



Arthropod assemblages in tree canopies: a comparison of orders on box mistletoe (*Amyema miquelii*) and its host eucalypts

Anna E Burns,^{1*} Saul A Cunningham² and David M Watson¹

¹School of Environmental Sciences and Institute for Land, Water and Society, Charles Sturt University, PO Box 789, Albury, NSW 2640, Australia.

²CSIRO Ecosystem Sciences, Canberra, ACT 2600, Australia.

Abstract

Parasitic plants, such as mistletoes, are important components of tree canopies, providing food and shelter for a range of vertebrates and invertebrates. Arthropods from several orders are known to inhabit mistletoes but no direct comparisons between these plants and their host plants have been conducted until present. In this study, the composition and abundance of arthropods occurring on hemi-parasitic box mistletoe, *Amyema miquelii* ((Lehm. ex Miq.) Tiegh., Loranthaceae), on *Eucalyptus* (L., Myrtaceae) trees from the south-west slopes region of eastern Australia were investigated. Here a comparison of the arthropod assemblages at the ordinal level is presented. Specimens of Insecta and Arachnida were sampled from box mistletoe and three of its most common host species, using restricted canopy fogging, in two consecutive years, in nine remnants of grassy-box woodlands. The same 10 arthropod orders were sampled from the mistletoes and their eucalypt hosts but the total density of arthropods was greater on the eucalypt foliage. The latter result might be attributed to the significantly greater nitrogen content of the eucalypt foliage than the mistletoe foliage. One year after de-faunation, all but one of the arthropod orders had re-colonised the mistletoe plants. The total abundance of arthropods (particularly Hemiptera and Hymenoptera) on the mistletoes was greater in the second year of sampling, in which drought conditions occurred. Future research of arthropod assemblages in tree canopies should be more inclusive of the full range of substrates or habitats within canopies. Furthermore, investigation of the nutritional quality of mistletoe foliage compared with their host trees is required for a better understanding of the factors driving variation in community composition of arthropod assemblages.

Key words arboreal, arthropod assemblage, box mistletoe, host plant, re-colonisation.

INTRODUCTION

After the development of methods for forest canopy research in the 1970s, and subsequent improvements, the huge diversity of arthropods inhabiting tree canopies began to be appreciated (e.g. Erwin & Scott 1980; Moran & Southwood 1982; Stork 1987; Basset & Arthington 1992; Colwell & Coddington 1994; Hammond 1994; Moffett & Lowman 1995; Stork *et al.* 1997; Ødegaard 2004). A wide variety of interactions between canopy arthropods and their host plants has been investigated, including host plant specificity, resource use, spatial and temporal variation in community composition, the effects of disturbance on arthropod diversity and re-colonisation dynamics (e.g. described in Stork *et al.* 1997; Basset *et al.* 2003). In addition to the trees themselves, a variety of other plants grow within canopies, including epiphytes, parasitic plants and lianas (Lowman & Rinker 2004). There have been

investigations of the arthropod assemblages inhabiting these groups of plants (Room 1972a,b; Whittaker 1982; Dejean *et al.* 1995; Richardson 1999; Kitching 2000; Yanoviak *et al.* 2003) but few direct comparisons between the arthropod assemblages inhabiting parasitic or epiphytic plants and their host plants have been made (Ødegaard 2000; Ellwood *et al.* 2002).

Mistletoes (i.e. aerial parasitic plants) and epiphytic plants have been proposed as keystone resources in the ecosystems in which they occur, because relative to their abundance and biomass they have a disproportionate influence on ecosystem functioning, and the ecology of vertebrate species in particular (Nadkarni 1994; Watson 2001). Mistletoes are an important food source and nesting site for many birds and mammals (Watson 2001; Cooney *et al.* 2006; Mathiasen *et al.* 2008) and have a positive effect on vertebrate diversity and distribution patterns in a wide range of habitat types (Watson 2002). However, the influence of mistletoes on the ecology and diversity of arthropods is poorly known. We are aware of just four community- or assemblage-level studies of arthropods inhabiting mistletoes (Room 1972a,b; Whittaker 1982; Tassone &

*Present address: School of Biological Sciences, Monash University, Clayton, Vic. 3800, Australia (anna.burns@monash.edu).

Majer 1997; Anderson & Braby 2009), compared with many hundreds of studies on mistletoe–vertebrate interactions (synthesised in Watson 2001). This is despite the existence of approximately 1400 species of mistletoes worldwide (Nickrent 2001) and mistletoe-specific arthropods in several orders (see Baloch & Mohyuddin 1969; De Baar 1985; McMillan 1987; Taylor 1999; Braby 2006). Although species-specific studies have revealed ecological interactions between mistletoes and arthropods, including herbivory, frugivory, pollination and tri-trophic relationships (Gregor *et al.* 1974; Penfield *et al.* 1976; Atsatt 1981; De Baar 1985; Aparicio *et al.* 1995; Braby 2000, 2005, 2006; Mooney 2003; French 2004; Robertson *et al.* 2005), it is unclear how these interactions affect community-scale variation in the distribution and diversity of canopy arthropods.

This study focused on arthropods inhabiting box mistletoe (*Amyema miquelii* (Lehm. ex Miq.) Tiegh., Loranthaceae) and three of its host tree species (*Eucalyptus polyanthemos* Schauer, *E. melliodora* Cunn. ex Schauer and *E. blakelyi* Maiden, Myrtaceae). It is the first comparative assemblage-level study of the composition and abundance of arthropods inhabiting a mistletoe species and its host plants. Box mistletoe occurs throughout mainland Australia, with the greatest frequency recorded in south-eastern Australia (Barlow 1984). Box mistletoe occurs on 125 recorded host plant species, primarily *Eucalyptus* species and a few species in each of nine other families (Downey 1998). The three *Eucalyptus* species included in this study are widely distributed in south-eastern Australia, and occur in woodlands and open forest, on gentle slopes and low hills (Chippendale 1988).

This paper represents one part of a larger study, which investigated the diversity, host specificity, spatial distribution and temporal dynamics of canopy arthropods inhabiting box mistletoes and their host plants (Burns 2009). The comparisons between arthropod assemblages in this paper are made at the taxonomic level of orders and address the questions: (1) Do arthropod assemblages differ in composition and abundance between mistletoe plants and their host trees? (2) Do foliage properties influence the community composition of arthropods on these plants? Furthermore, to begin to understand the community assembly of arthropod assemblages on mistletoes we include a comparison of the original assemblages and those sampled 1 year after de-faunation. Subsequent papers will address these issues and other aspects of the broader study with species-level data for selected groups of herbivorous and predatory arthropods.

MATERIALS AND METHODS

Study area

The study was conducted in the Upper Billabong Creek Catchment, in the south-west slopes of New South Wales, Australia (near the township of Holbrook: 35°44'S, 147°19'E, Fig. 1). The region has a temperate climate with the highest precipitation in winter and spring (June–October). Sampling occurred in the spring season of two consecutive years: November 2005

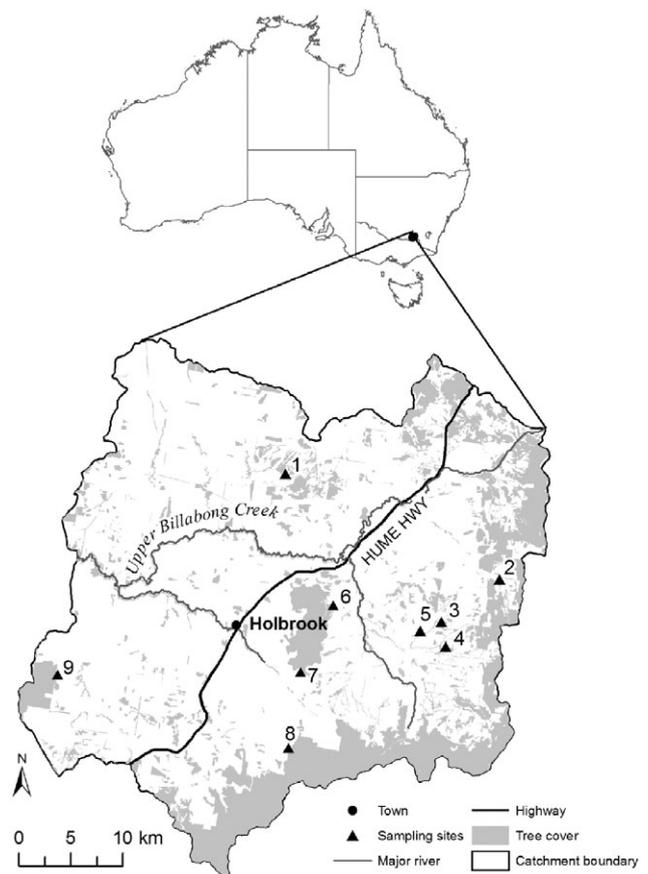


Fig. 1. Location of the study sites in the Upper Billabong Creek Catchment, southern New South Wales, Australia (centre of catchment: 35°43'S, 147°22'E).

and November 2006, because arthropod abundance is expected to peak at this time (Woinarski & Cullen 1984; Recher *et al.* 1996b). It was not feasible to collect samples in more than one season per year in this study.

Sampling took place at nine sites, 4–43 hectares in size, consisting of remnant woodlands on private land, surrounded by grazed pastures, crops or natural woodland (Fig. 1). The remnant woodlands were dominated by red box (*E. polyanthemos*), which is the primary host of box mistletoe (*A. miquelii*) in the region. Other tree species at the sites included yellow box (*E. melliodora*), Blakely's red gum (*E. blakelyi*), red stringybark (*E. macrorhyncha*), white box (*E. albens*), apple box (*E. bridgesiana*) and long-leaved box (*E. goniocalyx*) and there was a sparse understorey of shrubs and grasses. Three other mistletoe species occurred in a few of the sites at very low densities: drooping mistletoe (*Amyema pendula*), fleshy mistletoe (*A. miraculosa* ssp. *boormanii*) and Kurrajong mistletoe (*Notothixos cornifolius*, Viscaceae). The densities of box mistletoe at the study sites ranged from 7 to 70 clumps per hectare and appeared to be greater at the edges, than the interior, of the remnant woodlands. The nine sites were selected on the basis that there were at least 40 box mistletoe plants at each site and the sites were accessible with a trailer-mounted hydraulic bucket hoist, which was used to access the

canopy. The geographic distances between site pairs ranged between 2.4 and 45 km.

Sampling protocol

Arthropod samples were collected from box mistletoe plants and three of its host tree species, red box, yellow box and Blakely's red gum, at the edges of remnant vegetation patches. Sampling occurred at site numbers 1–5 (Fig. 1) over 9 days in November 2005, between 10 AM and 3 PM daily. In 2006, sampling occurred at all sites over 12 days in November between 9 AM and 2 PM daily. All samples were collected on sunny days with calm conditions or light winds. A restricted canopy fogging technique was used to collect the arthropods, similar to Basset (1990). In this technique, the plant foliage was fully enclosed in a plastic collection bag and then sprayed for 20 s with a pyrethrin-based insecticide, after which the opening of the bag was sealed with masking tape. After 20 min, the foliage was shaken vigorously to dislodge arthropods remaining on the foliage; the collection bag was unsealed, removed from the foliage and the collected material was transferred to a container of 75% ethanol. Large leaves, twigs and fruit in the sample bags were shaken over the bag and inspected for arthropods remaining on the surface, which were removed and included in the sample. All arthropod specimens (adults and larvae) were identified to order according to taxonomic guides for Australian invertebrates (Harvey & Yen 1989; Naumann 1991; Zborowski & Storey 1995; New 1996).

Restricted canopy fogging was the most appropriate method for collection of arthropods because mistletoe foliage is so close to the foliage of the host tree. This technique allows one to express the data in terms individuals per leaf area and is thought to be a more effective method than unrestricted insecticidal knock-down for collecting small specimens and spiders (Basset 1990). However, active flying specimens are likely to be underestimated by restricted canopy fogging because they are likely to alight from the foliage as the researcher tries to envelop the sample in the collection bag.

The type of plastic bag and insecticide differed slightly between years. In 2005, black plastic rubbish bin-liners were used, 1.30 m long by 1.12 m wide. In 2006, clear plastic bags were used that were 1.16 m long by 0.89 m wide and 50 µm thick (sourced from a packaging supply company). In 2005, Baygon Natural Insecticide (® S.C. Johnson & Son INC), containing naturally sourced pyrethrins (i.e. from pyrethrum), was used but this could not be used in 2006 due to discontinuation of the product, so Raid Fly and Mosquito Killer (® S.C. Johnson & Son INC) was used in 2006, which contains synthetic pyrethrins (i.e. pyrethroids): Tetramethin (4 g/kg), Phenothrin (0.9 g/kg) and Allethrin (0.9 g/kg); and Ethanol (291 g/kg). Pyrethrins, both naturally sourced and synthetic, degrade rapidly in sunlight and air (within a few hours or a few days, respectively), are low in toxicity to mammals and birds and are non-residual (NPIC 1998; Anonymous 2000).

The abundance of arthropods can vary according to the aspect of the tree (Richardson *et al.* 1999; Stork *et al.* 2001); therefore, mistletoe plants were sampled randomly from all

aspects of the trees, from 2 to 12 m above ground (i.e. to the maximum extent of the trailer-mounted hydraulic bucket hoist). Where possible, arthropods were sampled from eucalypt foliage within approximately 3 m of a mistletoe plant that was sampled in the same tree, at a similar height above ground and depth in the canopy. A distance of approximately 3 m was within the reach of the boom arm of the bucket hoist, without having to move its base on the ground. A labelled metal tag was attached to each branch of mistletoe and eucalypt that was sampled and the geographic coordinates of each sample were recorded with a hand-held GPS (4–5 m accuracy).

In November 2005, we sampled arthropods from 4–10 mistletoe plants and 2–6 eucalypt trees per site, giving a total of 30 box mistletoe samples and 19 eucalypt samples (i.e. from 12 red box, 4 yellow box and 3 Blakely's red gum trees). We sometimes sampled two mistletoes in the same tree, and in some cases the eucalypt foliage of a given tree was too high above ground to sample. In cases where two mistletoes were sampled in the same tree, the one located closest to the eucalypt sample was used in the data analyses, resulting in 19 paired samples of mistletoes and eucalypts. In November 2006, the same branches of the mistletoe plants sampled in 2005 were re-sampled (except for four mistletoes that had died *in situ* or fallen from the tree). In addition, 35 new mistletoe plants were sampled at four new sites (i.e. sites 6–9, Fig. 1) and three of the original sites, to obtain reference samples with which to compare the re-sampled mistletoe plants and to increase the range of distances between sites. Of the new mistletoe samples, only in three instances were two mistletoe samples collected in the same tree.

Estimation of leaf mass and area

To determine the density of arthropods on the plant foliage, the dimensions of the sampled foliage were recorded (to estimate foliage volume); then the relationships between foliage volume, leaf mass and leaf area were determined from subsamples of foliage of box mistletoe and each eucalypt tree species ($n = 5–10$ per plant species, see Table 1). Foliage volume was estimated according to the method of March and Watson (2007), using the following equation (adapted from the equation for the volume of an ellipsoid):

$$\text{Foliage quantity index} = \frac{1}{6} \times \pi \times a \times b \times c \times \text{density} \quad (1)$$

Table 1 Regression equations for leaf dry mass (y) as a function of the foliage quantity index (x , see text, Eqn 1) and mean (1 SE) specific leaf area (SLA) determined from the subsample of leaves of box mistletoe and each eucalypt species

Plant species	n	Regression equation	R^2	SLA† (cm ² /g)
Box mistletoe	10	$y = 373x + 8.8$	0.87	29.7 (1.2)
Red box	8	$y = 214x + 8.1$	0.84	42.5 (3.1)
Yellow box	9	$y = 137x + 11.1$	0.93	50.1 (2.8)
Blakely's red gum	5	$y = 186x + 3.8$	0.90	37.5 (1.5)

†SLA: area of one side of leaves.

where a , b and c are width, breadth and vertical depth of the foliage sample, respectively. The density of the foliage was assigned a score from 1 to 5, where 1 = less than 10% of the maximum foliage density, 2 = 10–30%, 3 = 30–60%, 4 = 60–90% and 5 = greater than 90% of the maximum foliage density. The foliage quantity index does not have units. March and Watson (2007) found a strong positive relationship between the foliage quantity index and leaf dry mass of box mistletoes ($r^2 = 0.91$, d.f._{1,18} $P < 0.001$).

The foliage subsamples were collected in December 2006. The above-mentioned were measured to obtain the foliage quantity index. The samples were then cut, placed in a plastic bag and in insulated containers with ice for transport to the laboratory, where they were weighed to record fresh weight and calculate percentage moisture of the foliage. Part of each sample was freeze-dried (for chemical analyses) and the remainder was oven-dried at 70°C. All samples were dried to constant weight, which was between 48 and 66 h for the oven-dried samples and between 96 and 120 h for the freeze-dried samples. Before oven-drying, the area of 10–20 leaves in each sample was measured with a portable leaf area meter (accurate to 2 cm²) and leaf thickness with digital callipers (accurate to 0.01 mm). These leaves were weighed separately to the rest of the sample to determine specific leaf area (SLA) and specific leaf weight. The majority of each sample consisted of mature leaves, with a small portion of juvenile leaves.

The relationship between leaf dry mass and foliage quantity index was determined from the foliage subsamples for each plant species separately. The regression equations (Table 1) were used to estimate the leaf dry mass of all the samples from which arthropods were collected. To estimate the leaf area of all the samples, the estimated leaf dry mass was multiplied by the mean SLA for the particular species (Table 1) and the value was doubled because arthropods occur on both sides of leaves. Using these data it was possible to express arthropod abundance as density of individuals per leaf area. Similar methods have been used previously (e.g. Woinarski & Cullen 1984; Basset & Arthington 1992). The mean SLA of red box and yellow box in the current study (Table 1) are within 1.5 cm²/g of published SLA values for these species (Gras *et al.* 2005). We could find no published values for the SLA of Blakely's red gum or box mistletoe.

Foliage chemistry

The total nitrogen and carbon content of the subsamples of mistletoe and eucalypt leaves was determined by quantitative combustion in a Carlo Erba EA-1110 CHN-O Elemental Analyser. Prior to analysis the leaves were freeze-dried to constant weight (96–120 h) and ground to a fine powder with a Cyclotec 1093 Sample mill grinder.

Statistical analysis

We used ANOVA for most analyses of variation in arthropod density between the sampled plants, except when the sampling design was too unbalanced, in which case we used restricted

maximum likelihood (REML) variance components analysis (with GenStat 12th edition). Data were log-transformed where necessary to meet the assumptions of normality and homogeneity of variances. Data collected from the three *Eucalyptus* species were pooled so we could compare arthropod density and ordinal composition at the level of host plant genus. The differences in mean density of all arthropods and each arthropod order, between the mistletoe and eucalypt samples, were assessed with ANOVA (fixed factor: host genus; random factor: pair). Inter-annual variation in the density of all arthropods and each arthropod order on the same mistletoe plants in 2005 and 2006 was tested with ANOVA (fixed factor: year; random factor: site). To determine the effect of de-faunation on variation in total arthropod density on the mistletoes sampled in 2006, the analysis was first restricted to sites that had both types of samples (i.e. arthropods from re-sampled and new mistletoes), and since there was no difference between sample types holding site constant ($P_{1,18,1} = 0.413$), then all sites were included in the analysis (REML fixed factor: sample type; random factor: site). The analysis was repeated for each arthropod order.

The leaf traits (total C and N content, specific leaf weight, leaf thickness and moisture content) were analysed with the non-parametric Kruskal–Wallis chi-squared rank test. This conservative test compares the medians of multiple samples; it does not require the data to be normally distributed and is appropriate for small and uneven samples sizes. For the leaf traits, *post hoc* tests of differences between all pair-wise combinations of the sampled plant species were conducted, with $\alpha = 0.01$ because multiple comparisons were conducted.

RESULTS

Variation in arthropod assemblage structure between mistletoes and eucalypts

A total of 5731 adult and larval arthropod specimens, belonging to 10 orders, were collected from the mistletoe and eucalypt foliage in 2005 (Fig. 2). The same orders occurred in both the mistletoe and eucalypt samples. The mean density of all arthropods was statistically significantly greater on the eucalypt foliage than the mistletoe foliage (host genus: $P_{1,18} < 0.001$). The mean density of five arthropod orders (Hemiptera, Thysanoptera, Coleoptera, Araneae and Hymenoptera) was significantly greater on the eucalypt foliage than the mistletoe foliage, but Acarina was significantly more abundant on the mistletoes (Fig. 2). The distribution of individuals among the arthropod orders was more even in the mistletoe assemblages than the eucalypt assemblages, due to the dominance of Hemiptera in the eucalypt assemblages. Hemiptera was the most abundant and frequently occurring order, comprising 40% and 50% of individuals in the mistletoe and eucalypt samples, respectively. The superfamily Psylloidea (psyllids) comprised 75% and 80% of the hemipteran individuals in the eucalypt and mistletoe samples, respectively. Individuals of Coleoptera, Hymenoptera (mostly

Fig. 2. Mean density (± 1 SE) of arthropod orders collected from the eucalypt tree foliage (white bars, $n = 19$) and box mistletoe plants (grey bars, $n = 19$). Statistical significance of the difference between the means: *** $P < 0.001$, ** $P < 0.01$.

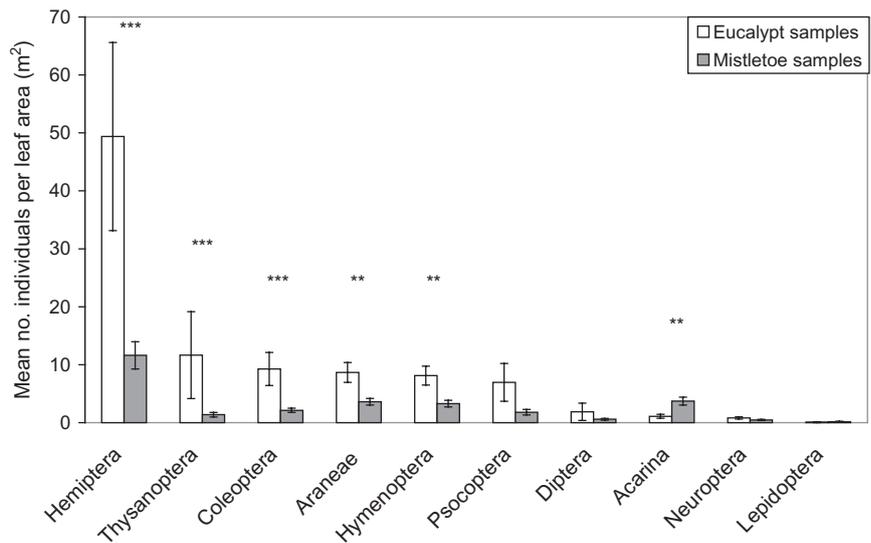
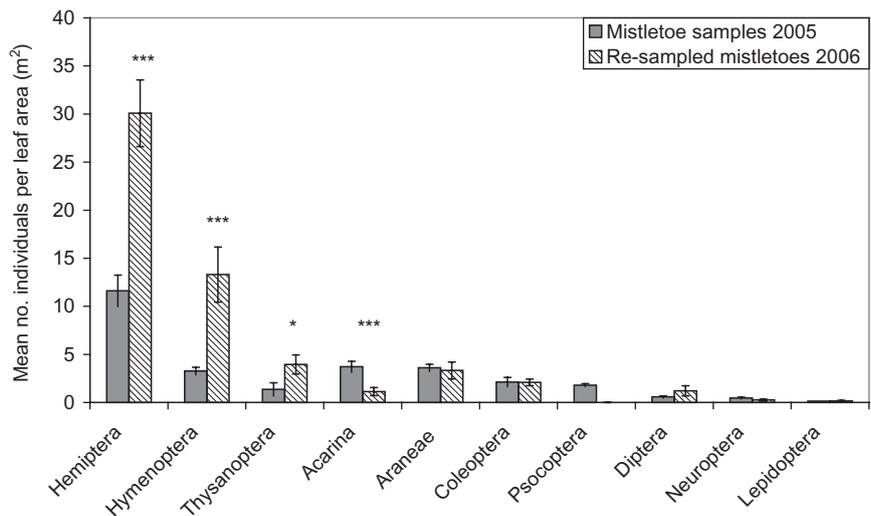


Fig. 3. Mean density (± 1 SE) of arthropod orders collected from the mistletoe plants in November 2005 (grey bars, $n = 30$) and re-sampled from the same mistletoes in November 2006 (hashed bars, $n = 26$). Significant differences between means: * $P < 0.05$, *** $P < 0.001$.



small wasps, <5 mm in length), Araneae, Acarina and Psocoptera also occurred frequently in the mistletoe and eucalypt samples. Thysanoptera were abundant and common in the eucalypt samples and approximately 90% of the thrips in the eucalypt and mistletoe samples were plague thrips, *Thrips imaginis* (L. Mound pers. comm. 2008). Lepidoptera was the least abundant order in both the mistletoe and eucalypt samples, with only two larvae in the eucalypt samples and two adults and 18 larvae in the mistletoe samples.

Temporal differences in arthropod assemblage structure on mistletoes

All arthropod orders except Psocoptera re-colonised the mistletoe branches that were sampled in 2005 (Fig. 3). The total density of arthropods was significantly greater on mistletoe plants in 2006 compared with the same plants in 2005 ($P_{1,50} < 0.001$, Fig. 4). There was a significantly greater density of Hemiptera, Hymenoptera and Thysanoptera, and a signifi-

cantly lower density of Acarina, on the re-sampled mistletoe branches in 2006 than in 2005 ($P_{1,54} < 0.05$, Fig. 3). Hemiptera was the most abundant order in both years.

A total of 4277 adult and larval arthropod specimens were sampled from the mistletoe plants in 2006. The same arthropod orders occurred on the new mistletoe plants as the re-sampled mistletoes and, in addition, one individual belonging to each of two orders, Pseudoscorpionida and Orthoptera, were collected on new mistletoe plants (not shown in Fig. 5). The mean density of all arthropods did not differ significantly between the mistletoe branches sampled for the first time in 2006 (new) and those re-sampled in 2006 ($P_{1,59.0} = 0.450$, Fig. 4). The mean densities of each arthropod order on the re-sampled and new mistletoe branches were also very similar (Fig. 5). Coleoptera was the only order for which there was a statistically significant difference in mean density between the new and re-sampled mistletoe branches, being greater on the new mistletoes (4.0 ± 0.6 and 2.1 ± 0.3 , respectively, $P_{1,59} < 0.05$, Fig. 5). These results confirm that the difference in

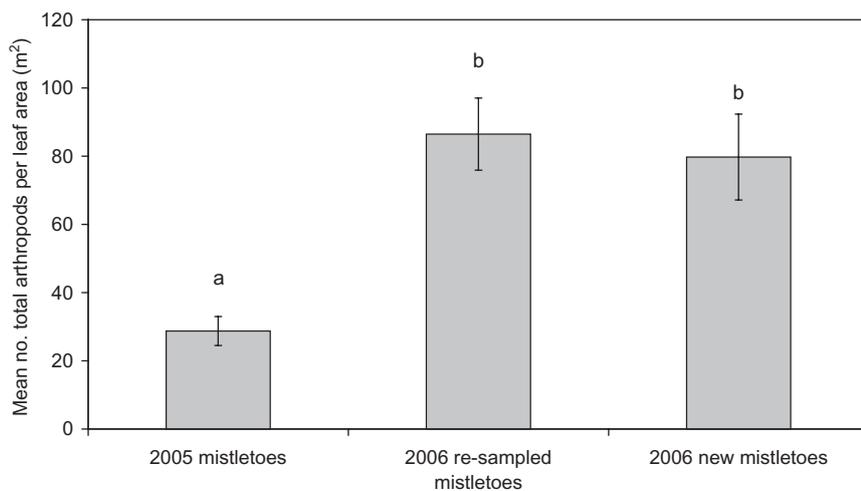


Fig. 4. Mean density (± 1 SE) of all arthropods on mistletoe plants sampled in 2005 ($n = 30$), on the same mistletoe branches re-sampled in 2006 ($n = 26$) and on new mistletoes sampled for the first time in 2006 ($n = 35$). Bars with different letters are significantly different ($P < 0.001$).

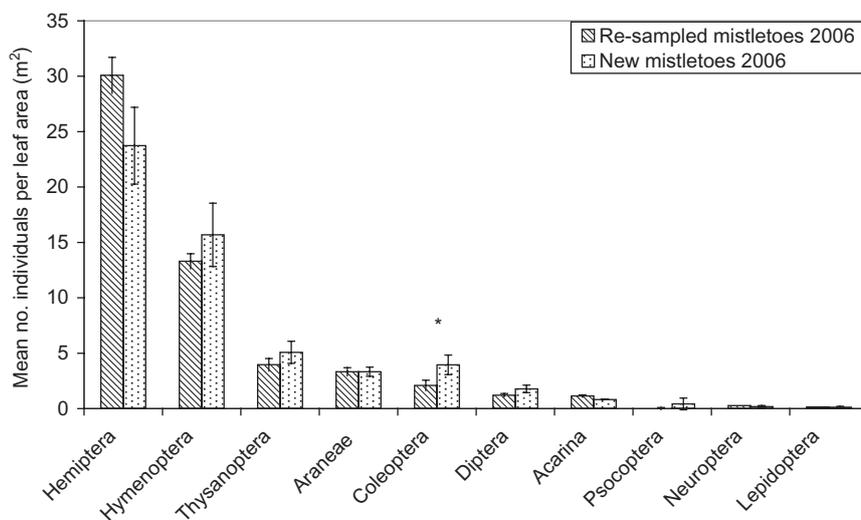


Fig. 5. Mean density (± 1 SE) of arthropod orders collected from the mistletoe plants in November 2006: 'Re-sampled' mistletoes (hatched bars, $n = 26$, i.e. originally sampled in 2005); and 'New' mistletoe plants (stippled bars, $n = 35$). Significant differences between means: * $P < 0.05$.

arthropod density on the same mistletoe branches between years was a year effect, not a de-faunation effect.

Foliage traits

The nitrogen content of the eucalypt leaves was significantly greater than that of the mistletoe leaves, for all eucalypt species combined and separately (comparing medians, $P < 0.01$, Table 2). Carbon content of the foliage was not significantly different between box mistletoe and the eucalypts (comparing medians, $P = 0.11$, Table 2). The SLA of the mistletoe leaves was significantly less than the eucalypt leaves, and the leaf thickness of the mistletoe leaves was significantly greater than the eucalypt leaves (comparing medians, $P < 0.01$, Table 2). Leaf thickness did not differ significantly between the eucalypt species but the SLA of the yellow box leaves was significantly greater than that of the red box and Blakely's red gum leaves (Table 2). The moisture content of the leaves was significantly greater comparing box mistletoe with all the eucalypts combined, and it differed between some but not all species pairs (Table 2).

Table 2 Leaf traits of box mistletoe and eucalypt trees in the study area

Plant species	N %	C %	SLA (cm ² /g)	Thickness (mm)	Moisture %
Box mistletoe	0.73a	51.4a	30.6a	0.478a	51.7a
All eucalypts	1.20b	51.2a	41.7b	0.284b	48.3b
Red box	1.27b	50.7a	37.7b	0.314b	49.6ab
Yellow box	1.15b	51.2a	52.2c	0.284b	49.6bc
Blakely's red gum	1.39b	51.7a	38.2b	0.264b	45.2c

Values are medians and those with different letters are significantly different ($P < 0.01$) according to a Kruskal–Wallis chi-squared rank sum test with *post hoc* comparisons between each plant species (box mistletoe: $n = 10$, each eucalypt species: $n = 5$). SLA, specific leaf area.

DISCUSSION

Comparison of arthropod assemblages inhabiting mistletoes and their host trees

The ordinal composition of the arthropods on box mistletoe and the host *Eucalyptus* trees was very similar, but the total

density of arthropods (per unit of leaf area) was greater on the eucalypts than the mistletoes. Four of the most abundant orders sampled, Hemiptera, Araneae, Hymenoptera and Coleoptera, were also the most abundant orders found in canopies of other temperate trees and mistletoe plants, using similar collection methods as our study (i.e. restricted canopy fogging, branch clipping or beating: Room 1972a; Whittaker 1982; Woinarski & Cullen 1984; Basset & Arthington 1992; Floren & Linsenmair 1997; Meades *et al.* 2002; Major *et al.* 2003). Similar to our results, psyllids have been the most abundant component of Hemiptera (80% or more of individuals) sampled from other *Eucalyptus* species (Woinarski & Cullen 1984; Majer & Recher 1988). There are few comparable studies of the density of arthropods on *Eucalyptus* and non-*Eucalyptus* plant species in Australia. Woinarski and Cullen (1984) found a greater total abundance of arthropods on non-*Eucalyptus* than *Eucalyptus* species (mainly contributed by Arachnida and Coleoptera); however, they excluded individuals <3 mm in size, which is a size class that formed a large component of the present study.

Other direct comparisons of arthropod assemblages between mistletoe species and their host plants are not available. However, similar arthropod orders to our study have been found in previous studies of arthropod assemblages on mistletoe plants (Room 1972a; Whittaker 1982; Tassone & Majer 1997; Anderson & Braby 2009). Eighteen arthropod orders were collected from *Nuytsia floribunda* (Loranthaceae; endemic to south-west Western Australia and the largest mistletoe species in the world), of which Psocoptera, Coleoptera, Hymenoptera, Acarina and Araneae were the most abundant (Tassone & Majer 1997). The most frequently occurring and species-rich orders inhabiting a tropical mistletoe species (*Decasynina signata*, Loranthaceae) in northern Australia were Hymenoptera, Hemiptera, Araneae and Lepidoptera (Anderson & Braby 2009). Their study found that the composition and taxonomic richness of arthropods did not differ significantly between individual mistletoes parasitising different host genera and species. Similarly, Araneae, Lepidoptera, Hymenoptera, Hemiptera and Coleoptera were the most species-rich orders collected from the foliage of a mistletoe species (*Tapinanthus bangwensis*, Loranthaceae) that parasitises cocoa (*Theobroma cacao*) in Ghana (Room 1972a). The abundance of each order was not reported in that study but the 26 most abundant insect species were ants and their associated Homopteran species (Room 1972a). Very few ants were sampled from box mistletoe in our study. Honeydew produced by psyllid larvae on mistletoes would be a potential food source for ants (Whittaker 1982; Paulson & Akre 1991; Novak 1994), but this type of feeding association was not evident in the present study. The only other published assemblage-level study of insects associated with a mistletoe species (*Phoradendron tomentosum*, Viscaceae, in south-western USA) found 40 species of herbivores, predators, parasitoids, and Homopteran-attendant ants in the orders Lepidoptera, Coleoptera, Hemiptera, Hymenoptera, Orthoptera and Neuroptera (Whittaker 1982).

Furthermore, several species of butterflies in the genera *Delias* and *Mylothris* (Pieridae), and *Ogyris* (Lycaenidae) spe-

cialise on Australian and African mistletoes as a larval food plant (Braby 2000, 2005, 2006). The caterpillars of several of these species of butterflies are attended by ants, which feed on exudates from the caterpillars (Eastwood & Fraser 1999; Braby 2000). Our study area is part of the distributional range of four butterfly species known to feed on box mistletoe, including one species which is attended by ants (Braby 2000), but few Lepidopteran caterpillars were collected from the box mistletoe plants in our study. This may be partly due to daytime collection and the sampling method, which was not conducive to collection of large flying insects. However, the lack of Lepidopteran caterpillars on the mistletoes and eucalypts may be related to the lack of food plants for adult Lepidoptera in the degraded remnant woodlands of this study.

Factors affecting arthropod densities

The greater density of arthropods, particularly the herbivorous Hemipteran insects, on the eucalypt foliage compared with the mistletoe foliage could be due to the greater total nitrogen concentrations of the eucalypt foliage. Our observations are in agreement with other studies, which found that arthropod abundance is positively correlated with foliar nutrient concentrations (Basset 1991; Recher *et al.* 1996a; Tassone & Majer 1997). Furthermore, differential levels of growth, reproduction and diversity of insects have been observed on plants with differing nutrient concentrations, particularly nitrogen (Ohmart 1991; Marvier 1996; Recher *et al.* 1996a; Lawler *et al.* 1997; Peeters 2002a). For example, the densities of sap-sucking insects, including psyllids, have been significantly positively correlated with leaf nitrogen levels of several plant species in an Australian forest (Peeters 2002a). Studies of two chrysomelid beetle species feeding on *Eucalyptus* established that 1% (Lawler *et al.* 1997) and 1.7% (Ohmart 1991) of foliar nitrogen (dry mass) was the critical threshold for larval growth and development, whereas nitrogen concentration in box mistletoe foliage sampled in this study (0.7%) falls below these critical thresholds. The average concentration of N in the box mistletoe foliage in this study was within 0.3% of the N content of foliage of the same species, reported by Ehleringer *et al.* (1986) and March (2007), and within 3% of the N content of foliage of congeneric species (Ehleringer *et al.* 1986). The proportion of nitrogen in the eucalypt foliage (1.2%) could also be marginal for herbivorous insects but it would still be advantageous for generalist herbivores to feed on the foliage of these eucalypt species rather than box mistletoe.

Leaf structural traits also impose limitations to feeding and can be more important determinants of insect densities than nutritional constituents of leaves (Peeters 2002b). The greater leaf thickness and lower SLA of the mistletoe leaves compared with the eucalypt leaves in the present study could limit insect herbivory and hence insect densities on the mistletoe foliage. However, the slightly greater moisture content of the box mistletoe foliage than the eucalypt foliage would be advantageous to insect herbivores. The only published study of the palatability of Australian mistletoes compared with their host

plants found that mistletoe foliage had significantly greater moisture content and toughness than the host foliage (Canyon & Hill 1997). In their study, leaf loss due to herbivory was significantly greater for one mistletoe species but not the other, compared with host foliage. The foliage of several mistletoe species (*Phoradendron* sp. and *Arceuthobium* sp.) in North America is considered highly digestible (especially to deer), with high carbohydrate content but low protein and mineral content (Urness 1969; Mathiasen 1996). However, direct correlations between foliage palatability and insect herbivory of these and other mistletoe species are not known.

The greater density of spiders on the eucalypt foliage than the box mistletoe foliage is likely to be due to the greater density of insect prey on the eucalypts than the mistletoes, since other studies of spider assemblages in forest canopies have found that the abundance and species richness of spiders is significantly correlated with prey abundance (Halaj *et al.* 1998; Horvath *et al.* 2005). The greater density of mites found in the mistletoe samples compared with the eucalypt samples could be due to the high incidence of predatory mites on one of the psyllid species (*Acizzia loranthaceae*), which is host-specific to *Amyema* mistletoes (Taylor 1999).

Re-colonisation patterns of arthropod assemblages

One year after the first sampling event, all the orders of arthropods, except Psocoptera, had successfully re-colonised the mistletoe branches that were de-faunated. The similar densities of the arthropod orders inhabiting the re-colonised mistletoes and the newly sampled mistletoes in the second year demonstrate that the arthropod densities on the re-colonised plants reflected the general densities of arthropods in that year. Moreover, overall abundances of arthropods were greater in the second year of sampling (2006) than the first (2005), particularly due to an increase in the density of hymenopteran and hemipteran insects. This result is intriguing, since the second year of sampling was hotter and drier than the first, and the average annual rainfall (270 mm) in 2006 was well below the long-term average (695 mm, BOM 2007). Drought causes physiological changes in plants that can be advantageous for insect herbivores, such as increased concentrations of essential nutrients (reviewed by Mattson & Haack 1987). These factors and associated changes in the thermal environment of drought-stressed plants (i.e. higher temperatures of the host plant and surrounding air) can cause increased growth rates and fecundity of phytophagous insects. Therefore, the climatic conditions in 2006 appear to have been favourable for the hemipteran insects inhabiting box mistletoe (i.e. mostly psyllids), and the abundance of these insects could have been favourable for predatory and parasitic arthropods, including parasitic wasps (Hymenoptera).

Similarly, Floren and Linsenmair (1997) found that the ordinal composition of arthropod communities in rainforest tree canopies recovered after 7 months since insecticide fogging; but the relative abundance of orders and the community structure at the species level changed during that period.

They regarded the environmental conditions immediately following de-faunation to be the most important drivers of the re-assembled community structure (Floren & Linsenmair 1997). In another re-colonisation study of the arthropods inhabiting a temperate tree species, the high dissimilarity in species composition of the arthropod assemblages during the collection period, up to 1 year since de-faunation, also suggested that stochastic processes were affecting the structure of the arthropod assemblages (Azarbayjani *et al.* 1999).

In conclusion, the arthropod assemblages inhabiting box mistletoes and their host eucalypt trees are similar in composition at the order level but differ in abundance. Further investigation of this dataset at the species level revealed information about patterns of host specificity and diversity of these arthropod assemblages (Burns 2009), which will be published in subsequent papers. We predict that herbivorous insects will be more host plant-specific than predatory arthropods due to the direct reliance of herbivores on plants. Comprehensive investigation of the nutritional and structural properties of mistletoe foliage (especially in the Loranthaceae family) is required, particularly in regards to the palatability of mistletoe foliage to insect herbivores in comparison with host plant foliage. This could be done by destructively harvesting mistletoe and host plant foliage from which insects are also sampled. A better understanding of these factors would help elucidate the key factors influencing the composition of arthropod assemblages on mistletoes compared with their host plants, and their contribution to whole canopy diversity.

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