	>10-<30s
Lauxaniidae				
undetermined sp. 1 moderately clothed scattered long curved stout setae and short, stout erect setae	1/14	cluster (4 grains) on forefemur	movements mainly within same cluster	>30s
undetermined sp. 2 integument with sparse, moderately long, stout curved setae	0/4		movements in same cluster	>10-<30s
Milichiidae				
undetermined sp. 1 integument moderately clothed with short adpressed setae and scattered longer curved stout setae	0/1		movement behaviour not recorded	>10-<30s
Muscidae				
undetermined sp. 1 ventral surface with moderately dense, moderately long setae, long, erect, stout setae elsewhere	0/1		movement behaviour not recorded	>10-<30s
undetermined sp. 2 whole body moderately clothed with stout curved setae	0/2		behaviour not recorded	
undetermined sp. 3 whole body moderately clothed with stout curved setae	0/1		movements within same cluster	not recorded
Platystomatidae				
genus near <i>Duomyia</i> sp. 1 integument densely clothed with short curved setae	4/4	scattered grains on legs, small clusters associated with mouthparts	movements mainly within same cluster	>10-<30s
<i>Euprosopia</i> sp. 1 with moderately dense setae on ventral surfaces	0/1		behaviour not recorded	
<i>Euprosopia</i> sp. 1? with moderately dense setae on ventral surfaces	0/1		behaviour not recorded	
<i>Euprosopia</i> sp. 2 integument with moderately dense setae on ventral surfaces	0/1		behaviour not recorded	
<i>Lamprogaster</i> sp. 1 upper thorax and abdomen moderately clothed with short curved setae, ventral surface smooth to scattered semi-erect setae	1/1	scattered grains (<10) associated with mouthparts	movements restricted to single flower cluster	>10-<30s
<i>Rivellia</i> sp. 1 integument moderately clothed with short curved setae	0/1		behaviour not recorded	

Taxa	n =	pollen placement	feeding behaviour	duration
Sarcophagidae				
<i>Sarcophaga</i> sp. 1 integument with numerous curved short setae and long stout curved setae	3/5	numerous scattered grains and small grain clusters (>20 grains) on mouthparts, face, fore and mid legs, mesopleuron	observable movements within single trees, movements mainly within single clusters	>10-<30s
undetermined sp. 2 integument with numerous curved short setae and long stout curved setae	1/1	small grain cluster (6 grains) associated with mouthparts	movements within same cluster	>10-<30s
Sepsidae				
undetermined genus sp. 1 integument generally smooth, but with scattered long erect bristles	0/3		behaviour not recorded	
Stratiomyidae				
<i>Odontomyia decipiens</i> (Guérin-Méneville) integument clothed with fine, short, adpressed setae, longer setae on face and mesopleuron	1/1	scattered grains (16) on proboscis, scattered grains on clypeus, procoxae, hind femur	movements mainly within same cluster	>10-<30s
<i>Odontomyia</i> sp. 1 integument clothed with fine, short, but dense, setae adpressed setae, especially on the ventral surface	0/1		behaviour not recorded	
Syrphidae				
<i>Ceriana macleayi</i> (Ferguson) integument densely clothed with very short, erect setae, with numerous coarsely punctate shallow pits	9/12	few scattered grains on eyes, clypeus, mouthparts, forelegs, sternopleuron, mesopleuron, cluster (>9 grains) on cheek	frequent movements between flowers, clusters and adjacent trees	>10-<30s
<i>Dideopsis aegrota</i> Fab. integument with numerous curved setae, especially on ventral surface of forebody	3/3	scattered single grains on mesopleuron, metacoxae, eyes, mouthparts, cheek, mid leg, large expelled pollen mass at apex of abdomen	commonly hovers in front of clusters before landing, frequent movements to adjacent trees following feeding bouts at single flowers and adjacent clusters	>10-<30s
<i>Eristalinus punctulatus</i> (Macquart) integument densely clothed with fine, moderately long setae	3/4	several grains associated with mouthparts, - numerous scattered grains on ventral surface of forebody	frequent movements to adjacent clusters	>10-<30s
<i>Eristalinus ?aurulans</i> (Wiedemann) integument densely clothed in short – moderately long, erect setae	2/2	numerous (>20->50) grains on proboscis and ventral surface of forebody	frequent movements to adjacent clusters	>10-<30s
<i>Melangyna</i> sp. 1 thorax, abdomen, and margin of head, densely clothed with short setae, mesopleuron and propleuron with dense, long, erect setae	1/1	scattered grains (<20) on forebody and ventral surface	movements to adjacent clusters	>10-<30s
<i>Melangyna</i> sp. 2 integument clothed with short – moderately long, erect, dense erect setae on margin of cheeks	1/1	2 small clusters on mouthparts, few scattered grains elsewhere	movements to adjacent clusters	>10-<30s
<i>Mesembrius hilaris</i> (Walker) integument with dense long setae on ventral surface, dense stout shorter setae on dorsal surface	5/9	numerous grains (>100) near mouthparts, also small pollen clusters and single grains on probosces, scattered single grains on forelegs, 1 individual with large expelled pollen mass near apex of abdomen	frequent interplant flights, feeding bouts at individual flowers long	>30s
? <i>Microdon</i> sp. 1 integument densely clothed with moderately long, erect setae	1/1	numerous scattered grains on hind femur, scattered grains on ventral surface of forebody	movements to adjacent clusters	>10-<30s

Taxa	n =	pollen placement	feeding behaviour	duration
? <i>Psilota</i> sp. 1 integument densely clothed with moderately long, erect setae	4/6	scattered single grains on eyes, face, mouthparts, ventral surface of forebody – pollen mass (>50 grains) on lower face, scattered grains elsewhere on all legs	movements to adjacent clusters	>10-<30s
? <i>Psilota</i> sp. 2 integument densely covered in semi erect – erect short to moderately long setae	0/1		behaviour not recorded	
<i>Syrirta luteinervis</i> de Meijere with curved adpressed setae	2/9	small clusters on mouthparts, single grains scattered on fore and mid legs and genal area	frequent hovering before alighting, movements to adjacent flowers and clusters	<10s
Tabanidae				
<i>Austroplex brevivalpis</i> Macquart abdomen densely clothed with moderately long adpressed setae, ventral surface and lateral margins of the thorax moderately clothed with semi erect setae	0/1		movements within single flower cluster	>30s
<i>Austroplex</i> sp. 1 integument densely clothed with long, erect setae	1/1	numerous scattered grains and small clusters on lower face, eyes, proboscis, forefemur	behaviour not recorded	
<i>Cydistomyia alternata</i> (Ferguson and Hill) integument densely clothed with long, erect setae	1/1	several grains on proboscis, forelegs	behaviour not recorded	
<i>Cydistomyia oculata</i> (Richardo) integument, including surface of eyes, densely clothed in long, erect setae	1/1	few grains on mid femur	behaviour not recorded	
? <i>Dasybasis</i> sp. 1 integument densely clothed with erect, curved setae	0/1		behaviour not recorded	
undetermined sp. 1 integument clothed in moderately long, fine, erect setae	1/1	several grains on clypeus, mouthparts	behaviour not recorded	
Tachinidae				
? <i>Austrophorocera</i> sp. near <i>grandis</i> Macquart integument densely clothed with stout curved setae	1/1	few scattered grains on eyes, mouthparts	movement behaviour not recorded	>10-<30s
<i>Rutilia lepida</i> Guérin-Méneville integument with dense setae on dorsal and ventral surfaces	2/4	>100->200 grains on mouthparts, scattered numerous single grains and clusters on forelegs, sternopleuron, mesopleuron and forecoxae	frequent interplant movements	>10-<30s
<i>Rutilia</i> sp. 1 integument generally clothed with dense moderately to long setae, and stout adpressed – erect bristles	0/1		movements generally within single clusters, followed by rapid flight to adjacent clusters	>10-<30s
<i>Saralba</i> sp. 1 dorsal and ventral surfaces, including legs, clothed with numerous curved but erect stout setae, setae more dense on genal area	6/10	few grains on mouthparts, small clusters on mouthparts, mesopleuron, hind legs	movements mainly to adjacent clusters	>10-<30s
undetermined sp. 1 integument with numerous curved, stout setae	5/6	occasional scattered grains – small clusters on proboscis and ventral surface	movement behaviour not recorded	>10-<30s
undetermined sp. 2 integument clothed with stout, long, erect setae	0/1		movement behaviour not recorded	>10-<30s

Taxa	n =	pollen placement	feeding behaviour	duration
undetermined sp. 3 integument with numerous long, stout setae	0/1		movement behaviour not recorded	>10-<30s
undetermined sp. 4 integument moderately clothed with short to long curved bristles	0/1		behaviour not recorded	
Tephritidae				
? <i>Bactrocera</i> sp. 1 integument densely clothed with short setae	1/1	scattered single grains on vertex, frons, base of antenna, foretibia	movements to adjacent flowers and clusters	>10-<30s
? <i>Bactrocera</i> sp. 2 scutellum densely clothed with very short adpressed setae, but integument generally smooth	0/4		movements generally within same cluster	>10-<30s
Therevidae				
<i>Anabarhynchus</i> sp. 1 integument with fine, short, erect setae, head with longer setae	4/5	scattered single grains, clusters on propleuron, mesopleuron, cheeks, forecoxae, forelegs	movements within cluster and to adjacent clusters	>10-<30s
<i>Anabarhynchus</i> sp. 2? integument with numerous erect, stout setae, and scattered erect, longer setae	0/1		behaviour not recorded	
Hemiptera				
Lygaeidae				
<i>Oncopeltus sordidus</i> (Dallas) integument with long setae on ventral surface, stout setae on legs	7/12	few - numerous grains (>100 on one indiv.) scattered on fore and mid legs, mid trochanter, pronotum and ventral surface in general	few inter-plant movements, prolonged feeding bouts at individual flowers and clusters, movements usually to adjacent clusters	>30s
Reduviidae				
<i>Pristhesancus plagipennis</i> Walker integument (excluding wings) moderately-densely clothed with curved and erect setae, ventrites mostly with short curved setae, legs with short erect setae	0/1		motionless on flower clusters, and foliage	
Rhopalidae				
<i>Leptocoris</i> sp. 1 integument densely clothed with fine, erect setae, setae on dorsal surface dense but minute	0/1		behaviour not recorded	
Hymenoptera – bees				
Apidae				
<i>Amegilla pulchra</i> (Smith) integument densely clothed in long, erect setae, but with adpressed setae on sternites	1/1	(female) several grains on mouthparts	rapid movements to adjacent flowers and clusters at lower levels, and to adjacent trees	<10s
<i>Apis mellifera</i> Linn. integument with dense long setae	7/9	small-large pollen masses in corbiculae, scattered grains elsewhere on ventral surface, legs and clypeus	mainly visiting adjacent open clusters within same tree	>10-<30s
<i>Braunsapis</i> sp. 1 integument generally clothed with numerous erect setae	2/2	(female) >200 – 1,000s grains in scopae on hind legs, single grains and masses on ventral surface, thorax, mid legs	movements to adjacent flowers and clusters in same tree	>10-<30s
<i>Exoneura</i> sp. 1 integument, especially ventral surface, with numerous moderately long erect setae	1/2	1,000s grains on hind leg scopae, numerous scattered grains on thorax and abdomen	movements to adjacent flowers and clusters in same tree	>10-<30s

Taxa	n =	pollen placement	feeding behaviour	duration
Colletidae				
<i>Amphylaeus nobilosellus</i> Cockerell upper surface of integument with small, shallow punctures, ventral surface with moderately dense, fine, erect, short setae	1/1	few grains on eye, penultimate sternite	movement to adjacent flowers and clusters in same tree	>10-<30s
<i>Heterapoides</i> sp. near <i>exleyae</i> Houston integument finely punctate, scattered setae on gena, abdomen, forelegs, forecoxae and propleuron	0/1		behaviour not recorded	
<i>Leioproctus irroratus</i> (Smith) integument generally clothed with dense, erect short to long setae	4/4	scattered grains on foretarsi – 1,000s grains in abdominal scopae and hind legs, scattered grains elsewhere	movements to adjacent flowers and clusters in same tree	>10-<30s
<i>Leioproctus</i> sp. nov.? ventral surface of integument, pronotum and head densely clothed with moderately long, erect setae	1/1	(male) scattered numerous grains on face, base of antennae, small clusters on forelegs and elsewhere on body	movements to adjacent flowers and clusters in same tree	>10-<30s
<i>Leioproctus</i> sp. nov.? (possibly same sp. as above) head, thorax, legs and ventral surface of abdomen and last abdominal sternite with dense, long setae	1/1	(female) scattered grains on ventral surface generally, few grains on mesoscutum	movements to adjacent flowers and clusters in same tree	>10-<30s
<i>Pachyprosopis haematostoma</i> Cockerell integument generally clothed with moderately sparse setae	1/1	(male) few grains scattered on forefemora, forecoxae, mandibles	then movements to adjacent flowers in same cluster	>10-<30s
Halictidae				
<i>Homalictus ?findersi</i> (Cockerell) integument generally clothed with long, erect setae	7/15	several scattered grains and pollen masses on gena, forelegs, mesoscutum, body generally - 1,000s grains in ventral scopae and on mid femur	same flower/cluster, then movements to clusters on same tree	>10-<30s
<i>Lasioglossum carbonarium</i> (Smith) integument densely clothed with short, erect setae	5/10	(males) individual grains - several grain clusters (>100 grains per cluster) on mouthparts; (females) numerous grains on forelegs and forecoxae, >200 grains on hindleg	movements mainly to adjacent flowers and clusters on same tree	>10-<30s
<i>Lipotriches</i> sp. 1 legs and ventral surfaces variously clothed in moderately long to short setae	8/24	(female 1) >1000 grains on hind tibiae, >100 grains on hind femur, scattered grains on ventral surface and mouthparts; (males) few (4 – 23) scattered grains on mouthparts	movements to adjacent flowers and clusters on same tree	>10-<30s
Hymenoptera –wasps				
Crabronidae				
<i>Bembicinus</i> sp. 1 with moderately long setae	3/4	scattered grains on forebody, especially vertex, mesoscutum, mesepisternum, mesepimeron	feeding bouts at single flowers followed by movements to other flowers on same tree	>10-<30s
<i>Bembix</i> sp. near <i>lamellatus</i> Handlirsch integument, especially forebody, with long setae	4/7	scattered grains on scape, eyes, genae, vertex, mesepisternum, pronotum, propleuron, forelegs.	rapid flights between flowers and adjacent trees	<10s
<i>Bembix promontorii</i> Lohrmann integument with long setae	0/2		swift patrolling flights between trees with few visits to flowers	
<i>Bembix</i> sp. 1 integument, especially forebody, with long setae	2/2	scattered grains on forebody, especially mesepisternum and pronotum.	rapid flights between flowers and adjacent trees	<10s
<i>Bembix</i> sp. 2? integument, especially forebody, with long setae	1/1	single grains on forefemur, eye and clypeus	movement behaviour not recorded	<10s

Taxa	n =	pollen placement	feeding behaviour	duration
<i>Cerceris</i> sp. near <i>antipodes</i> Smith integument deeply, coarsely punctate, clothed with dense erect, moderately long, setae	1/1	large clusters (>300 grains) on base of clypeus, gular region, mouthparts, propleuron, scattered single grains on ventral surface of forebody	frequent flights between clusters at lower strata on same tree	>10-<30s
? <i>Ectemnius</i> sp. 1 integument coarsely but finely rugose – rugulose, dense, moderately long setae on forecoxae and especially mesepisternum	1/1	several grains on mouthparts, cheeks	rapid flights between adjacent clusters on same tree	<10s
? <i>Ectemnius</i> sp. 2 integument with coarsely but finely rugose – rugulose punctures, dense, moderately long setae on forecoxae and especially mesepisternum, with longer setae on anterior margin of cheeks	6/9	scattered grains on mesopleuron, plus scattered occasional grains (<10) on head, mouthparts, forelegs, mesepisternum - >100 grains on mouthparts, cheeks, mesepisternum	rapid flights between adjacent clusters on same tree	<10s
<i>Pison</i> ? <i>ruficorne</i> Smith except for longer setae on clypeus integument only with short, fine setae	2/4	few scattered grains on mandibles, mouthparts, vertex, forefemora	rapid flights between adjacent clusters on same tree	<10s
<i>Sphodrotes</i> sp. 1 integument deeply punctate, each puncture separated by about 1 width	5/8	single scattered grains or small grain clusters on mouthparts, clypeus, fore and hind femora, propodeum and mesepisternum	frequent flights between clusters at lower tree strata on same tree	<10s
<i>Tachysphex fanuiensis</i> Pulawski integument clothed with very short, fine, setae, those on mesepisternum and forecoxae longer	2/2	numerous grains (>250) on mouthparts only – numerous grains on mouthparts, several grains on frons, forelegs	rapid flights between adjacent clusters in same tree	<10s
<i>Tachysphex</i> sp. 1 integument clothed with very short, fine ‘micro setae’, setae on clypeus more conspicuous	1/1	3 grains on clypeus	rapid flights between adjacent clusters on same tree	<10s
<i>Tachysphex</i> sp. 2 whole of integument densely clothed with (often long) setae	1/1	large pollen masses on mandible, scattered single grains on legs, eyes, clypeus, and especially ventral surface	rapid flights between adjacent clusters on same tree	<10s
<i>Tachysphex</i> ? <i>pilosulus</i> Turner integument clothed with fine, dense, setae, especially on head, thorax and fore and mid tibiae	1/1	scattered grains on mouthparts, genal area, forecoxae, propleuron, forefemora	rapid flights between adjacent clusters on same tree	<10s
? <i>Tachysphex</i> sp. 1 forebody clothed with short, fine and dense setae (especially on mesepisternum)	1/2	numerous grains on frons, clypeus, mesepisternum, mesopleuron, fore and mid legs	rapid flights between adjacent clusters on same tree	<10s
? <i>Tachysphex</i> sp. 2 integument mainly smooth, but with fine, short, setae (mainly restricted to frons, clypeus, mesepisternum)	1/2	>300 grains on prementum, scattered grains on clypeus, scape, propleuron and ventral surface of forebody generally	rapid flights between adjacent clusters on same tree	<10s
? <i>Tachysphex</i> sp. 3 mesoscutum and metapleuron without setae, integument otherwise clothed with very short, fine, adpressed setae, metapleuron distinctly wrinkled	1/1	single grains and small clusters on cheeks, mouthparts, propleuron	rapid flights between adjacent clusters on same tree	<10s
undetermined sp. 1 integument densely clothed in moderately long erect fine setae	1/1	scattered grains (<20) associated with mouthparts, including mandibles	behaviour not recorded	
undetermined sp. 2 integument densely covered with very short setae, ventral surface of abdomen with a few moderately long erect setae	1/1	small cluster on foreleg, few scattered grains on gena	behaviour not recorded	

Taxa	n =	pollen placement	feeding behaviour	duration
Evaniidae				
<i>Evania</i> sp. 1 integument coarsely rugose – punctate, with numerous dense short setae	4/5	scattered few grains on clypeus, mouthparts – numerous (>50) grains on mouthparts, forecoxae, forelegs	rapid flights between adjacent clusters on same tree	>10-<30s
Formicidae				
? <i>Paratrechina</i> sp. 1 integument with scattered long stout setae	0/2		rapid flights between adjacent clusters on same tree	>30s
undetermined Dolichoderinae sp. 1 integument generally smooth, but with few sparse setae	0/4		movements restricted to single cluster	>30s
Gasteruptiidae				
<i>Gasterupton pallidicus</i> Kieff ventral surface of integument with dense flattened setae	2/4	few scattered grains on mouthparts, mandibles and anterior margin of clypeus	movements to adjacent clusters and trees, usually at lower tree strata	>10-<30s
<i>Gasterupton</i> sp. 1 integument densely clothed with short adpressed setae	1/1	scattered grains associated with mouthparts	movements to adjacent flowers in same cluster on same tree	>10-<30s
Ichneumonidae				
<i>Lissopimpla excelsa</i> (Costa) integument with fine shallow punctures, generally without obvious setae	1/1	numerous (>100) grains on propleuron, pronotum, scattered grains on gena, forelegs, mesepisternum and metacoxae	movements to adjacent clusters on same tree	>10-<30s
? <i>Lissopimpla</i> sp. 1 integument clothed in minute, adpressed setae, otherwise surface appears smooth	0/1		movements to adjacent flowers and leaves on same tree	>10-<30s
? <i>Theronia</i> sp. 1 integument generally clothed in minute, adpressed setae, moderately long setae on clypeus, otherwise surface appears smooth	0/1		movements to adjacent flowers and leaves on same tree	>10-<30s
<i>Xanthopimpla terminalis</i> Brulle integument appears smooth, but is densely clothed with minute setae, especially the ventral surface of the thorax	0/1		occasional landings on adjacent clusters on same tree	<10s
Pergidae				
? <i>Pterygophorus cinctus</i> (Klug) integument appearing smooth, but clothed with dense, fine, curved setae	2/2	scattered single grains on clypeus, base of antennae, small cluster (12 grains) on metacoxa; >100 grains associated with mouthparts, >50 grains scattered on forelegs and clypeus	occasional movements to other flowers in same cluster on same tree	>30s
Pompilidae				
<i>Alocurgus aurifrons</i> (Smith) long setae on vertex, genae, forecoxae, forefemora and mouthparts	0/1		frequent flights between trees, usually at upper canopy level	>10-<30s
<i>Calopompilus defensor</i> (Smith) integument clothed with conspicuous long setae	1/2	>100 grains on mouthparts, scattered numerous grains on propleuron	frequent flight between trees, at upper canopy level	>10-<30s
<i>Ctenotegus</i> sp. 1 integument clothed in minute, adpressed setae, with a few longer, erect setae on cheeks and propleuron	1/2	several grains on mandible	agitated movements while feeding at individual flowers on same tree	>10-<30s
? <i>Ctenotegus</i> sp. 1 integument clothed in minute, adpressed setae but otherwise appearing smooth	1/1	c. 24 grains on mouthparts	agitated movements while feeding at individual flowers on same tree	>10-<30s

Taxa	n =	pollen placement	feeding behaviour	duration
<i>Ferreola handschinii</i> Haupt except for long setae on genal area integument with only minute setae,	5/7	scattered numerous single grains or small masses on pronotum, propleuron, genae, mouthparts, forecoxae, base of antennae, clypeus	frequent flight to adjacent trees	>10-<30s
<i>Ferreola ?handschinii</i> Haupt prothorax , back of head and frons clothed with dense short 'fur-like' setae, scattered long setae elsewhere on body	1/1	pollen cluster (>10) on maxilla	frequent flight to adjacent trees	>10-<30s
<i>Heterodontonyx bicolor</i> (Fab.) integument, except dorsal surface of abdomen and scutum, with numerous long setae	6/8	scattered grains or small clusters on mouthparts, forecoxae; >100 grains associated with mouthparts, forecoxae, gena, propleuron	frequent movements to near or more distant trees, flights usually at upper canopy level	>10-<30s
<i>Heterodontonyx</i> sp. 1 long setae on forecoxae, pronotum, vertex, clypeus and mandibles	3/3	small clusters (>10 - <50) and scattered single grains on mouthparts, forecoxae and propleuron	frequent flights between trees, usually at upper canopy level	>10-<30s
<i>Turneromyia frontalis</i> (Fab.) vertex, genal area and scutum with dense, adpressed setae, otherwise with minute setae	1/1	scattered grains on mouthparts, genae, vertex, scutum	frequent movements to adjacent trees	<10s
<i>Paracyphononyx</i> sp. 1 scattered long, erect setae on head, dorsal surface of thorax and ventral surface of abdomen and apex of last abdominal sternite	0/1		agitated movements while feeding at individual flowers on same tree	>10-<30s
undetermined sp. 1 integument clothed in minute, adpressed setae but otherwise appearing smooth	0/1		agitated movements while feeding at individual flowers on same tree	>10-<30s
undetermined sp. 1? integument clothed in minute, adpressed setae, with a few longer, erect setae on cheeks and propleuron	1/1	>50 grains in several distinct clusters and scattered single grains	agitated movements while feeding at individual flowers on same tree	>10-<30s
Scoliidae				
<i>Austroscolia</i> sp. 1 integument clothed in dense stout setae and bristles	0/2		frequent interplant movements, usually at upper canopy level	not recorded
<i>Scolia verticollis</i> (Fab.) integument clothed in dense stout setae and bristles	1/2	several grains on mouthparts	frequent interplant movements, usually at upper canopy level	<10s
Sphecidae				
<i>Sceliphron laetum</i> (Smith) dense moderately long setae on thorax and head, dense adpressed seatae on head	2/2	large clusters (>100 grains) on mouthparts and genae; scattered grains on clypeus	frequent movements to and between adjacent trees, usually at intermediate – upper levels	>10-<30s
<i>Sphex ephippium</i> (Fab.) with dense long setae	1/1	single grain on propodeum	rapid interplant flights with short feeding bouts at individual flowers	<10s
<i>Sphex fumipennis</i> Smith with dense long setae	2/4	few scattered grains on forefemur - small clusters on fore trochanter , forecoxae, few single grains on mouthparts	rapid interplant flights with short feeding bouts at individual flowers	<10s
Thynnidae				
<i>Acanthothynnus ater</i> Brown integument (especially ventral surface) clothed in long, dense, fine setae	1/1	>20 grains on clypeus, scattered grains elsewhere on forebody	frequent movements to adjacent trees	>10-<30s
<i>Anthobosca</i> sp. 1 body clothed with moderately dense, long erect setae especially on legs	1/1	scattered grains on cheeks, frons and clypeus	behaviour not recorded	

Taxa	n =	pollen placement	feeding behaviour	duration
<i>Diamma bicolor</i> Westwood integument (especially ventral surface) with moderately dense, long fine setae	1/1	(male) >100 grains on mouthparts, clypeus and frons, scattered occasional grains on forefemora, forecoxae and ventral surface generally	behaviour not recorded	
<i>Epactiothynnus tasmaniensis</i> (Saussure) integument (especially ventral surface) with long, moderately dense setae	0/1		frequent movements to adjacent trees	not recorded
<i>Epactiothynnus ?tasmaniensis</i> (Saussure) integument with dense moderately shallow punctures, moderately clothed with short erect setae	1/1	scattered grains (<20) on face, mouthparts and forecoxae	movements to adjacent flowers and clusters	not recorded
<i>Rhagigaster</i> sp. near <i>kiandrensis</i> Given integument coarsely punctate, clothed with dense, fine, erect setae	6/6	few scattered single grains on mouthparts and ventral surface of body – numerous grains (>50) on mouthparts, face, forelegs, mesopleuron, pronotum	frequent movements to adjacent flowers, clusters and trees, usually seen feeding at lower strata	>10-<30s
<i>Rhagigaster ?mutatus</i> Turner integument (especially ventral surface) clothed in long, dense, fine setae	3/4	scattered numerous single grains (>300 on one individual) on head including, mouthparts, forelegs, propleuron and ventral surface generally	frequent movements to adjacent clusters and trees	>10-<30s
? <i>Rhagigaster</i> sp. 1 integument heavily punctate, with numerous setae	3/3	scattered single grains on fronto-clypeal region and mouthparts - >300 grains on head and numerous scattered grains on ventral surface of thorax	frequent interplant movements	>10-<30s
<i>Zeleboria xanthorrei</i> (Smith) integument with dense, short, fine setae, those on forecoxae and gular area longer	2/2	few grains at base of antennae, pronotum, mesopleuron - >50 grains among setae at apex of abdomen	frequent movements to adjacent flowers, clusters and adjacent trees	>10-<30s
undetermined sp. 1 integument coarsely rugose – punctate, with numerous moderately long, stout setae	1/1	numerous grains (>50) on mouthparts, frons, clypeus, mesopleuron, forelegs	movements to adjacent flowers and clusters	>10-<30s
undetermined sp. 2 thorax densely punctate, integument generally with moderately long erect setae (dorsal surface of abdomen less so)	1/1	several grains on forefemur	behaviour not recorded	
Vespidae				
<i>Abispa splendida</i> (Guérin-Méneville) integument strongly and coarsely punctate, surface clothed with dense fine setae	0/1		movements to adjacent trees, at upper canopy level	not recorded
<i>Bidentodynerus bicolor</i> (Saussure) integument deeply pitted	5/7	few single grains on forefemur, fore and mesocoxae, clypeus and mouthparts; <50 grains associated with mouthparts	frequent movements between trees and flower clusters	>10-<30s
genus near <i>Elimus</i> integument densely covered with punctures and dense, fine and short setae	0/1		behaviour not recorded	
<i>Paralastor</i> sp. 1 thorax densely punctate, otherwise body clothed with very fine short setae	1/1	numerous (>50) grains associated with mouthparts, and <50 grains in single mass between base of antennae	behaviour not recorded	

Taxa	n =	pollen placement	feeding behaviour	duration
<i>Polistes humilis</i> (Fab.) with short setae, otherwise integument appears smooth	6/8	small pollen clusters on vertex, frons, clypeus, scattered grains on fore and mid legs, mesoscutum; >100 grains associated with mouthparts, mandibles, forelegs and anterior margin of clypeus	prolonged feeding at single flowers, followed by movements to adjacent flower clusters on same trees or nearest adjacent tree	>30s
<i>Pseudabispa confusa</i> v.d. Vecht integument strongly punctate	0/1		movements to adjacent trees, at upper canopy level	not recorded
<i>Rhopalidia</i> sp. near <i>plebiana</i> Richards integument clothed in minute, adpressed setae, surface with shallow punctures	0/1		movements to nearest flower clusters on same tree	>10-<30s
<i>Rhynchium ?mirabile</i> Saussure integument strongly punctate	1/1	numerous grains on mouthparts	movements to adjacent trees, at upper canopy level	not recorded
Lepidoptera				
Erebidae				
<i>Amata</i> sp.	0/1		movements usually within single clusters	>30s
Lycaenidae				
<i>Hypochrysops cyane</i> (Waterhouse and Lyell) integument densely clothed with long curved setae and adpressed scales	0/1		generally movements to adjacent clusters or trees	>30s
Zygaenidae				
<i>Pollanisus</i> sp. 1 integument densely clothed with scales	0/1		movements to flowers on same cluster	>10-<30s

Table 1.2. Summary of examined taxa carrying *Avicennia marina* pollen loads (from Table 1.1).

	total no. spp. examined	no. of families	total spp. with pollen	no. of families
Coleoptera	20	11	14	8
Diptera	~64	20	36	14
Hemiptera	3	3	1	1
Hymenoptera	~78	14	62	13
Lepidoptera	3	3	0	0
approx. total	~168	51	113	36

Table 1.3. Summary of observed movement patterns and foraging duration periods (approximate numbers of species only) (from Table 1.1).

Species observed undertaking frequent inter-tree may also undertake prolonged foraging bouts at single flower clusters and within single trees. Likewise, species observed undertaking 'within tree' movements may also move eventually to other trees.

	mainly movements in same cluster or tree	frequent movements to other trees	<10s foraging duration	>10-<30s foraging duration	>30s foraging duration
Coleoptera	9	6	0	0	16
Diptera	27	6	4	36	6
Hemiptera	2	0	0	0	1
Hymenoptera - bees	11	1	1	11	0
Hymenoptera - wasps	29	27	19	28	4
total all Hymenoptera	40	28	20	39	4
Lepidoptera	2	1	0	1	2
approx. total	80	41	24	76	29

Comparison with littoral rainforest records

Sampling intensity (i.e. daily and hourly sample events) for the 6 comparative rainforest species studied by me during 1990–1994 (Williams 1995) varied considerably and so the total flower-visiting fauna cited for each (Appendix 2) does not allow definitive comparative assessment. Nevertheless it does provide an indication of the composition of individual assemblages, and the taxonomically broad pool of potentially available pollinators.

Only *Alphitonia excelsa* reliably flowers annually and in the same months (January-March) as *Avicennia marina*. *Euroschinus falcata* (Oct.-Dec.), *Scolopia braunii* (Oct.), *Syzygium smithii* (Nov.-Jan.), *Alectryon coriaceus* (Dec.-Feb.) and *Guioa semiglauca* (Nov.-Jan.) usually cease flowering before January and do not necessarily flower each year (Williams 1995). Of the ~173 insect species recorded from *Avicennia marina* 34 species were also recorded from the adjacent rainforest community (Table 2); most of these being species that undertake frequent interplant flight, and from which *Avicennia marina* pollen had been isolated (Table 1). This total is an underestimate owing to many of the species collected by me during the previous rainforest study (Williams 1995) being only determined to family or genus, and not being available again for comparison. Coleoptera observed visiting the flowers of *Avicennia marina* reflected little of the diversity recorded from flowering rainforest trees, the greatest sharing of taxa being with Hymenoptera. It is of interest to note the collective diversity of ants, beetle families, hylaeine bees and microhymenoptera recorded from the six flowering rainforest trees (this itself a small subset of total shrubs and trees recorded from the site; see Williams 1993, 1995), yet their individual absence or poor representation at *Avicennia marina* flowers. However, a more extensive sampling at both the rainforest and the mangrove communities may illuminate a greater confederacy of shared pollinators. Regardless, Appendix 2 demonstrates a diversity of flower-visiting, potentially pollinating, insect fauna occurring in adjacent littoral rainforest, from which a network of taxa may be shared with flowering *Avicennia marina*.

Table 2. Insect species jointly recorded from flowering *Avicennia marina* and adjacent littoral rainforest.

Key: Families listed alphabetically under order.

Coleoptera	Species
Buprestidae	<i>Castiarina neglecta</i>
Cantharidae	<i>Chaulignathus flavipennis</i>
Cerambycidae	<i>Tropocalymma dimidatum</i>
Chrysomelidae	<i>Monolepta australis</i>
Melyridae	<i>Dicranolauis cinctus</i>
Scarabaeidae	<i>Eupoecila australasiae</i> , <i>Neorrhina punctata</i>
Diptera	
Bibionidae	<i>Bibio imitator</i>
Calliphoridae	<i>Amenia chrysame</i> , <i>Stomorhina xanthogaster</i>
Stratiomyidae	<i>Odontomyia decipiens</i>
Syrphidae	<i>Dideopsis aegrota</i> , <i>Eristalinus maculatus</i> , <i>Mesembrius hilaris</i> , <i>Syritta luteinervis</i>

Coleoptera	Species
Hemiptera	
Reduviidae	<i>Pristhesancus plagipennis</i>
Hymenoptera – bees	
Apidae	<i>Apis mellifera</i>
Colletidae	<i>Amphylaeus nubilosellus</i> , <i>Heterapoides</i> sp. near <i>exleyae</i> , <i>Leioproctus irroratus</i>
Halictidae	<i>Homalictus ?flindersi</i>
Hymenoptera – wasps	
Crabronidae	<i>Bembix promentorii</i>
Gasteruptidae	<i>Gasteruption pallidicollis</i>
Pompilidae	<i>Ferreola handschini</i>
Scoliidae	<i>Scolia verticollis</i>
Thynnidae	<i>Acanthothynnus ater</i> , <i>Diamma bicolor</i> , <i>Epactiothynnus tasmaniensis</i> , <i>Rhagigaster</i> sp. near <i>kiandrensis</i> , <i>Rhagigaster ?mutatus</i> , <i>Zeleborea xanthorrhoei</i>
Vespidae	<i>Abispa splendida</i> , <i>Polistes humilis</i> , <i>Pseudabispa confusa</i>

Discussion

Although *Avicennia* flowers are bisexual, Clarke and Myerscough (1991b) noted that individual flowers were protandrous, partly self-compatible (though geitonogamy is favoured), were open for 2-5 days, and that individual clusters had open flowers for 2-4 weeks. Homer (2009), observed that flowers remained open for slightly longer (average 6.3 days) at several sites in the NSW Northern Rivers. Studies by Raju *et al.* (2012) in the Godavari mangrove forests of Andhra Pradesh State, India, also noted that *Avicennia marina* flowers were protandrous and partly self-compatible and that flowering events extended for a period of about three months in the Northern Hemisphere spring-summer. *Avicennia marina* populations in northern Australia commence flowering in October/November-December (Coupland *et al.* 2005), with flowering shifting to May-June in temperate locations (Duke 1990). The populations studied by Homer (2009) flowered over a similar seasonal period to the Harrington population, but some trees that flowered heavily at her sites in one year failed to flower in the following season. This aspect was not studied at Harrington, but from casual observations flowering appeared to occur in most trees each season, though flowering intensity of individual trees may have varied.

Although partly self-compatible, *Avicennia marina* is considered pollinator-dependent (Homer 2009), with plants making a high investment in flower production to attract pollinators (Clarke 1992, Holland *et al.* 2003, Homer 2009). However, the potential for self-compatibility suggests that within-cluster movements by small ecologically unspecialised flower visitors (such as Chrysomelidae, Melyridae, Scirtidae; see Table 1.1) may result in pollen transfer to receptive stigmas. The sticky nature of *Avicennia marina* pollen likely excludes dispersal by wind, indicating dependence on biotic agents for transport.

Few birds were observed visiting *Avicennia marina* flowers at the study site and were usually absent during individual periods of observation. More than 200 bird species have been recorded from Australian mangroves, but fewer than 30 are restricted to, or largely confined, to this habitat (Saenger *et al.* 1977). Schodde *et al.* (1982) suggest that the relative uniformity of mangrove structure may provide limited foraging opportunities, accounting for the small number of avian visitors, but the entomophilous flower structure and the nature and quantity of floral resources that flowering *Avicennia marina* plants offer, may be more important limiting factors to recruitment (Williams & Adam 2010; Willmer 2011). Nevertheless, over extended periods of time birds may make contributions to the total number of pollen grains transferred, their movements, relative to the distances traversed by anthophilous insect visitors, potentially facilitating long distance gene flow between highly dispersed plants. This contention is supported by Buelow and Sheaves (2015) who considered that the mobility of mangrove-associated bird communities links mangrove forests to other mangrove, terrestrial and marine-pelagic systems, with migratory species linking systems on a regional spatial scale. Wee *et al.* (2014) highlight the connection between fragmentation of mangrove stands (a possible factor at Harrington), low bird pollinator visitation rates, and subsequent pollination failure, and stress the importance of mangrove habitat connectivity to enhance pollination in otherwise isolated stands. Mohd-Azlan *et al.* (2012) suggest that the structure of mangrove-associated bird assemblages is influenced by mangrove flowering phenology, the type and diversity of mangrove zones, and the nature of the matrix surrounding mangroves. However, those flower-visiting species observed during the Harrington study were not a subset of the avian fauna found in adjacent rainforest (discussed in Williams 1993), rather, being a distinctive assemblage of species characteristic of the local mangrove forest itself (e.g. *Lichmera indistincta*, *Phylidonyris nigra*), or species (e.g. *Gerygone* spp., *Anthochaera carunculata*, *Rhipidura leucophrys*) found in woodland or open areas generally. Regardless of the infrequent visitation to *Avicennia marina* flowers at Harrington, birds are widely reported as pollinators of mangroves. For example, sunbirds and honeyeaters are variously recorded as visitors and pollinators of species of *Bruguiera* (Rhizophoraceae) in northern Australia, Borneo, Malaysia and South Africa (Noske 1993), sunbirds are recorded as pollinators of *Avicennia ilicifolius* in southern India (Raju 1990), and of *Bruguiera gymnorrhiza* in Singapore (Wee *et al.* 2014); *Bruguiera* possessing more complex bird-adapted flowers than the entomophilous 'open' flower structure of *Avicennia*.

No indication of nocturnal bat visitation (i.e. soiled leaves, broken crown and lateral branches, day time roosting by individuals) was observed during this study. However, in the absence of night observations their possible role in pollination cannot be completely discounted. Nectar-feeding bats (*Eonycteris spelaea*) are reported as likely pollinators of *Sonneratia alba* and *S. ovata* (Sonneratiaceae) in Peninsular Malaysia (Zalipah *et al.* 2016), and Hutchings and Recher (1981) record the flying foxes *Pteropus poliocephalus* and

P. alecto commonly entering mangroves to feed on nectar and to roost. Law (1994a) records the Queensland blossom bat *Syconycteris australis*, a pollen and nectar-feeding specialist (Law 1994b), feeding on the inflorescences of *Banksia integrifolia* (Proteaceae) only several kilometres north-east from my study site. He noted that the abundance of *Syconycteris australis* corresponded with the rise in *Banksia integrifolia* in flower, with bat numbers, as a consequence of increased resource availability, peaking during winter. In summer, blossom bats at Harrington were absent (Law 1994a), this likely owing to bats needing to track food resources because of their high metabolic rates and daily energy demands (McNab 1980); which the flowers of *Avicennia marina*, with their relatively minute nectar and pollen quantities, are unlikely to meet, yet representing resources suitable for use by insects owing to their lower energy demands (Willmer 2011).

Insects visiting *Avicennia marina* flowers, and also recorded from adjacent rainforest (Appendix 2), are able to carry significant pollen loads (Table 1.1 in this study; Table 11.3 in Williams 1995, Williams & Adam 1998). None were seen to damage floral structures, though herbivores (e.g. moth larvae, cantharid beetles) have been reported elsewhere eating anthers and destroying whole buds (Clarke 1992). Observed foraging activities during this study, and the broader floral spectrum that the recorded species are known to visit, suggests many are able to function as potential pollinators. However, although this study provides insight into the foraging behaviour and movement patterns of flower visitors (Table 1) it did not attempt to determine whether individual species, or higher taxon ranks (e.g. orders, families), contributed more significantly to geitonogamous (within-plant) or xenogamous (between-plant) pollen movement. Dependence on insects as the primary agents of pollination for numerous mangrove species is widely recorded (Ali 2012, Clarke & Myerscough 1991b, Hermansen *et al.* 2014b, Homer 2009, Landry 2013, Primack *et al.* 1981, Raju 2020, Raju *et al.* 2012, Sun *et al.* 1998), yet size and isolation of individual mangrove stands may have a negative impact on the abundance and ecological and taxonomic diversity of flower visitors, levels of pollen movement and deposition (Hermansen *et al.* 2014a, Menz *et al.*, 2011, Wee *et al.* 2014), and consequent vulnerability to elevated expressions of inbreeding (Hermansen *et al.* 2015). But the factors of stand size and fragmentation, though of interest, were outside the aims of this study.

The ability of many of the insect species investigated during this project to acquire, transport and transfer pollen between flower clusters and conspecific flowering *Avicennia* trees (Tables 1.1, 1.2, 1.3) mirrors flower visitor assemblages and pollinator networks dominated by taxonomically diverse small- to large-sized insect assemblages studied elsewhere in the region (e.g. Williams 1995, Williams & Adam 1995, 1997, 2019) and recorded in diverse flowering plant communities, including rainforests, world-wide (reviewed in Williams & Adam 2010). The apparent insect-driven pollination theme observed at Harrington is reported for *Avicennia marina* throughout its distribution. Raju (2013), for example, records bees, wasps, flies and butterflies as flower visitors and pollinators of *Avicennia marina* in India,

but except for bees which foraged for both nectar and pollen, all other insects only collected nectar. Homer (2009) found that *Avicennia marina* trees growing in far northern NSW were largely dependent on insects as agents of pollination and consequent fruit set; recording 48 species of insects and arachnids visiting flowers, though most were represented by single or few individuals. In her study Diptera had the greatest number of species but Hymenoptera were the most abundant in terms of numbers of individuals. This was largely the situation at Harrington (Table 1.2, Appendix 2). In Homer's study, overall the alien honeybee *Apis mellifera*, the ant genera *Camponotus*, *Tapinoma* and *Ochtellus*, and thomisid spiders were the most plentiful. There is a rich spider fauna associated with Australian coastal wetland communities (Grimshaw 1982), however, spiders were rarely observed on either flowers or foliage at Harrington. Spiders recorded elsewhere from mangroves also occur in other terrestrial zones, with McCormick (1978) and Hutchings and Recher (1981) suggesting that the spider fauna found in mangroves might be highly seasonal in occurrence and restricted in areas frequently inundated, with the mangrove-associated spider fauna being recruited from adjacent habitats.

Homer (2009) recorded a diversity of small-sized insects visiting *Avicennia marina* flowers, however, she noted that her aspirator sampling method was unsuitable for collecting large fast-flying insects such as wasps (Homer 2009), a group well documented as pollinators (Brodmann *et al.* 2008, Shuttleworth and Johnson 2012) and a diverse and often conspicuous group at Harrington. Wasps include numerous nectar feeders (e.g. Thynnidae [Brown and Phillips 2013]), and predatory species that frequently feed on nectar (e.g. Crabronidae, Pompilidae, Sphecidae), which are effective in transporting pollen between dispersed trees (House 1985, Vithanage & Ironside 1986, Williams & Adam 1995, 1998); thus are potentially important in facilitating gene flow. Homer did observe six species of ants at her study plants (*Paratrechina*, *Myrmecorhynchus*, *Anonychomyrma*, in addition to those earlier cited), but this group was generally absent at Harrington. This may be owing to the expanse of tidally-prone open grassy saltmarsh habitat that ants would have to traverse been the mangrove stand and the adjacent rainforest and thin band of *Casuarina glauca*/*Banksia integrifolia*-dominated woodland. Although plant architecture, dispersed placement of individual plants within populations, ant foraging patterns, and the potential biocidal nature of body secretions may serve to limit the role of particular ants as pollinators, nevertheless some species can function as pollinators and also influence herbivore presence and activity (Gomez *et al.* 1996, Huxley & Cutler 1991, Williams & Adam 2010). Ants, especially species of *Polyrhachis*, are frequently encountered on flowering trees and shrubs (e.g. *Alectryon coriaceus* – Sapindaceae) in the adjacent rainforest (Williams 1995); in particular the arboreal leaf-nesting *Polyrhachis pilosa* (Williams 1993). *Polyrhachis pilosa* absence on *Avicennia marina* may be due to the leathery texture of its leaves; these being unsuitable for nest construction. The absence of ant species on all but one of the investigated *Avicennia marina* trees may explain the often common occurrence of the hemipteran *Oncopeltus*

sordidus (Lygaeidae), for ant foraging patterns and behaviour can act to 'defend' plants (Hölldobler and Wilson 1990) and so would likely deter herbivores.

Clarke and Myerscough (1991b) list a suite of ants, wasps, bugs (Lygaeidae, Miridae), beetles (Cantharidae), flies (Bombyliidae, Cecidomyiidae) and moths (Pylalidae) as visitors to flowering *Avicennia marina* at their New South Wales study sites, however *Apis mellifera*, as in Homer's (2009) study, was the most common insect visitor. Hermansen *et al.* (2014a, 2014b) sampled numerous insects visiting flowers of *Avicennia marina* populations growing in the Sydney region of New South Wales. Of the 38 species of flower-visiting insects that they recorded (Coleoptera 6 spp., Diptera 11 spp., Hemiptera 1 sp., Hymenoptera 15 spp., Lepidoptera 5 spp.) (Hermansen *et al.* 2014b) pollen was found on only two species of native insects (*Carphurus* sp. – Melyridae, *Iridomyrmex* sp. – Formicidae); *Carphurus* being recorded from Harrington (Table 1.1). The introduced and invasive honeybee *Apis mellifera* carried large pollen loads and was the most abundant species observed at flowers. Consequently they contended that *Apis* was the only effective pollinator, a proposition that overlooks the common occurrence of *Avicennia marina* in the Sydney region prior to the European occupation of 1788 (indicating prior effective pollination by native species) and the later introduction of *Apis mellifera* (P. Adam pers. comm.). However, *Apis mellifera*, if present in large numbers, may readily disturb foraging native insects (Williams 1995, Williams & Adam 1997), and in so doing reduces the potential for these to acquire pollen loads. Invasive species can adversely impact plant-pollination relationships (Arroyo-Correa *et al.* 2019; Cause *et al.* 2013; Gilpin 2017). Cause *et al.* (2013) found that removal of the invasive wasp *Vespa pensylvanica* from flowering *Metrosideros polymorpha* (Myrtaceae) in Hawaii allowed the restoration of plant-native pollinator mutualisms (at least as much as surviving Hawaiian pollinators would allow); an outcome potentially pertinent to the conservation and management of *Avicennia marina* populations and their associated anthophilous biota, and the impact that *Apis mellifera* may be having on the displacement and foraging patterns of native pollinators — as Hermansen *et al.* (2014b) also opined. In addition Hermansen *et al.* (2014b) posited that the reduction of mangrove diversity at higher latitudes (only *Avicennia marina* reaches Victoria) may cause a reduction in pollinator richness, thus explaining the supposed absence of effective native pollinators during their study. But this view artificially positions *Avicennia marina* in a functionally-isolated context in which other pollinator-dependent flowering plants are absent or sit ecologically independent of one another. Rather, throughout its range *Avicennia marina* is a member of diverse interactive plant complexes, with individual plant participants drawing upon locally-unique taxonomic pollinator assemblages.

The findings of Hermansen *et al.* (2014b) contrast with observations at Harrington, where numerous native species carried *Avicennia marina* pollen; with many species occurring in large numbers and undertaking frequent between-plant movements (Tables 1.1, 1.2, 1.3). World-wide *Apis mellifera* is an abundant component of anthophilous

insect faunas (Hung *et al.* 2018), is widely recorded from numerous mass-flowering rainforest trees in the Manning Valley (Williams & Adam 1997), may compete with native flower-visiting insects for resources (Goulson 2003), and is commonly reported elsewhere foraging on *Avicennia marina* flowers (Ali 2012, Clarke & Myerscough 1991; Saenger 2002, Tomlinson 2016) and those of other mangrove species (Chen 2000, Landry 2013). It has also been considered a nectar/pollen thief (see Carleial *et al.* 2015), and though *Apis mellifera* displays a diverse floral foraging spectrum, and individuals can forage over long distances (8km or so) (Visscher and Seeley 1982), the majority of pollen carried is held as a compacted mass within their corbiculae (Michener 2007) and this is generally not available for pollination; so that the contribution of *Apis* to pollination and long-distance gene flow may be overstated if assessed solely on the basis of possible flight distance.

Pollination by insects is also widely reported for other mangrove species, and in the case of *Rhizophora mangle* (Rhizophoraceae) studied in northern Pernambuco (Brazil) dual insect–wind pollination is also recorded (Nadia & Machado 2014). In a study of mangrove phenology and pollination in two mangrove forests at Zanzibar, East Africa, Raju *et al.* (2006) observed that *Nomia* bees (Halictidae) and *Odynerus* wasps (Vespidae) were pollinators of the obligate outcrossing species *Ceriops decandra* (Rhizophoraceae). Raju (2020) noted that hawkmoths (Sphingidae) were the principal pollinators of *Xylocarpus granatum* and *X. mekongensis* (Meliaceae) in India, and that butterflies and bees served as supplementary pollinators. Ali (2012) found that, in addition to visiting *Avicennia marina*, numerous insect species were pollinators of *Bruguiera gymnorrhiza*, *Ceriops tagal*, and *Rhizophora mucronata* (Rhizophoraceae). *Apis mellifera* was common at all four. Landry (2013) noted that bees, wasps, butterflies and flies were visitors to co-flowering *Avicennia germinans* (Acanthaceae) and *Laguncularia racemosa* (Combretaceae) in Florida, but again, that *Apis mellifera* was the most common visitor to both species; representing about 75 percent of all individuals visiting *Laguncularia racemosa* and 87 percent of all individuals visiting *Avicennia germinans*.

Although no night observations were undertaken at Harrington, differences in the diversity and frequency of diurnal versus nocturnal visitors to flowering mangroves have been recorded by Pandit and Choudhury (2001). They observed that although *Sonneratia caseolaris* (Sonneratiaceae) in India flowered both during day and night, diurnal visitors were more diverse and occurred with greater frequency; suggesting this was related to higher nectar volume and energy value in the morning. Significantly, Hermansen *et al.* (2014b) noted that diurnal pollen deposition on the stigmas of *Avicennia marina* they studied in the Sydney region was more important than nocturnal deposition; their experiments revealing that only 4% of stigmas carried nocturnally-deposited pollen.

Regardless of the absence of nocturnal observations during this study the species recorded from both *Avicennia marina* and adjacent rainforest trees suggest that a network of

potential pollinators is more widely available within the surrounding landscape, and that the constant January–March flowering pattern exhibited by *Avicennia marina* may function to provide a food resource for anthophilous insects beyond the dominant spring–early summer flowering patterns displayed by most local rainforest trees and shrubs (Williams 1995). Only *Alphitonia excelsa* flowers at the same time as *Avicennia marina*. Thus there is limited potential for seasonal competition for pollination services between tree species.

Although pollen was not observed on the specimens of the culicid mosquito *Aedes vigilax* collected for examination (Table 1), nevertheless, its episodic occurrence in 2020 on flowering *Avicennia marina* is of interest. This mosquito is closely associated with tidally influenced wetlands, especially saltmarsh and mangrove communities where eggs are laid in vegetation or substrates and hatch following inundation by spring tides or rainfall (Gislason & Russell 1997). The species can be exceptionally abundant, is one of the mosquitoes of greatest pest and public health concern in Australia, and can disperse many kilometres from wetlands (Webb & Russell 2019, Webb *et al.* 2016). There is a paucity of information available on the sugar feeding of *Ae. vigilax* in the field or its role in pollination (C. Webb pers. commun.), however, mosquitoes do feed on flowers and this behaviour has been identified as playing a role in the pollination of some plants (Peach & Gries 2016, 2020). It is probable that there was a substantial increase in *Aedes vigilax* following rainfall in early February 2020 and the specimens collected were likely to have been among a local cohort of emerged adult mosquitoes. *Aedes vigilax* adults generally do not live long, less than 3 weeks and male mosquitoes have substantially shorter lives (Webb *et al.* 2016), but given the exceptional abundance of *Aedes vigilax* at times, they may play an important role in pollination of estuarine plant species; however, future research should address the substantial gaps in our understanding of this role (C. Webb pers. comm.).

Conclusion

Visitation by a broad assemblage of anthophilous insects, rather than dependency on a specific pollinator or taxonomically-constrained assemblage (as with *Bruguiera gymnorrhiza* [Wee *et al.* 2014]), allows flexibility in local-scale pollinator recruitment, such that should individual species be absent a subset is likely to be available to undertake pollen transfer. Irrespective of whether individual species or individuals only carry small pollen loads, or be unpredictable or infrequent visitors, collectively the native insect flower-visiting assemblage identified in this study functions to provide a reliable pool of potential pollinators that may facilitate successful plant reproduction outcomes. However, some insect visitors (e.g., obligate ground nesting Halictidae [Houston 2018]) recorded visiting the flowers of *Avicennia marina* are dependent on terrestrial microhabitats (e.g., dry soil substrates, permanent layers of leaf litter and detritus, rotting fallen timber, specific larval food plants) for at least part of their larval development (e.g., Braby 2000, Lawrence and Ślipiński 2013, Naumann 1991). These are

microhabitat requirements which the *Avicennia marina* community at Harrington does not provide. Thus adjacent rainforest potentially serves to furnish a source of native insect pollinators for colonising *Avicennia marina* plants in a tidally inundated habitat otherwise generally unable to sustain terrestrial-dependent pollinator life cycles.

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Appendix 1 Plant Description – *Avicennia marina* subsp. *australasica*

Avicennia marina has a widespread global distribution and in tropical zones can reach a height up to 40 m (Tomlinson 2016). It is the most common mangrove growing in New South Wales, being present in all but one of the sixty-nine estuaries listed by West *et al.* (1984, 1985). The wide presence of *Avicennia marina* in mangrove communities throughout the Indo-Pacific region is attributed to its ability to grow in a diverse range of climatic and environmental conditions and to produce (often annually) large numbers of buoyant, readily dispersed, propagules (Raju *et al.* 2012). In Australia *Avicennia marina* is a small tree or shrub growing to about 9-12 m in height (Coupland *et al.* 2005, Duke 1991, Harden 1992), though trees at the study site were generally less than 6 m. Peg-like projecting pneumatophores, arising from horizontal cable roots in the soft sediment, were numerous and conspicuous. Trees may produce stilt-roots in response to long-term flooding (Allaway *et al.* 2002), however, no plants at the study site exhibited this attribute. The species disperses and colonises via floating propagules, with studies by Clarke and Myerscough (1991a) indicating that most propagules establish near parent trees, and with long distance dispersal subject to the uncertainty of oceanic currents and propagule longevity. Nevertheless long distance

movement of propagules does permit colonisation of new sites — although most long distance movement takes them to the ‘wrong’ place. Developing propagules may suffer high mortality rates (Clarke 1992). Leaves are leathery, opposite, and shiny above. Below there is a dense covering of hairs (tomentum) which makes them look grey/glaucous. Anthesis is reported to occur sequentially from top to bottom (Raju 2013). Flowers are musty — fragrant during peak flowering, inflorescences are axillary cymes or in terminal panicles with flowers being sessile, actinomorphic and bisexual. The corolla is shallow, 4-lobed, with a thick wall, and fused in the basal half forming a partly fused readily accessible tube; its internal face pale yellow-orange in colour when open. Nectar, or nectar-like secretion, is found near the base of the corolla. Ovules 4, the gynoecium pointed at its apex, but not conspicuously furcated or broadened (Clarke & Myerscough 1991b, Harden 1992, G. Williams pers. obs.). Fruit a capsule, usually consisting of 1, rarely 2, embryos surrounded by a thin pericarp (Clarke 1992), crypto-viviparous (P. Adam pers. commun.) Each anther produces about 16,000 pollen grains (Clarke & Myerscough 1991b). Pollen grains are tricolporate (see Faegri *et al.* 1992), about 30µm across (Tomlinson 2016), whitish, sticky rather than dry, and are exuded in a mass before the style becomes receptive (Homer 2009). Anthers turn brown when dehiscent (G. Williams pers. obs.).

Appendix 2 Insect visitors to flowering *Avicennia marina* and comparison with species recorded from an adjacent littoral rainforest (from Williams 1995).

Key: Codes indicate plant records for individual insect species. Single species unless otherwise indicated in parentheses.

Uncertain determinations clumped as 'sp./spp.', with number of apparent species given in parentheses.

Microhymenoptera records indicated as '?>1' = 1 species, or more than 1 species present.

Plant species		
Ac. <i>Alectryon coriaceus</i> (Sapindaceae)		
Ae. <i>Alphitonia excelsa</i> (Rhamnaceae)		
Am. <i>Avicennia marina</i> (Acanthaceae)		
Ef. <i>Euroschinus falcata</i> (Anacardiaceae)		
Gs. <i>Guioa semiglaucula</i> (Sapindaceae)		
Sb. <i>Scolopia braunii</i> (Salicaceae)		
Ss. <i>Syzygium smithii</i> (Myrtaceae)		
Taxa		
BLATTODEA		
Blattellidae		
<i>Balta</i> ? <i>mundicolor</i>		Ef
<i>Balta</i> sp.		Gs
<i>Ectoneura pallidula</i>		Ss, Ae
<i>Ellipsoidion femoratum</i>		Ef, Gs
sp.		Ss, Ae
COLEOPTERA		
Aderidae		
<i>Aderus</i> spp.		Gs(2)
? <i>Aderus</i> sp./spp.		Ef, Ae
sp./spp.		Ef, Ae
Anthicidae		
<i>Anthicus</i> ? <i>brevicollis</i>		Gs
<i>Anthicus</i> ? <i>obliquefasciatus</i>		Sb
<i>Anthicus</i> spp.	Am	Ef(?>1), Ss, Sb(2), Gs
Attelabidae		
<i>Auletobius</i> sp.		Ae
? <i>Euops</i> sp.		Ss
Belidae		
<i>Belus punctulatus</i>		Ac
<i>Belus semipunctulatus</i>		Gs
<i>Belus tenuis</i>		Gs
Buprestidae		
<i>Castiarina acuminata</i>		Ss, Ae, Gs
<i>Castiarina cydista</i>		Sb
<i>Castiarina neglecta</i>	Am	Ae
<i>Castiarina producta</i>		Ef, Sb, Gs
<i>Neocuris</i> sp. nov.		Ef
<i>Neocuris</i> sp.		Ae
<i>Torresita cuprifera</i>		Ae
Cantharidae		
<i>Chauliognathus flavipennis</i>	Am	Ef, Gs
<i>Chauliognathus</i> ? <i>flavipennis</i>		Ae, Sb
<i>Chauliognathus</i> sp.		Ss
<i>Heteromastix</i> sp.		Ef

Carabidae		
<i>Amblytelus amplipennis</i>		Ss
<i>Sarothrocrepis</i> sp./spp.		Ef, Ae(2)
? <i>Sarothrocrepis</i> sp./spp.		Ef
Cavognathidae		
<i>Cavognatha</i> sp.		Ss
Cerambycidae		
<i>Aridaeus thoracicus</i>	Am	
<i>Demonisis</i> sp.		Gs
<i>Hesthesis variegata</i>	Am	
<i>Iphra</i> spp.		Ef, Ae
<i>Notoceresium setistriatus</i>		Ef
<i>Stenocentrus ostricilla</i>		Ss
<i>Stenocentrus</i> ? <i>ostricilla</i>		Gs
<i>Syllitus</i> sp.		Ss
<i>Tessaromma nanum</i>		Sb
<i>Tropocalymma dimidatum</i>	Am	Ss
<i>Zoedia</i> ? <i>longipes</i>		Sb
Chrysomelidae		
<i>Aporocera iridipennis</i>		Ae
<i>Aulacophora</i> sp.	Am	
<i>Ditropidus concolor</i>		Gs
<i>Ditropidus</i> sp./spp.		Ef, Ss, Ae, Gs
? <i>Edusella</i> sp.		Ef
<i>Monolepta australis</i>	Am	Ef, Ae, Sb, Gs
<i>Monolepta miniuscula</i>		Ss
<i>Monolepta</i> ? <i>miniuscula</i>		Ae, Gs
<i>Monolepta</i> sp. nr. <i>modesta</i>	Am	
<i>Monolepta</i> sp. nr. <i>nigra</i>		Ae
<i>Monolepta</i> sp./spp.	Am	Ef, Ae(>1)
<i>Pedethma</i> sp.		Gs
Clambidae		
<i>Clambus</i> sp./spp.		Ss, Gs
Cleridae		
<i>Tarsostenodes simulator</i>		Gs
Coccinellidae		
<i>Cryptolaemus montrouzieri</i>		Ae
<i>Diomus ementitor</i>		Ae
<i>Diomus notescens</i>		Ef
<i>Epilachna</i> sp.		Ae
<i>Rhizobius</i> sp. nr. <i>nigrovarious</i>		Ef, Ae, Ac
<i>Rhizobius</i> sp.		Ef, Ss(>1), Ae(2), Sb, Ac, Gs(2)
? <i>Rhizobius</i> spp.		Ae(3)
<i>Rodalia koebelei</i>		Ae, Gs
<i>Rodalia</i> ? <i>koebelei</i>		Ae
sp.		Gs
Colydiidae		
sp.		Sb
Corylophidae		
<i>Sericoderus</i> sp./spp.		Ef(2), Ss, Ae, Gs
Curculionidae		
<i>Balanerhinus problematicus</i>		Sb
<i>Balanerhinus</i> sp./spp.		Ae, Gs
<i>Cyttalia</i> sp.		Ef
? <i>Cyttalia</i> sp.		Ef
<i>Meriphus</i> sp. 1		Ef, Ss, Sb, Gs

<i>Meriphys</i> sp. 2		Ef
<i>Meriphys</i> sp. 4		Ac
<i>Meriphys</i> sp. 5		Ss, Ac
<i>Neolaemosaccus</i> sp.		Ae
<i>Neomelanterius carinicolis</i>		Ef
<i>Storeus</i> sp. 1		Ac
<i>Storeus</i> sp. 3		Sb
<i>Storeus</i> sp. 4		Ss, Gs
<i>Storeus</i> sp. 5		Gs
<i>Storeus</i> sp. 6		Ss, Gs
<i>Storeus</i> sp. 7		Gs
<i>Tychiini</i> sp. 4		Ss, Ac
<i>Tychiini</i> sp. 4?		Ef, Gs
<i>Tychiini</i> sp. 5		Sb, Ac
<i>Tychiini</i> sp. ?5		Ef
<i>Tychiini</i> sp. 7		Ae
<i>Tychiini</i> sp. ?7		Ef, Ac
<i>Tychiini</i> sp. 8		Ac
<i>Tychiini</i> sp. ?8		Ef
<i>Tychiini</i> sp. 9		Ef, Ac
<i>Tychiini</i> sp. 13		Ss
- Ceutorhynchinae		
sp./spp.		Ef, Ae, Gs
- Scolytinae		
sp.		Ae
Dermestidae		
<i>Anthrenocerus</i> spp.		Ef(3), Ss(2), Ae
? <i>Anthrenocerus</i> spp.		Ef, Ae(3), Sb
<i>Anthrenus</i> sp. nr. <i>socius</i>		Gs
<i>Thaumaglossa nigricans</i>		Ae
<i>Trogoderma</i> sp./spp.		Ef, Ss, Gs
? <i>Trogoderma</i> sp./spp.		Ef, Sb, Gs
Elateridae		
<i>Megapenthes futilis</i>		Gs
<i>Microdesmes angulatus</i>		Ef, Ss
<i>Microdesmes collaris</i>		Ef, Gs
<i>Microdesmes ?collaris</i>		Gs
<i>Ophidius histrio</i>		Ae
sp.		Ae
Hydraenidae		
<i>Hydraena</i> sp.		Gs
Hydrophilidae		
<i>Pseudohydrobius flavus</i>		Ae
Latridiidae		
<i>Aridius</i> sp.		Ss
? <i>Bicava</i> sp.		Ss
<i>Corticaria</i> sp./spp.		Ef, Ss, Ae, Sb, Gs
?Leiodidae		
sp.		Gs
Lycidae		
<i>Metriorrhynchus</i> spp.		Ef(2), Ss(2), Sb
Meloidae		
<i>Palaestria ?rubripennis</i>	Am	
Melyridae		
<i>Carphurus</i> sp. nr. <i>azureipennis</i>	Am	
<i>Carphurus</i> sp./spp.		Ae, Ac, Gs
? <i>Carphurus</i> sp.		Ac

<i>Dicranolaius cinctus</i>	Am	Ef
<i>Dicranolaius ?cinctus</i>		Ae
<i>Helcogaster insignicornis</i>		Ef
<i>Helcogaster ?insignicornis</i>		Ef
<i>Helcogaster</i> sp./spp.		Sb
<i>Neocarphurus ?angustibasis</i>		Ef, Ae
<i>Neocarphurus</i> sp./spp.		Ss, Gs
Mordellidae		
? <i>Austromordella</i> sp.		Ef
<i>Hoshihananomia</i> sp.		Ae
<i>Mordella auronotata</i>		Gs
<i>Mordella humeralis</i>		Gs
<i>Mordella ?humeralis</i>		Sb
<i>Mordella inusitata</i>		Gs
<i>Mordella ?promiscua</i>		Gs
<i>Mordella</i> spp.		Ef(>1), Ss(2), Ae(>1), Sb(?>3), Gs(>1)
<i>Mordellistena</i> sp./spp.		Ef, Ss, Gs(>1)
? <i>Mordellistena</i> sp.		Ae
<i>Tomoxia aterrima</i>		Ae
<i>Tomoxia</i> sp./spp.		Ef, Gs
? <i>Tomoxia</i> sp.		Ae
Nitidulidae		
<i>Epuraea eyrensis</i>		Sb
<i>Epuraea</i> spp.		Ef(2), Ae
<i>Notobrachypterus</i> sp.		Ss
? <i>Rixerodes</i> sp.		Ef
sp.		Ae
Phalacridae		
<i>Litochrus ?maculatus</i>		Ef, Ae
<i>Litochrus</i> sp./spp.		Ef, Ss, Ae(>1), Gs
? <i>Litochrus</i> spp.		Ef(>1), Ss(2), Ae(2), Sb
<i>Olibroporus</i> spp.		Ef, Ss(3), Ae, Gs
? <i>Phalacrinus</i> sp./spp.		Ss, Sb(?>1)
<i>Phalacrus</i> sp.		Gs
? <i>Phalacrus</i> sp./spp.		Ae, Sb
sp./spp.	Am	Ef
Pselaphidae		
? <i>Rhybaxis</i> sp.		Ef
Ripiphoridae		
<i>Macrosiagon</i> sp.		Ae
Salpingidae		
? <i>Lissodema</i> sp.		Ef
Scarabaeidae		
- Cetoniinae		
<i>Eupoecila australasiae</i>	Am	Ae
<i>Glycyphana brunnipes</i>	Am	
<i>Neorrhina punctata</i>	Am	Ae
- Melolonthinae		
<i>Automolius</i> sp. nr. <i>valgoides</i>		Ss
<i>Cheiragra ruficollis</i>		Ef, Ss, Ae, Sb, Gs
<i>Cheiragra ?ruficollis</i>		Ef
<i>Heteronyx</i> sp./spp.		Ef
? <i>Heteronyx</i> sp./spp.		Ef, Ae
<i>Phyllotocus australis</i>		Ss, Sb, Gs
<i>Phyllotocus ?australis</i>		Ae
<i>Phyllotocus ?marginipennis</i>		Ef

Scirtidae		
<i>Pseudomicrocara</i> sp./spp.	Am	Ae(2), Sb
? <i>Pseudomicrocara</i> sp./spp.		Ae, Gs
<i>Scirtes</i> spp.		Ae(2)
sp./spp.	Am	Ae(2)
Scraptiidae		
<i>Scraptia</i> sp.		Ef
Staphylinidae		
- Aleocharinae		
? <i>Oligota</i> sp.		Gs
spp.		Ef(2), Ss(2)
Tenebrionidae		
- Alleculinae		
<i>Atoichus bicolor</i>		Ae, Sb
<i>Atoichus</i> sp.		Ae, Sb
<i>Nocar</i> sp. nr. <i>depressiusculus</i>		Ef, Gs
<i>Nocar</i> sp.		Sb
<i>Tanychilus dubius</i>	Am	
- Lagriinae		
? <i>Euomma</i> sp.		Ae
<i>Ommatophorus</i> sp.		Ae
DIPTERA		
Asilidae		
? <i>Tricella</i> sp.		Ef
sp.		Ef
Bibionidae		
<i>Biblio imitator</i>	Am	Ae, Sb
spp.		Sb(2), Gs(2)
Bombyliidae		
<i>Geron</i> spp.	Am(1/?2)	Ef(2), Ss(2), Ae, Gs
<i>Ligyra bombyliiformis</i>	Am	Ae
<i>Pseudopenthes fenestrata</i>		Ae
<i>Villa fuscicostata</i>	Am	
<i>Villa</i> sp. 1	Am	
Calliphoridae		
<i>Amenia chrysame</i>	Am	Ss, Gs
<i>Amenia</i> sp. near <i>dubitalis</i>	Am	
<i>Calliphora hillii</i>		Gs
<i>Calliphora</i> sp.		Gs
<i>Chlororhinia exempta</i>		Ef
<i>Chrysomya megacephala</i>		Ae
<i>Chrysomya</i> ? <i>megacephala</i>	Am	
<i>Chrysomya</i> sp. 1	Am	
? <i>Lucilia</i> sp.		Gs
<i>Paramenia</i> sp./spp.		Ss, Ae, Ac
<i>Stomorphina melastoma</i>		Ae
<i>Stomorphina xanthogaster</i>	Am	Ac
<i>Stomorphina</i> sp./spp.	Am	Ef(2), Ae(>1), Sb, Ac, Gs
genus near <i>Stomorphina</i>	Am	
sp./spp.	Am(2)	
Cecidomyiidae		
sp./spp.		Ef, Ae, Gs
Chironomidae		
sp./spp.	Am	Ss, Gs(>1)
Chloropidae		
<i>Apotropina</i> sp. 1		Ac, Gs
<i>Apotropina</i> sp. 2		Ss

<i>Apotropina</i> sp. 3		Ae
<i>Pemphigonotus mirabilis</i>	Am	
sp.		Ae
Conopidae		
<i>Microconops</i> sp.	Am	
Culicidae		
<i>Aedes vigilax</i>	Am	
<i>Toxorhynchites speciosus</i>		Gs
sp./spp.		Ae(2)
Dolichopodidae		
<i>Austroscleropus</i> sp.		Ef
<i>Krakatauia macalpinei</i>		Ef, Ss, Ae, Gs
Drosophilidae		
<i>Drosophila flavohirta</i>		Ae
<i>Drosophila</i> sp./spp.		Ss, Ae, Ac
? <i>Drosophila</i> sp.		Gs
<i>Leucophena cooperensis</i>		Ae
sp./spp.		Ef(?>1)
Empididae		
<i>Empis</i> spp.		Ef(2)
<i>Tachydromia</i> sp. 1	Am	
sp./spp.		Ae, Ac, Gs
Ephydriidae		
sp./spp.	Am	Ae
Lauxaniidae		
<i>Homoneura</i> sp./spp.		Ae, Gs
<i>Melanina</i> sp./spp.		Ef(?>1), Sb, Ac, Gs
? <i>Melanina</i> sp.		Ae
<i>Sapromyza nigriceps</i>		Ae, Sb
<i>Sapromyza</i> ? <i>nigriceps</i>		Ef, Ae, Ac
<i>Sapromyza sciomyzina</i>		Sb
<i>Sapromyza</i> ? <i>sciomyzina</i>		Ef
<i>Sapromyza</i> sp./spp.		Ss, Ac, Gs
? <i>Sapromyza</i> sp./spp.		Ss, Gs
<i>Steganopsis melanogaster</i>		Ae, Gs
<i>Tephritisoma</i> spp.		Ef, Ae, Ac
sp./spp.	Am(2)	Ae(2), Ac
Lonchaeidae		
<i>Lamprolonchaea</i> sp.		Gs
Milichiidae		
sp.	Am	
Muscidae		
<i>Musca</i> spp.	Am(3)	Ae, Gs
Mycetophilidae		
sp./spp.		Ae
Nemestrinidae		
<i>Cyclopsidea</i> sp.		Ae
Phoridae		
spp.		Ef(2), Ss(2), Ae(2), Sb, Ac, Gs
Platystomatidae		
<i>Duomyia picta</i>		Ae, Ac, Gs
<i>Duomyia</i> ? <i>picta</i>		Gs
<i>Duomyia</i> sp. nov.?		Ae
<i>Duomyia</i> sp./spp.		Ss(2), Ae(2), Gs
genus near <i>Duomyia</i>	Am	
<i>Euprosopia remota</i>		Ae
<i>Euprosopia</i> spp.	Am(2)	

<i>Lamprogaster</i> sp.	Am	
<i>Microepicausta</i> sp./spp.		Ss, Ae, Gs
<i>Pogonortalis doclea</i>	Am	Ss, Ae
<i>Rivellia</i> spp.	Am	Ae(2)
Psychodidae		
sp.		Ae
?Rhagionidae		
sp.		Ss
Sarcophagidae		
<i>Sarcophaga</i> spp.	Am	Ef, Ae(2)
sp.	Am	
Scatopsidae		
? <i>Scatops</i> sp.		Ss
sp./spp.		Ss, Ae
?Scatopsidae		
sp.		Ef
Sepsidae		
<i>Australosepsis niveipennis</i>		Ae
<i>Lasionemapoda hirsuta</i>		Gs
? <i>Lasionemapoda hirsuta</i>		Ae
? <i>Parapalaeosepsis plebeia</i>		Ae
<i>Sepsis dissimilis</i>		Ae, Gs
<i>Sepsis ?dissimilis</i>		Ae
<i>Sepsis</i> sp.	Am	Ae
sp.	Am	
Stratiomyidae		
<i>Hermetia ?illucens</i>		Ae
<i>Odontomyia decipiens</i>	Am	Ae
<i>Odontomyia laterimaculata</i>		Ae
<i>Odontomyia ?sydneyensis</i>		Ae
<i>Odontomyia</i> spp.	Am	Ae(2)
Syrphidae		
<i>Ceriana macleayi</i>	Am	
<i>Ceriana</i> sp.		Gs
<i>Dideopsis aegrota</i>	Am	Ae
? <i>Episyrphus</i> sp.		Ac
<i>Eristalinus ?aurulans</i>	Am	
<i>Eristalinus maculatus</i>	Am	Ae
<i>Eristalinus punctulatus</i>	Am	
<i>Eristalinus</i> sp.		Ae
<i>Mesembrius hilaris</i>	Am	Ef, Ss
? <i>Graptomyza</i> sp.		Ac
<i>Melangyna</i> sp. 1	Am	
<i>Melangyna</i> sp. 2	Am	
? <i>Microdon</i> sp.	Am	
<i>Psilota</i> sp./spp.		Ef, Ss
? <i>Psilota</i> sp./spp.	Am(2)	
<i>Syritta luteinervis</i>	Am	Ac
? <i>Xanthogramma</i> sp./spp.		Ae, Ac
sp./spp.		Ae, Gs
Tabanidae		
<i>Austroplex brevipalpis</i>	Am	
<i>Austroplex</i> sp. 1	Am	
<i>Cydistomyia alternata</i>	Am	
? <i>Cydistomyia alternata</i>		Ae
<i>Cydistomyia oculata</i>	Am	
? <i>Dasybasis</i> sp.1	Am	

<i>Scaptia auriflua</i>		Ae
? <i>Tabanus</i> sp.		Ae
sp.	Am	
Tachinidae		
<i>Austrophorocera</i> sp.		Ae
? <i>Austrophorocera</i> sp. nr. <i>grandis</i>	Am	
<i>Blepharella</i> sp.		Ae(2)
? <i>Blepharella</i> sp.		Ae
<i>Blepharipa</i> sp.		Ae
? <i>Palexorista</i> sp.		Gs
<i>Prosenia</i> sp.		Ae
<i>Rutilia ?inusta</i>		Ae
<i>Rutilia lepida</i>	Am	
<i>Rutilia</i> sp./spp.	Am	Ae
<i>Saralba</i> sp.	Am	
<i>Senostoma</i> sp.		Ae
<i>Tritaxis</i> sp.		Gs
spp.	Am(4)	Ss, Ae, Gs
Tephritidae		
? <i>Bactrocera</i> sp./spp.	Am(2)	Ae
<i>Spathulina</i> sp./spp.		Ae, Gs
<i>Trupanea glauca</i>		Ae
Therevidae		
<i>Anabarhynchus</i> sp. 1	Am	
<i>Anabarhynchus</i> sp. 2?	Am	
sp./spp.		Ef, Ae, Sb, Gs
Tipulidae		
sp./spp.		Ss, Ae(>1), Gs
?Trichoceridae		
sp./spp.		Ss, Ae(>1), Ac, Gs(>1)
HEMIPTERA		
Cicadellidae		
<i>Ishidaella</i> sp.		Gs
sp.		Ae
Cicadidae		
<i>Arunta perulata</i>		Ae
<i>Cicadetta ?arenaria</i>		Gs
?Cixiidae		
? <i>Oliarus</i> sp.		Ef
Eurymelidae		
sp.		Ae
Flatidae		
<i>Massila</i> sp.		Gs
<i>Siphanta ?acuta</i>		Sb
<i>Siphanta</i> sp./spp.		Ss, Gs
Issidae		
<i>Chlamydopteryx</i> sp. nr. <i>vulturinus</i>		Ef
Lygaeidae		
<i>Arocatus</i> sp. 1		Ef
<i>Oncopeltus sordidus</i>	Am	
Membracidae		
sp.		Ae
Miridae		
spp.		Ef(4), Ss, Ae(>1), Ac, Gs
Orsillidae		
<i>Nysius</i> sp./spp.		Ef, Ss, Ae, Gs

Psyllidae		
spp.		Ae, Ac(3), Gs(2)
Reduviidae		
<i>Pristhesancus plagipennis</i>	Am	
Rhopalidae		
<i>Leptocoris</i> sp.1	Am	
Tessaratomidae		
<i>Lyramorpha</i> sp.		Gs
Tingidae		
<i>Teleonemia scrupulosa</i>		Ef, Gs
<i>Teleonemia</i> spp.		Ac(2)
sp.		Ss
HYMENOPTERA		
microhymenoptera		
Agonidae		
sp./spp.		Ss, Ae(>1), Gs
Bethylidae		
spp.		Ss, Ae(2), Gs(>1)
?Bethylidae		
sp.		Ef
Braconidae		
? <i>Agathis</i> sp.		Ae
<i>Bracon</i> sp./spp.		Ae(2)
<i>Iphaulax</i> sp.		Ae
? <i>Iphaulax</i> sp.		Gs
? <i>Rogas</i> spp.		Ae, Gs(2)
sp./spp.		Ef(>1), Ss, Sb(>1)
Ceraphronidae		
sp./spp.		Ae(>1)
Chalcididae		
spp.		Ef, Ss, Ae(>3), Gs(>1)
Chrysididae		
? <i>Praestachysis</i> sp.		Ae
<i>Stilbum</i> sp.		Ae
sp./spp.		Ae(>1)
Diapriidae		
sp./spp.		Ae(>1), Sb(>1)
Dryinidae		
sp./spp.		Ef(>1)
Encyrtidae		
sp./spp.		Ef(>1), Ae(>1), Sb(>1), Gs(>1)
Eulophidae		
sp./spp.		Ef(>2), Ss, Ae(>2), Gs(>1)
Eupelmidae		
sp./spp.		Ae(>1)
Eurytomidae		
<i>Mesamotura</i> sp.		Ae
sp./spp.		Ae(>1)
Figitidae		
sp./spp.		Ef(>1), Ae(>2), Gs(>1)
Mymaridae		
sp./spp.		Ae(>1)
Ormyridae		
sp./spp.		Ef(>1)
Platygastridae		
sp./spp.		Ef(>2), Ae(>2), Gs(>1)

Pteromalidae		
sp./spp.		Ef(>1), Ss, Ae(>1), Sb(>1), Gs(>1)
Torymidae		
sp./spp.		Ss, Ae(>1), Gs(>1)
generally larger species		
Braconidae		
? <i>Agathis</i> sp.		Ae
<i>Bracon</i> sp./spp.		Ae(2)
<i>Iphaulax</i> sp.		Ae
? <i>Iphaulax</i> sp.		Gs
? <i>Rogas</i> spp.		Ae, Gs(2)
sp./spp.		Ef(>1), Ss, Sb(>1), Gs(>1)
Crabronidae		
<i>Acanthostethus</i> sp./spp.		Ef, Ae(>1)
<i>Bembicinus</i> sp./spp.	Am	Ef, Ae
<i>Bembix</i> sp. nr. <i>lamellatus</i>	Am	
<i>Bembix</i> sp. nr. <i>lamellatus</i> ?	Am	
<i>Bembix promontorii</i>	Am	Ae
<i>Bembix</i> sp. 1	Am	
<i>Bembix</i> spp.		Ae(2)
<i>Cerceris</i> sp. nr. <i>antipodes</i>	Am	
<i>Ectemnius reginellus</i>		Ae
? <i>Ectemnius</i> sp. 1	Am	Ae
? <i>Ectemnius</i> sp. 2	Am	
? <i>Ectemnius</i> sp. 3		Ae
<i>Larra</i> sp.		Ae
<i>Pison</i> ? <i>ruficornis</i>	Am	
<i>Sericophorus</i> sp.		Ae
<i>Sphodrotes</i> sp. 1	Am	
<i>Sphodrotes</i> sp./spp.		Ef, Ae(>1)
? <i>Sphodrotes</i> spp.		Ae(2)
<i>Tachysphex fanulensis</i>	Am	
<i>Tachysphex</i> ? <i>pilosus</i>	Am	
<i>Tachysphex</i> sp. 1	Am	
<i>Tachysphex</i> sp. 2	Am	
<i>Tachysphex</i> spp.		Ef, Ae(2), Ac
? <i>Tachysphex</i> sp. 1	Am	
? <i>Tachysphex</i> sp. 2	Am	
? <i>Tachysphex</i> sp. 3	Am	
? <i>Tachysphex</i> sp./spp.		Ae(>1)
<i>Williamsita</i> sp.1		Ae
<i>Williamsita</i> sp.2		Ae
sp./spp.		Ef, Ac
Evaniidae		
<i>Evania</i> sp./spp.	Am	Ss, Ae, Gs
? <i>Evania</i> spp.		Ae(2)
Gasteruptionidae		
<i>Gasteruption pallidicus</i>	Am	Ss
<i>Gasteruption</i> sp./spp.	Am	Ac
Ichneumonidae		
<i>Echthromorpha intricatoria</i>		Ae
<i>Lissopimpla excelsa</i>	Am	
? <i>Lissopimpla</i> sp.	Am	
? <i>Theronia</i> sp. 1	Am	
<i>Xanthopimpla terminalis</i>	Am	

?Ichneumonidae		
sp.		Gs
Mutillidae		
<i>Euphutomorpha</i> sp. 1		Ae
<i>Euphutomorpha</i> sp. 2		Ae
<i>Euphutomorpha</i> sp. 3		Gs
sp.		Gs
Pergidae		
<i>Pterygophorus cinctus</i>		Ss
? <i>Pterygophorus cinctus</i>	Am	
Pompilidae		
<i>Alocurgus aurifrons</i>	Am	
<i>Calopompilus defensor</i>	Am	
' <i>Chirodamus</i> ' spp.		Ae(2)
<i>Ctenotegus</i> sp. 1	Am	
<i>Ctenotegus</i> sp. 1?	Am	
? <i>Ctenotegus</i> sp. 1	Am	
<i>Ferreola handschirii</i>	Am	Ae
<i>Ferreola</i> ? <i>handschirii</i>	Am	
<i>Heterodontonyx bicolor</i>	Am	
<i>Heterodontonyx</i> sp. 1	Am	Ae
<i>Heterodontonyx</i> spp.		Ae(>3)
? <i>Heterodontonyx</i> sp.		Ae
<i>Paracyphononyx</i> sp. 1	Am	
<i>Turneromyia frontalis</i>	Am	
spp.	Am(1/?2)	Ef, Ss(3), Ae, Ac
Scoliidae		
<i>Austroscolia</i> sp. 1	Am	
<i>Radumeris</i> ? <i>tasmaniensis</i>		Ae
? <i>Radumeris</i> sp.		Ac
<i>Scolia verticollis</i>	Am	Ae
<i>Scolia</i> spp.		Ae(3)
Sphecidae		
<i>Sceliphron laetum</i>	Am	
<i>Sphex ephippium</i>	Am	
<i>Sphex fumipennis</i>	Am	
Thynnidae		
<i>Acanthothynnus ater</i>	Am	Ae
<i>Acanthothynnus</i> ? <i>ater</i>		Ae
<i>Anthobosca signata</i>		Ae
? <i>Anthobosca signata</i>		Ae
<i>Anthobosca</i> sp. 1	Am	
<i>Diamma bicolor</i>	Am	Ae, Ac
<i>Dimorphothynnus dimidiatus</i>		Ss, Ae, Gs
<i>Dimorphothynnus</i> ? <i>dimidiatus</i>		Ae
<i>Epactiothynnus tasmaniensis</i>	Am	Ae
<i>Epactiothynnus</i> ? <i>tasmaniensis</i>	Am	Ss, Ae
? <i>Epactiothynnus</i> sp.		Ae
<i>Rhagigaster</i> sp. nr. <i>kiandrensis</i>	Am	Ss, Ae, Gs
<i>Rhagigaster</i> ? <i>mutatus</i>	Am	Ae
? <i>Rhagigaster</i> sp. 1	Am	
<i>Tmesothynnus dispersus</i>		Ae
<i>Thynn Turneria</i> sp. nr. <i>umbripennis</i>		Ae
? <i>Thynn Turneria</i> sp.		Ae
<i>Zaspilothynnus</i> sp. nr. <i>campanularis</i>		Ae
<i>Zeleboria</i> ? <i>contigua</i>		Ss, Ae, Gs

<i>Zeleboria xanthorrhoei</i>	Am	Ss, Ae
? <i>Zeleboria</i> sp.		Ae
spp.	Am(2)	
Vespidae		
<i>Abispa splendida</i>	Am	Ae
<i>Bidentodynerus bicolor</i>	Am	
genus near <i>Elimus</i>	Am	
? <i>Epiodynerus</i> sp.		Ae
<i>Leptomenoides</i> sp.		Ae
<i>Paralastor</i> sp. 1	Am	Ae
<i>Paralastor</i> sp. 2		Ae
<i>Paralastor</i> sp. 2?		Ae
<i>Paralastor</i> spp.		Ef, Ss, Ac(2)
? <i>Paralastor</i> sp.		Ef
<i>Polistes humilis</i>	Am	Ae, Ac
<i>Polistes</i> ? <i>humilis</i>		Ae
<i>Polistes tepidus</i>		Ae
<i>Pseudabispa confusa</i>	Am	Ae
<i>Rhopalidia</i> sp. nr. <i>plebiana</i>	Am	
<i>Rhynchium</i> ? <i>mirabile</i>	Am	
Apoidea		
Apidae		
<i>Amegilla pulchra</i>	Am	
<i>Apis mellifera</i>	Am	Ef, Ss, Ae, Sb, Ac, Gs
<i>Braunsapis</i> sp. 1	Am	
<i>Exoneura lawsonii</i>		Ae
<i>Exoneura</i> sp. 1	Am	
Colletidae		
- Colletinae		
<i>Leioproctus cristatus</i>		Gs
<i>Leioproctus</i> ? <i>cristatus</i>		Ef, Ae, Ac
<i>Leioproctus irroratus</i>	Am	Ef, Ae, Ac
<i>Leioproctus</i> ? <i>irroratus</i>		Ef
<i>Leioproctus</i> sp. nr. <i>irroratus</i>		Ae
<i>Leioproctus</i> sp. nov.?	Am	
- Hylaeinae		
<i>Amphylaeus nubilosellus</i>	Am	Ef, Ae, Sb, Ac, Gs
<i>Amphylaeus</i> ? <i>nubilosellus</i>		Ef
<i>Hemirhiza melliceps</i>		Ac
<i>Heterapoides</i> sp. nr. <i>exleyae</i>	Am	Ef, Ae, Ac, Gs
<i>Heterapoides</i> ? <i>nigriconcava</i>		Ef
<i>Hylaeus amiculiformis</i>		Sb
<i>Hylaeus cyanophilus</i>		Ae
<i>Hylaeus</i> ? <i>cyanophilus</i>		Ef
<i>Hylaeus</i> ? <i>jacksoniae</i>		Ae
<i>Hylaeus</i> ? <i>microphenax</i>		Ef
<i>Hylaeus primulipictus</i>		Ef
<i>Hylaeus rotundiceps</i>		Ef, Ae
<i>Hylaeus</i> sp./spp.		Ef, Sb
- Euryglossine		
<i>Pachyprosopis haematosoma</i>	Am	
Halictidae		
<i>Homalictus flindersi</i>		Ae, Ac, Gs
<i>Homalictus</i> ? <i>flindersi</i>	Am	Ac
<i>Homalictus megastigmus</i>		Ae, Sb, Ac
<i>Homalictus</i> ? <i>megastigmus</i>		Ef
<i>Homalictus</i> ? <i>sphecodoides</i>		Gs

<i>Lasioglossum carbonarium</i>	Am	
<i>Lipotriches</i> sp. 1	Am	
Formicoidea		
Formicidae		
<i>Camponotus</i> sp.		Ae
? <i>Camponotus</i> sp.		Gs
<i>Crematogaster</i> spp.		Ae(2), Ac(2), Gs
<i>Iridomyrmex</i> sp./spp.		Ef, Ss, Ae, Gs
? <i>Iridomyrmex</i> spp.		Ef(2)
<i>Myrmecia nigrocincta</i>		Ef, Ae, Sb, Ac
? <i>Paratrechina</i> sp.	Am	
? <i>Pheidole</i> sp.		Gs
<i>Polyrhachis ammon</i>		Ae
<i>Polyrhachis</i> sp. nr. <i>ammon</i>		Ae
<i>Polyrhachis clio</i>		Ef, Ae, Ac, Gs
<i>Polyrhachis hookeri</i>		Ae
<i>Polyrhachis ?pilosa</i>		Ac
<i>Polyrhachis</i> sp./spp.		Ef, Ae, Sb, Ac, Gs
? <i>Polyrhachis</i> spp.		Ae, Ac(2)
<i>Rhytidoponera metallica</i>		Ac
sp./spp.	Am	Ae
LEPIDOPTERA		
Erebidae		
<i>Amata</i> sp./spp.	Am	Gs
? <i>Amata</i> spp.		Ss(2), Ae(2), Sb(>1), Ac
<i>Asura</i> sp.		Ss
<i>Nyctemera amica</i>		Ef, Gs
Hesperiidae		
sp./spp.	Am(2)	Ae
Lycaenidae		
<i>Candalides ?absimilis</i>		Ae
<i>Candalides consimilis</i>		Ac
<i>Erysichton l. lineata</i>		Ae
<i>Erysichton ?l. lineata</i>		Ae
<i>Hypochrysops cyane</i>	Am	
<i>Jalmenus</i> sp.		Ac
<i>Paralucia ?aurifera</i>		Ac
sp.	Am	
Nymphalidae		Ae
<i>Danaus affinis</i>	Am	
<i>Danaus chrysippus</i>	Am	
<i>Hypocysta metirius</i>		Ae
<i>Junonia villida callibe</i>		Ae
<i>Tirumala hamata</i>	Am	

Papilionidae		
<i>Graphium eurypylus lycaon</i>		Ae
Pieridae		
<i>Catopsilia pomona</i>	Am	
<i>Catopsilia</i> sp.		Ae
<i>Delias nigrina</i>		Ac
Geometridae		
? <i>Aeolochroma</i> sp.		Ae
Zygaenidae		
<i>Pollanisis</i> sp. 1	Am	
Mantispidae		
<i>Callomantispa picta</i>		Ef
? <i>Spaminta</i> sp.		Gs
ORTHOPTERA		
Gyrllacrididae		
sp.		Ae
PSOCOPTERA		
Ectopsocidae		
<i>Ectopsocus</i> sp. nr. <i>briggsi</i>		Ae, Gs
THYSANOPTERA		
Aeolothripidae		
<i>Desmothrips bagnalli</i>		Ef
<i>Desmothrips</i> sp.		Ef
Phlaeothripidae		
<i>Haplothrips ?victoriensis</i>		Ef
<i>Haplothrips</i> sp.		Ef
<i>Heliothrips haemorrhoidalis</i>		Ss, Ae, Gs
sp.		Gs
Thripidae		
<i>Partenothrips dracaenae</i>		Ef
<i>Thrips ?australis</i>		Ss, Gs
<i>Thrips hawaiiensis</i>		Ef
<i>Thrips setipennis</i>		Ef, Ss, Gs
<i>Thrips</i> sp.		Ss, Gs
? <i>Thrips</i> sp./spp.		Ef, Gs(>1)