Diversity and dynamics of the arthropod assemblages
inhabiting mistletoe in eucalypt woodlands

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A thesis submitted in fulfilment of the requirements
for the degree of Doctor of Philosophy
Charles Sturt University
Australia
March 2009

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Dedicated to all the creatures that depend on mistletoe plants as a primary food source or habitat
(including Australian Jezebel butterflies which inspired me to do this PhD research)

Cover photo (© Anna Burns): Acizzia amyemae (G.S. Taylor; Hemiptera: Psyllidae)
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I, ____________________________________________,

Hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person nor material which to a substantial extent has been accepted for the award of any other degree or diploma at Charles Sturt University or any other educational institution, except where due acknowledgment is made in the thesis. Any contribution made to the research by colleagues with whom I have worked at Charles Sturt University or elsewhere during my candidature is fully acknowledged.

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Acknowledgements

I would like to sincerely thank and acknowledge my supervisors for their advice and guidance during my doctoral candidature. Firstly, my principal supervisor, Associate Professor David M. Watson (Charles Sturt University) particularly for detailed and critical editorial advice about this thesis, and assistance with grant applications and conference presentations. I also thank my co-supervisor, Dr Saul A. Cunningham (CSIRO Division of Entomology), for very helpful advice about sampling methods, data analyses and the key results, plus editorial advice about my thesis and conference presentations. I also appreciated the back-up supervisory assistance and encouragement of Dr Paul Humphries (Charles Sturt University).

I acknowledge the very helpful assistance of the following people with various components of the research:

- Landholders of the Holbrook district for permission to work on their properties.
- Field site selection and training in use of mechanical equipment: Matt Herring.
- Field work: Craig Reid, Peter Bowdren, Kerry Whitworth, Colin Payne, Kelly Dunn, Rebecca Durant, Alison Skinner, Sue Burns and Saul Cunningham.
- Sorting of arthropod samples collected in 2006 to order-level: Brendan Kelly, Hugh McGregor, Terry Korodaj.
- Arthropod identifications (family to species levels): Kimberi Pullen, Dr Gary Taylor, Cathy Car, Graham Milledge, Dr Barry Richardson, Piotr Trebicki.
- Statistical analyses: Simon McDonald, Dr Simon Ferrier and Glenn Manion.
- Acquisition of spatial–environmental data and construction of maps: Deanna Duffy and Simon McDonald in the Spatial Analysis Unit at Charles Sturt University.
- Photo editing: Toby Grant. All images in the thesis were taken by the author except the image in Figure 2.5c, which was sourced from David M. Watson.
- Carbon & nitrogen analyses: analytical laboratory at the Australian National University (Research School of Biological Sciences).

I also appreciated the friendship of the other post-graduate students at CSU and the interest and encouragement of other friends and my family during this PhD journey.
Abstract

Patterns of biological diversity, including gradients of species richness and changes in community composition over different spatial and temporal scales (i.e. beta-diversity), have been elucidated for a variety of organisms. However, patterns and determinants of the beta-diversity of arthropods, i.e. insects, arachnids and other related animals (the most diverse organisms on Earth), have only recently been examined. The arthropod fauna inhabiting mistletoe plants and their host trees are a useful association with which to investigate patterns and determinants of beta-diversity. The hemi-parasitic box mistletoe, *Amyema miquelii*, infects several *Eucalyptus* species and is widespread in south-eastern Australia. The association between these plants and arthropods provides an ideal opportunity to investigate the diversity, host-specificity and spatial and temporal turnover of arthropod assemblages. This is the first community-level, systematic study investigating the diversity and host-specificity of insects and spiders inhabiting a mistletoe species in comparison to its host-plants. Previous investigations of the interactions between mistletoes and vertebrates led to the proposal that mistletoes are keystone resources; however, the importance of the interactions between mistletoes and invertebrates is not well known.

Arthropods were sampled from box mistletoe and three of its host-tree species, in remnant woodlands in a temperate region of south-eastern Australia. The nine sites that were sampled over two years were separated by up to 40 km. The composition and density of arthropod orders were determined, along with the family and feeding guild composition of beetles (Coleoptera), and the species richness and composition of herbivorous insects (psyllids: Hemiptera) and spiders (Araneae). Analyses included the relative influence of host-plant traits, habitat variables and distance between samples on the rate of change in community composition among the psyllid and spider assemblages.

The composition of arthropod orders was very similar between the assemblages inhabiting the box mistletoe and eucalypt trees, but densities of arthropods were greater on the eucalypt hosts. These differences in density corresponded with a significantly greater concentration of nitrogen in the eucalypt foliage compared to the mistletoe foliage. Small differences in beetle family composition and feeding guilds were found between the mistletoes and eucalypts.
ABSTRACT

Species-level identifications of the most abundant arthropod taxa in different trophic levels: herbivorous psyllid insects and predacious spiders, led to detection of finer-scale differences in community composition between the host-plants.

The species composition of psyllids differed greatly between the host-plant taxa and this was apparent after determination of ‘tourist’ vs. ‘resident’ psyllid species. Two psyllid species inhabiting the mistletoes (*Acizzia loranthacae* and *A. amyemae*) were confirmed as ‘residents’ and specialists on box mistletoe (those which complete their whole life-cycle on that host-plant). Ten of the 17 psyllid species collected from box mistletoe were deemed as tourist species (those which cannot complete their life-cycle on that host-plant). In contrast, only 2 of the 20 psyllid species inhabiting the eucalypt canopies were determined as tourist species. None of the 42 species of spiders could be differentiated as host-specific to box mistletoe or the eucalypt tree species. Thus, the average similarity in community composition among the resident psyllid assemblages inhabiting the mistletoes and eucalypt hosts was less than one percent. In contrast, the average similarity of the spider assemblages between the mistletoes and eucalypts was forty percent.

Niche and patch-scale properties such as host-plant taxon, proximity of neighbouring trees and mistletoe age had the strongest influence on the assemblages and patterns of re-colonisation and beta-diversity of the herbivorous insects. Of the measured habitat variables, potential prey abundance had the strongest influence on the variation in community composition of the spider assemblages. The null model of increasing community dissimilarity with increasing geographic distance among assemblages was not supported for the herbivorous insects studied, confirming previous findings of low beta-diversity of herbivorous insects among congeneric host-plants. However, the spatial separation of assemblages did have a small influence on the beta-diversity among the spider assemblages.

This research has confirmed that the arthropod fauna inhabiting mistletoe plants contributes a small but significant amount to canopy arthropod diversity, particularly due to the presence of host-specific herbivorous insects. Thus, protection of the taxonomic and structural diversity of vegetation, such as mistletoes and other epiphytic plants in tree canopies, is important to ensure the conservation of animals that are dependent on different plant forms and species, and thus biodiversity as a whole. Emerging research is revealing that the occurrence patterns of host-specific
arthropods are primarily determined by the taxonomic affinities and distribution of their hosts. In contrast, occurrence patterns of generalist arthropods are more affected by niche properties and local environmental conditions. Areas of research that require further investigation include the interaction between the spatial distribution of habitat and dispersal scales of arthropod taxa; the influence of plant chemistry on community composition of herbivorous insects associated with mistletoes and their host-plants; and lastly, the evolutionary history of mistletoe-specific arthropod species.
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Chapter 1

Introduction

1.1 Patterns of biological diversity

For generations, scientists and natural historians have pondered questions about the patterns of biological diversity, such as: What is the distribution and abundance of different organisms? Are there more species in the tropics than temperate zones? What are the patterns of spatial and temporal species turnover? Are there different patterns of species turnover in different habitats, ecosystems and parts of the world? How does habitat or host-plant specificity influence patterns of species turnover?

General patterns of biological diversity have been elucidated for a variety of taxa, over different scales of space and time, particularly relating to variations in numbers of species. For instance, species richness declines from the equator to higher latitudes, either north or south; and species diversity increases with habitat diversity and is greatest at intermediate levels of disturbance (Rosenzweig 1995 and references therein). While patterns of variation in species richness or within-habitat richness (i.e. alpha-diversity) are valuable for our understanding of biological diversity; it is even more informative to determine patterns of variation in species composition and abundances of organisms among different locations, i.e. patterns of beta-diversity. These two components, alpha- and beta-diversity, combine to provide a fuller picture of patterns of diversity from local to global scales.

General patterns of beta-diversity have emerged from recent research involving a range of taxa belonging to different kingdoms, inhabiting different realms (i.e. terrestrial, marine, freshwater) and regions of the world; with different biological characteristics (e.g. dispersal ability, trophic position, body size and thermal regulation); and over varying scales of study extent (Nekola and White 1999, Soininen et al. 2007a, Soininen et al. 2007b and references therein). Established null
models of beta-diversity patterns relating to characteristics of the environment and spatial factors include: beta-diversity increases with increasing rate of environmental change and increasing geographic distances between habitat units of the organisms. Null models of beta-diversity patterns relating to biological characteristics of organisms include: the greater the dispersal ability of organisms the lower the beta-diversity among assemblages; and the wider the niche breadth and thus overlap of taxa, the lower the beta-diversity among assemblages (Nekola and White 1999). Emerging research is identifying rates of change of beta-diversity as a function of these variables (Ferrier and Guisan 2006, Jones et al. 2006, Ferrier et al. 2007, Bohlman et al. 2008, Laliberte et al. 2009).

Furthermore, different patterns of beta-diversity have been found at different spatial scales. In a meta-analysis comparing the decay in similarity of assemblages located less than 1 km apart (small scale) and greater than 1 km apart (large scale), Soininen et al. (2007) found that beta-diversity was higher in the tropics than temperate areas at small scales, but lower in the tropics over larger scales. Other patterns they found include that beta-diversity was highest among assemblages of small organisms and poor dispersers at small scales, but at larger scales there was no significant effect of body size or dispersal ability on beta-diversity. Therefore, further research is required to determine the interactions and relative influences of environmental and spatial variables and organism characteristics on patterns of beta-diversity.

1.1.1 Beta-diversity patterns of arthropod assemblages

Invertebrate animals constitute more than three-quarters of the diversity of life on Earth. Insects, spiders and related invertebrate animals (i.e. arthropods) account for approximately 1.4 million of the 1.8 million named species of living organisms (Stork 1993, 1997); however, the true number of arthropods is estimated to be up to 10 million species, as numerous species await discovery, identification and description (Ødegaard 2000a, Novotny et al. 2002a). Considering that arthropods constitute the bulk of biodiversity, studying beta-diversity patterns of these organisms is important for our understanding of global biodiversity. Beta-diversity patterns of arthropod assemblages can be determined for a range of trophic levels, a wide variety of habitats and over varying spatial and temporal scales (Novotny et al. 2002b, Summerville and Crist 2003, Novotny and Weiblen 2005, Beck and Khen 2007, Lindo and N.
Winchester 2008). However, the majority of beta-diversity research published in the last twenty years has focused on plant communities; equating to five times more studies than those involving insects (ISI Web of Science search: ‘beta-diversity and insects’: 71; ‘beta-diversity and plants’: 321). Due to the fundamental differences between arthropods and plants, beta-diversity patterns of plant assemblages (or vertebrate assemblages) cannot be directly extrapolated to arthropod communities. However, interactions between arthropods (particularly insects and arachnids) and plants are a useful system in which to investigate patterns of beta-diversity, due to their close associations. Arthropods and plants have various mutualistic and antagonistic relationships, e.g. relating to herbivory, insectivory (i.e. fly-traps), reproduction, shelter, and nutrient cycling; and varying degrees of specificity. However, the cryptic nature and overwhelming richness of arthropods makes empirical research all the more challenging.

Most studies documenting patterns of beta-diversity of arboreal arthropods have been restricted to Lepidoptera and Coleoptera, and have occurred in both tropical regions (e.g. Devries et al. 1999, Wagner 2000, Novotny et al. 2002b, Brehm et al. 2003, Ødegaard 2006, Beck and Khen 2007, Novotny et al. 2007, Hulcr et al. 2008) and temperate regions (e.g. Gering et al. 2003, Summerville et al. 2003, Barness et al. 2006, Baselga and Jimenez-Valverde 2007, Hirao et al. 2007, Baselga 2008, Summerville et al. 2008). Although comparison of these studies is challenging due to the variety of different beta-diversity indices and analytical techniques, some common and significant determinants of beta-diversity can be elucidated. These factors include vegetation composition and structure, the history of disturbance, variation in precipitation and ambient temperature (which are often correlated with elevational gradients), and geographic distance between sites (Wagner 2000, Brehm et al. 2003, Gering et al. 2003, Ødegaard 2006, Baselga and Jimenez-Valverde 2007, Beck and Khen 2007). When controlling for variations in elevation, climate, soil and vegetation composition; levels of host-specificity and host-plant taxonomic relationships have been the most important factors influencing beta-diversity among insect assemblages (i.e. increasing beta-diversity among assemblages sampled from plants of increasing taxonomic distance) (Novotny et al. 2002b, Novotny et al. 2007). Furthermore, the dispersal ability of insect taxa has been used to explain patterns of spatial turnover among insect assemblages; either high dispersal ability contributing
to low beta-diversity or species turnover, and low dispersal ability leading to higher beta-diversity (Novotny et al. 2007, Baselga 2008).

Comprehensive research by Novotny and co-workers (2007) over large extents of continuous lowland rainforest led to the discovery of low average beta-diversity among assemblages of arboreal herbivorous insects. These assemblages included Lepidopteran caterpillars inhabiting widespread congeneric host-plants; ambrosia beetles feeding on fungi on decaying wood; and fruitflies. The patterns of low beta-diversity among assemblages were thought to be underpinned by the relatively low host-specificity of the insect taxa (i.e. genus- and family-specialists), widespread occurrence of their host-plants or habitats, and non-limiting dispersal of the insect taxa. Over smaller spatial scales of less than 20 km, low beta-diversity of herbivorous insects was also documented among Lepidopteran assemblages on congeneric host-plants, and was attributed to dominance of a few widespread species (Novotny et al. 2002b). However, in the same study, high beta-diversity was documented among assemblages of caterpillars from host-plants in different genera and families. Similarly, low beta-diversity was found among assemblages of arboreal Lepidoptera in oak-hickory forests separated by approximately 10 km (but sampled by indiscriminate light trapping), with low beta-diversity attributed to dominance of a small proportion of moth species (Summerville et al. 2008).

Further research is required to determine patterns of beta-diversity of a wider variety of arthropod taxa, in different habitats or ecosystems, at different geographical scales and among host-plant taxa with differing levels of diversity and distributional ranges (Novotny and Weiblen 2005).

1.2 Arthropod diversity among components of tree canopies

After the advent of methodologies for forest canopy research in the 1970s, and subsequent improvements, the huge diversity of arthropods (and other organisms) inhabiting tree canopies began to be discovered (Erwin and Scott 1980, Moran and Southwood 1982, Stork 1987, Basset and Arthington 1992, Moffett and Lowman 1995, Stork et al. 1997, Ødegaard 2004). Canopy arthropod studies have investigated a wide variety of aspects of the association between arthropods and plants, including host- and habitat-specificity, resource use, vertical stratification of assemblages, spatial and temporal variation in community composition, effects of human-mediated
disturbance on arthropod diversity and recovery of assemblages after disturbance (e.g. described in Stork et al. 1997, and Basset et al. 2003). The invertebrate communities inhabiting components of tree canopies such as epiphytic plants have also been investigated. This research has revealed that epiphytic plants support a wide variety of invertebrate orders, including some that do not otherwise occur in tree canopies, such as aquatic invertebrates and terrestrial detritivores (Cotgreave et al. 1993, Dejean et al. 1995, Richardson 1999, Kitching 2000, Ellwood et al. 2002, Yanoviak et al. 2003). The diversity of invertebrates inhabiting epiphytes results from the variety of structural forms of epiphytes (e.g. baskets, rosettes, tanks and mats), which provide shelter, nutrients and water to a diversity of organisms (Benzing 1990, Nadkarni 1994).

In this thesis, the diversity of arthropod fauna inhabiting mistletoe plants in the canopy of eucalypt woodlands will be examined. Mistletoe plants and their host-trees provide an opportune system in which to investigate patterns of change in species richness, composition and abundance among arboreal arthropod assemblages. Mistletoes, which are obligate parasitic plants, are an ideal and intriguing substrate with which to investigate arthropod diversity in temperate woodlands because they are relatively small, discrete patches of foliage located within an otherwise homogeneous canopy. There have been relatively few studies examining the interactions between mistletoes and arthropod fauna, despite the existence of approximately 1400 species of mistletoes worldwide (Nickrent 2001). There are particularly few studies comparing the diversity and host-specificity of arthropods on mistletoes versus the mistletoes’ host-plants, or on any epiphytic plant compared to its host-plant. Therefore, intriguing questions include: How do the assemblages of arthropods on mistletoe plants come about? Are there species that are host-specific to mistletoes and, if so, are they dispersal limited? Or are the assemblages on mistletoes simply a subset of the assemblage of arthropods already inhabiting the host-plant?

Mistletoes 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; however the influence of mistletoes on the ecology and diversity of invertebrates is not fully
known (Mathiasen 1996, Watson 2001, Cooney and Watson 2005). There have only been three other systematic, community level studies of the diversity of arthropods associated with mistletoe species: one involving a mistletoe that parasitises cocoa plants in Ghana (Room 1972a, b); another of a mistletoe that parasitises mesquite trees in south-western USA (Whittaker 1982); and a study of arthropods inhabiting a tropical species of mistletoe in northern Australia (Anderson and Braby 2009). These studies did not also sample the arthropods inhabiting the host-plants of the mistletoes; but host-specific insects were identified in one of the studies based on published literature and expert knowledge (Whittaker 1982). Therefore, this doctoral research is the first direct, comparative community-level study of the diversity of arthropods inhabiting a mistletoe species and the canopy of its host-plants. Also there have only been two other studies comparing the community composition of arthropods between epiphytic plants and their host trees (Ødegaard 2000b, Ellwood et al. 2002).

1.2.1 Mistletoes

Mistletoe plants are aerial, stem-parasites that belong to the order Santalales and families Loranthaceae, Viscaceae, Misodendraceae and Santalaceae, with most species belonging to the first two families (Nickrent 2001). In Australia, there are 92 species of mistletoes, 71 of which are endemic, belonging to two families (Loranthaceae, Viscaceae and Santalaceae) and 15 genera (Barlow 1984a, b, Downey 1998, Downey and Wilson 2004). *Amyema* (Loranthaceae) is the most diverse genus, with 36 species occurring throughout mainland Australia (Barlow 1984a, Shaw et al. 2004). Most Loranthaceous mistletoes are pollinated by birds, which are attracted to their showy colourful flowers (Mathiasen et al. 2008 and references therein); however insects are pollinators of some mistletoe species, particularly Viscaceous mistletoes, which have less conspicuous flowers. Insect pollinators include flies, thrips, ants, wasps and bees (Gregor et al. 1974, Penfield et al. 1976, Aparicio et al. 1995, French 2004, Robertson et al. 2005). Furthermore, birds are the major dispersal agents of mistletoe seeds, which are enclosed in fleshy nutritious fruits, and in many parts of the world co-evolutionary relationships have developed between mistletoes and frugivorous birds (Calder 1983, Mathiasen et al. 2008). After the sticky seed is deposited on a host-branch, germination commences under the right conditions and mechanical penetration of host tissue follows if the seed has been deposited on a suitable host (most likely determined by bark properties and cell to cell connections,
Calder 1983). Cellular connections between the mistletoe and host-plant results in the formation of a haustorium (or holdfast) and transfer of water, minerals and sometimes carbohydrates from host to parasite (Calder and Bernhardt 1983). Haustoria develop into a range of forms and in some host-mistletoe associations, such as *Eucalyptus* and *Amyema* species, the host-branch distal to the haustorium dies as a result of diversion of vascular flow to the mistletoe (Shaw et al. 2004, Mathiasen et al. 2008).

Mistletoes are often morphologically similar but physiologically different to their host-plants. Mistletoes often resemble their host-plants to such a degree that they are said to mimic their hosts’ foliage and branching structure (Atsatt 1983, Canyon and Hill 1997). Leaf shape of mistletoes can be indistinguishable from that of their hosts, particularly for species of *Amyema* (illustrated in Shaw et al. 2004, Watson 2004, and references therein). However, the foliage of mistletoes and their hosts often differs in concentrations of nutrients, water and defensive chemicals. The foliage of many mistletoe species contains a higher concentration of nutrients than that of their host-plants, including nine of fourteen measured elements, excepting nitrogen (Lamont and Bernhardt 1983, Ehleringer et al. 1986, Kuppers 1992, March 2007). Mistletoes are thought to have few structural defenses and the secondary chemistry of mistletoes is mostly known from studies of the immunological properties of Viscaceous mistletoes (Watson 2001, Mathiasen et al. 2008, and references therein). Some mistletoe species contain condensed tannins and other phenolic compounds and can extract nitrogen-based secondary chemicals from their host-plants, but the influence of these compounds on mistletoe herbivores is unknown (Khanna et al. 1968, Atsatt 1977 and references therein, Salatino et al. 1993). Mistletoe plants are a favoured food source of many vertebrate and invertebrate animals, which feed on all parts of the mistletoe plant (reviewed by Watson 2001).

The foliage of several mistletoe species is an important and often exclusive food source for the larvae of many species of Lepidoptera throughout the world. In Australia, 25 species of butterflies (in families Pieridae and Lycaenidae) and at least 4 species of moths (in families Saturniidae, Agaristidae, Lymantriidae and Noctuidae) feed on a range of mistletoe species (De Baar 1985, Braby 2000). An additional 20 species of *Delias* (Pieridae) have been recorded feeding on mistletoes in the families Loranthaceae or Viscaceae in the Asian region (Braby 2006); 14 species of *Mylothris* (Pieridae) feed on mistletoes in Africa (Braby 2005); and 5 species of Lepidopteran
larvae feed on dwarf mistletoes in the USA (Mooney 2003). An interesting tritrophic relationship exists between Australian mistletoes, Lycaenid butterflies and ants. The caterpillars of several Lycaenid butterfly species, which feed on mistletoes, are attended by a range of ant species (Eastwood and Fraser 1999, Braby 2004). The ants defend the caterpillars and eggs of the butterflies and feed on secretions from the caterpillars. Butterflies of *Ogyris amaryllis* preferentially oviposit on mistletoes (*Amyema* species) that are occupied by ants (*Iridomyrmex* species) (Atsatt 1981), and the larvae and pupae of other mistletoe-feeding *Ogyris* species even live in ant nests (Kitching 1991).

Other herbivorous arthropods associated with mistletoe plants throughout the world, which feed on mistletoe foliage, fruit, nectar, stems, or wood of the haustorium, belong to the orders Hemiptera, Coleoptera, Orthoptera, Hymenoptera, Diptera, and Acari (Baloch and Mohyuddin 1969, Room 1972a, Whittaker 1982, De Baar 1985, Williams 1985, McMillan 1987, Mathiasen 1996). Predatory arthropods have also been collected from mistletoes, including web-spinning and hunting spiders (Araneae), lacewings (Neuroptera) and coccinellid beetles (Coleoptera), which are likely to feed on the herbivorous insects inhabiting mistletoe plants (Room 1972a, Whittaker 1982, Jennings et al. 1989).
1.3 Research Protocol

1.3.1 Research aim and questions

The aim of this thesis is to determine the diversity and distinctiveness of the arthropod assemblage inhabiting mistletoe plants, compared with the arthropod assemblages inhabiting the mistletoes’ host trees. The patterns of alpha- and beta-diversity of the arthropod assemblages will be determined by examining the host-specificity and spatial and temporal turnover of the assemblages. Furthermore, the factors that influence these patterns will be investigated, such as host-plant and habitat traits and the dispersal ability of the arthropods. The specific research questions that will be addressed are:

1. What is the community composition of the arthropod fauna inhabiting box mistletoe and the host eucalypt trees? (Chapters 2 & 3)

2. How does trophic position influence host-plant specificity of arthropods and patterns of beta-diversity of assemblages among and between host-plant taxa? (Chapter 3)

3. What are the relative influences of host-plant identity, habitat traits and spatial separation on variation in community composition (i.e. beta-diversity) among the arthropod assemblages? (Chapter 4)

Throughout this thesis the use of the term host-plant refers to the plant that the arthropod specimens were collected from, unless specifically referring to the host-plant of the mistletoe. It is expected that herbivorous insects will differentiate more between the plant taxa than will predatory arthropods. Therefore, it is predicted that the community composition of specialised herbivorous insects will vary more between the different plant taxa than the community composition of generalist herbivores or predatory arthropods (i.e. higher beta-diversity among assemblages of specialised herbivorous insects between different host-plants, than among assemblages of non-specialised arthropods). However, the similarity among arthropod assemblages is expected to increase with increasing plant taxonomic affinity. Therefore, lower beta-diversity is predicted among arthropod assemblages inhabiting congeneric plants than from plants in different genera or families.
CHAPTER 1

It is expected that host-plant taxon will be the most important determinant of beta-diversity for assemblages of host-specific arthropod taxa. In contrast, it is predicted that habitat traits will be more important determinants of beta-diversity among generalist and predatory arthropods, than host-plant taxon, according to the niche requirements of the arthropods. The influence of spatial variables will depend on the dispersal ability and other biological traits of the arthropod taxa, i.e. greater spatial turnover in community composition is expected among assemblages consisting of arthropods with low dispersal ability and aggregated distribution patterns.

1.3.2 Thesis outline and scope of the study

This thesis consists of five chapters in total. Chapters 2 to 4 address components of the research questions and are similar in style to separate papers. Chapter 5 is a concluding chapter for the whole thesis. The study occurred in a pastoral and cropping landscape, with remnant eucalypt woodlands and scattered trees. The sampling sites were located 2 to 45 km apart in remnant woodlands on private properties. One species of mistletoe was sampled: *Amyema miquelii* (Lehm. Ex Miq.) Tiegh., box mistletoe; and three species of *Eucalyptus* trees which box mistletoe parasitises (*Eucalyptus polyanthemos* red box, *E. melliodora* yellow box and *E. blakelyi* Blakely’s red gum). The samples from the *Eucalyptus* trees were combined for analyses because it was not possible to sample the same number of each tree species due to the uneven distribution of the species and the dominance of red box trees. Therefore, the comparison of arthropod assemblages is between those inhabiting box mistletoe plants and the mistletoes’ host *Eucalyptus* trees. Sampling by restricted canopy fogging occurred in one season of the year (spring), over two years, to assess the spatial and temporal variation in community composition and the factors influencing assembly of the arthropods on de-faunated mistletoe plants.

Chapter 2, which addresses the first research question, begins with comparison of arthropod orders between the sampled plants and moves on to comparison of the incidence and abundance of beetle families between plants. Identification of selected arthropods at genus and morphospecies level proceeds in Chapter 3, regarding the most abundant herbivorous and predatory arthropods, i.e. psyllids (Hemiptera) and spiders (Araneae). Identification of taxa at this higher level of resolution enabled analysis of host-specificity of the arthropods (in different trophic groups) and
elucidation of fine-scale patterns of beta-diversity among the assemblages inhabiting the mistletoe and eucalypt plants. The analyses and results of this thesis concern two types of measures – presence or abundance, regardless of the taxonomic level of entities.

Some of the factors that could influence variation in assemblage composition and abundance were investigated, such as foliage properties of the mistletoe and eucalypt plants; habitat properties, such as proximity of neighbouring trees and mistletoes; and other environmental factors such as landform and solar radiation. The influence of these variables on arthropod diversity is discussed in Chapters 2 and 3 but particularly in Chapter 4. In Chapter 4, the beta-diversity of the psyllid insect and spider assemblages is related to variation in host-plant traits, environmental factors and geographic distance between the assemblages. The sampling sites were similar in topography, climate, vegetation and soil composition, so as to focus on the influence of spatial separation and selected patch-scale variables on patterns of beta-diversity among the arthropod assemblages. The influence of these variables on the re-colonisation dynamics of the psyllid insects on the mistletoe plants is also investigated in Chapter 4.
1.4 References


CHAPTER 1


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Kuppers, M. 1992. Carbon discrimination, water-use efficiency, nitrogen and phosphorus-nutrition of the host mistletoe pair Eucalyptus behriana F. Muell
and *Amyema miquelii* (Lehm. Ex Miq.) Tiegh. at permanently low plant water status in the field. Trees - Structure and Function 7:8-11.


Chapter 2

Contribution of component communities to canopy arthropod diversity

2.1 Introduction
The pioneering work of entomologists such as Erwin and Scott (1980, 1983), Futuyma and Gould (1979), Janzen (1973, 1988), Moran and Southwood (1982), Stork (1987a, b), Majer and Recher (1988), Basset (1990), and Kitching et al. (1993) led to the discovery of the huge contribution of canopy-dwelling insects to total species diversity, particularly in tropical forests. Their research involved examination of the similarity of insect assemblages on different host-plants or forest types, leading to estimates of tropical arthropod richness of between 30–80 million species (Erwin 1982, Stork 1988). After more recent detailed research on the host-specificity of herbivorous insects, the estimates of global arthropod richness have been downsized to 2.4–10.2 million species (Basset et al. 1996, Stork 1999, Ødegaard 2000a, Novotny et al. 2002). These studies were based on the species richness and host-specificity of insects to tree species in forests but there is a lack of this information regarding arthropods on other plant forms in forests, e.g. epiphytic or parasitic plants, which form ‘component communities’ of tree canopies (Basset 1997, Stuntz et al. 2002). Therefore, the arthropod diversity of component communities is represented by guesses or estimates from only one epiphyte–host study in estimates of total arthropod diversity (Ødegaard 2000a).

Epiphytic plants are very diverse in forest canopies around the world, i.e. 23,400 species including mistletoes (Benzing 1990), and they have been proposed as ecological keystones because of their contribution to forest diversity and ecosystem functioning (Nadkarni 1994, Watson 2001). The abundance of epiphytes in forest canopies has been proposed as an influential factor on the diversity of canopy-dwelling arthropods (Stork...
1987a), but there are few published empirical studies to quantify the contribution of epiphytic-dwelling arthropods to overall forest diversity. The structure of some epiphytic plants enables them to hold water, litter and other organic debris; therefore they support invertebrate animals that do not otherwise occur in tree canopies, such as aquatic invertebrates and terrestrial detritivores (Cotgreave et al. 1993, Dejean et al. 1995, Richardson 1999, Kitching 2000, Ellwood et al. 2002, Yanoviak et al. 2003). It has been estimated that epiphytes can at least double the biomass of invertebrates in the entire rainforest canopy, from a study that revealed a single Bird’s nest fern can contain the same biomass of invertebrates as the whole tree canopy (Ellwood and Foster 2004). However, there is only one published study directly comparing the compositional similarity of arthropod assemblages between epiphytic plants and tree canopies (Ødegaard 2000b). In the latter study of herbivorous beetles associated with lianas and trees in a tropical forest, Ødegaard (2000b) found that only 24% of beetle species were associated with both the trees and the lianas. Lianas hosted a greater proportion of specialised phytophagous beetles, and trees hosted a greater proportion of wood-eating beetles. The difference in beetle composition between the lianas and trees is thought to be due to differences in rates of leaf production. Differences in abundance of invertebrates between different types of epiphytes have been related to quantities of nutrients and changing structure of plant parts with age (Richardson et al. 2000). This is similar to other studies of plant–insect interactions, which have found that the development, reproduction and abundances of insects are limited by foliage nutrient concentrations and structural properties (Ohmart 1991a, White 1993, Recher et al. 1996a, Peeters 2002a, b).

Mistletoes are one form of epiphytic plant, which are parasitic on their hosts and are common in forests and woodlands worldwide. Mistletoes have been proposed as a keystone resource for vertebrates in forests and woodlands (Watson 2001); however, their importance for invertebrates has not been thoroughly investigated. There are no published comparative, community-level studies of the host-specificity and diversity of invertebrate assemblages inhabiting mistletoes and the mistletoe’s host-plants. Mistletoes are often structurally similar to their hosts in leaf form and branching structure but differ in nutrient content. The foliage of many mistletoe species contains a higher concentration of nutrients than that of their host-plants, including nine of
fourteen measured elements (Lamont and Bernhardt 1983, March 2007); however, the foliage of *Amyema miquelii* often contains a lower concentration of nitrogen than its *Eucalyptus* host-plants (Ehleringer et al. 1986, Kuppers 1992, March 2007). Mistletoe foliage is thought to contain fewer structural and chemical defenses than host-plant foliage, and is consumed by a range of mammals and insects (Watson 2001, Mathiasen et al. 2008, and references therein).

In this chapter, I describe an exploratory, observational study addressing the question: do arthropod assemblages differ in composition and abundance between mistletoes and the tree canopies; and what factors might influence those patterns? Comparisons are made at the taxonomic level of orders and also the family and guild composition of Coleoptera (beetles). Furthermore, the re-colonisation of mistletoes by arthropods following de-faunation is examined to explore the factors influencing the diversity and distributional patterns of arthropods inhabiting mistletoes. In Chapter 3, the two most abundant herbivorous and predatory groups of arthropods, psyllids and spiders, are identified to species level. Identification of these taxa to a higher resolution enabled finer-scale differences in community composition to be elucidated between the assemblages on the mistletoe and eucalypt plants. Chapter 4 describes the relative roles of host-plant traits and environmental and spatial factors shaping the arthropod communities, over the spatial and temporal scales examined in this thesis.
2.2 Methods and Materials

2.2.1 Location

The study was conducted in the Upper Billabong Creek Catchment, in the south west slopes of New South Wales, Australia (Figure 2.1). The town of Holbrook (35° 43’ 36” S, 147° 18’ 50” E) is near the centre of the catchment and is 55km NE of Albury. Climatic data from the nearest meteorological station, Hume Weir (50 km SW of Holbrook, 36.10° S, 147.03° E), were obtained from the Australian Bureau of Meteorology. The region is characterised by hot summers (December–February) and cool winters and rainfall is greatest in winter and spring (June–October; Fig. 2.0). The total annual rainfall in the first year of sampling (2005) was slightly above the long-term average: 871mm compared to 695mm long-term annual average for 1922–2007; and it was well below average in the second year of sampling (2006): 270 mm. In the month of the first sampling event, November 2005, the average minimum and maximum temperatures (12.8°C and 25.6°C) and total rainfall (56.2 mm) were similar to the long-term averages for November (Fig. 2.0). However, for the second sampling event in November 2006, the average monthly minimum and maximum temperatures (14.0°C and 31.3°C) were above the long-term averages for that month and the monthly rainfall (34.6 mm) was below the long-term average.

![Figure 2.0](image-url) **Figure 2.0** Mean monthly minimum (white bars) and maximum (black bars) temperatures and rainfall (black line), between 1922 and 2007, recorded at the Hume Weir Meteorological Station.
Figure 2.1 Location of the study sites in the Upper Billabong Creek Catchment, in New South Wales, Australia.
2.2.2 Site selection and description

Sampling took place at nine sites, which consist of grazed remnant woodlands on private land, surrounded by paddocks used for grazing or cropping, or by un-grazed native woodland (Figure 2.0, Table 2.0). Most of the woodlands were dominated by trees of *Eucalyptus polyanthemos* (red box), which is the primary host for box mistletoe (*Amyema miquelii*) in the region. The other tree species that occurred at the study sites, which are also host-plants for box mistletoe, were *Eucalyptus blakelyi* (Blakely’s red gum), *E. melliodora* (yellow box), *E. macrorhyncha* (red stringybark), *E. albens* (white box), *E. bridgesiana* (apple box) and *E. goniocalyx* (long-leaved box). Three other mistletoe species *Amyema pendula* (drooping mistletoe) and *A. miraculosa* subsp. *boormanii* (fleshy mistletoe) both in the Loranthaceae and *Notothixos cornifolius* (Kurrajong mistletoe) in the Viscaceae also occurred at a few of the sites, at very low densities. The nine sites were selected on the basis that there were at least 40 box mistletoe plants at each site; the sites covered a range of spatial distances between sites from 2.4 and 45 km; and that the sites were accessible with a trailer-mounted hydraulic bucket-hoist, which was used to access the canopy. The sites sampled in 2005 are part of an ongoing study investigating the effect of mistletoe on the diversity of woodland birds, mammals and reptiles (Resources in Fragmented Landscapes Experiment, ARC Discovery Project, D.M. Watson). The study sites occur on gently sloping or undulating footslopes or plains, with soil types consisting of Chromosols and Kurosols in all of the soil landscape types except Mountain Creek, which mainly consists of Sodosols and Dermosols (Table 2.1, Figure 2.2).
Table 2.0 Site and sampling information. Tree species codes: RB: red box, YB: yellow box, BRG: Blakely’s red gum. Soil types are described in Table 2.1.

<table>
<thead>
<tr>
<th>Site No.</th>
<th>Size (ha)</th>
<th>Tree species sampled from</th>
<th>Surrounding land use</th>
<th>Soil type</th>
<th>No. mistletoe samples</th>
<th>No. eucalypt samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>11</td>
<td>RB, YB, BRG</td>
<td>Grazing &amp; cropping</td>
<td>Lloyd</td>
<td>6 5</td>
<td>5 (2RB, 3YB, 1BRG)</td>
</tr>
<tr>
<td>6</td>
<td>15</td>
<td>RB, YB</td>
<td>Grazing, improved pasture</td>
<td>Mountain Creek</td>
<td>5 5</td>
<td>3 (2RB, 1YB)</td>
</tr>
<tr>
<td>10</td>
<td>18</td>
<td>RB, YB, BRG</td>
<td>Grazing, improved pasture</td>
<td>Mountain Creek &amp; Castlestead</td>
<td>10 12</td>
<td>6 (3RB, 2BRG, 1YB)</td>
</tr>
<tr>
<td>11</td>
<td>15</td>
<td>RB</td>
<td>Grazing, improved pasture</td>
<td>Lloyd</td>
<td>5 5</td>
<td>2 RB</td>
</tr>
<tr>
<td>23</td>
<td>4</td>
<td>RB</td>
<td>Cropping &amp; grazing</td>
<td>Lloyd</td>
<td>4 4</td>
<td>3 RB</td>
</tr>
<tr>
<td>43</td>
<td>32</td>
<td>RB, YB</td>
<td>Un-grazed woodland &amp; cropping</td>
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<td>6</td>
<td></td>
</tr>
<tr>
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<td>RB, BRG</td>
<td>Grazing and un-grazed woodland</td>
<td>Yarra Yarra</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>45</td>
<td>42</td>
<td>BRG, YB</td>
<td>Grazing and un-grazed woodland</td>
<td>Yarra Yarra</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>46</td>
<td>43</td>
<td>RB, BRG</td>
<td>Grazing and un-grazed woodland</td>
<td>Lloyd</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.1 Descriptions of the soil landscapes in which the study sites are located, from Doughty (2003).

<table>
<thead>
<tr>
<th>Soil Landscape Grouping</th>
<th>Soil Landscape Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Castlestead</td>
<td>Undulating footslopes adjacent to Devonian sandstones and conglomerates. Local relief 10–30 m, altitude 230–330 m, slope gradients 2–10%. Well drained Red and Brown Chromosols and Kurosols on upper slopes, Brown and Yellow Chromosols and Kurosols on mid and lower slopes and Sodosols in drainage depressions.</td>
</tr>
<tr>
<td>Lloyd</td>
<td>Rolling low hills on Ordovician metasedimentary rocks. Local relief 30–90 m, altitude 200–450 m, slopes 10–20%. Moderately well drained Paralithic Leptic Rudosols and Red Kurosols on upper slopes, Red Chromosols and Kurosols on mid to lower slopes, and Brown Kurosols in drainage lines.</td>
</tr>
<tr>
<td>Mountain Creek</td>
<td>Very gently undulating alluvial plains. Local relief &lt;5 m, altitude 240–350 m, slopes 0–2%. Moderately well drained Brown, Yellow and Grey Sodosols on higher terraces, Yellow and Brown Dermosols on lower terraces, and Stratic Rudosols in recent channels.</td>
</tr>
<tr>
<td>Yarra Yarra</td>
<td>Gently inclined footslopes and fans adjacent to Silurian granite. Local relief 10–70 m, altitude 170–520 m, slopes 2–8%. Imperfectly to moderately well drained Red, Brown and Yellow Chromosols on upper and mid slopes, Sodosols and Kurosols on lower slopes, and very deep Orthic Tenosols on fans.</td>
</tr>
</tbody>
</table>
2.2.3 Sampling technique

Selection of mistletoe and eucalypt foliage

Arthropod and foliage samples were collected from box mistletoe plants (*Amyema miquelii* (Lehm. ex Miq.) Tiegh.), and red box (*Eucalyptus polyanthemos* Schauer), yellow box (*E. melliodora* Cunn. ex Schauer) and Blakely’s red gum (*E. blakelyi* Maiden) hosts. The samples were taken from trees at the edges of remnant vegetation patches, or within 50 m of the edge of the patch. The mistletoe plants were sampled haphazardly from all aspects of the trees, since the abundance of arthropods can vary with aspect in the tree but not in a consistent manner (Richardson et al. 1999, Stork et al. 2001). The samples were taken from 2 to 12 metres above ground. The eucalypt foliage that was sampled was within 3 m of a mistletoe plant sampled in that tree, at the same height above ground and depth of canopy. *Amyema miquelii* (Loranthaceae) plants occur throughout mainland Australia, with the greatest frequency recorded in south-east Australia (Barlow 1984). *Amyema miquelii* occurs on 125 recorded host-plant species, primarily *Eucalyptus* species in the family Myrtaceae and also a few species in each of
nine other families (Downey 1998). The three *Eucalyptus* species from which samples were collected are widely distributed in south-east Australia, including the states Victoria, New South Wales and Queensland, and occur in woodlands and open forest, on gentle slopes and low hills (Chippendale 1988).

**Arthropod collection and identification**

Sampling of arthropods took place in the spring season of the southern hemisphere, in November 2005 and November 2006, because the abundance of arthropods is highest in spring in south-eastern Australia (Woinarski and Cullen 1984, Recher et al. 1996b). The sampling period in 2005 consisted of 9 days of sampling, from the 14th to 25th November, and sampling occurred between 10am and 3pm. Minimum and maximum daily temperatures during the sampling period were 9–17°C and 22–30°C, respectively. In 2006, sampling occurred over 12 days, from the 17th November to 1st December, between 9am and 2pm. Minimum and maximum daily temperatures during the sampling period in 2006 were 7–19°C and 25–37°C, respectively. All samples were collected on sunny days with calm conditions or light winds. In 2006, the mistletoe plants that were sampled in 2005 were re-sampled (except four plants that had died or fallen from the tree). In addition, 30 new mistletoe plants were sampled at four new sites (numbers 43–46, Figure 2.0, Table 2.0), to obtain reference samples with which to compare the re-colonised mistletoe plants and to increase the range of distances between sites.

A restricted canopy fogging technique was used to collect the arthropods, similar to Basset (1990). Because mistletoe foliage is so close to the foliage of the host tree, restricted canopy fogging was the most appropriate method for collection of arthropods. In this technique, foliage is fully enclosed in a collection bag before spraying (Fig. 2.3). Restricted canopy fogging 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.
A trailer-mounted hydraulic bucket-hoist was used to access the tree canopy ("Nifti-lift", with a 12 m telescoping boom arm, Figure 2.3). Foliage of the samples was enclosed in a plastic bag and pyrethrin-based household insecticide was sprayed into the bag for 20 seconds, then the opening of the bag was sealed with masking tape. After 20 minutes the foliage was shaken vigorously to dislodge arthropods remaining on the foliage. The bag was unsealed and removed from the foliage, then resealed and stored in the vehicle. 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 pyrethrin, 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: Tetramethrin (4g/kg), Phenothrin (0.9g/kg) and Allethrin (0.9g/kg); and Ethanol (291g/kg). Pyrethrin is non-residual, breaks down in sunlight and is not toxic to vertebrates. A metal tag with a unique number was attached to a branch at the top of each foliage sample. At the end of the daily collection period the contents of the sample bags were transferred to 80% 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 specimens were sorted to order, according to "The Insects of Australia" (Naumann 1991) and using insect taxonomic guides by New (1996) and Zborowski and Storey (1995). All beetles were identified to family by a para-taxonomist, Kim Pullen (CSIRO Entomology), and assigned to trophic groups according to the published feeding habits of each family (Lawrence and Britton 1994). The psyllids (Hemiptera: Psylloidea) and spiders (Araneae) were identified to morphospecies by the author, and subsequent identifications and analysis of these taxa are described in the following chapter.
Figure 2.3 Sampling method: (a) hydraulic bucket hoist used to access the tree canopy, (b) mistletoe plant with part of foliage enclosed in sampling bag to collect arthropods.
Estimation of leaf mass and area

For most samples it was not possible to include the entire mistletoe clump, thus a portion of the mistletoe foliage was sampled. The width, breadth and vertical depth of the sampled foliage were recorded. The density of the foliage was assigned a score from 1–5, 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 density score was combined with the width, breadth and vertical depth of the foliage to calculate a foliage quantity index (Equation 1), adapted from the equation of the volume of an ellipsoid (March and Watson 2007).

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

Where \(a\), \(b\) and \(c\) are width, breadth and vertical depth respectively.

The foliage quantity index does not have units. March and Watson (2007) found a strong positive relationship between the foliage quantity index and dry mass of the sample: \(r^2 = 0.91, P < 0.001\) (\(F_{1,18} = 180.1\)).

In December 2006, I collected foliage samples to determine the relationship between sample volumes, leaf mass and leaf area. Ten box mistletoe samples and five to eight samples from each of the host eucalypt species were collected. The width, breadth and vertical depth of each sample were measured, a foliage density score was assigned and then the sample was cut from the tree and placed in a plastic bag. The samples were placed in insulated containers with ice and taken to the Charles Sturt University laboratory (1 hour from the study area). At the laboratory, the samples 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 degrees Celsius. All samples were dried to constant weight, which was between 48 and 66 hours for the oven dried samples and between 96 and 120 hours for the freeze dried samples. Before oven-drying, the area of 10–20 leaves in each sample was measured with a CI-202 Portable Leaf Area Meter (CID Inc.), and these leaves were weighed separately to the rest of the sample to determine specific leaf area and weight. The majority of each sample consisted of mature leaves, with a small portion of juvenile leaves.
The measurements of the foliage samples collected in 2006 were used to estimate the leaf dry mass and area of the foliage from which arthropods were collected. The leaf dry mass of the foliage samples from the box mistletoe and each eucalypt species were plotted separately against the foliage quantity index, and the regression equations from the fitted lines (equations 2 to 5) were used to estimate the leaf dry mass of the 2005 and 2006 samples.

Box Mistletoe: Leaf dry mass = 373.18*foliage quantity + 8.7719, $r^2 = 0.874$

Red Box: Leaf dry mass = 214.45*foliage quantity + 8.1049, $r^2 = 0.836$

Yellow Box: Leaf dry mass = 137.92*foliage quantity + 11.086, $r^2 = 0.929$

Blakely's Red Gum: Leaf dry mass = 186.73*foliage quantity + 3.7719, $r^2 = 0.889$

To estimate the leaf area of the samples I took the estimated leaf dry mass (from each regression model, equations 2–5), multiplied it by the mean specific leaf area for that species (Table 2.2) and then doubled the value to reflect the fact that insects can use both sides of each leaf. Using these data it was possible to express arthropod abundance as density per leaf area. The mean specific leaf area (SLA) of red box and yellow box in the current study (Table 2.2) are within 1.5 cm$^2$ g$^{-1}$ of published SLA values for these species (Gras 2005): mean SLA (±SE) of adult red box leaves was 41.5 (± 1.9) and of yellow box leaves was 51.5 (± 6.3) (N = 5 for each species). There are no published values of the SLA of Blakely’s red gum or box mistletoe.

Table 2.2 Mean specific leaf area (±SE) of the sub-sample of leaves of box mistletoe and each eucalypt species (area of one side of leaves).

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Mean specific leaf area (cm$^2$ g$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Box mistletoe (N = 10)</td>
<td>29.7 (1.2)</td>
</tr>
<tr>
<td>Red box (N = 8)</td>
<td>42.5 (3.1)</td>
</tr>
<tr>
<td>Yellow box (N = 8)</td>
<td>50.1 (2.8)</td>
</tr>
<tr>
<td>Blakely’s red gum (N = 5)</td>
<td>37.5 (1.5)</td>
</tr>
</tbody>
</table>
Nitrogen and carbon content of foliage

The nitrogen and carbon content of the sub-sample of mistletoe and eucalypt leaves collected in 2006 were determined by a laboratory at the Australian National University. Prior to analysis the leaves were freeze-dried to constant weight (96 and 120 hours) and ground to a fine powder with a Cyclotec 1093 Sample mill grinder. Approximately 2mg of leaf tissue of the 10 mistletoe and 15 eucalypt samples were analysed for carbon and nitrogen content by quantitative combustion in a Carlo Erba EA-1110 CHN-O Elemental Analyser.

Measurement of habitat variables

A range of variables were measured to encompass characteristics of the sampled mistletoes and trees and the surrounding habitat of the sampled trees (Table 2.3, Figure 2.4). The ‘index of mistletoe age’ was the diameter of the host tree branch adjacent to the haustorium of the sampled mistletoe (measured at 100 mm from the haustorium for a standard measure) (Fig. 2.5). Since mistletoe seeds only germinate on young branches the diameter of the host branch is regarded as a reliable indication of the relative age of the mistletoe (Reid et al. 1995). The measurement of distances to the nearest four trees was based on the point-quarter method for measuring habitat variables (Etchberger and Krausmann 1997), i.e. the area around each sampled tree was divided into quarters according to the compass points, with the sampled tree at the centre (Fig. 2.4), and the distance to the nearest tree in each quarter was measured (trees ≥ 10 cm DBH; distance estimates were made for trees more than 100 m from the sampled tree). The health of the sampled mistletoe and tree were scored from 1–5 (i.e. 1: vigorous, covered in new growth; 2: healthy, some new growth; 3: old foliage, no new growth; 4: some dead leaves & twigs; 5: dead branches). The phenology of the sampled tree and mistletoe were recorded as the presence of buds, flowers and/or fruit. The geographical co-ordinates of the samples were recorded with a Garman® eTrex Summit™ hand-held GPS with 4–5 m accuracy. The elevation, degrees and aspect of the slope, topographic relief moisture index and solar radiation were derived from remotely-sensed data, including the digital elevation model, at the geographic location of each sample in ESRI® ArcMap™ 9.2.
Table 2.3 Sample and habitat variables measured for the mistletoe and eucalypt samples, either directly at the site (D), using a GPS, or derived from remotely-sensed data (R).

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>Code</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree height</td>
<td>TreeHgt</td>
<td>D</td>
</tr>
<tr>
<td>Tree diameter at breast height</td>
<td>TreeDBH</td>
<td>D</td>
</tr>
<tr>
<td>Height of sample above ground</td>
<td>HtAbvGd</td>
<td>D</td>
</tr>
<tr>
<td>Aspect of sample in the tree</td>
<td>AspectSA</td>
<td>D</td>
</tr>
<tr>
<td>Index of mistletoe age, i.e. host-branch diameter</td>
<td>HostBrDi/Mtoe age</td>
<td>D</td>
</tr>
<tr>
<td>Number of mistletoe in sampled tree</td>
<td>No.Mist</td>
<td>D</td>
</tr>
<tr>
<td>Distance to nearest mistletoe plant</td>
<td>NNDmtoe</td>
<td>D</td>
</tr>
<tr>
<td>Distance to the nearest tree</td>
<td>NNDtree</td>
<td>D</td>
</tr>
<tr>
<td>Average of distances to the nearest tree in each compass quadrant</td>
<td>AveNND</td>
<td>D</td>
</tr>
<tr>
<td>Number of trees in 15m radius around sampled tree</td>
<td>Trees15m</td>
<td>D</td>
</tr>
<tr>
<td>Health of tree &amp; mistletoe</td>
<td>Health T/M</td>
<td>D</td>
</tr>
<tr>
<td>Phenology of tree &amp; mistletoe (flowers, fruits or buds)</td>
<td>FL FR BD</td>
<td>D</td>
</tr>
<tr>
<td>Understorey (leaf litter, grass or shrubs)</td>
<td>LL GR SH</td>
<td>D</td>
</tr>
<tr>
<td>Longitude of sample</td>
<td>LONG, X</td>
<td>GPS</td>
</tr>
<tr>
<td>Latitude of sample</td>
<td>LAT, Y</td>
<td>GPS</td>
</tr>
<tr>
<td>Elevation</td>
<td>Elevation</td>
<td>R</td>
</tr>
<tr>
<td>Slope</td>
<td>Slope</td>
<td>R</td>
</tr>
<tr>
<td>Aspect of the slope</td>
<td>AspectSL</td>
<td>R</td>
</tr>
<tr>
<td>Topographic relief moisture index</td>
<td>TRMI</td>
<td>R</td>
</tr>
<tr>
<td>Solar radiation</td>
<td>SolarRad</td>
<td>R</td>
</tr>
</tbody>
</table>
Figure 2.4 Diagram of a sampled tree (dark green line) and the measurements recorded for each mistletoe and eucalypt sample (not to scale). M1: sampled mistletoe, M2: nearest mistletoe to M1, E1: sampled eucalypt foliage. Refer to table 2.3 for description of variable codes.
Figure 2.5 Development of the mistletoe haustorium and the relationship between the diameter of the host branch and mistletoe age. These images display the progression from mistletoe seed germination to establishment and growth of the haustorium; which indicates the range in size of the host branch diameter with progression in mistletoe age. (a) Mistletoe seed germinating on a small branch (approx. 1 cm diameter). (b) Mistletoe haustorium established and portion of host branch distal to haustorium (left side) greatly reduced. (c) Haustorium of an older mistletoe and the thicker branch of its host-plant. (d) The distal end of this infected branch has atrophied and fallen off, with the broken end of the branch covered by the mistletoe. (Note: these photos are not of the same mistletoe or host-plant).
2.2.4 Statistical analysis

*Kruskal-Wallis non-parametric test for differences between sample groups*

Differences between the mistletoe and eucalypt samples in density of individuals of each arthropod order, and the foliage variables, were assessed with the Kruskal-Wallis chi-square rank test. It is a non-parametric test to compare the medians of multiple samples and does not require normality of the data; and observations can be on any scale of measurement. A post-hoc test of differences between all pair-wise combinations of the host-plants was conducted for the foliage variables, with $\alpha = 0.01$ because multiple comparisons were conducted.
2.3 Results

2.3.1 Ordinal composition and abundance

In November 2005, 5731 arthropod specimens, both adults and larvae, were collected from the mistletoe and eucalypt foliage. The majority of these specimens were less than 5 mm in length. The mean densities of the arthropod orders, except Acarina, were greater in the eucalypt samples than the mistletoe samples; with significant differences for 6 of the 10 orders ($P < 0.01$) between the mistletoe and eucalypt samples (Fig. 2.6).

![Figure 2.6 Mean density (± 1SE) of arthropod orders. Black bars represent the eucalypt samples ($N = 19$) and white bars represent the mistletoe samples ($N = 30$). Results of the Kruskal-Wallis chi-square rank test of difference between the medians of the sample groups shown above the bars: ns = not significantly different, ** = $P < 0.01$, *** = $P < 0.001$.](image)

Hemiptera was the most abundant order, in terms of the density of individuals per leaf area, comprising 49% of the individuals in the eucalypt samples and 40% in the mistletoe samples. Hemipteran individuals occurred in every sample. The superfamily Psylloidea, i.e. psyllids, comprised 75% and 80% of the abundance of Hemipteran individuals in the eucalypt and mistletoe samples, respectively. The eucalypt samples contained a significantly greater density of total Hemipteran individuals than the mistletoe samples. But the density of the psyllids was not statistically significantly different between the sample groups due to the large variation in density among the
eucalypt samples (ranging from 0 to 246 individuals per square metre). In the mistletoe samples, Acarina, Araneae, Hymenoptera and Coleoptera were the next most abundant orders, and individuals of each of these orders occurred in 90–100% of samples. These orders, except Acarina, were also the next most abundant and frequently occurring orders in the eucalypt samples, as well as Thysanoptera. However, the mean density of individuals in the orders Thysanoptera and Psocoptera, in the eucalypt samples, were inflated by very large abundances of larvae in one sample for each order. The mean densities of Thysanoptera and Psocoptera excluding the abundant samples are reduced by a third or half, to 4.2 and 3.8 individuals per m², respectively. Approximately 90% of the thrips in the mistletoe and eucalypt samples were plague thrips, *Thrips imaginis* (Laurence Mound, personal communication). Lepidoptera was the least abundant order in both the mistletoe and eucalypt samples, with only 2 larvae in the eucalypt samples and 2 adults and 18 larvae in the mistletoe samples. It is likely that there were few adult Lepidoptera collected because the sampling method was not conducive to collecting actively flying insects and most Lepidoptera are active at night. Only a few adult and larval Lepidopterans were observed on the plants at the time of collecting.

The mistletoe plants that were sampled in 2005 were re-colonised by all orders except Psocoptera during the following year (Fig. 2.7). The overall density of arthropods was significantly greater in 2006 ($P < 0.001$) and the dominance structure of the orders differed between years but Hemiptera remained the most abundant order collected in 2006 (Fig. 2.7). There was a greater density of Hemiptera and Hymenoptera and a lower density of Acarina on the mistletoe plants in 2006 compared to 2005 (Fig. 2.7).
Figure 2.7 Mean density (± 1SE) of arthropod orders collected from the mistletoe plants in November 2005 (white bars, N = 30) and re-sampled from the same plants in November 2006 (hashed bars, N = 26). Results of Kruskal-Wallis chi-square rank test of difference between the medians of the sample groups shown above the bars: ns = not significantly different, * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

In the comparison of the density of orders collected from the re-sampled mistletoes and the new mistletoes that were sampled for the first time in 2006 (Fig. 2.8), the densities of all orders were very similar between the mistletoe sample groups. One specimen each of the orders Pseudoscorpionida and Orthoptera were sampled from the new mistletoe plants. The median densities of Coleoptera and Hemiptera (all Hemiptera and psyllids only) were statistically significantly different between the new and re-sampled mistletoes (P < 0.05 Kruskal-Wallis chi-square test). A total of 4424 individuals were collected in 2006 from all the mistletoe plants that were sampled.
2.3.2 Relative abundance of beetle families and feeding guilds

221 beetles were collected in the 30 mistletoe samples and 262 beetles in the 19 eucalypt samples (in 2005); most of which were adult life-stages, with less than 1% larvae. A total of 19 families are represented, with 16 families in the mistletoe samples and 15 families in the eucalypt samples. The most abundant families in both sample groups were Lathridiidae (mycophagous) and Coccinellidae (‘ladybird beetles’, predacious) (Fig. 2.9). Beetles in the families Curculionidae (weevils, phytophagous) and Phalacridae (mycophagous) were relatively more abundant on the eucalypt foliage than the mistletoe foliage; and Chrysomelidae (phytophagous) and Melyridae (predacious and phytophagous) were relatively more abundant on the mistletoe foliage (Fig. 2.9). Individuals of Brentidae (a weevil family) were also relatively abundant in the mistletoe samples but were not present in the eucalypt samples. Hence, the majority of beetles collected belong to families that are mycophagous, phytophagous and predacious (Fig. 2.10). Some beetles also belong to families that primarily feed on nectar, pollen and fruit, or scavenge on remains of animal matter. The proportions of
beetles in each feeding guild were similar between the mistletoe and eucalypt samples.

![Pie chart](image-url)  

**Figure 2.9** Relative abundance (percentage of individuals in each family) of beetle families in (a) the eucalypt samples (N = 19) and (b) the mistletoe samples (N = 30).
Figure 2.10 Relative abundance of feeding guilds of beetles (percentage of individuals in each guild, from family classifications) in (a) the eucalypt samples ($N = 19$) and (b) the mistletoe samples ($N = 30$).
2.3.3 Foliage traits

The median percentage nitrogen content of the mistletoe leaves was significantly lower than that of the eucalypt leaves, for all eucalypt species combined and separately (Table 2.4); and the same pattern was observed for the mean percentage leaf nitrogen (Fig. 2.11). The median percentage carbon content of the foliage was not significantly different between the mistletoe and eucalypt foliage (Table 2.4). The median specific leaf area 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 (Table 2.4). The median percent moisture content of the leaves differed significantly between the mistletoe leaves and all of the eucalypt leaves combined but not necessarily between each plant species (Table 2.4).

**Table 2.4** Leaf traits of the box mistletoe and eucalypt trees ($N = 5–10$ per plant species). Values are medians and those with different letters are significantly different ($P < 0.01$), according to the Kruskal-Wallis chi-square rank sum test (with post-hoc comparisons between each plant species).

<table>
<thead>
<tr>
<th></th>
<th>N %</th>
<th>C %</th>
<th>SLA (cm²/g)</th>
<th>Thickness (mm)</th>
<th>Moisture %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mistletoe</td>
<td>0.73 a</td>
<td>51.4 a</td>
<td>30.6 a</td>
<td>0.478 a</td>
<td>51.7 a</td>
</tr>
<tr>
<td>All eucalypts</td>
<td>1.20 b</td>
<td>51.2 a</td>
<td>41.7 b</td>
<td>0.284 b</td>
<td>48.3 b</td>
</tr>
<tr>
<td>Red box</td>
<td>1.27 b</td>
<td>50.7 a</td>
<td>37.7 b</td>
<td>0.314 b</td>
<td>49.6 ab</td>
</tr>
<tr>
<td>Yellow box</td>
<td>1.15 b</td>
<td>51.2 a</td>
<td>52.2 c</td>
<td>0.284 b</td>
<td>49.6 bc</td>
</tr>
<tr>
<td>Blakely’s red gum</td>
<td>1.39 b</td>
<td>51.7 a</td>
<td>38.2 b</td>
<td>0.264 b</td>
<td>45.2 c</td>
</tr>
</tbody>
</table>

![Mean percent leaf nitrogen](image)

**Figure 2.11** Mean percentage leaf nitrogen ($± 1$ SE) for each plant species and all eucalypts combined. Mistletoe samples: $N = 10$; Eucalypt samples: $N = 5–8$ for each eucalypt host species (red box, yellow box and Blakely’s red gum).
2.4 Discussion

2.4.1 Composition and abundance of arthropod orders inhabiting mistletoes and tree canopies

The ordinal composition of the arthropods inhabiting box mistletoe and its host *Eucalyptus* trees was very similar, but the densities of all orders except Acarina were greater in the *Eucalyptus* canopies. The orders Hemiptera, Araneae, Hymenoptera and Coleoptera, which contained the most abundant inhabitants of mistletoe and the eucalypts, are also the most abundant orders found in canopies of other temperate and sub-tropical trees, using similar collection methods as the present study (i.e. restricted canopy fogging, branch clipping or beating: Woinarski and Cullen 1984, Basset and Arthington 1992, Floren and Linsenmair 1997, Meades et al. 2002, Major et al. 2003). In comparison, whole-canopy fogging tends to result in collection of a higher proportion of Diptera than restricted canopy fogging, but Hemiptera, Hymenoptera and Coleoptera have also been the dominant orders sampled by whole-canopy fogging of tropical and temperate trees (Southwood et al. 1982, Stork 1991, Recher et al. 1996b, Hill and Cermak 1997, Stork and Hammond 1997, Southwood et al. 2005). Araneae are often not effectively sampled by whole-canopy fogging because spiders have drag lines that prevent them falling into the collecting trays. However, with restricted canopy fogging, the insecticide can contact the spiders more directly and the foliage was shaken vigorously to dislodge arthropods from the foliage. In some forests, a higher proportion of Collembola, Psocoptera and Thysanoptera are also sampled by canopy fogging (Kitching et al. 1993, Watanabe 1997, Southwood et al. 2005). Similar to my results, psyllids have formed 80% or more of the individuals belonging to Hemiptera sampled from other *Eucalyptus* species (Woinarski and Cullen 1984, Major and Recher 1988).

The arthropod orders inhabiting box mistletoe also inhabit other species of mistletoes, but the relative abundance and composition differs somewhat to the present study. One of the few other comprehensive studies of the invertebrate diversity associated with mistletoe plants involved a mistletoe species (*Tapinanthus bangwensis*, Loranthaceae) which parasitises cocoa plants in Ghana (Room 1972). It revealed that Araneae, Lepidoptera (mainly larvae), Hymenoptera (two-thirds ants), Hemiptera and Coleoptera were the most species rich orders collected from the foliage (Room 1972). The abundance of each order was not measured in that study but the twenty-six most
abundant species were dominated by ants and their associated Homopteran species. There was a distinct lack of ants sampled from mistletoe in the present study, perhaps because the mistletoes were not in flower at the time of sampling. However, the honeydew produced by the psyllids on mistletoes would be a good resource for ants and there are three published accounts of ant-attendance of psyllids for honeydew (Whittaker 1982, Paulson and Akre 1991, Novak 1994), but this was not evident in the present study. The only other study of the community composition of insects associated with a mistletoe species (*Phoradendron tomentosum*, Viscaceae, in south-western USA), determined 22 species of herbivores (including 12 specialists), 12 species of predators and parasitoids and 6 species of Homopteran-attendant ants; in the orders Lepidoptera, Coleoptera, Hemiptera, Orthoptera, Neuroptera and Hymenoptera (Whittaker 1982). This study found that interactions between herbivore, predator and parasitoid species, differences in dispersal ability and some resource partitioning allowed coexistence of specialist herbivore species with overlapping niches.

Furthermore, several species of butterflies in the genera *Delias* and *Mylothris* (Pieridae), and *Ogyris* (Lycaenidae) specialise on Australian and African mistletoes as a larval food plant (Braby 2000, Braby 2005, Braby 2006). The caterpillars of several of these species of butterflies are attended by ants, which feed on exudates from the caterpillars (Kitching 1991, Eastwood and Fraser 1999, Braby 2000). My study area is part of the distributional range of four butterfly species known to feed on *Amyema miquelii* including one species which is attended by ants (Braby 2000), but few Lepidopteran caterpillars were collected from the box mistletoe plants in this study.

Other epiphytic plants support similar invertebrate orders as those found on mistletoes, and also additional orders or classes including aquatic and soil-dwelling invertebrates (Cotgreave et al. 1993, Dejean et al. 1995, Richardson 1999, Kitching 2000, Ellwood et al. 2002, Yanoviak et al. 2003). This is due to the structural properties of epiphytic plants, which enables them to accumulate water and organic matter. Since epiphytic plants are often structurally different to their host-plants they are likely to support different arthropod taxa to their host-plants. There are only two published studies of the comparison of invertebrate communities between epiphytic plants and their host-plants, one comparing the abundance of orders and the other the species composition of herbivorous insects (Ødegaard 2000b, Ellwood and Foster 2004). These
studies demonstrated that epiphytic plants can support at least the same abundance of invertebrates as the tree canopy; and that lianas support different species of herbivorous insects to those inhabiting the host species. However, mistletoe plants are structurally similar to their host-plants, particularly Australian Loranthaceous mistletoes which are known to mimic the habit and leaf morphology of their hosts (Shaw et al. 2004, Watson 2004). Hence, the invertebrate faunal composition is likely to be more similar between mistletoes and their host-plants compared with other epiphytic plants and their hosts. Indeed, the incidence of arthropod orders was the same on the mistletoes and eucalypts in the present study. However, the composition of the arthropod assemblages inhabiting box mistletoe and its’ host eucalypts might differ at higher levels of taxonomic resolution, which will be the subject of the next chapter.

2.4.2 Density of arthropods related to leaf properties

Is the greater density of arthropods on eucalypts related to higher nitrogen in eucalypt leaves?

The greater density of arthropods, particularly the herbivorous Hemipteran insects, on the eucalypt foliage compared with the mistletoe foliage could be due to the significantly higher nitrogen content of the Eucalyptus leaves. Differential levels of growth, reproduction, abundance and diversity of insects have been observed on plants with differing nutrient concentrations (Ohmart 1991a, Marvier 1996, Recher et al. 1996a, Richardson et al. 2000, Peeters 2002a). Aphids feeding on parasitic plants had a greater survival rate and produced more offspring on the plants with the highest nitrogen concentration (Marvier 1996). A critical level of nitrogen in foliage, of 1.7%, was found for the larval growth and development of a chrysomelid beetle species (Ohmart 1991b). Furthermore, the densities of sap-sucking insects, including Psylloidea (Hemiptera), were significantly positively correlated with leaf nitrogen levels of several plant species in an Australian forest (Peeters 2002a). However, although the percentage content of nitrogen in the eucalypt leaves in this study was greater than the mistletoe leaves, it was still much lower than the general nutritional requirement of insects (Mattson 1980, Schoonhoven et al. 1998). The nitrogen content of insects is approximately 10% of dry weight; therefore herbivorous insects must consume large amounts of plant material and concentrate the available nitrogen. This is particularly so for sap-sucking insects, as the nitrogen content of phloem and xylem sap is lower than
other parts of the leaf blade and the rest of the plant (Mattson 1980, Schoonhoven et al. 1998). Sap-sucking insects, such as psyllids, excrete up to eighty percent of ingested carbohydrates as honey-dew (Hodkinson 1974). Therefore, since the nutritional requirements of the herbivorous insects are limiting on both the mistletoes and the *Eucalyptus* trees, other factors must be contributing to the differences in abundance between the arthropod communities.

**Influence of chemical and structural defences and leaf longevity on insect densities**

The growth and reproduction of insects, and hence insect densities, can be reduced by plant secondary metabolites (Schoonhoven et al. 2005). Leaf structural traits also impose limitations to feeding and can be more important determinants of insect densities than nutritional constituents of leaves (Peeters 2002b). *Eucalyptus* leaves contain a cocktail of secondary chemicals, including cyanogenic glycosides, terpenoids, and phenolic compounds; and numerous structural defences such as high concentrations of lignin and cellulose (Landsberg et al. 1997, Lawler et al. 1998, Gleadow et al. 2008). However, these chemicals do not always have a deterrent effect on herbivory and their effects can be unclear, e.g. phenolic levels are positively correlated with the C:N ratio of foliage, thus high phenolic levels are associated with low N levels (Landsberg et al. 1997, Burns et al. 2002, Gleadow and Woodrow 2002). A multitude of herbivores, both insects and mammals, consume eucalypt foliage and have overcome the constraints of the low nutritional quality and palatability of eucalypt foliage (reviewed by Landsberg and Cork 1997). For example, folivorous arboreal marsupials have nitrogen conserving mechanisms in their hindgut and a low metabolic rate (Cork and Foley 1991). Other marsupials supplement their diet with insects and many herbivores including insects feed on young foliage when available (which often contains greater N and fewer defences than mature foliage) (Ohmart et al. 1987, Ohmart and Edwards 1991, Landsberg et al. 1997). Herbivores are also likely to benefit from the continuous availability of eucalypt foliage and recurrent flushing of new leaves whenever environmental conditions are suitable (Landsberg et al. 1997).

Mistletoe plants are considered to have few structural defences (Mathiasen et al. 2008); and there is a distinct lack of research regarding the secondary chemistry of mistletoes in the Loranthaceae family. However, condensed tannins and other phenolics
have been measured in the foliage and stems of non-Australian Loranthaceae mistletoes (Tilney and Lubke 1974, Salatino et al. 1993). The lower specific leaf area and greater leaf thickness 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. Leaf turnover rates are three times greater for box mistletoe than red gum eucalypts in the local area of this study (March and Watson 2007), which is likely to also apply to the eucalypt species sampled in this study. Whole mistletoe plants are also usually shorter lived than their host trees (Watson 2001). Therefore, the combination of these factors (particularly greater nitrogen concentration of the eucalypt foliage than mistletoe foliage, and greater availability of eucalypt than mistletoe foliage) might explain the higher densities of insects, and hence predacious arthropods, on the eucalypt foliage than the box mistletoe foliage in this study.

2.4.3 Re-colonisation patterns of arthropod orders

After one year since the first sampling event, all the orders of arthropods, except Psocoptera, had successfully re-colonised the mistletoe plants that were ‘de-faunated’. The densities of orders on the de-faunated mistletoes were also similar to those on the non de-faunated mistletoe plants, sampled at the same time. Unlike other de-faunation experiments, the entire patch (in this case, clump) was not de-faunated: rather, just a portion of it was, so re-colonisation would be far easier (from unaffected parts of the same mistletoe clump, rather than some other mistletoe elsewhere). The change in relative abundance of orders between sampling events could lend itself towards supporting a stochastic non-equilibrium model of community structure, driven by environmental conditions and other ‘starting constraints’ (Floren and Linsenmair 1997). This model regards the presence of taxa at the most favourable time as the most important factor driving community composition. The significantly greater densities of Hemiptera and Hymenoptera on the re-colonised mistletoes compared with the original assemblages could reflect the favourable environmental conditions in the first year of sampling. The above average rainfall in the first year of sampling could have led to high fecundity of the insects in that year, resulting in greater abundances in the following year. Furthermore, the specimens of Hymenoptera, which mainly consisted of wasps, could have been favoured by the abundance of Hemipteran prey.
The similar densities of the arthropod orders inhabiting the re-colonised mistletoes and the newly sampled mistletoes in the second year, shows that the arthropod densities on the re-colonised plants reflected the general densities of arthropods in that year. Similarly, Floren and Linsenmair (1997) found that the ordinal composition of arthropod communities in rainforest tree canopies recovered after seven months since insecticide fogging, but the relative abundance of orders and the community structure at the species-level changed during that period. They attributed these patterns to the stochastic non-equilibrium model. In another re-colonisation study of the arthropods inhabiting a tree species, the high dissimilarity in species composition of the arthropod assemblages for the whole collection period up to one year since de-faunation, also suggested that stochastic processes were affecting the structure of the arthropod assemblages (Azarbayjani et al. 1999). Therefore, the results of this chapter lend themselves towards supporting the stochastic non-equilibrium model of community structure, rather than a deterministic equilibrium model. However, this hypothesis could change upon identification of taxa at the species level. Subsequent analyses of the similarity in species composition among the assemblages in relation to properties of the mistletoes and surrounding habitat, and spatial separation of the mistletoes, could reveal that deterministic factors also influence the assembly and maintenance of diversity of the arthropod communities.

It is expected that some of the herbivorous insects will be host-specific to either the mistletoe or eucalypt species. Therefore, the assembly and diversity of these insects would be more strongly influenced by deterministic factors of floristic composition in habitat patches and host-plant traits. Re-colonisation and community composition of the arthropod assemblages on mistletoes will also depend on the proximity of source populations to the de-faunated mistletoe plants and dispersal ability of the arthropod taxa. These factors will be explored for the psyllid assemblages on the mistletoe plants in Chapter 4, after examination of species-level data and host-specificity of psyllids in Chapter 3.
2.4.4 Finer-scale differences in arthropod composition between plant taxa

The beetle specimens were identified to family and feeding guild categories. Differences in the taxonomic and functional composition of the beetle families inhabiting the mistletoes and eucalypts have provided further evidence that the arthropod community of mistletoes differs to that inhabiting the eucalypt trees. While the two most abundant beetle families were the same among the assemblages on the mistletoes and eucalypts, specimens from seven families were collected either only on mistletoes or only on eucalypts. However, finer taxonomic resolution is still required to determine variation in species richness and composition between the arthropod assemblages on the plants in this study, and therefore the uniqueness or otherwise of the arthropod assemblages inhabiting box mistletoes compared to their host-trees. This will be the subject of the next chapter, regarding the community composition of the most abundant groups of arthropods in two trophic levels: the herbivorous psyllids (superfamily Psylloidea: Hemiptera) and the predacious spiders (Araneae).

2.5 Conclusion

In conclusion, the arthropod community inhabiting mistletoe plants consists of the same orders that inhabit *Eucalyptus* trees; however, the abundance of arthropods is less on the mistletoes than the eucalypts. Factors such as the chemical and structural properties of the plant foliage, the longevity of foliage and whole plants, and the abundance of the host-plants could all influence the variation in abundance of the arthropod communities between the host-plants. Further identification of selected groups of arthropods to species levels, will enable elucidation of finer-scale differences of the assemblages among the mistletoe and eucalypt plants; and thus the contribution of mistletoes to the diversity of canopy-dwelling arthropod communities.

It is expected that herbivorous insects will differentiate more between the plant taxa than spiders. Therefore, it is likely that the mistletoe plants will host specialist herbivorous insects and that the community composition of the herbivorous insects will vary more between the different plant genera, than will the community composition of the spiders. Thus, it is expected that host-plant taxon will be the most important determinant of beta-diversity among assemblages of host-specific arthropod taxa. In contrast, it is predicted that habitat traits will be more important determinants of beta-
diversity among generalist or predatory arthropods, than host-plant taxon, according to the niche requirements of the arthropods. Spatial and temporal patterns of variation in arthropod community composition will depend on the dispersal ability and other biological traits of the arthropod taxa. Therefore, greater homogeneity (lower beta-diversity) among assemblages is expected for more mobile taxa. Of the two arthropod groups examined in detail in the next chapter, psyllids are sedentary as larvae and mobile as adults; while spiders are mobile in all life-stages. Consequently there might be more homogeneity in community composition among the spider assemblages.
2.6 References


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Chapter 3

Arthropod assemblages of mistletoe in eucalypt woodlands: islands, sub-sets or something in-between?

3.1 Introduction

In the previous chapter I reported that the arthropod assemblages inhabiting mistletoe plants and eucalypt trees did not differ in the composition of orders. Therefore identification at lower taxonomic levels is required to examine host-plant specificity of the arthropods. Identifications of taxa at the species-level allow elucidation of patterns of species richness and other components of diversity from local to global scales. Although species-level identifications are particularly difficult for super-diverse taxa such as arthropod fauna, due to lack of species descriptions and availability of taxonomic expertise, this level of taxonomic resolution is more informative and enables more powerful comparative research (Austin 1999). The use of morphospecies (or ‘repeatable taxonomic units’) has provided amateur taxonomists a means of identifying specimens to a high taxonomic resolution with reasonable accuracy (Oliver and Beattie 1996, Pik et al. 1999) and has been particularly useful for ecological studies of diverse taxa (e.g. Longino and Colwell 1997, Lawton et al. 1998, Majer et al. 2000, Yanoviak et al. 2003, Novotny et al. 2007). Species or morphospecies identifications, together with ecological information, enable determination of fine-scale differences in the composition of arthropod assemblages between host-plants or habitats, and thus patterns of alpha- and beta-diversity among and between different host-plants or habitats.

When sampling diverse organisms such as invertebrates, a problem still remains that it is almost impossible to determine the true abundance and distribution of all species of an ecosystem or habitat. Therefore, estimates of true species diversity are derived from the species richness and abundance of communities sampled in small
areas. Studies of a variety of taxa have estimated true species richness (or alphadiversity) from extrapolation of species accumulation curves, parametric estimates from models of the relative abundance distributions of species, and non-parametric estimates from observed species incidence and abundances (Colwell and Coddington 1994, Magurran 2004). These techniques allow not only estimation of true species richness, but can be useful for measuring sampling adequacy.

The change in species composition between samples or sites is assessed by differentiation diversity or beta-diversity. In its original form, beta-diversity was proposed as the change in species composition along environmental gradients (Whittaker 1960). Since then, the concept has been applied to biological dissimilarity between any spatially separated samples, habitats or landscapes, irrespective of environmental gradients (Whittaker 1977, Harrison et al. 1992, Vellend 2001, Koleff et al. 2003, Magurran 2004). Here, beta-diversity of arthropod assemblages will be assessed for samples collected from different host-plant genera, i.e. *Amyema* mistletoes vs. *Eucalyptus* trees; and among samples from individuals of the same host-plants separated by varying distances. A hypothesis regarding the beta-diversity of herbivorous insects proposed by Novotny and Weiblen (2005) is that communities on widespread, dominant plant taxa in temperate and tropical forests will exhibit low beta-diversity. Research by Novotny et al. (2007) supports this hypothesis, as they found low beta-diversity (i.e. greater than 50% average similarity) among assemblages of Lepidopteran caterpillars inhabiting widespread host-plant genera in lowland continuous rainforest. This is related to the finding that most herbivorous tropical insects are specialised at the level of host-plant genus or family, rather than to individual plant species (Novotny et al. 2002a). Further research is required to determine patterns of beta-diversity of other arthropod taxa, particularly more specialised herbivores, in different habitats, at different geographical scales and among host-plant taxa with differing levels of diversity and distributional ranges (Novotny and Weiblen 2005).

To determine the true species richness and complementarity of arthropod communities, the host- or habitat-specificity of the arthropods needs to be determined. The host-specificity of herbivorous insects is usually defined according to dietary specialisation, that is, the number and taxonomic relationship of the host-plants upon which an insect feeds: i.e. association with only one host-plant species
(monophagous), a few host-plant species in the same family (oligophagous), or many host species in different families (polyphagous). The host-specificity of insects is best determined by observations of host-feeding and oviposition, in the species’ whole geographical range. However, this information is usually not available and is difficult to obtain, therefore we often rely on distributional data and statistical estimations to determine or predict host and habitat associations (Fagan et al. 2006, Stork and Grimbacher 2006).

Insects can be associated with plants for reasons other than feeding and oviposition, for example they may be attracted to a plant for shelter, sun-basking, sexual display or protection from natural enemies (Moran and Southwood 1982, Schoonhoven et al. 1998). Insects that fit into these categories and those that occur on a plant incidentally, are termed ‘tourist’ or ‘transient’ species in diversity studies (Moran and Southwood 1982, Stork 1987, Basset and Arthington 1992, Novotny et al. 2002a, Ødegaard 2004). These studies have determined host-specificity and tourist species by feeding trials, larval rearing, gut contents analysis, field observations and published host records. In the present study, host-specificity and, thus, putative ‘tourist’ species and ‘resident’ species will be determined from information in the published literature and with a statistical method (indicator species analysis) that assesses whether the frequency and abundance of species with respect to different hosts is greater than would be expected by chance.

The group of herbivorous insects that I studied in detail for this thesis are psyllids, in the order Hemiptera, superfamily Psylloidea (also known as jumping plant-lice or lerp insects). There are 354 described species of Psylloidea in Australia and 100 or more species awaiting description, which is more than 10% of the world fauna. The superfamily Psylloidea is thought to have originated from a southern fauna probably on Gondwana (Eastop 1978, Hodkinson 1989, Hollis 2004). Psyllids feed exclusively on phloem and most psyllid species are either monophagous or oligophagous, developing on a single host-plant species or a group of congeneric species. While several psyllid species have been recorded on more than one host genus, none are known to feed on more than one host family (Hodkinson 1974, Hollis 2004, Percy et al. 2004). While all psyllid species exhibit a narrow host range, host-plants from many different families can be found in one psyllid genus, e.g. Acizia. A psyllid host-plant is defined as a species on which the psyllid completes its
development from egg to fertile adult (Hodkinson 1974, Hollis 2004). Adult psyllids (which can fly) can feed on more than one plant species but return to their true host-plants to copulate and oviposit (Hollis 2004), but the wingless nymphs are typically restricted to the one plant for their entire development (Hodkinson 1974, Hollis 2004). Therefore, these patterns of host-specificity of psyllid insects will be examined regarding host-plants that are closely integrated (i.e. *Amyema miquelii* mistletoes in *Eucalyptus* trees) but which belong to different families.

The host-specificity and diversity of herbivorous insects will be contrasted with that of generalist predatory arthropods: spiders. In Australia, there are about 2,000 described species of spiders but it is estimated that there are at least 10,000 species (Raven et al. 2002). The host-specificity of arthropods other than herbivores such as predators, parasitoids and scavengers can be determined by evaluating specificity to substrate, habitat or prey. The distribution and population density of spiders in their habitats is not random, but sculpted by physical conditions, such as temperature, humidity, wind and light intensity, and biological factors such as type of vegetation, food supply, competitors and enemies (Foelix 1982). The spatial structure of the environment is especially important for web-building spiders. Furthermore, there is often a vertical stratification in spider species distribution that corresponds with the vertical stratification of different vegetation types, from the soil zone to the canopy (Foelix 1982). Species and families of spiders exhibit preferences for different habitat types shown by differences in species richness, composition and activity density between habitats (Öberg et al. 2007). Some spiders are also preferentially associated with certain plant species which have structural features that are advantageous for their survival. For example, lynx spiders in the genus *Puecetia* (Oxyopidae) preferentially dwell on plants with glandular trichomes, which are thought to aid prey capture of insects (Vasconcellos-Neto et al. 2007). In addition, several species of jumping spiders (Salticidae) specifically use bromeliad plants over a wide geographic range in South America, with some jumping spiders almost exclusively inhabiting a particular bromeliad species, while other species inhabit 7–8 bromeliad species (Romero 2006). The architecture of the leaves of the bromeliads is thought to be beneficial to the spiders for shelter, mating, foraging, egg-laying and as a nursery for spiderlings. However, spiders that inhabit the canopy of trees are not necessarily host-plant-specific. The similarity in species composition of spiders inhabiting the canopy of five rainforest tree species, in four families, was not
influenced by the taxonomic relationship between the trees (Russell-Smith and Stork 1995). In a study of spiders inhabiting dwarf mistletoes, none of the spider species were restricted to the mistletoes, they were also common on the hosts of the mistletoes and many other conifer species (Jennings et al. 1989).

Mistletoes exhibit a mosaic of features that are variously similar or different to their hosts. Leaf shape of mistletoes can be indistinguishable from that of their hosts, particularly for species of *Amyema* (illustrated in Shaw et al. 2004, Watson 2004, and references therein), but the foliage of mistletoes and their hosts can differ in concentrations of nutrients, water and defensive chemicals. Several mistletoe species contain higher nitrogen concentrations than their host-plants, including species of *Amyema* (Lamont and Bernhardt 1983, Ehleringer et al. 1986b). However, the foliage of *Amyema miquelii* often contains a lower concentration of nitrogen than its *Eucalyptus* host-plants (Ehleringer et al. 1986b, Kuppers 1992, March 2007), as was also found in this study (Chapter 2). There is a lack of studies of the secondary chemistry of Loranthaceous mistletoes, but the existing studies have revealed that mistletoes contain condensed tannins and other phenolic compounds and can extract nitrogen-based secondary chemicals from their hosts (Khanna et al. 1968, Atsatt 1977 and references therein, Salatino et al. 1993). Foliage of *Eucalyptus* trees contains a range of secondary chemicals such as phenolics, including condensed and hydrolysable tannins, terpenoids and cyanogenic glycosides, and is highly lignified (Landsberg et al. 1997, Lawler et al. 1998, Gleadow et al. 2008). These foliage traits have not limited and perhaps have promoted the diversification of insects associated with *Eucalyptus* species (Morrow 1977, Majer et al. 1997). Of the studies of insects associated with mistletoe plants, several species of butterflies have been documented as feeding on mistletoes in their larval stages, either exclusively or as a large part of their diet (De Baar 1985, Braby 2000, Braby 2005). While there are no direct studies of the influence of structural properties of mistletoes on invertebrate animals; a study simulating the structure of witches’ brooms in Douglas-fir branches (which are induced by mistletoe infection) found that community composition of spider assemblages was related to variation in foliage structure, e.g. hunting and sheet-web spiders showed clear micro-habitat preferences based on vegetation structural properties (Halaj et al. 2000).
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This is an exploratory study to investigate the contribution of box mistletoe plants to the arthropod diversity of *Eucalyptus*-dominated woodlands, and the influence of host-specificity on patterns of alpha- and beta-diversity of the arthropod assemblages. Two trophic guilds of arthropods have been selected: herbivorous insects and predaceous spiders, which have differing degrees of host-plant specificity. The host-plant system investigated is a hemi-parasitic plant, box mistletoe (*Amyema miquelii*), and three of its host-tree species which all belong to the genus *Eucalyptus*. The overall question addressed in this chapter is: do assemblages of arthropods in two trophic guilds differ in their host-specificity, species richness, species composition and abundance between a mistletoe species and the mistletoes’ host-trees? After examining the influence of host-plant species on the community composition of the herbivorous and predatory arthropod assemblages in the present chapter, I will use these comparisons to generate further insight into the ecology of canopy-dwelling arthropods, including factors determining their assembly and occurrence patterns in the following chapter.
3.2 Methods

3.2.1 Arthropod identification

The arthropods were collected as described in Chapter 2. I sorted the Psylloidea (Hemiptera) specimens to morphospecies that were subsequently identified to genus and species by taxonomist Dr Gary Taylor (The University of Adelaide, South Australia). I identified the Araneae specimens to family and morphospecies, and taxonomists Cathy Car (Charles Sturt University) and Graham Milledge (Australian Museum) agreed with most of my morphospecies boundaries but four morphospecies were combined into one morphospecies and they assigned genus names to four morphospecies. The Salticidae specimens were identified to genus by Dr Barry Richardson (CSIRO Entomology). The other tentative generic names for the spiders were assigned from Shield (2001) (i.e. those denoted with “?” in Table 3.4).

3.2.2 Species richness and diversity estimation

Species richness indices

The true species richness of the psyllid and spider communities associated with the mistletoe and eucalypt hosts was estimated by five indices and extrapolation from the species-accumulation curve, and compared with the observed species richness. I used the non-parametric estimators based on species incidence data that have performed reasonably well in other studies: Chao2, Incidence-based coverage estimator (ICE) and Jackknife 2, and the Michaelis-Menten model of the species-accumulation curve (Magurran 2004). Since abundance data were also collected in the present study the Chao1 and abundance-based coverage estimator (ACE) were also evaluated and all of these indices were calculated by the EstimateS 7.5.1 © statistical package (Colwell 2006).

The Chao1 estimator (equation 6) (Chao 1984, Colwell and Coddington 1994) incorporates the observed number of species plus a ratio of rare species in the samples.

\[
\text{Chao1} = S_{obs} + \frac{a^2}{2b}
\]  

(6)

Where \( S_{obs} \) is the observed number of species and \( a \) and \( b \) are the number of species that are represented by only one individual and exactly two individuals,
respectively (i.e. singleton and doubleton species: (Colwell and Coddington 1994). The estimated true number of species equals the observed number of species when all species are represented by at least two individuals.

The Chao2 estimator (equation 7) (Chao 1984, Colwell and Coddington 1994) incorporates the observed number of species plus a ratio of infrequent species in the samples.

$$\text{Chao 2} = S_{\text{obs}} + \left( \frac{L^2}{2M} \right)$$  \hspace{1cm} (7)

Where $S_{\text{obs}}$ is the observed number of species and $L$ and $M$ are the number of species that occur in only one sample and exactly two samples, respectively (i.e. unique and duplicate species: (Colwell and Coddington 1994). The estimated true number of species equals the observed number of species when all species are present in at least two samples.

The second order Jackknife estimator (equation 8) is also calculated from incidence data and incorporates an expression based on the number of species that occur in only one sample and exactly two samples (Colwell and Coddington 1994).

$$\text{Jackknife 2} = S_{\text{obs}} + \left[ \frac{L(2n - 3)}{n} - M \left( \frac{n - 2}{n(n - 1)} \right) \right]$$  \hspace{1cm} (8)

Where $n$ is the number of samples and $L$ and $M$ are as above.

The equation of the incidence-based coverage estimator of species richness (Colwell 2006 Appendix B) is:

$$S_{\text{ice}} = S_{\text{freq}} + \frac{S_{\text{infr}}}{C_{\text{ice}}} + \frac{Q_1}{C_{\text{ice}}} \nu_{\text{ice}}^2$$  \hspace{1cm} (9)

Where $S_{\text{freq}}$ is the number of species in greater than 10 samples (frequent species) and $S_{\text{infr}}$ is the number of species in 10 or fewer samples (infrequent species) (Magurran 2004). The sample coverage estimate, i.e. the proportion of all individuals in infrequent species that are not uniques, is:

$$C_{\text{ice}} = 1 - \frac{Q_1}{N_{\text{infr}}}$$,
where \( N_{\text{inf}} = \sum_{j=1}^{10} jQ_j \) (i.e. the total number of individuals in infrequent species)

and \( Q_j \) is the number of species that occur in \( j \) samples. The term that estimates the coefficient of variation of the \( Q_j \)'s, is

\[
\gamma_{\text{icr}}^2 = \max \left[ \frac{S_{\text{inf}}}{C_{\text{icr}} (m_{\text{inf}}-1)} \left( \sum_{i=1}^{10} \frac{j(j-1)Q_j}{N_{\text{inf}}} \right)^2 - 1,0 \right]
\]

The abundance-based coverage estimator of species richness (Colwell 2006 Appendix B) is:

\[
S_{\text{acc}} = S_{\text{abund}} + \frac{S_{\text{rare}}}{C_{\text{ace}}} + \frac{F_1}{C_{\text{ace}}} \gamma_{\text{acc}}^2
\]

Where \( S_{\text{abund}} \) is the number of species with greater than 10 individuals and \( S_{\text{rare}} \) is the number of species with 10 or fewer individuals (Magurran 2004). The sample coverage estimate, i.e. the proportion of all individuals in rare species that are not singletons, is:

\[
C_{\text{acc}} = 1 - \frac{F_1}{N_{\text{rare}}},
\]

where \( N_{\text{rare}} = \sum_{i=1}^{10} iF_i \) (i.e. the total number of individuals in rare species)

and \( F_i \) is the number of species with \( i \) individuals. The term that estimates the coefficient of variation of the \( F_i \)'s, is:

\[
\gamma_{\text{ace}}^2 = \max \left[ \frac{S_{\text{rare}}}{C_{\text{ace}} (N_{\text{rare}})(N_{\text{rare}}-1)} \left( \sum_{i=1}^{10} \frac{i(i-1)F_1}{N_{\text{rare}}} \right)^2 - 1,0 \right]
\]
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The number of species expected to accumulate with increasing sampling effort can be extrapolated by fitting an asymptotic curve to the observed data (Colwell and Coddington 1994). The Michaelis-Menten model for the species accumulation curve was used in this study:

\[ S(n) = \frac{S_{\text{max}} + n}{B + n} \]

(11)

Where \( S(n) \) is the number of species observed in \( n \) samples, \( S_{\text{max}} \) is the total number of species in the assemblage and \( B \) is the sampling effect required to detect 50% of \( S_{\text{max}} \) (Magurran 2004).

Species diversity and evenness indices

The diversity and evenness of the psyllid and spider assemblages in the mistletoe and eucalypt samples were evaluated with Simpson’s Diversity and Evenness indices. Simpson’s Diversity index emphasises the dominance of the species in the assemblage. In its original form Simpson’s Diversity index is the probability that two randomly chosen individuals belong to the same species:

\[ D = \sum p_i^2 \]

Or, for a finite community

\[ D = \sum \left( \frac{n[n-1]}{N[N-1]} \right) \]

(12)

where \( p_i \) is the proportion of individuals in the \( i \)th species, \( n_i \) is the number of individuals in the \( i \)th species and \( N \) is the total number of individuals. Simpson’s diversity is often reported as \( 1-D \) or \( 1/D \) so that the index increases as the diversity of the samples increases (Magurran 2004) and it is reported in the reciprocal form in this thesis.

Simpson’s Evenness index is a measure of the evenness of the abundance of individuals across the species. It is calculated as:

\[ E_{1/D} = \frac{(1/D)}{S} \]

These indices were computed in EstimateS 7.5.1 © (Colwell 2006) with 50 randomisations of the sample accumulation order. Two eucalypt samples that did not
contain any adult psyllids and one mistletoe sample that did not have any spiders were excluded from the analyses of species richness and diversity because EstimateS does not accept rows with zero totals.

3.2.3 Estimation of host-specificity

Indicator species analysis was used to estimate the host-specificity of the psyllids and spiders by determining whether each taxon had a non-random distribution with regard to each host, i.e. mistletoe vs. eucalypts. The indicator species values are based on the average relative abundance and frequency of the taxa in each group of samples. The indicator value \( IV \) of taxa \( j \) in host group \( k \) (McCune and Grace 2002) is calculated as:

\[
IV_{kj} = (\text{Relative abundance}_{kj} \times \text{Relative frequency}_{kj}) \times 100
\]

where the relative abundance and frequencies are expressed as proportions.

The statistical significance of the highest indicator value for a given taxon across the host groups \( IV_{\text{max}} \) was evaluated by a Monte Carlo randomisation test. Maximum indicator values were calculated from 4999 permutations of the data matrix, to test the null hypothesis that \( IV_{\text{max}} \) for taxa \( j \) in host group \( k \) is no larger than would be expected by chance. The significance values are the proportion of randomized trials with indicator values equal to or exceeding the observed indicator value. PC-ORD 5.07 © (McCune and Mefford 2006) was used for this analysis.
3.2.4 Similarity in species composition and abundance

**Observed and estimated true similarity between samples**

The observed similarity in species composition and relative abundances of the arthropod assemblages, within and between the mistletoe and eucalypt samples was calculated using three similarity indices: the Jaccard index (equation 14), for similarity in species composition derived from incidence data, the Bray-Curtis or Sørensen quantitative index (equation 15), and the Morisita-Horn index (equation 16) to determine the similarity in relative abundances of species between samples. The density of individuals per leaf area (m²) was used in calculation of the Bray-Curtis and Morisita-Horn indices. The indices were computed in EstimateS 7.5.1 © (Colwell 2006) from comparisons of all sample combinations.

**Jaccard index**

\[ \text{Jaccard index} = \frac{a}{(a + b + c)} \]  

Where \( a \) is the number of species present in both samples, and \( b \) and \( c \) are the number of species only in sample 1 and only in sample 2, respectively (Magurran 2004).

**Bray-Curtis index**

\[ \text{Bray-Curtis index} = \frac{2jN}{(N_a + N_b)} \]  

Where \( jN \) is the sum of the lower of the two abundances (i.e. densities) for each species found in both samples, and \( N_a \) and \( N_b \) are the total density of individuals in samples A and B, respectively (Magurran 2004).

**Morisita-Horn index**

\[ \text{Morisita-Horn index} = \frac{2\sum (a_i \cdot b_i)}{(d_a + d_b) \cdot (N_a \cdot N_b)} \]  

Where \( a_i \) is the density of individuals in the \( i \)th species in sample A; \( b_i \) is the density of individuals in the \( i \)th species in sample B; \( N_a \) and \( N_b \) are as above; and \( d_a \) (and similarly \( d_b \)) is calculated as follows (Magurran 2004):

\[ d_a = \frac{\sum d_i^2}{N_a^2} \]

The true similarity in species composition and abundance of the arthropod assemblages was estimated with the Jaccard abundance-based estimator (Chao et al.
2005), which takes into account the effect of unseen shared species. The value of the index is weighted based on the frequencies of rare, shared species in the samples because the greater their frequencies, the more likely it is that additional shared species are present in both true assemblages but are absent from one or both samples (Chao et al. 2005). The standard deviation of the Jaccard abundance-based estimator was calculated with a bootstrap procedure, from the recommended 200 times re-sampling of the data in EstimateS 7.5.1 © (Colwell 2006).

Two eucalypt samples that did not contain any adult psyllids and one mistletoe sample that did not have any spiders were excluded from the analyses because EstimateS does not accept rows with zero totals.

**Visualisation of similarity among samples: non-metric multidimensional scaling**

The similarity between and among the sample groups was visualised with non-metric multi-dimensional scaling (NMDS) using the software PC-ORD 5.07 © (McCune and Mefford 2006). NMDS is the most appropriate ordination technique for ecological data that contains many species and large variation in species abundances (McCune and Grace 2002) and it allows identification of the dominant patterns in the data set. It determines the rank similarities between all samples in species composition and abundances (depending on the similarity index of choice), thereby avoiding assumptions of normality and linear relationships between species, which are required by other ordination techniques such as principal co-ordinates analysis (Clarke 1993, McCune and Grace 2002). Furthermore, any dissimilarity index can be used with this technique. I used 250 runs with the real data and 250 runs with the randomized data, a maximum of 6 dimensions, random starting co-ordinates, maximum 500 iterations, and a stability criterion of <0.000001 (i.e. the value of the standard deviation of stress over the final 10 iterations). The runs with the randomized data resulted from randomization of the observed data among the species variables; this was the process used to evaluate whether NMS extracted stronger axes than expected by chance. The dissimilarity in species composition and abundance between all samples was calculated with the Bray-Curtis index, from untransformed species densities. Square-root transformed and log transformed data were assessed but results from the transformed data were no more robust or informative than the results from the untransformed data. Samples without any taxa were removed from the data set because PC-ORD does not accept rows with zero totals.
Determination of the influence of each taxon on the arrangement of samples in the NMDS ordination was evaluated by the correlations of the taxa with each axis. The values of the non-parametric Kendall’s rank correlation coefficient, \( \tau \), were assessed against the critical values of Kendall’s \( \tau \), accepting a Type I error of \( \alpha = 0.05 \) (Table 3.0).

<table>
<thead>
<tr>
<th></th>
<th>Psyllids</th>
<th>Spiders</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mistletoe samples</td>
<td>0.255 ((N = 30))</td>
<td>0.261 ((N = 29))</td>
</tr>
<tr>
<td>Eucalypt samples</td>
<td>0.368 ((N = 17))</td>
<td>0.333 ((N = 19))</td>
</tr>
<tr>
<td>Mistletoe &amp; Eucalypt samples</td>
<td>0.218 ((N \geq 40))</td>
<td>0.218 ((N \geq 40))</td>
</tr>
</tbody>
</table>

**Independence of samples**

To test the assumption of the independence of observations within each sample group, which is required for statistical tests of the variation within and between sample groups, a Mantel Test was conducted to determine the spatial correlation of the samples. This involved regression of two matrices: the compositional dissimilarity between samples and the geographic distance between samples, to determine whether there is a linear relationship between the matrices. Mantel’s Test assesses how often randomisation of one matrix results in a correlation as strong or stronger than the observed correlations between the matrices (McCune and Grace 2002). Separate matrices for the mistletoe and eucalypt samples were compiled, and the Jaccard and Bray-Curtis dissimilarity indices were used for differences in species composition and relative abundances between samples. Mantel’s asymptotic approximation method was used to evaluate the test statistic, calculated with PC-ORD 5.07 © (McCune and Mefford 2006).
Statistical test for difference between groups: multi-response permutation procedure

The null hypothesis of no difference in observed species composition and abundance of the arthropod assemblages between the mistletoe and eucalypt samples (i.e. beta-diversity) was tested with the multi-response permutation procedure (MRPP). This procedure is a non-parametric statistical test that is well suited to testing for differences between groups of samples of ecological multivariate data. MRPP does not assume normality in the distribution of the data, or homogeneity of variances under the alternative hypotheses and does not require a balanced experimental design (Zimmerman et al. 1985, McCune and Grace 2002). Therefore, MRPP is more appropriate than MANOVA or PERMANOVA for analysis of my data sets. The only assumption of MRPP is that the sample units are independent. This procedure tests the probability that the average observed within-group dissimilarity is significantly less than would be expected by chance, from permutation of the data set. The weighted mean within-group compositional dissimilarity, $\delta$, of the observed data, is compared to the expected $\delta$ derived from multiple permutations of the data in which samples are randomly assigned to groups. A test statistic, $T (\text{observed } \delta - \text{expected } \delta)/\text{SD expected } \delta$, is compared to the distribution of all possible deltas resulting from permutation of the data. The effect size of the difference between groups is determined by the ‘chance-corrected within-group agreement’ statistic, which describes the within-group homogeneity compared to the random expectation (McCune and Grace 2002). Bray-Curtis and Jaccard dissimilarity indices were used in the analyses to encompass both differences in species incidence and abundance (i.e. untransformed species densities) between samples; computed with PC-ORD 5.07 © (McCune and Mefford 2006). Blocked MRPP was used to test the differences between the psyllid and spider assemblages inhabiting mistletoe and eucalypt foliage sampled in the same tree. Only the Euclidean dissimilarity (i.e. the absolute difference in abundance) is available for use in Blocked MRPP.

Statistical test for variation within groups: multivariate dispersions test

To evaluate whether the arthropod fauna inhabiting mistletoe and eucalypt foliage display different patterns of variation in species composition and abundance within each sample group (i.e. internal beta-diversity), a distance-based test of homogeneity of multivariate dispersions was used (Anderson 2006). Differences in dispersion between sample groups may reflect different levels of heterogeneity in
host-plant or habitat qualities. For each host-plant and faunal group, the distance in compositional dissimilarity from each observation to the group centroid was determined in ordination space (the least-squares residuals). The group centroid is the point which minimises the sum of squared distances to points within that group. A $P$-value was obtained by permutation of the least-squares residuals, to avoid making assumptions about the distribution of distances. Any dissimilarity index can be used in the test, so the Jaccard and Bray-Curtis dissimilarity indices were used to encompass both qualitative and quantitative differences in species composition. The only assumption of the test is independence of the observations. The test was performed with the PERMDISP2 computer program (Anderson 2004). This method is more suitable for determining the variation between samples within the same host group, compared to a significance test of the normal arithmetic mean and variance of all pair-wise comparisons of dissimilarity between samples, because the data for the latter test would not be independent. The lack of independence of observations is avoided in the multivariate dispersions test due to determination of the group centroid and calculation of distances from each observation to the group centroid.
3.3 Results

In the first sampling period, November 2005, arthropods were collected from both mistletoe and eucalypt foliage. The results of the analyses of the most abundant herbivorous group (the psyllids) and the most abundant predatory group (the spiders) are presented here.

Part A - Psyllids

3.3.1 Comparison of species richness, diversity and host-specificity of psyllids in the mistletoe and eucalypt assemblages

A total of 21 morphospecies, belonging to 12 genera were found in the mistletoe and eucalypt samples (Table 3.1). All but one species, *Schedotrioza distorta* (Triozidae), belong to the family Psyllidae. The mistletoe samples contained 17 morphospecies, while 20 morphospecies were found in the eucalypt samples. Sixteen of the total morphospecies occurred in both the mistletoe and eucalypt samples. Seventeen of the psyllid morphospecies were sampled from the red box trees (*N* = 12), which were the largest sample group of the eucalypt hosts. The samples from the other eucalypt hosts: yellow box and Blakely’s red gum, contained 11 and 4 morphospecies, respectively.

The host records of the psyllid morphospecies identified to species and genera were examined from the published literature. Two of the psyllid species, *Acizza loranthacae* and *A. amyemae* (Fig. 3.1a,b, Table 6.0, Appendix), which are considered host-specific to mistletoes (*Amyema* spp., Loranthaceae) (Taylor 1999) were abundant and frequent in the mistletoe samples (Table 3.1). This study is the first confirmed record of these two species on *Amyema miquelii*. These two species, *Acizza loranthacae* and *A. amyemae*, only occurred as one and two individuals in the eucalypt samples (Table 3.1). The mistletoe samples also contained psyllid species that are only known to occur on *Eucalyptus* species, i.e. *Platyobria adustalata* (MS5), *P. lewisi* (MS14), *Anoeconeossa communis* (MS8), *Schedotrioza distorta* (MS13), *Cardiaspina retator* (MS19) and *C. albicollaris* (MS26) (Table 6.0, Appendix), and all of these species occurred in the eucalypt samples. The other morphospecies collected in the eucalypt and mistletoe samples (only identified to genus), belong to genera containing species that have been recorded on *Eucalyptus* species or other hosts in the Myrtaceae family (Hollis 2004) (Table 6.0, Appendix). This includes the two most abundant morphospecies in the eucalypt samples: *Australopsylla* sp.1 (MS3,
Fig. 3.1c) and *Australopsylla* sp.2 (MS10, Fig. 3.2j), which belong to a genus that has only been recorded on *Eucalyptus* host species. However, these two morphospecies were also abundant in the mistletoe samples.

To further determine which psyllid species are ‘tourists’ and which are ‘residents’ on each host-plant, indicator species analysis was conducted. Three species and four morphospecies were found to have a non-random distribution with respect to one of the host-plant groups (Table 3.2). The highly significant indicator species values of *Acizzia loranthaceae* and *A. amyemae* (*P* < 0.01) confirms the host-specificity of these two species on mistletoe; therefore they are considered tourist species on the eucalypt hosts sampled in this study. The two most abundant morphospecies: *Australopsylla* sp.1 (MS3, Fig.3.1c), *Australopsylla* sp.2 (MS10, Fig.3.2j), and three other morphospecies: *Anoeconeossa* sp.1 (MS6, Fig.3.1f), *Blastopsylla* sp.1 (MS7, Fig.3.1g) and *Anoeconeossa communis* (MS8, Fig.3.2h), occurred at a significantly greater density and frequency in the eucalypt samples than the mistletoe samples (*P* < 0.05, Table 3.2). Therefore, these five morphospecies will be considered tourist species on mistletoe in this study. The six species that have only been recorded on *Eucalyptus* species, as listed in the previous paragraph, will also be considered tourists on mistletoe (i.e. MS 5, 8, 13, 14, 19 and 26 in Table 3.1). The five other morphospecies in the mistletoe samples (i.e. MS 4, 18, 21, 22 and 23) belong to genera that contain species that have been recorded on *Eucalyptus* species and other species in the Myrtaceae family (Table 6.0, Appendix). These morphospecies did not occur abundantly or frequently enough on a particular host in this study to result in significant indicator species values; therefore they will be considered residents on the mistletoe and eucalypt hosts in the present study but their host relations are unclear. From this point forward the term ‘species’ will be used for taxa identified to species or morphospecies.
Figure 3.1 Psyllid taxa collected from box mistletoe and the eucalypt host trees. (a) *Acizzia loranthacae*, MS 1; (b) *Acizzia amyemae*, MS 2; (c) *Australopsylla* sp.1, MS 3; (d) *Phyllopsylla* sp. MS 4; (e) *Platyobria adustalata* MS 5; (f) *Anoeconeossa* sp.1, MS 6; (g) *Blastopsyilla* sp.1, MS 7.
Figure 3.2 Psyllid taxa collected from box mistletoe and the eucalypt host trees, continued: (h) *Anoeconeossa communis*, MS 8; (i) *Platyobria* sp.1, MS 9; (j) *Australopsylla* sp.2, MS 10; (k) *Australopsylla* sp.3, MS 11; (l) *Schedotrioza distorta*, MS13; (m) *Platyobria lewisi*, MS 14; (n) *Acizza* sp.1, MS 16; (o) *Creiis* sp.1, MS 15.
Figure 3.3 Psyllid taxa from box mistletoe and the eucalypt host trees, continued: (p) Ctenarytaina sp., MS 18; (q) Cardiaspina retator, MS 19; (r) Protorya sterculiae, MS 20; (s) Glycaspis sp., MS 21; (t) Hyalinaspis sp., MS 22; (u) Blastopsylla sp.2 (near multisetulae), MS 23 (v) Acizia sp.2, MS 24; (w) Creiis sp.2, MS 25; (x) Cardiaspina albicollaris, MS 26; (y) Spondylaspis plicatuloides, MS 27; (z) Cryptoneossa sp.?, MS 17.
Table 3.1 Species inventory of psyllid assemblages collected from box mistletoe and its *Eucalyptus* hosts. Comparison of abundance (total no. individuals), average density (no. individuals m$^{-2}$ leaf area, dry weight) and percent frequency of psyllid morphospecies in the mistletoe ($N=30$) and eucalypt ($N=19$) samples. Tourist species were determined from the literature and indicator species analysis.

<table>
<thead>
<tr>
<th>Morphospecies / Species</th>
<th>Mistletoe samples</th>
<th>Eucalypt samples</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Abundance</td>
<td>Density</td>
</tr>
<tr>
<td>MS1 <em>Acizzia loranthacae</em></td>
<td>294</td>
<td>2.99</td>
</tr>
<tr>
<td>MS2 <em>Acizzia amyemae</em></td>
<td>103</td>
<td>0.98</td>
</tr>
<tr>
<td>MS3 <em>Australopsylla</em> sp.1</td>
<td>279</td>
<td>2.67</td>
</tr>
<tr>
<td>MS4 <em>Phyllolyma</em> sp.</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS5 <em>Platyobria adustalata</em></td>
<td>8</td>
<td>0.10</td>
</tr>
<tr>
<td>MS6 <em>Anoeconeossa</em> sp.1</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS7 <em>Blastopsylla</em> sp.1</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS8 <em>Anoeconeossa communis</em></td>
<td>4</td>
<td>0.04</td>
</tr>
<tr>
<td>MS9 <em>Platyobria</em> sp.1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>MS10 <em>Australopsylla</em> sp.2</td>
<td>117</td>
<td>1.20</td>
</tr>
<tr>
<td>MS11 <em>Australopsylla</em> sp.3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>MS13 <em>Schedotrioza distorta</em></td>
<td>1</td>
<td>0.01</td>
</tr>
</tbody>
</table>
### Mistletoe samples

<table>
<thead>
<tr>
<th>Morphospecies / Species</th>
<th>Abundance</th>
<th>Density</th>
<th>Frequency</th>
<th>Tourist</th>
<th>Abundance</th>
<th>Density</th>
<th>Frequency</th>
<th>Tourist</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS14 <em>Platyobria lewisi</em></td>
<td>4</td>
<td>0.04</td>
<td>10</td>
<td>Y</td>
<td>3</td>
<td>0.13</td>
<td>16</td>
<td>N</td>
</tr>
<tr>
<td>MS15 <em>Creis</em> sp.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
<td>1</td>
<td>0.07</td>
<td>5</td>
<td>N</td>
</tr>
<tr>
<td>MS16 <em>Aczzarella</em> sp.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
<td>1</td>
<td>0.04</td>
<td>5</td>
<td>?</td>
</tr>
<tr>
<td>MS18 <em>Ctenarytaina</em> sp.</td>
<td>2</td>
<td>0.03</td>
<td>7</td>
<td>?</td>
<td>3</td>
<td>0.05</td>
<td>11</td>
<td>N</td>
</tr>
<tr>
<td>MS19 <em>Cardiaspina retator</em></td>
<td>1</td>
<td>0.02</td>
<td>3</td>
<td>Y</td>
<td>1</td>
<td>0.02</td>
<td>5</td>
<td>N</td>
</tr>
<tr>
<td>MS21 <em>Glycaspis</em> sp.</td>
<td>6</td>
<td>0.08</td>
<td>17</td>
<td>?</td>
<td>5</td>
<td>0.22</td>
<td>16</td>
<td>N</td>
</tr>
<tr>
<td>MS22 <em>Hyalinaspis</em> sp.</td>
<td>1</td>
<td>0.01</td>
<td>3</td>
<td>?</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>MS23 <em>Blastopsylla</em> sp.2</td>
<td>2</td>
<td>0.02</td>
<td>7</td>
<td>?</td>
<td>13</td>
<td>0.45</td>
<td>16</td>
<td>N</td>
</tr>
<tr>
<td>MS26 <em>Cardiaspina albicollaris</em></td>
<td>1</td>
<td>0.01</td>
<td>3</td>
<td>Y</td>
<td>2</td>
<td>0.06</td>
<td>11</td>
<td>N</td>
</tr>
</tbody>
</table>

**Total abundance & Average density**

<table>
<thead>
<tr>
<th></th>
<th>Mistletoe samples</th>
<th>Eucalypt samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance</td>
<td>826</td>
<td>645</td>
</tr>
<tr>
<td>Density</td>
<td>8.21</td>
<td>28.22</td>
</tr>
</tbody>
</table>

**Number of morphospecies**

<p>| |</p>
<table>
<thead>
<tr>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mistletoe samples</td>
</tr>
<tr>
<td>Eucalypt samples</td>
</tr>
</tbody>
</table>
Table 3.2 Psyllid morphospecies with significant indicator species values. The values were calculated from the density of individuals m$^{-2}$ leaf area in the mistletoe and eucalypt samples ($N = 30$ and $N = 19$, respectively).

<table>
<thead>
<tr>
<th>Morphospecies</th>
<th>Indicator Group ^</th>
<th>Percent mean relative abundance &amp; frequency +</th>
<th>P value *</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS1 <em>Acizzia loranthacae</em></td>
<td>Mistletoe</td>
<td>85</td>
<td>0.0002</td>
</tr>
<tr>
<td>MS2 <em>Acizzia amyemae</em></td>
<td>Mistletoe</td>
<td>61</td>
<td>0.0012</td>
</tr>
<tr>
<td>MS3 <em>Australopsylla</em> sp. 1</td>
<td>Eucalypts</td>
<td>61</td>
<td>0.0340</td>
</tr>
<tr>
<td>MS6 <em>Anoeconeossa</em> sp. 1</td>
<td>Eucalypts</td>
<td>28</td>
<td>0.0044</td>
</tr>
<tr>
<td>MS7 <em>Blastopsylla</em> sp. 1</td>
<td>Eucalypts</td>
<td>34</td>
<td>0.0022</td>
</tr>
<tr>
<td>MS8 <em>Anoeconeossa communis</em></td>
<td>Eucalypts</td>
<td>55</td>
<td>0.0002</td>
</tr>
<tr>
<td>MS10 <em>Australopsylla</em> sp. 2</td>
<td>Eucalypts</td>
<td>48</td>
<td>0.0366</td>
</tr>
</tbody>
</table>

^ The group of samples that contain the maximum indicator value for each morphospecies.

* Derived from multiplication of the average relative abundance and average relative frequency of each morphospecies among the mistletoe samples and the eucalypt samples.

* Proportion of randomized trials with an indicator value equal to or exceeding the observed indicator value, from a Monte Carlo test with 4999 permutations of the data.

Consequently, upon exclusion of the tourist species, the observed total species richness of the psyllid assemblage collected from the mistletoes was 7 species and for the assemblage collected from the eucalypt it was reduced to 18 species (Table 3.3, Fig. 3.4). The estimated true species richness of the non-tourist psyllid assemblage on mistletoe ranged from 7–9 species, with a 95% confidence interval of the Chao1 and Chao2 estimates of 7–18 species. The estimated species richness of the non-tourist eucalypt assemblage reached a maximum average of 36 species, with a 95% confidence interval of the Chao1 and Chao2 estimates of 22–88 species. The diversity of the psyllid assemblage collected on mistletoe became less than that of the eucalypt assemblage upon exclusion of the tourist species (Table 3.3). The evenness of the psyllid assemblages, with regard to relative abundance of species, was greater for the assemblages inhabiting mistletoe than the eucalypt hosts (Table 3.3).
**Table 3.3** Species richness, evenness and diversity of the psyllid assemblages associated with the host-plants, with and without tourist species. Number of samples: N; species richness: S; Estimated S range: the mean species richness estimated by each of the indices described in the text; Simpson’s diversity (D) & evenness (E).

<table>
<thead>
<tr>
<th>Sample group</th>
<th>N</th>
<th>Observed S</th>
<th>Estimated S range</th>
<th>Simpson’s D</th>
<th>Simpson’s E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mistletoe, with tourists</td>
<td>30</td>
<td>17</td>
<td>18–29+</td>
<td>3.63</td>
<td>0.21</td>
</tr>
<tr>
<td>Mistletoe, no tourists</td>
<td>30</td>
<td>7</td>
<td>7–9^</td>
<td>1.73</td>
<td>0.25</td>
</tr>
<tr>
<td>Eucalypts, with tourists</td>
<td>19</td>
<td>20</td>
<td>25–32*</td>
<td>2.47</td>
<td>0.12</td>
</tr>
<tr>
<td>Eucalypts, no tourists</td>
<td>19</td>
<td>18</td>
<td>22–36#</td>
<td>2.45</td>
<td>0.14</td>
</tr>
</tbody>
</table>

+ Maximum estimate from the Chao1 & Chao2 indices; ^ max. Jackknife 2 & ACE indices; * max. Jackknife 2 & Chao2 indices; # max. Chao1 index.

**Figure 3.4** Relative abundance distribution of the psyllid assemblages, with and without tourist species, displayed as density of psyllid species per m$^2$ leaf area in the mistletoe and eucalypt samples ($N = 30$ and $N = 19$, respectively). The order of species ranking is different for each assemblage.
3.3.2 Similarity in psyllid species composition and abundance between the mistletoe and eucalypt assemblages

The observed and estimated true similarity between the psyllid assemblages inhabiting the different hosts resulted in the same patterns, therefore only the results of the Jaccard abundance-based estimator of true similarity are shown (Figure 3.5). The mistletoe samples were more similar to each other in psyllid species composition and abundance than the eucalypt samples were to each other. This result was even more pronounced when the tourist species were excluded from the assemblage comparisons. When tourist species were included in the comparisons, the psyllid assemblages of the mistletoe and eucalypt samples collected in the same tree were more similar to each other, than were all random comparisons of the assemblages on the hosts (Figure 3.5). There was less than 1% similarity between the assemblages of non-tourist psyllid species inhabiting the mistletoe and eucalypt foliage.

Figure 3.5 Mean estimated true percentage similarity (±1SE) in psyllid species composition and abundance, calculated with the Jaccard abundance-based estimator, between the sample groups identified on the X-axis. (Number of pair-wise comparisons between each sample group: Mistletoes 400, Eucalypts 136, Mistletoe vs. Eucalypt within tree 19, Mistletoe vs. Eucalypts unpaired comparisons 510.)
The similarity in observed psyllid species composition between samples was visually displayed through ordination of the data, with non-metric multi-dimensional scaling, using the Bray-Curtis index for dissimilarity in observed relative abundance of species. The ordination with all psyllid species (Fig. 3.6) shows that most of the mistletoe and eucalypt samples form two different groups (primarily separated from each other along Axis 2). The final stress of the 3-dimensional solution was 14.2%, which is considered fair (McCune and Grace 2002) and the probability that an ordination produced by randomisation of the data would have the same or lower stress was $P = 0.028$, however the instability criterion for variation in the stress values was not met after 500 iterations. The cumulative total of the variance represented by the three axes was $r^2 = 0.81$ (and the proportion of variance represented by each axis: Axis 1 $r^2 = 0.22$, Axis 2 $r^2 = 0.21$, Axis 3 $r^2 = 0.38$). The most abundant species or morphospecies, i.e. *Australopsylla* sp.1 (MS3), *Australopsylla* sp.2 (MS10), *Acizzia loranthacae* (MS1) and *A. amyemae* (MS2), had the most influence on the arrangement of the samples in the ordination, with *A. loranthacae* and *A. amyemae* strongly positively correlated with Axis 2; and *Australopsylla* sp.1 and *Australopsylla* sp.2 were strongly negatively correlated with Axis 3 and positively correlated with Axes 1 and 2.
Figure 3.6 Non-metric multidimensional scaling ordination of the dissimilarity in species composition and abundances of all psyllid species in the mistletoe and eucalypt samples. The Bray-Curtis dissimilarity index was used. Host 1 (purple symbols): Mistletoe samples ($N = 30$); Host 2 (green symbols): Eucalypt samples ($N = 17$). Dissimilarities were calculated with the Bray-Curtis index, from untransformed densities. The vectors represent the taxa. Stress = 14.2%.

The ordination of psyllid assemblages, without the tourist species (Figure 3.7), shows that the mistletoe and eucalypt samples are more tightly clustered due to higher similarity between samples after removal of the tourist species. The final stress of this 3-dimensional ordination was 12% and the instability criterion of the stress values was met after 166 iterations (SD < 0.000001). The cumulative total of the variance represented by the three axes was $r^2 = 0.84$ and the proportion of variance represented by each axis was: Axis 1 $r^2 = 0.17$, Axis 2 $r^2 = 0.31$, Axis 3 $r^2 = 0.36$. The two psyllid species that are mistletoe specialists, *Acizzia loranthacae* and *A. amyemae*, were strongly positively correlated with Axis 3. The most abundant morphospecies in the eucalypt samples, *Australopsylla* sp.1 and *Australopsylla* sp.2, were strongly negatively correlated with Axis 3 and negatively correlated with Axis 2.
A Mantel Test was used to evaluate the assumption of independence of sample units. There was no significant correlation between the dissimilarity in species composition and the spatial distance between samples. Therefore the mistletoe and eucalypt samples were not spatially correlated to each other, in a linear relationship, and the assumption of independence of sample units was met. The results hardly differed between the Jaccard and Bray-Curtis dissimilarities so only the Bray-Curtis results are listed here: Mistletoe samples: Mantel $Z = 0.52 \times 10^7$, $P = 0.34$, Mantel $r = -0.09$; Eucalypt samples: Mantel $Z = 0.22 \times 10^7$, $P = 0.49$, Mantel $r = -0.08$. Therefore, the results of the following tests are valid.

The null hypothesis of no difference in compositional dissimilarity between the mistletoe and eucalypt samples was rejected, as a result of the statistical test from the multi-response permutation procedure. The average within-group dissimilarity of the psyllid assemblages in the two host groups was smaller than would be expected by chance ($P < 0.0001$), based on both incidence and abundance data. This result is true
both when tourist species were included and excluded from the data sets, however the effect size \((A)\) of the difference between sample groups was greater when the tourist species were excluded from the analysis (i.e. \(A = 0.17\) for resident assemblages; \(A = 0.08\) for assemblages with tourists). The compositional dissimilarity of the psyllid assemblages collected within the same tree was also significantly different between the hosts (Euclidean distance, \(P < 0.001\)).

The variation in observed dissimilarities within each sample group was subjected to significance testing with the distance-based test of homogeneity of multivariate dispersion. The results of this test showed that the variation in community composition of the resident psyllid assemblages was significantly greater amongst the eucalypt samples than the mistletoe samples \((P < 0.01)\). When all psyllid species were included in the analyses, the variation in species incidence amongst the samples was not significantly different (Jaccard dissimilarity, \(P = 0.072\)) but the variation in relative abundance was significantly greater amongst the eucalypt samples than the mistletoe samples (Bray-Curtis dissimilarity, \(P < 0.05\)). Therefore, dissimilarity in community composition was greater among the psyllid assemblages inhabiting the eucalypts than the mistletoes.
Part B - Spiders

3.3.3 Comparison of species richness, diversity and host-specificity of spiders in the mistletoe and eucalypt assemblages

Forty-two morphospecies of spiders in 7 families were identified in all of the samples, with 33 morphospecies in the mistletoe samples and 30 morphospecies in the eucalypt samples (Table 3.4, Fig. 3.8). Twenty-one morphospecies were shared between the mistletoe and eucalypt samples, while 12 morphospecies were sampled only from the mistletoe foliage and 9 were collected only from the eucalypt foliage (Fig. 3.8). The morphospecies that occurred only in the mistletoe or eucalypt samples were represented by only one to three individuals each. Six out of seven of the spider families occurred at a greater density of individuals on the eucalypt foliage than the mistletoe foliage. Individuals of the family Araneidae, in the orb-weaving guild, occurred at very similar densities on the mistletoe and eucalypt foliage. All the families except Thomisidae occurred more frequently in the eucalypt samples (Table 3.4). The family Araneidae was the most species rich family, containing 18 morphospecies. The most abundant and frequently occurring morphospecies in both the mistletoe and eucalypt samples was MS39 in the family Clubionidae (sac spiders) (Table 3.4). The second most abundant morphospecies in both sample groups were MS55 *Achaearanea* sp.2, in family Theridiidae (comb-footed spiders), and MS36 *Cymbacha ocellate*, in family Thomisidae (crab spiders). Similar to the psyllid assemblages, approximately half of the morphospecies in each sample group were represented by only one or exactly two individuals, and occurred at a density of less than 0.1 individuals per square metre (Fig. 3.9). Both guilds of spiders, web-building spiders and hunting spiders occurred at a greater density on the eucalypt foliage than the mistletoe foliage. The web-building spiders, those in the families Araneidae, Theridiidae and Tetragnathidae, occurred at a greater density on the eucalypt hosts than the mistletoe plants: 3.5 and 1.7 individuals per square metre of foliage, respectively. Similarly, the density of the hunting spiders, in the families Clubionidae, Salticidae and Thomisidae, on the eucalypt foliage was more than double that of the hunting spiders on the mistletoe foliage: 4.8 compared to 1.7 individuals per square metre of foliage, respectively.
Figure 3.8 Number of morphospecies of spiders unique and common to the mistletoe and eucalypt samples, $N = 30$ and $N = 19$ respectively.

Figure 3.9 Relative abundance distribution of the psyllid assemblages, displayed as density of spider species per m$^2$ leaf area in the mistletoe and eucalypt samples, $N = 30$ and $N = 19$, respectively. (The order of species ranking is different for each assemblage).
Table 3.4 Species inventory of spider assemblages collected from box mistletoe and its *Eucalyptus* hosts. Comparison of abundance (total no. individuals), average density (no. individuals m\(^{-2}\) leaf area, dry weight) and percent frequency of spider families and morphospecies in the mistletoe (*N*=30) and eucalypt (*N*=19) samples.

<table>
<thead>
<tr>
<th>Morphospecies</th>
<th>Mistletoe samples</th>
<th>Eucalypt samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family Araneidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MS31 ?Cyrtophora sp.1</td>
<td>12</td>
<td>0.11</td>
</tr>
<tr>
<td>MS32 ?Cyrtophora sp.2</td>
<td>31</td>
<td>0.32</td>
</tr>
<tr>
<td>MS33 ?Cyrtophora sp.3</td>
<td>10</td>
<td>0.08</td>
</tr>
<tr>
<td>MS34</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS35 Archemorus sp.1</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS37 Archemorus sp.2</td>
<td>9</td>
<td>0.05</td>
</tr>
<tr>
<td>MS43 ?Cyrtophora sp.4</td>
<td>7</td>
<td>0.07</td>
</tr>
<tr>
<td>MS44 ?Cyrtophora sp.5</td>
<td>3</td>
<td>0.04</td>
</tr>
<tr>
<td>MS45 Dolophones sp.1</td>
<td>20</td>
<td>0.17</td>
</tr>
<tr>
<td>MS50</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS52</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS53</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS54</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>MS57</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS58</td>
<td>2</td>
<td>0.02</td>
</tr>
<tr>
<td>MS66 ?Cyrtophora sp.6</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>MS73 ?Dolophones sp.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>MS76</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td><strong>Total Araneidae</strong></td>
<td><strong>102</strong></td>
<td><strong>1.00</strong></td>
</tr>
<tr>
<td>Family Clubionidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MS39</td>
<td>104</td>
<td>0.93</td>
</tr>
<tr>
<td>MS75</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total Clubionidae</strong></td>
<td><strong>104</strong></td>
<td><strong>0.93</strong></td>
</tr>
<tr>
<td>Family Linyphiidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MS74</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Family Salticidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MS40 Simaethula sp.2</td>
<td>3</td>
<td>0.04</td>
</tr>
<tr>
<td>MS42 Rhombonotus sp.1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>MS46 Opisthoncus sp.1</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS49 Opisthoncus sp.2</td>
<td>4</td>
<td>0.04</td>
</tr>
<tr>
<td>MS51 Simaethula sp.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Morphospecies</td>
<td>Mistletoe samples</td>
<td>Eucalypt samples</td>
</tr>
<tr>
<td>---------------</td>
<td>------------------</td>
<td>------------------</td>
</tr>
<tr>
<td></td>
<td>Abundance</td>
<td>Density</td>
</tr>
<tr>
<td>MS64 Rhombonotus sp.2</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS69 (new species?)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>MS70 (new species?)</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>Unidentifiable juveniles</td>
<td>19</td>
<td>0.16</td>
</tr>
<tr>
<td><strong>Total Salticidae</strong></td>
<td>29</td>
<td>0.11</td>
</tr>
<tr>
<td><strong>Family Tetragnathidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MS41 Phonognatha sp.</td>
<td>24</td>
<td>0.15</td>
</tr>
<tr>
<td><strong>Family Theridiidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MS48 ?Achaearanea sp.1</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS55 ?Achaearanea sp.2</td>
<td>39</td>
<td>0.42</td>
</tr>
<tr>
<td>MS56 ?Achaearanea sp.3</td>
<td>5</td>
<td>0.09</td>
</tr>
<tr>
<td>MS60</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS61</td>
<td>8</td>
<td>0.07</td>
</tr>
<tr>
<td>MS67 ?Achaearanea sp.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total Theridiidae</strong></td>
<td>54</td>
<td>0.59</td>
</tr>
<tr>
<td><strong>Family Thomisidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MS36 ?Cymbacha ocellata</td>
<td>61</td>
<td>0.61</td>
</tr>
<tr>
<td>MS38 ?Diaea sp.</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS47</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>MS59</td>
<td>7</td>
<td>0.06</td>
</tr>
<tr>
<td>MS68</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>MS72</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Unidentifiable adults</td>
<td>5</td>
<td>0.03</td>
</tr>
<tr>
<td><strong>Total Thomisidae</strong></td>
<td>70</td>
<td>0.69</td>
</tr>
<tr>
<td><strong>Total abundance &amp; Average density</strong></td>
<td>386</td>
<td>3.62</td>
</tr>
<tr>
<td><strong>Number of morphospecies</strong></td>
<td>33</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.10 Spider taxa collected from box mistletoe and the eucalypt host trees (MS = morphospecies): (a) MS31 (5mm grid), (b) MS32 (c) MS33 (5mm grid) (d) MS34 (e) MS35 Archemorus sp.1 (f) MS36.
Figure 3.11 Spider taxa collected from box mistletoe and the eucalypt host trees, continued (MS = morphospecies): (g) MS37 Archemorus sp.2 (h) MS38 (i) MS39 (j) MS40 (k) MS41 (l) MS43 (m) MS44.
Figure 3.12 Spider taxa collected from box mistletoe and the eucalypt host trees, continued (MS = morphospecies): (n) MS45 (o) MS46 (p) MS47 (q) MS48 (r) MS49 (s) MS50.
Figure 3.13 Spider taxa collected from box mistletoe and the eucalypt host trees, continued (MS = morphospecies): (t) MS51 (u) MS52 (v) MS53 (w) MS54 (x) MS55 (y) MS56 (z) MS57.
Figure 3.14 Spider taxa collected from box mistletoe and the eucalypt host trees, continued (MS = morphospecies): (A) MS58 (B) MS59 (C) MS60 (D) MS61 (E) MS62 (F) MS63 (G) MS64 (H) MS65.
Figure 3.15 Spider taxa collected from box mistletoe and the eucalypt host trees, continued (MS = morphospecies): (I) MS66 (J) MS67 (K) MS68 (L) MS69 (M) MS70 (N) MS71 (O) MS72 (P) MS73 (Q) MS74 (R) MS75.
Only two morphospecies of spiders had a non-random distribution with respect to the host species, as determined by indicator species analysis: MS39 and MS41. MS39 (family Clubionidae) had a significant maximum Indicator Value of 73% (P = 0.005) for the eucalypt host group. This morphospecies occurred frequently in both the mistletoe and eucalypt samples but it occurred at a higher density on the eucalypt foliage (Table 3.4). MS41 Phonognatha sp. (family Tetragnathidae) had a significant maximum Indicator Value of 33% (P = 0.024) for the eucalypt host group. However, neither of these morphospecies will be regarded as host-specific to the eucalypt hosts, or tourist species on mistletoe, because no further information is available from the published literature about their host specificity. MS39 has not even been identified to genus and no information about the host specificity of the genus Phonognatha is available in the published literature. None of the spider families were identified as indicator families for either the mistletoe or eucalypt samples.

There was a large amount of variation in the estimated true species richness predicted for the spider assemblage inhabiting the mistletoe plants (Table 3.5). The highest estimation of 161 species (95% C.I.: 55–784), calculated with the Chao1 and Chao2 indices, was due to the large ratios of singleton to doubleton and unique to duplicate species (both 16:1) observed in the mistletoe samples. The rarefied species richness estimates of Chao1 and Chao2 for the mistletoe assemblage, i.e. from the equivalent number of samples as the total number of eucalypt samples, were 70 (95% C.I.: 36–242) and 54 species (95% C.I.: 33–150), respectively. The 95% confidence interval of the mean Chao1 estimate is 35–117 for the eucalypt samples. Therefore, the estimates of rarefied species richness of the spider assemblages on the mistletoe and eucalypt hosts are not significantly different. The estimates of true species richness for the spider assemblage on all hosts combined, ranged from 45 to 83 species (95% C.I.: 54–183, Chao1 & 2 indices). The Simpson’s diversity index for the spider assemblages inhabiting the mistletoe and eucalypt hosts was twice as much as that of the psyllid assemblages on the respective hosts. However, the evenness of the spider assemblages was similar to that of the psyllid assemblages on the corresponding hosts.
Table 3.5 Species richness, evenness and diversity of the spider assemblages associated with the host-plants. Number of samples: \( N \); species richness: \( S \); Estimated \( S \) range: the mean species richness estimated by each of the indices described in the text; Simpson’s diversity (\( D \)) & evenness (\( E \)).

<table>
<thead>
<tr>
<th>Sample group</th>
<th>( N )</th>
<th>Observed ( S )</th>
<th>Estimated ( S ) range</th>
<th>Simpson’s ( D )</th>
<th>Simpson’s ( E )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mistletoe</td>
<td>30</td>
<td>33</td>
<td>38–161(^+)</td>
<td>7.25</td>
<td>0.22</td>
</tr>
<tr>
<td>Eucalypts</td>
<td>19</td>
<td>30</td>
<td>37–50(^\wedge)</td>
<td>5.17</td>
<td>0.17</td>
</tr>
</tbody>
</table>

\(^+\) Maximum estimate from the Chao1 & Chao2 indices; \(^\wedge\) max. Chao1 index.

3.3.4 Similarity in spider species composition and abundance between the mistletoe and eucalypt assemblages

The estimated true similarity between the spider assemblages collected from the mistletoes and eucalypts was 40% (comparison between all samples, measured with the Jaccard abundance-based estimator), which was intermediate between the similarity of assemblages among congeneric plants (Fig. 3.16). The similarity between the spider assemblages collected in the same tree, from mistletoe and eucalypt foliage, was not significantly different to the similarity between mistletoe and eucalypt samples from different trees (Fig. 3.16). The spider assemblages inhabiting the eucalypt foliage were slightly more similar to each other in estimated true similarity than were the spider assemblages inhabiting the mistletoes (Fig. 3.16). The same patterns of similarity occurred for the observed similarity in relative abundances of the assemblages, determined with the Bray-Curtis index and the Morisita-Horn index. However, there was little difference purely in similarity of spider species composition among each host group, measured by the classical Jaccard index (i.e. 22–25% similarity among and between the sample groups).
Among Mistletoes Among Eucalypts Mistletoes vs. Eucalypts, within same tree Mistletoes vs. Eucalypts, all comparisons

Figure 3.16 Mean (±1SE) estimated true percentage similarity in spider species composition, among and between the mistletoe and eucalypt samples, calculated with the Jaccard abundance-based estimator. (Number of pair-wise comparisons between each sample group: Mistletoes 410, Eucalypts 175, Mistletoe vs. Eucalypt in same tree 17, Mistletoe vs. Eucalypt all comparisons 555.)

Non-metric multidimensional scaling showed that there was a large amount of variation in compositional similarity amongst the samples of spiders collected on the mistletoe and eucalypt hosts (Fig. 3.17). The two morphospecies highlighted by the indicator species analysis were correlated with the arrangement of the eucalypt samples in the ordination. MS41 *Phonognatha* sp. was significantly negatively correlated with axes 1 and 2 and positively correlated with axis 3; and MS39 was significantly negatively correlated with axis 2 and positively correlated with axis 3. The variance in the original data that was represented in the ordination came to a cumulative total of $r^2 = 0.78$, and each axis contributed as follows: Axis 1 $r^2 = 0.17$, Axis 2 $r^2 = 0.28$, Axis 3 $r^2 = 0.34$. The stress value of the ordination was 15%, with a $P$ value of 0.008, and the final instability in the stress values was 0.05 after 500 iterations.
Figure 3.17 Non-metric multi-dimensional scaling ordination of the dissimilarity in spider species composition and abundance among the mistletoe and eucalypt samples. Host 1 (purple symbols) = Mistletoe samples ($N = 29$); Host 2 (green symbols) = Eucalypt samples ($N = 19$). Dissimilarities were calculated with the Bray-Curtis index, from untransformed densities. The vectors represent the taxa. Stress = 15%.

The MRPP test for a difference in the mean compositional dissimilarity of the spider assemblages between the sample groups, resulted in a significant difference between the mistletoe and eucalypt samples for both observed dissimilarity in species incidence (Jaccard index, $P < 0.0001$, effect size $A = 0.03$) and relative abundance (Bray-Curtis index, $P < 0.0001$, effect size $A = 0.05$). The mean compositional dissimilarity of the spider assemblages collected from the mistletoe and eucalypt foliage, within the same trees, was also significantly different (Euclidean distance, $P < 0.01$, effect size $A = 0.05$).

The variation within each sample group (mistletoes and eucalypts) in observed dissimilarities was subjected to significance testing with the distance-based test of homogeneity of multivariate dispersion. There was not a significant difference in the variance of dissimilarity in species composition or relative abundance within the mistletoe or eucalypt sample groups (Jaccard index $P = 0.89$, Bray-Curtis index $P = 0.196$). Therefore, the differences in assemblage composition between the sample groups are due to differences in the mean or ‘location’ of the sample groups, not differences in dispersion within each group.
3.4 Discussion

The results of this study showed that the mistletoe plants are hosts to a few specialised herbivorous psyllid insects but no spider species were host-specific to the box mistletoe. Other insect herbivores such as Lepidopteran caterpillars are also known to be specialist feeders on mistletoe species (Braby 2005, Braby 2006). This study provides further evidence that mistletoes make important contributions to the diversity of canopy arthropods at lower rather than higher trophic levels. However, the species richness and density of the herbivorous psyllid insects were greater on the *Eucalyptus* trees than on the mistletoe plants. Similarly, the densities of most spider families were greater on the eucalypts but the species richness of the spider assemblages was similar between mistletoes and eucalypts. These patterns led to high compositional turnover, or beta-diversity, of the psyllid assemblages between the mistletoe and eucalypt plants. There was lower beta-diversity between the spider assemblages on the mistletoes and eucalypts compared with the psyllid assemblages. The driving factors behind these patterns and the implications of these findings for other mistletoe– and epiphyte–host–plant associations will be discussed.

3.4.1 Patterns of alpha-diversity and niche differentiation of herbivorous insect assemblages between host-plants

The alpha-diversity of a true or self-maintaining community is determined by niche differentiation between species, which allows the coexistence of different species in the one habitat (Shmida and Wilson 1985). It is also influenced by factors such as habitat size and stability (Strong et al. 1984). Since the species richness of psyllids was greater on the *Eucalyptus* trees than the mistletoe plants, it seems that there is greater niche differentiation of psyllids on eucalypts than mistletoes.

Psyllid species differ in their use of host-plant resources by differences in developmental biology, for example development of larvae under lerps, in galls or leafcurls, or free-living larvae; and differences in oviposition sites and feeding on different aged leaves (Taylor 1992, White 1993, Hollis 2004). The two psyllid species that are host-specific to mistletoe have free-living larvae (and the other five species that occurred on mistletoe, but of inconclusive host-specificity, have free-living and lerp-
forming larvae). In comparison, the psyllid species inhabiting the sampled *Eucalyptus* trees display all forms of larval development on their hosts.

Furthermore, psyllid species may have encountered more *Eucalyptus* trees than mistletoe plants over time. The species-area relationship predicts that species richness increases with habitat area or sampled geographic area and has been demonstrated for a wide range of taxa including insects (Strong et al. 1984, Rosenzweig 1995). The abundance and/or geographic range of plants are equivalent to area sampled in the species-area relationship for insects and plants; and the encounter-frequency hypothesis was developed to account for the greater species richness of insects on widespread, abundant plants (Southwood 1961, cited in Strong et al. 1984). Mistletoe plants have a patchy and contagious distribution and are necessarily less abundant than trees in the forests and woodlands in which they occur (Watson 2001); including in the catchment area of this study (March 2007). Therefore, psyllid insects are more likely to encounter and exploit the canopies of *Eucalyptus* trees than box mistletoe plants.

Mistletoe plants are also a less stable habitat than eucalypt trees, which is likely to influence the species richness of herbivorous insect communities. Leaf turnover rates are three times greater for box mistletoes than red gum eucalypts in the local area of this study (March and Watson 2007) and mistletoes are usually shorter lived than their host trees (Watson 2001). Furthermore, Australian mistletoes are more sensitive to fire and frost than their hosts and are also susceptible to drought (Reid and Lange 1988, Reid et al. 1995). These factors would contribute to mistletoes being a less stable habitat than eucalypt trees for phytophagous insects. Not only could this partially explain the lower densities of psyllids on box mistletoes but also the lower species richness of psyllids on mistletoe than the eucalypt trees, due to less opportunity for speciation of psyllids on mistletoes.

The differences in species richness and density of the psyllids between the mistletoe and eucalypt foliage could also be related to the differences in nutritional quality and structural properties of the host foliage. The higher density of psyllids on the eucalypt foliage compared to the mistletoe foliage could be partially explained by the higher concentration of nitrogen in the eucalypt leaves (see Chapter 2). Box mistletoe leaves are thicker and have a lower area to weight ratio than the leaves of the eucalypt
hosts, which could influence the feeding ability of psyllid insects if the thickness of leaves affects the penetration of psyllid stylets to phloem vessels. A study of herbivorous insects, including phloem feeders, on evergreen shrubs and trees found that densities of insects were negatively correlated with leaf structural traits that could limit feeding, including specific leaf weight, vascular tissue depth, lamina and cuticle thickness and stomate length (Peeters 2002). However, the foliage of *Eucalyptus* trees contains strong structural defences (such as high concentrations of lignin and cellulose) and a concoction of secondary metabolites (such as phenolics, cyanogenic glycosides and terpenes: Landsberg et al. 1997, Lawler et al. 1998, Gleadow et al. 2008). In contrast, mistletoes are thought to have few structural defenses (Mathiasen et al. 2008) and the secondary chemistry of *Amyema* mistletoes is largely unknown. The defences in eucalypt foliage appear not to have limited the abundance of psyllid species on eucalypts and have perhaps enhanced diversification of psyllid species on these host-plants.

These factors might also contribute to explaining the greater proportion of tourist species on mistletoes than eucalypts. Sixty percent of the psyllid species collected on box mistletoe consisted of tourist species, while only ten percent of psyllid species on the eucalypts were tourist species. The secondary metabolites in eucalypt foliage may be a deterrent to the mistletoe-specialist psyllids, whereas the less-defended mistletoe foliage could be more exploitable by the eucalypt psyllid species. It is possible that psyllids which usually occur on eucalypt trees could supplement their feeding on mistletoes. The transpiration rate of mistletoes is often higher than their host-trees, particularly under conditions of water stress (Fisher 1983, Ehleringer et al. 1986a); therefore it is likely that phloem conductance rates are higher in mistletoes than their host-trees, which could be advantageous to the tourist (phloem-feeding) psyllids. Other studies of canopy-dwelling arthropods have found a large proportion of tourist species in tree canopies, from 10–70% (Moran and Southwood 1982, Stork 1987, Basset and Arthington 1992, Majer et al. 2000, Ødegaard 2004, Southwood et al. 2005), including 70% of the psyllid species inhabiting willow trees (Jager and Topp 2002).

The occurrence of tourist species can also be related to the ‘mass effect’, that is “the establishment of species in sites where they cannot be self-maintaining” (Shmida and Wilson 1985). The mass effect results from a combination of the dispersal ability of
species, the reproductive success of species in adjacent areas, the heterogeneity of the biota and environmental conditions in the sampled area (Shmida and Wilson 1985). The close spatial proximity of mistletoes and their host tree canopies, and the high density of some psyllid species in the eucalypt canopies, make them perfect candidates for the occurrence of mass effects. Adult psyllids can jump a few metres in the air and disperse longer distances by wind (Hollis 2004). Therefore, they are able to easily move between mistletoe and eucalypt foliage, particularly within the same tree. The result of greater similarity between assemblages of psyllids collected in the same tree compared with similarity between all tree–mistletoe combinations provides support for the mass effect (see Fig. 3.3, the assemblages with tourist species). Mass effects can also lead to the perception of increased alpha-diversity of a particular community, which was observed in the current study.

3.4.2 Patterns of beta-diversity of herbivorous insects

The high beta-diversity (i.e. very low similarity) of the ‘resident’ psyllid assemblages between the host-plant genera is striking. The pattern of increasing beta-diversity, or decreasing similarity, among the psyllid assemblages with decreasing taxonomic relatedness of the host-plants, is similar to other studies of herbivorous insects. The similarity of assemblages of herbivorous beetles in the canopy of tropical forests, decreased from 55% between conspecific host-plant species to 25% between congeneric hosts, 15% between confamilial hosts and 12% between hosts of different families (Ødegaard et al. 2005). Likewise, the similarity between assemblages of phytophagous Lepidopteran caterpillars on tropical host-plant species was 34% between congeneric hosts and only 1% between confamilial and allofamilial host-plants (Novotny et al. 2002b). The similarity of the psyllid assemblages corresponds well with this pattern: 65% among the conspecific mistletoe plants, 35% among the congeneric eucalypt hosts, and 0.5% between the mistletoe and eucalypt hosts (i.e. different genera and families).

The results of this study partially support the hypothesis of low beta-diversity among widespread congeneric host-plants (Novotny and Weiblen 2005, Novotny et al. 2007). The psyllid community inhabiting mistletoes exhibited low beta-diversity (i.e. greater than 50% average similarity among assemblages on individual mistletoes); whereas the psyllid community inhabiting the *Eucalyptus* trees exhibited higher beta-
diversity (35% average similarity). This result reflects the higher species richness and variation in abundance of the psyllid species among the host eucalypts than among the mistletoe plants; which was influenced by collection of arthropods from three species of eucalypts but one species of mistletoe. The greater variation in densities of psyllid species among the eucalypt samples was due to very high densities in three samples; it was not an effect related to a particular *Eucalyptus* species. Despite the fragmentation of the woodlands and separation of host-plants by up to twenty-three kilometres, host-plant identity seems to be more important than spatial separation of assemblages in determining the similarity in community composition of the psyllid assemblages between host-plants. The spatial influence on the beta-diversity of the arthropod assemblages will be tested explicitly in the following chapter.

### 3.4.3 Patterns and drivers of the alpha- and beta-diversity of spider assemblages

Habitat heterogeneity and prey abundance influence the distribution and abundance of spider species (Foelix 1982, Greenstone 1984, Gunnarsson 1990, Halaj et al. 1998). However, since none of the spider species in the present study were found to be host-specific to the mistletoe or eucalypt hosts and the species richness of the spider assemblages did not differ significantly between the hosts, it could be assumed that there are not enough structural and micro-habitat differences between the mistletoe plants and the eucalypt canopies to lead to differential host-plant preferences by the spider species. The only other study of spider assemblages inhabiting mistletoe plants and their hosts, similarly found that none of the spider species were restricted to the dwarf mistletoe species, they also occurred widely on the conifer host species (Jennings et al. 1989). However, in other studies of forest canopies, the species richness and abundance of spider assemblages was greater on structurally more complex tree species, and hunting and sheet-web spiders showed clear micro-habitat preferences based on vegetation structural properties (Halaj et al. 1998, 2000). Some species of spiders also display preferences for particular plant species, if they contain structural properties conducive to the spiders’ survival and reproduction, e.g. sticky trichomes or cavities in bromeliad plants (Romero 2006, Vasconcellos-Neto et al. 2007).
Therefore, further research could be conducted to determine the occurrence of micro-habitat differences between mistletoes and the tree canopies that might influence the structure of spider assemblages, such as sampling the mistletoe haustorium and rigid branches adjacent to the haustorium, and curled or folded leaves, which were not adequately sampled in the present study but might house specific spider species. Birds are important predators of canopy-dwelling spiders, including having differential effects on the abundance of particular spider guilds and species, which can influence the overall abundance and composition of spider assemblages (Gruner and Taylor 2006, Mooney and Linhart 2006, Gunnarsson 2007). Hence, further research could include bird-exclusion experiments to test the influence of bird predation on the abundance and composition of spider assemblages inhabiting mistletoes versus the tree canopy.

The greater density of most of the spider families on the eucalypt foliage than the mistletoe foliage could be related to the higher density of prey on the eucalypts, since all of the insect orders occurred at a greater density on the eucalypt foliage than the mistletoe foliage. Other studies of spider communities 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 influence of prey densities on the similarity in species composition and abundance among the spider assemblages will be examined in the next chapter.

Spiders are active dispersers and are generally less host-plant specific than herbivorous insects. These characteristics would lead to greater mixing of spider species between similar habitats and thus lower beta-diversity of spider assemblages between the habitats (i.e. mistletoes vs. eucalypts) compared with herbivorous insect assemblages, as was observed in this study. The distribution of the spiders seems to be random, since the similarity of the spider assemblages among the eucalypts and among the mistletoes, separately, did not differ much from the similarity of the assemblages between the eucalypts and mistletoes (Fig. 3.8). Furthermore there was no effect of whether samples occurred in the same tree or not. Similarly, a study of the diversity of spiders inhabiting five species of tropical trees found that the similarity of spider assemblages did not differ significantly between related and unrelated host-plant species (Russell-Smith and Stork 1995). There is a paucity of studies investigating the beta-diversity of spider assemblages between host-plants or habitats. Therefore, since host-
plant identity was not as important for determining the composition of spider assemblages as it was for the psyllid assemblages in this study, I want to find out which of the measured variables might influence the beta-diversity of spiders, such as habitat traits, prey abundance and spatial distance between assemblages, which will be explored in the following chapter.

3.4.4 Implications for other mistletoes and epiphytes compared to their hosts

Mistletoe foliage and branching structure is often structurally similar, but physiologically different, to the foliage of their host-plants (Ehleringer et al. 1986b, Shaw et al. 2004); whereas a lot of epiphytic plants are both structurally and physiologically different to their host-plants. Epiphytic vegetation is often sclerophyllous and succulent and therefore likely to be less palatable and nutritious compared to the host tree foliage. Little is known about the herbivory or secondary metabolism of epiphytes but extensive defoliation is rare in neotropical epiphytes (Benzing 1990). Epiphytes also display a range of growth habits including creeping (e.g. figs and orchids), water-filled tanks and rosettes (e.g. bromeliads) and baskets (e.g. ferns) (Benzing 1990). Therefore, epiphytic plants are likely to support different assemblages of arthropods compared to their host-plants, at a range of trophic levels, because they provide an environment that is both physiologically and structurally different to the host-tree canopies. Indeed, they are known to support aquatic and terrestrial detritivore invertebrates which do not usually occur in the canopy of trees (Cotgreave et al. 1993, Richardson 1999, Kitching 2000). In contrast, mistletoe plants are likely to support different assemblages of herbivorous insects compared with their host-plants, but similar assemblages of arthropods in other trophic levels. This is because mistletoes display greater differences to their host-plants in foliage physiology than structure. Therefore, plant structure and physiology appear to be important drivers of trophic differences between the arthropod communities inhabiting plants. Herbivorous insects discriminate between plant taxa based on fine-scale physiological and structural properties of plant foliage, whereas predatory, parasitic and omnivorous arthropods are more influenced by plant structure, micro-habitats and prey abundance.
3.5 Conclusion

This study has revealed detailed information about the diversity and host-specificity of arthropod assemblages inhabiting mistletoe plants and their host trees. The arthropod assemblages on mistletoes are not ‘island assemblages’ or just a sub-set of the arthropod community inhabiting the tree canopy – they are something in-between. Arthropod assemblages on mistletoe plants include herbivorous insects specialised to the mistletoes; and also herbivorous insects from the tree canopy that temporarily occur on the mistletoes but cannot complete their lifecycle on mistletoes, i.e. ‘tourist species’. Identification of tourist psyllid species enabled a more accurate examination of patterns of variation in community composition among the host-plants. Mistletoes are also home to predatory arthropods that inhabit both the mistletoes and the tree canopies – no host-specific spiders were identified. Thus, the species turnover or beta-diversity of the arthropod assemblages between the mistletoe plants and eucalypt foliage was greater among the psyllid assemblages than the spider assemblages.

Having established that host-plant identity has differential influence on the host-specificity and community composition of arthropods in different trophic levels (related to physiological and structural properties of the plants); the next chapter will explore the habitat and spatial factors influencing the variation in beta-diversity of the psyllid and spider assemblages among host-plants. Generalisations regarding the beta-diversity of arthropods are allusive and more empirical studies in this area are needed to aid the conservation of these super-diverse organisms (Novotny and Weiblen 2005).
3.6 References


CHAPTER 3


March, W. A. 2007. The impact of an Australian mistletoe, Amyema miquelii (Loranthaceae), on nutrient cycling in eucalypt forests and woodlands. Charles Sturt University, Albury, Australia.


Chapter 4

Beta-diversity patterns of arthropod assemblages across a landscape

4.1 Introduction

Having established patterns of beta-diversity of the psyllid and spider assemblages regarding the differences between the two host-plant genera (*Amyema* mistletoes and *Eucalyptus* trees) in the previous chapter; I now seek to elucidate relative influences of environmental and spatial factors on the beta-diversity patterns. It is expected that assemblages of taxa will vary between different types of habitat or along environmental gradients, but a more intriguing question is: how much variation is there between different patches of the same habitat that are spatially separated? In terms of conservation this addresses the issue of whether it is sufficient to conserve one or a few patches of a habitat type or ecosystem, or if many patches of the habitat are required at particular scales of spatial separation, to ensure that complementary assemblages of taxa are conserved. It is expected that communities located close together will be more similar than communities located far apart, due to dispersal limitation and/or spatial structuring along environmental gradients, i.e. spatial autocorrelation (Legendre 1993). This chapter is as much about elucidating factors that might explain patterns within the samples from each of the host-plants, as it is about explaining differences between host-plants.

Studies of spatial patterns in community ecology seek to understand the drivers of spatial patterns, and the relative influence of such drivers. Is variation in community composition (i.e. beta-diversity) directly related to geographic distance between communities and is this a result of dispersal limitation and/or other biological processes such as competition, predation and contagious modes of growth or reproduction? Or is beta-diversity among biological communities a result of spatially-
structured environmental conditions, such as rainfall or soil type? Or is beta-diversity related purely to non-spatially structured environmental heterogeneity, i.e. niche properties? Disentangling the direct and indirect drivers of spatial turnover is complex, but data analysis techniques have advanced such that variation in beta-diversity among assemblages can be partitioned into the variation explained by variation in geographic distances, spatially-structured environmental heterogeneity, and pure environmental heterogeneity (Borcard et al. 1992, Legendre 1993, Tuomisto and Ruokolainen 2006, Ferrier et al. 2007). Researchers have found that both environmental and biotic processes influence variation in community composition among geographically separated communities of a range of taxa including vertebrates, invertebrates and vascular plants. Spatial patterns in community composition of these taxa have been attributed to dispersal of organisms and disease transmission; and spatially-structured environmental gradients, e.g. precipitation; while variation in community composition has also been attributed to environmental heterogeneity such as variation in plant community composition, edaphic composition, climate and habitat size (Tuomisto et al. 2003, Parris 2004, Bahn et al. 2006, Chust et al. 2006, Jones et al. 2006, Steinitz et al. 2006, Baselga and Jimenez-Valverde 2007, Baselga 2008, Ernst and Rödel 2008).

The study of the determinants of beta-diversity of invertebrate animals is in its infancy and few generalisations have been proposed due to the small number of empirical studies. One hypothesis proposed by Novotny and Weiblen (2005) regarding the beta-diversity of arboreal herbivorous insects is that communities on widespread, dominant plant taxa in temperate and tropical forests will exhibit low beta-diversity (except in cases of intra-specific aggregation). This was proposed because many vegetation types are dominated by widespread plant taxa and most herbivorous insects are specialised at the level of plant genera and families. Subsequent research by Novotny et al. (2007) has provided evidence to support this hypothesis, because low average beta-diversity was found among Lepidopteran larval assemblages inhabiting congeneric host-plants, located up to 500 km apart in continuous lowland tropical rainforest. I will be testing this hypothesis with regards to the psyllid insect communities inhabiting box mistletoe plants and the three *Eucalyptus* tree species, which are widely distributed in south-eastern Australia. While this hypothesis has been proposed for herbivorous insects, I am not aware of
any hypotheses regarding the beta-diversity of spider assemblages. However, it is likely that spider assemblages will display low beta-diversity among widespread host-plants, similar to vagile generalist insects (Hulcr et al. 2008), depending on the dispersal ability of the spider taxa. It was identified in the previous chapter that host-plant identity did not have as strong an influence on the variation in community composition among the spider assemblages, as among the psyllid assemblages. An aim of this chapter is to determine which of the measured habitat variables influenced the variation in beta-diversity among the spider and psyllid assemblages. Furthermore, analysis of the beta-diversity of the psyllid assemblages among the re-colonised mistletoe plants, also addressed in this chapter, will examine the relative influence of habitat and spatial factors on re-colonisation dynamics.

Comparisons between beta-diversity studies are difficult due to the use of different forms of beta-diversity analysis, i.e. partitioning the variance in community composition versus additive partitioning of gamma- or alpha-diversity (as outlined by Tuomisto and Ruokolainen 2008). However, a short review of arthropod beta-diversity studies is as follows. The few arthropod studies to incorporate both the effects of spatial patterns and environmental heterogeneity on beta-diversity among assemblages have focused on large scales: entire continents or countries, using environmental variables derived from climate data (Baselga and Jimenez-Valverde 2007, Baselga 2008). Other arthropod beta-diversity studies that have investigated spatial patterns have divided sampling areas into hierarchical spatial scales but the size and spatial separation of the nested classes were not explicitly identified (e.g. Summerville et al. 2003); or the studies have occurred at very small spatial scales (i.e. < 2km, Fournier and Loreau 2001, Crist et al. 2006). Furthermore, while several studies have examined the beta-diversity of arthropod assemblages among different habitats, few have examined the beta-diversity of arthropods among different host-plants by identifying host-specific taxa (but see Frenzel and Brandl 2001, Novotny et al. 2002, Novotny et al. 2005, Summerville et al. 2006, Novotny et al. 2007). There are similar numbers of published beta-diversity studies of canopy-dwelling arthropods in tropical and temperate regions, but these are mainly restricted to Lepidoptera and Coleoptera. Beta-diversity studies of ground-dwelling arthropods have primarily occurred in temperate regions and mainly include beetles, ants and spiders. Therefore, more studies of the environmental and spatial factors influencing the patterns of beta-
diversity of arthropod assemblages are required, involving different orders and guilds of arthropods, in both temperate and tropical areas and at local and regional scales.

**Analysing beta-diversity**

The analysis of beta-diversity in terms of variation in community composition can be analysed at two levels. The first level addresses the questions: Why is there beta-diversity among sites? Or, why does community composition vary among sites? And, can the variation in community composition be explained by the variation in environmental factors or geographical location of sites? These questions can be statistically analysed with multiple regression analyses, including canonical analyses (e.g. redundancy analysis or canonical correspondence analysis, when linear or unimodal relationships are expected, respectively), which produce constrained ordinations (Tuomisto and Ruokolainen 2006). The expected species composition or abundance at a new site can then be predicted if the environmental conditions or geographical location of the site are known. The second level addresses the following ecological questions: Why is there variation in beta-diversity among groups/pairs of sites?; and “can variation in beta-diversity be explained by variation in environmental difference or geographical distance?” (Tuomisto and Ruokolainen 2006). At this level, the expected beta-diversity between two new sites can be predicted if the environmental difference and/or geographical distance between the sites are known.

The main difference between the two levels of abstraction is the response variable. At the first level, the response variable is a table of the sites (or samples) x species data, in the form of species incidence or abundance. At the second level, the response variable is a matrix of the pair-wise dissimilarities in community composition between all sites or samples. Another difference is that in addressing questions at the first level, the actual values of the environmental variables and the geographical location of sites are used in analyses; whereas, at the second level, the differences in the environmental variables and geographical locations between sites are used. In this chapter of my thesis I am addressing the questions at the second level of abstraction and will use generalised dissimilarity modelling to do so. Other statistical analyses used to address the questions at the second level include the Mantel test (for linear or monotonic correlations) and multiple regressions on distance matrices (to fit linear regressions).
Generalised dissimilarity modelling (GDM) is a form of multiple matrix regression; however, in GDM more complex relationships between the response and predictor variables can be determined, rather than just linear or unimodal relationships. Furthermore, GDM has two advanced features compared to other modelling techniques, which address two types of “nonlinearity commonly encountered in ecological data” (Ferrier et al. 2007). Firstly, GDM explicitly accounts for the curvilinear relationship between compositional dissimilarity and ecological separation among samples. The curvilinear relationship occurs because the dissimilarity indices are bounded by zero and one, and compositional dissimilarity reaches its asymptote before the maximum ecological separation between sites or samples is reached. That is, ecological separation between sites will continue despite maximum compositional dissimilarity being reached (for example see Fig. 4.0a). Secondly, GDM accommodates variation in the rate of compositional turnover along environmental gradients, rather than assuming it stays constant along the whole range of the environmental gradient, as in linear matrix regression. It does this by fitting non-linear functions (derived from I-spline basis functions) directly to the environmental variables, rather than to the ‘environmental distances’ between pairs of sites (Ferrier et al. 2007). In the latter case, environmental distances are often calculated as Euclidean distances between pairs of sites for each environmental predictor. Therefore, site pairs with environmental distances of the same magnitude are treated the same in dissimilarity matrices, despite differences in the actual values of the variables of the pair-wise combinations and variation in compositional dissimilarity along the environmental gradient (e.g. two pairs of sites with 100 and 200mm vs. 1300 and 1400mm would be ranked the same in traditional matrix regression, i.e. environmental distance = 100). In contrast, GDM transforms compositional dissimilarity as a function of variation in the actual values of the ecological predictors. Furthermore, GDM incorporates the geographical distance between samples as a predictor variable (calculated from the geographic coordinates), thus allowing determination of the influence of spatial separation on the compositional turnover of species assemblages.
4.2 Methods

4.2.1 Statistical analyses

*Relationships between compositional dissimilarity and environmental and spatial variables*

In order to identify which variables are most likely to influence the observed patterns of beta-diversity of the arthropod assemblages, I used generalised dissimilarity modelling (Ferrier et al. 2007). The response variable was a matrix of the compositional dissimilarity among all pair-wise combinations of the samples, for each of the community data sets of the psyllid and spider assemblages (Table 4.0). The predictor variables were the differences in the measured host and habitat variables, the spatially-derived environmental data (from remote sensing) and the geographical distance between samples (Table 4.1). Therefore, the environmental variables encompass traits of the host-plants and the surrounding vegetation, position of the sample in the tree and topographic site characteristics. The difference in leaf area of the samples was included as a predictor variable for analysis of species incidence data to account for the different sample sizes of plant foliage. Leaf area was already incorporated into analysis of the abundance data because abundance was expressed as density of individuals per leaf area of the samples. The geographic distance between samples was the spatial component of the models. The arthropod samples collected in 2005 (and the mistletoe plants re-sampled in 2006) were located between 4 m and 23 km apart, and in 2006 the samples from the new mistletoe plants were located between 4 m up to 30 km apart.

Model selection and evaluation proceeded as follows. Initially all of the predictor variables were included in the modelling, and then those variables that did not contribute to the model or contributed very little were removed (i.e. variables for which the sum of the coefficients of the three I-spline basis functions were less than 0.01). Furthermore, for the predictor variables that were inter-related (e.g. NNDtree, AveNND and no. trees in 15 m radius) only the variable that contributed the most to the initial model was kept for the subsequent model. Automated variable selection and significance testing are not currently available in the GDM software. However, the GDM software produces scatter-plots of observed compositional dissimilarity versus predicted ecological distance and observed compositional dissimilarity vs. predicted...
compositional dissimilarity between all sample-pairs to assess the overall fit of the models (see Fig. 4.0 for example). It also plots the variation in compositional dissimilarity as a function of each predictor variable in the model, holding other variables constant, using three I-spline basis functions (generating smoothed monotonic functions, see Fig. 4.2 for example). These plots display the total magnitude of change in compositional dissimilarity associated with each predictor variable (holding the other variables constant); and the rate of compositional turnover at different positions along each predictor variable (from the slope of the fitted functions). Thus, the compositional dissimilarity between a sample pair as a function of a particular predictor variable can be deduced from these plots by locating the values of the predictor variables for the samples on the x-axis, and calculating the difference in the corresponding values on the y-axis.

The proportion of variance in observed compositional dissimilarity that was correlated with the variance in the predicted model of compositional dissimilarity was separated into four proportions of statistically explained variance: (i) purely by the environmental variables, (ii) purely by the geographic distance between samples, (iii) purely by the host-plant type (i.e. mistletoe vs. eucalypt); and (iv) shared by the environmental, spatial and/or host variables (due to correlations between these variables) (Borcard et al. 1992). This was done by running the analyses with and without these variables or sets of variables and comparing the amount of variation explained by the models. For example, to determine the proportion of variation in observed compositional dissimilarity explained purely by host-plant type and purely by the environmental variables: I derived the Null Deviance (N) and the GDM Deviance (T) from a model with the environmental variables and host-plant type, then the GDM Deviance of a model with only host-plant type (H), then the GDM Deviance from a model with only the environmental variables (E). (The GDM deviance is the amount of deviance in the Null model of observed compositional dissimilarity that is not explained by the GDM model). The following calculations were made to determine the proportion of observed compositional variation explained: purely by host-plant type $H' = (E-T)/N$; purely by environmental variables $E' = (H-T)/N$; and shared between host-plant type and environmental variables $S' = [(N-T)/N] - (H'+E')$ (i.e. the proportion of variation explained by the fitted GDM model with all variables, which is not explained purely by host-plant type or environmental variables). The
variation explained by a single environmental variable or a group of environmental variables was also determined for the variables that were indicated as having the strongest correlation(s) with compositional dissimilarity (by the sum of the coefficients of the I-spline functions).

GDM was operated in R statistical freeware v.4.8.0 (obtained from: http://cran.r-project.org/) with functions and scripts obtained from http://www.biomaps.net.au/gdm/ (Ferrier et al. 2007). The Bray-Curtis dissimilarity index (for species abundance data; i.e. the complement of Equation 15, Chapter 3) and the Sørensen dissimilarity index (for species incidence data, i.e. qualitative; Equation 17) were used in the GDM analyses.

\[
\text{Sørensen dissimilarity index} = 1 - \frac{2a}{a+b+c} \tag{17}
\]

Where \(a\) is the number of species present in both samples, and \(b\) and \(c\) are the number of species only in sample 1 and only in sample 2, respectively.

<table>
<thead>
<tr>
<th><strong>Host-plant</strong></th>
<th><strong>Arthropod taxa</strong></th>
<th><strong>No. species</strong></th>
<th><strong>No. samples</strong></th>
<th><strong>Year sampled</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mistletoe</td>
<td>Psyllid species</td>
<td>7 residents, 10 tourists</td>
<td>30</td>
<td>2005</td>
</tr>
<tr>
<td>Eucalypts</td>
<td>Psyllid species</td>
<td>18 residents*</td>
<td>19</td>
<td>2005</td>
</tr>
<tr>
<td>Mistletoe</td>
<td>Psyllid species – on de-faunated plants*</td>
<td>4 residents, 12 tourists</td>
<td>26</td>
<td>2006</td>
</tr>
<tr>
<td>Mistletoe</td>
<td>Psyllid species – on new plants</td>
<td>5 residents, 6 tourists</td>
<td>34</td>
<td>2006</td>
</tr>
<tr>
<td>Mistletoe</td>
<td>Spider species</td>
<td>33</td>
<td>30</td>
<td>2005</td>
</tr>
<tr>
<td>Eucalypts</td>
<td>Spider species</td>
<td>30</td>
<td>19</td>
<td>2005</td>
</tr>
</tbody>
</table>

* The tourist species in the eucalypt samples were not included in analyses because there were only 2 species, which occurred as 1 and 2 individuals.
+ The de-faunated plants were the mistletoe plants that were originally sampled in 2005 (apart from 4 plants that had died in situ or fallen from the tree).
Table 4.1 Predictor variables used in the generalised dissimilarity modelling, measured directly at the site (D), using a GPS, or derived from remotely-sensed data (R).

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>Code</th>
<th>Source</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Index of mistletoe age (host branch diameter)</td>
<td>HostBrDi</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Tree height</td>
<td>TreeHgt</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Tree diameter at breast height</td>
<td>TreeDBH</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Height of sample above ground</td>
<td>HtAbvGd</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Number of mistletoe in sampled tree</td>
<td>No.Mist</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Distance to nearest mistletoe plant</td>
<td>NNDmtoe</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Distance to the nearest tree</td>
<td>NNDtree</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Average distance to nearest tree in each compass quadrant</td>
<td>AveNND</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Number of trees in 15m radius around sampled tree</td>
<td>Trees15m</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Aspect of sample in the tree</td>
<td>AspectSA</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Prey abundance (number of insects and mites per m(^{-2}) leaf area)</td>
<td>PreyAbund</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>Latitude of sample</td>
<td>LAT., Y</td>
<td>GPS</td>
<td></td>
</tr>
<tr>
<td>Longitude of sample</td>
<td>LONG., X</td>
<td>GPS</td>
<td></td>
</tr>
<tr>
<td>Elevation</td>
<td>Elevation</td>
<td>R</td>
<td></td>
</tr>
<tr>
<td>Slope</td>
<td>Slope</td>
<td>R</td>
<td></td>
</tr>
<tr>
<td>Aspect of slope</td>
<td>AspectSL</td>
<td>R</td>
<td></td>
</tr>
<tr>
<td>Topographic relief moisture index</td>
<td>TRMI</td>
<td>R</td>
<td></td>
</tr>
<tr>
<td>Solar radiation</td>
<td>SolarRad</td>
<td>R</td>
<td></td>
</tr>
</tbody>
</table>
Figure 4.0 An example of the fit of the generalised dissimilarity model to the observed data displayed as relationships of (a) observed compositional dissimilarity vs. predicted ecological distance and (b) observed vs. predicted compositional dissimilarities, for all pair-wise combinations of the psyllid assemblages collected in samples from the mistletoe and eucalypt plants ($N = 49$, Sørensen index). The predicted ecological distance is derived from the combination of selected predictor variables used in the generalised dissimilarity modelling.
4.3 Results

4.3.1 Relative influence of host-plant type, environmental and spatial variables on the beta-diversity of the psyllid and spider assemblages

*Psyllids inhabiting mistletoes and eucalypts*

The variation in beta-diversity among samples was analysed in terms of the variation in species composition and abundances combined (with the Bray-Curtis index) and species composition only (with the Sørensen qualitative index). Since both sets of results were very similar for the psyllid and spider assemblages, the results for species composition only are shown in the graphs in this section. The results of the modelling confirmed that the type of host-plant taxon has a strong influence on the dissimilarity in species composition of the resident psyllid assemblages; while the environmental variables contributed a small proportion to explaining the variation in dissimilarity between the psyllid assemblages inhabiting the mistletoe and eucalypt plants (Fig. 4.1). (I use the term ‘explain’ in a statistical sense, not inferring a causal relationship).

Comparing the analyses of the assemblages on each host-plant separately, the model for which the most variation in beta-diversity was explained was among the assemblages of tourist psyllid species on the mistletoe plants (which consisted of up to 10 species). The estimate of mistletoe age explained 16% of the total compositional dissimilarity among these tourist assemblages, approximately a third of that explained by the environmental variables (Fig. 4.1). Compositional dissimilarity or turnover among the assemblages of tourist psyllid species increased with increasing difference in mistletoe age between pairs of samples (as indicated by the diameter of the host branch, Fig. 4.2). Figure 4.3 displays the overall fit of the model to the data for the tourist psyllid assemblages inhabiting the mistletoe plants.

For all of the psyllid assemblages, the variation in proximity of surrounding trees and the height of the sample above ground were two of the environmental variables for which a large magnitude of change in compositional dissimilarity was recorded (Table 4.2). As seen in Figure 4.4, the rate of change in compositional dissimilarity was high between pairs of samples for which the average distance to the nearest tree was up to approximately 60 m, and either did not vary or was lower between pairs of samples for which the proximity of the nearest trees was greater than 60 m, depending on the assemblage data set (Fig. 4.4 a vs. b). Similar relationships
occurred between compositional dissimilarity and proximity of surrounding trees for the other psyllid assemblage data sets (graphs not shown). The rate of change in compositional turnover of the psyllid species in the mistletoe and eucalypt samples as a function of the height of samples above ground varied along the range of measured heights (Fig. 4.5), and different relationships were modelled for each of the psyllid assemblage data sets (graphs not shown). The spatial distance between samples did not explain any of the variation in any of the models of psyllid species composition, and it explained less than 1% of the variation in species abundances.

![Figure 4.1 Proportions of variation in psyllid species composition explained and not explained by groups of predictor variables, for five community data sets (sampled in 2005, Table 4.0). The proportion of observed variation in compositional dissimilarity among the psyllid assemblages was partitioned into the variation explained purely by the environmental predictor variables, purely by type of host-plant (i.e. mistletoe or eucalypt, for the data sets including both hosts), shared between the environmental and host-plant variables, and the proportion of variation not explained by the predictor variables. See Table 4.2 for the environmental predictor variables that contributed to each of the models. Compositional dissimilarity was calculated with the Sørensen qualitative index and partitioning of variance was conducted with generalised dissimilarity modelling.](image-url)
Table 4.2 Maximum magnitude of change in compositional dissimilarity among the psyllid assemblages as a function of each of the predictor variables. These assemblages are from the samples collected in 2005 (Table 4.0), and were analysed with the Sørensen qualitative index in generalised dissimilarity modelling.

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>Assemblage comparisons</th>
<th>Mistletoes &amp; Eucalypts</th>
<th>Mistletoes</th>
<th>Eucalypts</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>All species</td>
<td>Residents</td>
<td>Tourists</td>
</tr>
<tr>
<td>Host plant</td>
<td>0.74</td>
<td>3.24</td>
<td>N/A*</td>
<td>N/A</td>
</tr>
<tr>
<td>Index of mistletoe age</td>
<td>N/A</td>
<td>N/A</td>
<td>0.15</td>
<td>2.16</td>
</tr>
<tr>
<td>Height above ground</td>
<td>0.59</td>
<td>0.55</td>
<td>0.64</td>
<td>1.30</td>
</tr>
<tr>
<td>Proximity of trees</td>
<td>0.81</td>
<td>0.30</td>
<td>0.34</td>
<td>0.80</td>
</tr>
<tr>
<td>Tree DBH or tree height</td>
<td>0.34</td>
<td>0.26</td>
<td>0.15</td>
<td>0.55</td>
</tr>
<tr>
<td>Leaf area of sample</td>
<td>0.31</td>
<td>0.60</td>
<td>0.15</td>
<td>0.11</td>
</tr>
<tr>
<td>No. mistletoe in tree</td>
<td>0.09</td>
<td>0.19</td>
<td>0.23</td>
<td>0.29</td>
</tr>
<tr>
<td>Aspect of sample</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.59</td>
</tr>
<tr>
<td>Elevation</td>
<td>0.00</td>
<td>0.03</td>
<td>0.13</td>
<td>0.22</td>
</tr>
<tr>
<td>Aspect of slope</td>
<td>0.43</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>TRMI</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.20</td>
</tr>
</tbody>
</table>

* N/A: not applicable to analysis of this data set (i.e. ‘host-plant’ variable didn’t apply to the data sets from only one type of host-plant; and ‘index of mistletoe age’ was not applicable to the samples from eucalypt foliage).
Figure 4.2 Compositional dissimilarity among the tourist psyllid assemblages from the mistletoe samples as a function of the host-branch diameter (i.e. ‘HostBrDi’ cm, the index of mistletoe age), holding all other variables constant (Table 4.2). The analysis was conducted with the Sørensen qualitative index in generalised dissimilarity modelling. Thus, compositional dissimilarity, or species turnover, among the assemblages of tourist species increased with increasing difference in mistletoe age between pairs of samples.
Figure 4.3 The fit of the model to the observed data of the tourist psyllid assemblages from the mistletoe samples displayed as relationships of (a) observed compositional dissimilarity vs. predicted ecological distance and (b) observed vs. predicted compositional dissimilarities. The data points area all pair-wise combinations of the samples ($N = 22$). The model was fit with generalised dissimilarity modelling using the Sørensen dissimilarity index. The predicted ecological distance is derived from the selected predictor variables combined (see Table 4.2).
Figure 4.4 Compositional dissimilarity among the psyllid assemblages as a function of the proximity of surrounding trees for (a) the tourist psyllid assemblages from the mistletoe samples and (b) assemblages with all psyllid species from the mistletoe and eucalypt samples. ‘AveNND’ is the average distance (m) to the nearest tree from the sampled tree. The analysis was conducted with the Sørensen qualitative index in generalised dissimilarity modelling. Thus, variation in pair-wise compositional dissimilarity among the assemblages of psyllids increased steeply between samples with up to approximately 60 m to the nearest tree, and either did not vary or increased at a lesser rate between samples with >75 m to the nearest trees. (See figures 4.3 and 4.0, respectively, for the fit of the model to all predictor variables combined for these assemblage data sets.)
Figure 4.5 Compositional dissimilarity among the assemblages of all psyllid species inhabiting the mistletoe and eucalypt plants as a function of the height of the sample above ground: ‘HtAbvGd’ (m). The analysis was conducted with the Sørensen qualitative index in generalised dissimilarity modelling. Thus, compositional turnover among the assemblages of psyllid species varies over the range of height above ground at which the assemblages were sampled. (See Fig. 4.0 for the fit of the model to all predictor variables combined for this assemblage data set.)
Spiders inhabiting mistletoes and eucalypts

The measured predictor variables contributed up to 37% to explaining the variation in beta-diversity among the spider assemblages, with the environmental variables explaining 32% of the variation among the assemblages on the eucalypts (Fig. 4.6). However, a large proportion of the variation was not explained by the measured predictor variables (Fig. 4.6). The mistletoe and eucalypt assemblages of spiders consisted of similar numbers of species (33 and 30, respectively), yet the proportion of explained variation was greater among the eucalypt assemblages than the mistletoe assemblages. This may be due to the greater variation in abundance of spiders among the eucalypt assemblages compared with the mistletoe assemblages. Among the eucalypt samples, the abundance of potential prey explained 14% and 21% of the variation in spider species composition and abundances, respectively. Among the eucalypt samples with prey densities of up to approximately 50 prey per m² of foliage (i.e. half of the samples), a steep rise in compositional dissimilarity; but there was no compositional dissimilarity among samples with prey densities between 50 and 350 prey per m² of foliage (Fig. 4.7). Prey abundance and the leaf area of the sample were the variables that contributed most to explaining the variation in beta-diversity among the mistletoe samples separately, and among the mistletoe and eucalypt samples combined (Table 4.3); and the relationship between compositional dissimilarity and prey abundance for these sample sets were similar to that among the eucalypt samples (i.e. Fig. 4.7). The relationship between observed compositional dissimilarity and all the selected predictor variables for the spider assemblages among the eucalypt samples is shown in Figure 4.8.

The geographic distance between the mistletoe and eucalypt samples contributed 3% or less to explaining the variation in spider species composition and abundances among the samples. The spatial structure in beta-diversity among the spider assemblages resulted from the higher dissimilarity between the samples that were separated by the greatest distances (i.e. the samples collected at site 23 compared to the samples at the other four sites, 19–23 km apart), and no compositional dissimilarity between samples less than 10 km apart (Fig. 4.9). The type of host-plant explained only a small portion of the variation in beta-diversity among the spider assemblages, that is, 0.4% of the variation in species composition and 2.6% of the variation in species abundances.
**Figure 4.6** Proportion of variation in observed compositional dissimilarity among the spider assemblages inhabiting the mistletoe and eucalypt plants explained purely by the spatial and environmental predictors, shared between the predictor variables and not explained by the predictor variables. See Table 4.0 for details of the assemblages and Table 4.3 for the environmental predictor variables that contributed to each of the models. Compositional dissimilarity was calculated with the Sørensen qualitative index and partitioning of variance was conducted with generalised dissimilarity modelling.

**Table 4.3** Maximum magnitude of change in compositional dissimilarity among the spider assemblages as a function of each of the predictor variables (analysed with the Sørensen index in generalised dissimilarity modelling).

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>Mistletoes &amp; Eucalypts</th>
<th>Mistletoes</th>
<th>Eucalypts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Host-plant</td>
<td>0.07</td>
<td>N/A*</td>
<td>N/A</td>
</tr>
<tr>
<td>Geographic distance</td>
<td>0.18</td>
<td>0.09</td>
<td>0.27</td>
</tr>
<tr>
<td>Prey abundance</td>
<td>0.36</td>
<td>0.43</td>
<td>0.51</td>
</tr>
<tr>
<td>Leaf area of sample</td>
<td>0.42</td>
<td>0.39</td>
<td>0.17</td>
</tr>
<tr>
<td>No. mistletoe in tree</td>
<td>0.20</td>
<td>0.23</td>
<td>0.32</td>
</tr>
<tr>
<td>No. or proximity of trees</td>
<td>0.22</td>
<td>0.35</td>
<td>0.23</td>
</tr>
<tr>
<td>TreeDBH</td>
<td>0.11</td>
<td>0.09</td>
<td>0.04</td>
</tr>
<tr>
<td>Height above ground</td>
<td>0.00</td>
<td>0.00</td>
<td>0.15</td>
</tr>
<tr>
<td>Slope</td>
<td>0.00</td>
<td>0.00</td>
<td>0.36</td>
</tr>
<tr>
<td>Aspect of slope</td>
<td>0.00</td>
<td>0.00</td>
<td>0.18</td>
</tr>
<tr>
<td>Elevation</td>
<td>0.03</td>
<td>0.24</td>
<td>0.11</td>
</tr>
<tr>
<td>TRMI</td>
<td>0.07</td>
<td>0.11</td>
<td>0.00</td>
</tr>
</tbody>
</table>

* N/A: not applicable to analysis of this data set, i.e. ‘host-plant’ variable didn’t apply to the data sets from only one type of host-plant.
Figure 4.7 Compositional dissimilarity among the assemblages of spiders in the eucalypt samples as a function of the abundance of potential prey in the samples (i.e. number of insects and mites per m\(^2\) leaf area). Variation in compositional dissimilarity among the spider assemblages reached an asymptote at approximately 50 prey specimens per m\(^2\) leaf area in the samples. The analysis was conducted with the Sørensen qualitative index in generalised dissimilarity modelling.
Figure 4.8 The relationship between observed compositional dissimilarity among the assemblages of spiders from the eucalypt samples vs. the predicted ecological distance among the samples (derived from the combined selected predictor variables, see Table 4.3). The data points area all pair-wise combinations of the samples (N = 19). The model was fit with generalised dissimilarity modelling using the Sørensen dissimilarity index.
Figure 4.9 Compositional dissimilarity among the assemblages of spiders inhabiting the eucalypt trees as a function of geographic distance between the sampled trees. The analysis was conducted with the Sørensen qualitative index in generalised dissimilarity modelling. Thus, the species turnover was greatest between the samples that were separated by the largest distances, 19–23 km (i.e. the samples collected at site 23 compared to the samples at the other four sites in 2005, Fig. 2.1 Chapter 2).
CHAPTER 4

4.3.2 Temporal variation in beta-diversity of the psyllid assemblages & relative influences of the predictor variables

In 2006, arthropod samples were collected from 26 of the mistletoe plants that were sampled in the previous year, and 34 ‘new’ mistletoe plants that were not previously sampled. The samples collected from the ‘re-colonised’ mistletoe plants included 16 species of psyllids: the 2 mistletoe-specialist species, 12 tourist species known to occur on *Eucalyptus* species (including the two most abundant tourist species sampled in the first year and three species not collected in the first year, Appendix A), and 2 psyllid species of uncertain host-specificity. Therefore, analysis of the re-colonisation assemblages included 4 resident species and 12 tourist species. The psyllid assemblage collected from the ‘new’ mistletoe plants consisted of 11 species (including 2 species not collected the previous year): i.e. the 2 mistletoe-specialist species, 6 tourist species known to occur on *Eucalyptus* species or *Brachychiton* species, and 3 species with unknown host-specificity or a broader host-range. These ‘new mistletoe’ assemblages were analysed based on 5 resident species and 6 tourist species. One of the tourist psyllid species (*Blastopsylla* sp.2, MS23) which was not very abundant or frequent in 2005 was the most abundant species collected from both the re-colonised and new mistletoes in 2006. The spatial variation among the sets of mistletoe samples was similar: between 0.004–23 km among the mistletoes sampled in 2005 and again in 2006; and between 0.004–30 km among the new mistletoes sampled in 2006.

The results for species composition and abundance are shown here, since a greater percentage of variation in beta-diversity was explained compared with analysis of species composition alone (but the relative partitioning of variation among the predictor variables was similar for both sets of analysis). Analysis of the psyllid assemblages that were sampled on the same mistletoe plants in both years of sampling, resulted in 23% percent of the variation in compositional dissimilarity explained by the variation in the measured environmental variables (Fig. 4.10). In these models, the index of mistletoe age, distances to the nearest mistletoe and tree, and solar radiation were the environmental variables that contributed the most to explaining the variation in beta-diversity among these psyllid assemblages (i.e. ‘Enviro subset’ for ‘2005v2006Recol’ in Fig. 4.10). Among the assemblages of psyllids on the re-colonised mistletoes in 2006 only, the variation in beta-diversity
was most influenced by the variation in distances to the nearest mistletoe and tree from the sampled mistletoe (i.e. ‘Enviro subset’ for ‘2006Recol’ in Fig. 4.10). The spatial distance between samples explained less than 1% of the variation in observed dissimilarity between the samples for all of these data sets. Analysis of the beta-diversity of the psyllid assemblages collected from the new mistletoe plants in 2006 resulted in less than 12% of variation in observed compositional dissimilarity explained by the predictor variables. Therefore, partitioning of variance was not conducted but it was noted that once again geographic distance among samples contributed only a small amount to the models.

![Figure 4.10](image)

Figure 4.10 Relative influence of the environmental variables on the variation in community composition among the psyllid assemblages collected on the same mistletoe plants over two years (i.e. ‘2005’: original assemblages collected in 2005 and ‘2006Re-col.’: assemblages collected in 2006 from the re-colonised mistletoes). The proportion of observed variation in beta-diversity among the psyllid assemblages was partitioned into the proportions of variation explained purely by subsets of environmental variables (i.e. ‘Enviro subset’ or ‘Other Enviro’), shared by all environmental variables, and not explained by the predictor variables. For analysis of the ‘2005v2006Recol’ assemblages ‘Enviro subset’ consisted of the index of mistletoe age, distances to the nearest mistletoe and tree, and solar radiation. For analysis of the ‘2006Recol’ assemblages separately, ‘Enviro subset’ consisted of the distances to the nearest tree and mistletoe. The analyses were conducted with generalised dissimilarity modelling using the Bray-Curtis dissimilarity index to calculate compositional dissimilarity.
4.4 Discussion

The determinants of beta-diversity of the arthropod assemblages varied between the assemblages belonging to the different trophic levels, according to the host-specificity of the arthropods, and the importance of different host-plant and habitat characteristics to the arthropod guilds. Host-plant genus was confirmed as a strong influence on the beta-diversity of the resident psyllid assemblages among the mistletoe plants and eucalypt trees, but only a weak influence on the beta-diversity of the spider assemblages. The variation in beta-diversity of the psyllid and spider assemblages was also partially explained by variation in the measured environmental variables. Mistletoe age and the proximity of neighbouring trees and mistletoes had the strongest influence on the beta-diversity among the psyllid assemblages; particularly influencing the tourist species assemblages and the re-colonisation patterns of the psyllid assemblages among the de-faunated mistletoes. In contrast, beta-diversity among the spider assemblages was most influenced by variation in the abundance of potential prey, but the density and proximity of neighbouring trees and some components of land-form also influenced the beta-diversity of the spider assemblages. The spatial separation of samples had a small influence on the beta-diversity of the arthropod assemblages, among samples located more than 10 km apart.

4.4.1 Spatial structuring of arthropod assemblages

The results of my research are mostly consistent with the few studies that have examined the spatial pattern of arthropod beta-diversity among host-plants at specific scales. Assemblages consisting mainly of Lepidoptera, Hemiptera, Coleoptera and Araneae have been more similar than expected by chance among *Eucalyptus marginata* trees less than 20 km apart (i.e. low beta-diversity), and more divergent than expected by chance at distances between 55 and 70 km apart (i.e. higher beta-diversity) (Burgman and Williams 1995). My results are consistent with these findings, in that the community composition of the psyllid and spider assemblages varied little among assemblages on congeneric host-plants separated by up to 23 km, and they were most dissimilar among assemblages with the greatest separation (19–23 km). Low average beta-diversity has also been recorded among assemblages of Lepidopteran caterpillars on congeneric host-plants at both small and large spatial
scales: among sites separated by less than 20 km and among sites separated by 60 to 500 km in continuous lowland rainforest (Novotny et al. 2002, Novotny et al. 2007).

While patterns of the beta-diversity of arboreal spiders have not been elucidated by other studies, the results of the present study can be compared with the few studies of the beta-diversity of ground-dwelling spiders and generalist herbivore insects. Studies of the beta-diversity of ground-dwelling arthropods, including spiders, have detected changes in community composition between spatially separated samples of the same forest type or land system, from 0.5 to 350 km apart, including significant positive relationships between beta-diversity and geographic distance (Oliver et al. 1998, Ferrier et al. 1999, Oliver et al. 2004). Two studies of generalist insect assemblages have documented low variation in community composition among spatially separated sites, over large scales, i.e. 500 and 1,000 km between rainforest sites for fungal-feeding beetle assemblages (Hulcr et al. 2008), and over a smaller scale of 10 km between managed temperate forests for adult moth assemblages (Summerville et al. 2008). Therefore, the relatively low spatial turnover of the spider assemblages among sites separated by up to 23 km in the present study is consistent with the latter results, but more studies of the beta-diversity of generalist and predatory arthropods are required to determine if there are consistent spatial patterns associated with these taxa. Elucidation of such patterns for arboreal versus ground-dwelling spiders and hunting vs. web-building spiders, over a range of scales could be used to inform conservation management of different assemblages of spiders.

Even though the influence of the spatial separation of samples on the beta-diversity of the arthropod assemblages was very low over the extent of the study area, some small-scale spatial structuring among the assemblages was detected. That is, the proximity of surrounding trees and mistletoes influenced the similarity of the assemblages, particularly for the psyllid assemblages that re-colonised the de-faunated mistletoe plants. Therefore, it is likely that the dispersal ability and local population dynamics of psyllids affects the structure of psyllid assemblages over a short time scale and local spatial scale. But it can be inferred that over many years the assemblages of psyllids on box mistletoes become similar, regardless of where the mistletoes occur in the landscape. The tight co-evolution of psyllid species and their host-plant species, and dominance of a few psyllid species in the assemblages are also likely to contribute to the distributional patterns of psyllids. Psyllid taxa have co-
evolved closely with their host-plants, leading to high levels of host-specificity (Percy 2003, Hollis 2004, Percy et al. 2004). Australian Psylloidea, *Eucalyptus* and *Amyema* mistletoe taxa all have a long biogeographical history, originating at least 38 million years ago (Eastop 1978, Hodkinson 1980, Barlow 1996, Ladiges 1997). Box mistletoe and the *Eucalyptus* species in this study occur widely throughout south-eastern Australia. Therefore, it is likely that the psyllid taxa host-specific to these plant species have tracked the distributional changes of the plant species over time and have also become widespread.

Consequently, the low spatial species turnover of psyllid assemblages on congeneric host-plants supports the hypothesis of low beta-diversity of herbivorous insects on widespread plant taxa (Novotny and Weiblen 2005). However, the low spatial turnover among the psyllid assemblages in the present study might not apply to other insect assemblages on host-plants with less widespread distributions. For example, several mistletoe species in Australia occur at only one location or a few locations separated by up to 100 km or more (e.g. *Amyema subcapitatum*, *A. hillianum*, *A. maidenii* subsp. *angustifolium*); and other species have a relatively wide spatial distribution but are found on a narrow range of hosts (e.g. *A. lucasii*) (Barlow 1984). Therefore, further research involving host-plants with varying geographic distributions, including mistletoe plants with narrow host-plant ranges, would elucidate other interesting patterns of beta-diversity among arthropod assemblages.

### 4.4.2 Relative influence of habitat factors on beta-diversity among arthropod assemblages

At the local scale, the environmental or habitat variables that influenced the beta-diversity among the arthropod assemblages were a combination of biotic and abiotic, stochastic and deterministic factors of the host-plants and surrounding habitat. The relative influence of these factors differed among the assemblages of resident and tourist psyllid species, and the spider assemblages.

**Psyllid assemblages**

Not surprisingly, host-plant identity had the greatest influence on beta-diversity among the assemblages of resident psyllid species inhabiting the mistletoes and eucalypts. To a lesser extent, the variation in community composition among the resident psyllid assemblages was influenced by proximity of neighbouring trees, the
height of sampled foliage above ground and the size of the sampled trees. The beta-
diversity of the tourist psyllid assemblages on the mistletoe plants was more strongly
influenced by the measured environmental and habitat variables. The variables with
the most influence on the tourist assemblages were the estimated age of the sampled
mistletoes; factors relating to the position of the mistletoe in the tree (i.e. variation in
height of the mistletoe above ground and aspect of the mistletoe in the tree); the size
of the sampled tree and the proximity of surrounding trees. It is unclear whether the
relationships between beta-diversity of the tourist psyllid assemblages and these
habitat factors are deterministic or stochastic.

I will examine the relationships between beta-diversity of the tourist psyllid
assemblages with two of the habitat variables in more detail: estimated mistletoe age
and proximity of surrounding trees. Firstly, the greatest difference in community
composition of tourist psyllid species was among mistletoes with the greatest
difference in estimated age. The age of a mistletoe plant is related to its size, with size
generally increasing with age but decreasing in senescing individuals (Reid et al.
1995). The greater the longevity and size of the mistletoes, the more likely tourist
species are to encounter mistletoes, leading to similarity in assemblage composition
among mistletoes of similar age and size. Secondly, the greatest variation in beta-
diversity of the tourist psyllid assemblages (on mistletoes) was among assemblages
with surrounding trees at close proximity (up to 60 m away); and there was little
variation among assemblages for which surrounding trees were at greater distances
from the sampled mistletoe and tree. The proximity of surrounding trees is an
indication of the proximity of potential source populations of tourist psyllid species.
Therefore, these results show that the assemblages of psyllid species in closely
neighbouring trees cause fluctuations in the community composition of tourist
assemblages on nearby mistletoes.

The variation in community composition of the tourist assemblages on
mistletoes was also influenced by the community composition of those psyllid species
in the canopy of the host-tree (Chapter 3); since mistletoe samples that had the highest
relative abundance of tourist psyllid species were collected in trees with high relative
abundance of those species. Furthermore, the re-colonisation of the originally de-
faunated mistletoes by psyllids was influenced by the estimated age of mistletoes and
the proximity of surrounding trees and mistletoes. Therefore, it appears that stochastic
factors of insect population demography and proximity of neighbouring trees and mistletoes, i.e. local population effects, interact with deterministic factors of mistletoe age and size to influence the composition and abundance of tourist psyllids that encounter mistletoes, and the re-colonisation dynamics of all of the psyllid species associated with mistletoes.

Tourist species have been recognised as an important guild in other canopy arthropod studies, constituting 10–70% of total species composition (Moran and Southwood 1982, Stork 1987, Basset and Arthington 1992, Ødegaard 2000, Jäger and Topp 2002, Ødegaard 2004, Southwood et al. 2005). Arthropod tourist species are defined as non-predatory species, which do not have an intimate or lasting relationship with a host-plant, but whose members may occur on plants due to random dispersal or for shelter, sun-basking, sexual displays and mating, or indirect sources of nutrition, e.g. honey-dew (Moran and Southwood 1982). Psyllid species are usually highly host-plant specific but adult psyllids occasionally feed on non host-plants (i.e. those on which the species cannot complete its whole lifecycle, Hollis 2004). Therefore, it is possible that psyllids which usually occur on eucalypt trees could supplement their feeding on mistletoes. Regardless of whether individuals of tourist species occur on mistletoes due to stochastic or directed dispersal, or mass effects (due to high relative abundance in the host-tree or surrounding trees); they form part of the biodiversity of arthropods inhabiting mistletoes and become part of the food web in that component of the canopy.

However, the majority of community ecology studies do not distinguish between resident and tourist species, and therefore they overlook some of the fine-scale diversity patterns and relationships such as determined in the present study. For example, studies of insect communities sampled with indiscriminate methods like whole canopy fogging, malaise traps or light traps, and/or which sample few plants or habitats, do not have the power to determine host or habitat specificity. Moreover, studies that distinguish insect tourist species do not usually investigate the occurrence patterns of such species (but see Ulrich and Zalewski 2006). Monitoring species assemblages over time can enable elucidation of resident and tourist species in assemblages and the relative abundance of these different components of assemblages (Magurran and Henderson 2003, Magurran 2007). In a study of a fish community over 21 years in the Bristol Channel (UK), core species persisted in the community for
more than 10 years and accounted for 99% of total abundance, whereas occasional species were recorded in the community for less than 10 years during that period and made up the remaining 1% of abundance (Magurran and Henderson 2003). The core and occasional species were distinguished as those usually occurring in different habitats (estuarine vs. deeper water) and the arrival of occasional species was related to stochastic weather conditions. In my study, the relative abundance and frequency of the tourist psyllid species in the mistletoe samples differed significantly between years but was much more consistent for the resident psyllid species. This observation, combined with the influence of the different host and habitat variables on the beta-diversity of the resident and tourist assemblages, lends support to the hypothesis that the structure and distribution of core/resident species assemblages is underpinned by biological factors, whereas that of occasional/tourist assemblages is more related to local, stochastic dispersal and chance events (Ulrich and Zalewski 2006, Magurran 2007).

**Spider assemblages**

The beta-diversity among the spider assemblages inhabiting the mistletoe and eucalypt plants was most strongly influenced by the abundance of potential arthropod prey. The relationship between variation in prey abundance and beta-diversity of the spider assemblages indicated that there is a threshold level of prey abundance, above which the variation in beta-diversity of the spider assemblages was not affected. Prey abundance is known to influence the abundance and species richness of spiders (Halaj et al. 1998, Horvath et al. 2005) but this is not always the case. In situations of non-limiting prey abundance this factor has had little influence on the diversity of web-spiders (Greenstone 1984). High abundance of prey on the host-plants could prevent competitive exclusion by a few species of spiders, allowing the co-existence of many species of spiders and little change in composition and abundance between host-plants. Birds also influence the community composition of spiders via predation; therefore further research could include bird-exclusion experiments to determine the relative influence of top-down and bottom-up determinants of the community composition of spiders inhabiting mistletoes and their hosts (similar to Gruner and Taylor 2006, and Mooney and Linhart 2006).

Community composition of spider assemblages has also been found to be influenced by inter-related factors of plant species composition, vegetation
architecture, shade and moisture levels (Halaj et al. 2000, Beals 2006, Entling et al. 2007, Schaffers et al. 2008). Other environmental factors that had a small influence on the beta-diversity of the spider assemblages in the present study include the density and proximity of neighbouring trees and mistletoes, and the elevation and slope of the land. These results indicate that climatic conditions and the proximity and abundance of neighbouring spider communities had some influence on the structure of the sampled spider communities.

4.4.3 Accounting for the unexplained variation in beta-diversity

Between thirty-six and ninety percent of the observed variation in beta-diversity among the arthropod assemblages was not related to the measured predictor variables. These results are comparable with other beta-diversity studies, which report proportions of unexplained variation in community composition of 36-70% for invertebrate assemblages (Baselga and Jimenez-Valverde 2007, Mykra et al. 2007, Baselga 2008, Hulcr et al. 2008), 53% for frog assemblages (Parris 2004) and 30-90% for vascular plant assemblages (Duivenvoorden et al. 2002, Tuomisto et al. 2003, Jones et al. 2006, Laliberté et al. 2009). Therefore, other variables that could be measured to account for the unexplained variation in beta-diversity the arthropod assemblages among mistletoes and eucalypts include the chemical and structural traits of the foliage of every sampled plant (for the influence on psyllid assemblages). And regarding the spider assemblages: measurement of microhabitat differences, e.g. micro-climatic conditions, structural supports and hiding spots, which might affect web-building versus hunting spiders. Some of the unexplained variation may also be due to stochastic variation in species composition and abundance between the assemblages unrelated to any measurable variable.
4.5 Conclusion

The results of this chapter revealed that the community composition of the resident psyllid assemblages was primarily driven by host-plant taxonomy and secondarily by habitat properties. The occurrence of tourist species in the psyllid assemblages was most strongly influenced by local habitat factors, such as proximity of neighbouring trees and mistletoes, and stochastic dispersal. The spatial separation of sampled host-plants over the whole study area was not a significant driver of beta-diversity among the arthropod assemblages. However, small-scale factors within the tree canopy and surrounding habitat shaped the community composition of assemblages, and the re-assembly of the psyllid communities. Therefore, it is likely that local population dynamics affect the structure of psyllid assemblages at local spatial scales and over short time periods; but over longer time scales the dominant psyllid species have become widespread due to tight co-evolution with their host-plants.

Host-plant taxon was confirmed as a weak influence on the beta-diversity of the spider assemblages. Of the measured habitat variables, potential prey abundance was had the strongest influence on the variation in community composition among the spider assemblages. A small amount of spatial turnover in community composition of the spider assemblages was observed over the extent of the study. Hence, the beta-diversity of spider assemblages was primarily influenced by niche properties (i.e. prey abundance and similarity in habitat architecture between the host-plants), but also partially by limited dispersal among spatially-separated assemblages.
4.6 References


Chapter 5

General discussion and conclusions

The diversity of arthropod fauna inhabiting plants is influenced by a multitude of interacting factors which drive variations in species richness, composition and abundance of arthropod communities over different spatial and temporal scales. These factors include host-plant specificity and plant taxonomic relationships (Frenzel and Brandl 2001, Novotny et al. 2002a, Schoonhoven et al. 2005); vegetation composition and architecture (Halaj et al. 2000, Basset 2001, Stuntz et al. 2002, Cunningham et al. 2005); quality and palatability of nutritional resources (Basset 1996, Richardson et al. 2000); apparency and abundance of plants (Strong et al. 1984); inter-trophic interactions among arthropods and other animals (Gruner and Taylor 2006, Mooney and Linhart 2006); spatial arrangement and environmental conditions of habitats (Major et al. 2003, Steinitz et al. 2006); and history of disturbance (Floren and Deeleman-Reinhold 2005). These are important factors to consider for conservation of arthropod diversity and thus the important ecological roles played by arthropod fauna.

5.1 Review of findings

The first part of this chapter begins with a review of the comparative similarity of arthropod assemblages sampled from mistletoe plants and their host trees. This includes examination of different orders of arthropods, belonging to different trophic levels, and the traits of the hosts that might be related to the observed differences in community composition among assemblages on different hosts (Chapters 2 and 3). The review also includes a synthesis of the patterns of beta-diversity among the sampled arthropod assemblages and the relative influence of host or habitat traits and spatial distribution on variation in beta-diversity among assemblages (Chapter 4). The second part of the chapter (section 5.2) consists of a comparison of the results of the
present study with those of other studies of component arthropod communities, and implications for further research.

5.1.1 Comparative similarity of arthropod assemblages on mistletoe and eucalypt trees

In Chapter 2, it was established that the ordinal composition of arthropod assemblages was the same between the mistletoe and eucalypt plants but the abundance of all orders except mites was greater on the eucalypt foliage. Upon examination of the nitrogen content of the mistletoe and eucalypt foliage, I suggested that the greater densities of arthropods in the eucalypt canopies could be due to the higher nitrogen content of the eucalypt foliage. Even though the nitrogen content of the eucalypt foliage is still low for the nutritional requirements of insects, it must be sufficiently greater than the mistletoe foliage to enable greater population densities of insects on the eucalypts and to override the influence of defensive traits of the eucalypt foliage. This is intriguing because mistletoe foliage is thought to be relatively undefended compared to eucalypt foliage and often contains higher concentrations of other mineral nutrients than its host trees (Lamont 1983, March 2007). However, the mistletoe foliage was significantly thicker than the eucalypt foliage, which could be an impediment to herbivorous insects, leading to lower densities of such insects and a flow-on effect to predatory arthropods. Other factors that could contribute to the disparity in arthropod abundances between the studied plants include the greater density of eucalypt trees than mistletoe plants in this landscape; and the greater longevity and hence stability of the eucalypt canopies than mistletoe plants (in terms of leaf and whole plant longevity).

Differences in the composition of the arthropod assemblages between the mistletoe and eucalypt plants were discovered at lower taxonomic levels of arthropod family, genus and species (Chapter 3). The composition and relative abundance of spiders differed slightly between the host-plants (at family to morphospecies levels) but the most striking differences were among the assemblages of herbivorous psyllid insects (at morphospecies level). The psyllid assemblage inhabiting box mistletoe was dominated by two mistletoe-specialist psyllid species and also consisted of several tourist species, which made up sixty percent of the seventeen species collected from the mistletoe plants. In contrast, only ten percent of the twenty psyllid species inhabiting the eucalypt canopies were determined as tourist species. Therefore, among
the resident psyllid assemblages inhabiting the mistletoes and the eucalypt canopies, there was less than one percent similarity in community composition. This revealed high beta-diversity of the psyllid assemblages between allo-familial host-plants. Further analysis of the similarity of community composition among the mistletoe and eucalypt assemblages separately, revealed greater similarity among psyllid assemblages from individuals of the same host-plant genus. The phenomenon of greater similarity among insect assemblages with increasing host-plant relatedness is becoming an established pattern among herbivorous insect assemblages (Novotny et al. 2002b, Novotny and Basset 2005, Ødegaard et al. 2005). However, further research is required to determine the patterns of variation in herbivorous insect assemblages among congeneric mistletoe species, to compare with patterns among congeneric eucalypt species (since only one species of mistletoe was sampled in the present study).

The assemblages of spiders inhabiting the mistletoes and eucalypts were much more similar in community composition than were the psyllid assemblages between the sampled plants. The results of the beta-diversity analysis (Chapter 4) confirmed that host-plant identity was not a strong predictor of the variation in species composition and abundance among the spider assemblages. These results are likely related to the similarity in plant structure or architecture between the mistletoes and the eucalypt canopies. Box mistletoes mimic the leaf and branching structure of their host-plants, resulting in few differences in habitat architecture between the sampled plants. Habitat architecture is known to have a strong influence on the composition and abundance of spider assemblages (Foelix 1982, Greenstone 1984, Halaj et al. 2000); therefore, further research is warranted to investigate micro-habitat differences between mistletoe plants and the canopies of their host-trees.

Of the measured habitat variables, potential prey abundance was found to have the strongest influence on the variation in community composition among the spider assemblages (Chapter 4). While prey abundance was a strong predictor of spider beta-diversity, a threshold level of prey densities was reached above which the beta-diversity of the spider assemblages was no longer influenced. These results correspond with other studies of the ecology of spider communities, in which prey abundance has been correlated with the variation in community composition of spider assemblages (Halaj et al. 1998, Horvath et al. 2005). However, prey abundance has
not always been a strong predictor of spider diversity, probably due to non-limiting prey abundance (Greenstone 1984).

5.1.2 Relative roles of niche properties and spatial patterns on community composition of arthropods

This thesis has also examined the relative influences of niche properties and dispersal ability of arthropod taxa, by evaluating the strength of relationships between beta-diversity of assemblages and habitat or spatial variables. Only a small amount of spatial turnover in community composition of the spider assemblages was observed over the extent of the study (up to 40 km between sites). The beta-diversity of the spider assemblages was primarily influenced by niche properties (i.e. prey abundance and similarity in habitat architecture), but also some limited dispersal among spatially-separated assemblages (Table 5.0). The stronger influence of spatial separation on the spider assemblages than the psyllid assemblages, was the result of slightly greater spatial turnover among the spider assemblages than the psyllid assemblages. This probably reflects the host-specificity of psyllids and thus closer matching of the spatial distribution of psyllids and their host-plants, compared with spiders and their host-plants or habitats.

Thus, the spatial separation of psyllid assemblages over the whole study area did not have a significant influence on the beta-diversity patterns of the psyllids. However, small-scale factors within the tree canopy and neighbouring trees shaped the community composition of psyllid assemblages, particularly that of tourist psyllid assemblages (Fig. 5.0). These factors included mass effects, that is, the abundance and proximity of source populations of insects; which influences the chance of such insects encountering their host-plants and also non host-plants (i.e. plants on which these species cannot be self-maintaining). These habitat factors also affected the re-assembly and community composition of psyllids on the de-faunated mistletoe plants. Moreover, the community composition between the original and new assemblages of psyllids varied less for the resident psyllid species than the tourist psyllid species. This confirmed the influence of deterministic factors on the community composition of resident psyllids versus stochastic factors affecting tourist species (Magurran 2007). Therefore, the community composition of resident psyllid assemblages was primarily driven by host-plant taxonomy and secondarily by habitat properties, leading to non-random distribution; whereas the occurrence of tourist species in the
psyllid assemblages was most strongly influenced by local habitat factors and stochastic dispersal (Table 5.0).

Table 5.0 The main determinants of alpha- and beta-diversity among the arthropod assemblages in this study.

<table>
<thead>
<tr>
<th>Determinants</th>
<th>Arthropod taxa most strongly affected</th>
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<tbody>
<tr>
<td>Host-plant taxonomic relationships</td>
<td>Psyllids (particularly resident* species)</td>
</tr>
<tr>
<td>Nutritional quality and structural properties of plant foliage</td>
<td>Psyllids</td>
</tr>
<tr>
<td>Proximity &amp; abundance of source populations (e.g. mass effects)</td>
<td>Psyllids (particularly tourist+ species)</td>
</tr>
<tr>
<td>Abundance, age, size &amp; longevity of plants</td>
<td>Psyllids (particularly tourist species)</td>
</tr>
<tr>
<td>Prey abundance</td>
<td>Spiders</td>
</tr>
<tr>
<td>Habitat architectural similarity</td>
<td>Spiders</td>
</tr>
<tr>
<td>Spatial separation of assemblages</td>
<td>Spiders</td>
</tr>
</tbody>
</table>

* Resident species: those species which are specialised to, or have a non-random distribution in regard to, a particular host-plant.
+ Tourist species: those species which occur occasionally on a particular host-plant and cannot complete their whole life-cycle on that host-plant.

5.2 Determinants of diversity of other component communities of arthropods

Other component communities of arthropods that have been studied include inhabitants of different species of epiphytic plants and ectoparasites on vertebrates. Studies comparing the arthropod species richness, abundance and faunal similarity between different species of epiphytic plants have found that the main determinants of variation in alpha-diversity and faunal similarity of arthropod assemblages between plants are: plant size and architecture, and direct and indirect nutrient resources (Dejean et al. 1995, Richardson 1999, Richardson et al. 2000, Stuntz et al. 2002). The effect of epiphytic plant size and architecture on alpha-diversity and faunal similarity is due to greater accumulation of water and plant debris in larger epiphytes. This in turn influences the structural complexity of the habitat, the availability of nutrients and the degree of niche partitioning in epiphytic microcosms. Direct sources of nutrients also influence compositional dissimilarity of arthropod fauna among different types of epiphytes, for example plant exudates and decaying flowers in
heliconia bracts provide resources to arthropods, but not in bromeliad plants (Richardson et al. 2000). Not only do these factors influence the species richness, composition and abundance of arthropods but also the composition of feeding guilds of arthropod assemblages. Stuntz et al. (2002) found that detritivores and predators constituted at least 80% of arthropods inhabiting three species of epiphytes; and the proportions of web-building and hunting spiders differed significantly between the plants. The variations in spider guild composition were related to the differences in plant forms between the epiphytic species, with the structure of bromeliads more amenable to hunting spiders, whereas that of orchids more suitable for web-building spiders (Stuntz et al. 2002). Therefore, interacting factors of plant species, size, architecture and resources influence the diversity of arthropod communities among epiphytic plants as well as mistletoe plants. These studies of epiphytic plants did not examine the influence of spatial factors on community similarity.

Communities of parasitic mites on mammals provide another interesting comparison with arthropod assemblages inhabiting mistletoe and other epiphytic plants. Vinarski et al. (2007) studied the relative influence of geographic distance, host-species composition and environmental factors on the compositional similarity among mite assemblages inhabiting 11 species of small mammals. They found that the similarity among component communities of mites, i.e. those inhabiting the same host-species, was mainly determined by similarity in the local environmental conditions (i.e. climatic variables); while the similarity between component communities (i.e. among the compound community) was mainly determined by host-species composition. Furthermore, the similarity among communities of mites was not affected by geographic distance, which was thought to eventuate from passive dispersal of the mites and tight co-speciation among the parasites and their hosts.

These results are similar to my findings for the psyllid and spider communities. Firstly, the geographic distance between the spider and psyllid assemblages only had a small influence on the compositional similarity among assemblages. The component communities of psyllids and spiders on congeneric host-plants were primarily influenced by habitat factors, such as mistletoe age for psyllids and prey abundance for spiders; whereas, the composition of the compound community of psyllids on both host-plant taxa was primarily determined by identity of the host-plants. However, the compositional similarity among the spider compound
community was not as strongly influenced by host-plant taxon. Similar to parasitic mites and their host-mammal species, psyllid taxa have co-evolved closely with their host-plants (Percy 2003, Hollis 2004, Percy et al. 2004).

5.3 Implications for conservation and further research

This research provides further evidence that mistletoe plants support a distinct assemblage of herbivorous insects; therefore, conservation of mistletoes and other epiphytic plants is important for the conservation of biodiversity. The distribution of the host-specific psyllid insects was closely linked to that of their host-plants in this study, thus conservation of host-specific insect assemblages could be achieved by conservation of viable populations of their host-plants. The conservation of arboreal spiders should be targeted towards conserving heterogenous habitats which support the biological requirements of spiders, at appropriate spatial configurations for their dispersal ability. Further research is required to determine the patterns and scales of spatial turnover of arthropod assemblages, and the interaction between habitat distribution and dispersal ability of taxa. Moreover, tourist or transient species should not be ignored in conservation strategies. Species might appear to be on the ‘wrong’ host-plant or habitat but that may be an important, albeit occasional, part of their biology and life-cycle. For example, different life-stages (adults vs. larvae) have different habitat requirements and can occur on different host-plants, and some taxa have different seasonal patterns of occurrence and niche requirements e.g. migratory birds.

Further research is required to determine the patterns and scales of spatial turnover of arthropod assemblages at a wide variety of scales, particularly for predatory arthropods and herbivorous generalist insects, and both epigeic and arboreal taxa. Some questions that need to be addressed and possible experimental designs and predictions are outlined below.

What is the interaction between habitat distribution and the dispersal ability of arthropod taxa? What is the effect of this interaction on beta-diversity or homogenisation of assemblages in a specified area? Does this interaction differ between taxa of different body sizes, trophic levels and habitat specificity?
An experiment to address these questions could involve placing new habitats (such as tree logs) in an area at differing distances to each other and to existing similar habitats; and measuring the colonisation of the new habitats, in conjunction with the distances to the nearest existing habitats to estimate dispersal abilities. For example, a study such as that by Gibb et al. (2006) involving collection of saproxylic beetles from experimentally placed logs, could be extended to a greater range of distances between new habitats, a larger extent of study area and arthropods in different trophic levels. To be more precise about dispersal abilities, the experiment could involve mark–recapture of arthropods, but this would limit the number of taxa and individuals that could be used in the experiment. Arthropods in different trophic levels could be assessed in the same habitat, e.g. saproxylic beetles, spiders and/or ants on tree logs, but different habitats would need to be used to include a wider variety of trophic levels. New vegetation habitats could be created by de-faunation, as in the present study, but the measurement of distances to surrounding similar habitats would have to be more extensive than in the present study (for best estimates of dispersal ability and proximity of source populations). Research of this kind would necessarily involve collaboration of ecologists, taxonomists, para-taxonomists, field assistants and many hours of fieldwork, identification of taxa and data analyses.

Body size and winged-ness of arthropods are two properties that influence dispersal ability and colonisation rate of new habitats. It is expected that colonisation rate would be positively correlated with dispersal ability of arthropods, which would be positively correlated with body size and winged-ness. However, there is currently no consensus on the influence of these factors on the occurrence of arthropod fauna and the interactions with successional age and spatial arrangement of habitats (Hurd and Fagan 1992, Gathmann et al. 1994, Steffan-Dewenter and Tscharntke 1997, Cunningham and Murray 2007). If the distribution of habitats is greater than the dispersal ability of taxa, this would promote greater beta-diversity between assemblages; but lower beta-diversity and thus homogenisation of assemblages under the opposite conditions. It is also expected that the interaction between dispersal ability and distances between habitats would be stronger for habitat specialists, which rely on particular habitats or host-plants to complete their life-cycle, compared with habitat generalists. Therefore, the variation in beta-diversity among habitat-specialist assemblages would increase at a greater rate than among habitat-generalist
assemblages, with increasing distances between habitats. However, there would also be an interaction with the dispersal ability of the taxa.

Other areas of further research could include extension of the re-colonisation part of the current study by sampling arthropod assemblages on mistletoes over different time periods since de-faunation, to examine the effect of time on community assembly in more detail. Furthermore, mistletoe volume, as well as leaf area, could be directly included in analyses of arthropod community composition, to assess the effect of both size and area of mistletoe foliage on the interception rate and species packing or carrying capacity of the mistletoe plants. Furthermore, the re-colonisation patterns of spiders collected from de-faunated mistletoes in the present study could be examined, after identification of the spider specimens to morphospecies. The relative influence of environmental and spatial variables on the guild composition of spiders (e.g. web-building versus hunting) could also be assessed with the current data set.

Another area of interesting research would be studies of the origins of mistletoe-specific insect taxa, i.e. examination of the relationships between insect species on different mistletoe species, and on a range of mistletoes versus host-plants. The psyllid species so far collected from *Amyema* mistletoes (on *Eucalyptus* species) are more closely related to psyllid species which inhabit *Acacia* species than *Eucalyptus* species, but *Acizzia* has not yet been recorded on mistletoes on *Acacia* (Taylor 1999, Yen 2002).

### 5.4 Conclusion

As the first systematic community-level study of the arthropod fauna inhabiting a mistletoe species and its host-plants, this research has provided important information about the diversity and host-specificity of arboreal arthropods in component communities. This research has confirmed that the arthropod fauna inhabiting mistletoe plants contributes a small but significant amount to canopy arthropod diversity, due to the presence of host-specific herbivorous insects. Mistletoe plants in general are predicted to host a different fauna of herbivorous insects compared with the mistletoes’ host-plants; due to the different physiological characteristics of mistletoe plants and their hosts. In contrast, other epiphytic plants are expected to support different arthropods in several trophic levels (e.g. detritivores, herbivores and
predators) compared to those inhabiting their host-plants; due to differences in both structural and physiological properties between epiphytic plants and their hosts.

Sampling over different spatial scales (from within-tree to between-patch scales up to 40 km apart) and over a one year period, enabled elucidation of the relative influence of spatial, host-plant and habitat variables on the variation in diversity among arthropod assemblages. Niche and patch-scale properties such as host-plant taxon, proximity of neighbouring trees and mistletoe age, had the strongest influence on the beta-diversity and assembly of the herbivorous insect assemblages. The community composition of resident psyllid assemblages was primarily driven by host-plant taxonomy and secondarily by habitat properties, leading to non-random distribution; whereas the occurrence of tourist species in the psyllid assemblages was most strongly influenced by the local habitat factors and stochastic dispersal. Prey abundance had the strongest influence on the beta-diversity among the spider assemblages on the different host-plants. The null model of increasing community dissimilarity with increasing geographic distance among assemblages was not supported for the herbivorous insects studied, confirming previous findings of low beta-diversity of herbivorous insects among congeneric host-plants. However, the spatial separation of assemblages did have a small influence on the variation in community composition among the spider assemblages.

Therefore, conservation of arthropod fauna and biodiversity in general, depends on conservation of habitats with different vegetation composition and structural forms, to encompass the full range of habitat components utilised by arthropods. The required spatial arrangement of habitat for arthropods depends on the biological characteristics of the target organisms, e.g. host-plant specificity and dispersal ability; and historical distribution and fragmentation of habitats. Further research examining these interacting factors would aid the conservation of the highly diverse arthropod taxa throughout the world.
5.5 References


Table 6.0 Extra information about the Hemipteran taxa sampled in this study from box mistletoe (*Amyema miquelii*) and the eucalypt trees: red box (*Eucalyptus polyanthemos*), yellow box (*E. melliodora*) and Blakely’s red gum (*E. blakelyi*). Identification and sources of information about psyllids: Dr Gary Taylor (University of Adelaide), Taylor (1999), Hollis (2004). Identification of Cicadellidae (leafhoppers) by Piotr Trebicki (Department of Primary Industries, Victoria).

<table>
<thead>
<tr>
<th>Morphospecies code</th>
<th>Species</th>
<th>Family</th>
<th>Known host plant(s)</th>
<th>Life history</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS01</td>
<td><em>Acizzia loranthacae</em> G.S. Taylor, 1999</td>
<td>Psyllidae</td>
<td><em>Amyema</em> spp.</td>
<td>Free-living</td>
<td>Known Distribution: ACT, NSW, SA, VIC</td>
</tr>
<tr>
<td>MS02</td>
<td><em>Acizzia amyemae</em> G.S. Taylor, 1999</td>
<td>Psyllidae</td>
<td><em>Amyema</em> spp.</td>
<td>Free-living</td>
<td>Distribution: ACT, SA, VIC</td>
</tr>
<tr>
<td>MS03</td>
<td><em>Australopsylla</em> sp.1 G.S. Taylor, 1999</td>
<td>Psyllidae</td>
<td><em>Eucalyptus</em> spp. (The 2 described <em>Australopsylla</em> species have been collected on <em>E. macrorhyncha</em>, <em>E. moluccana</em> &amp; <em>E. capitellata</em> in NSW &amp; on other species in other states.)</td>
<td>lerp-former, leaf-curler or gall-inducer</td>
<td></td>
</tr>
<tr>
<td>MS04</td>
<td><em>Phyllolyma</em> sp. (Crystal lerp)</td>
<td>Psyllidae</td>
<td><em>Eucalyptus</em> spp., <em>Melaleuca</em> sp.</td>
<td>lerp former – young stems. Crystalline lerps, covered in honey dew, aggregate &amp; patchy distribution</td>
<td>Poorly described group</td>
</tr>
<tr>
<td>MS05</td>
<td><em>Platyobria adustalata</em> Taylor, 1987</td>
<td>Psyllidae</td>
<td><em>Eucalyptus polyanthemos</em> and <em>?E. melliodora</em> (Hollis, 2004)</td>
<td>free-living - young, newly expanded leaf</td>
<td>Distribution: ACT</td>
</tr>
<tr>
<td>MS06</td>
<td><em>Anoeconeossa</em> sp.1</td>
<td>Psyllidae</td>
<td><em>Eucalyptus</em> spp.</td>
<td>Under abandoned lerps and galls of other psyllid species.</td>
<td></td>
</tr>
<tr>
<td>MS07</td>
<td><em>Blastopsylla</em> sp.1</td>
<td>Psyllidae</td>
<td><em>Eucalyptus</em> spp., <em>Melaleuca</em> spp.</td>
<td>Lerp-formers or free-living</td>
<td>This could be a new species. (There are no setae on the ‘elbow’ of the paramere, as in <em>Blastopsylla</em> sp.2, MS23.)</td>
</tr>
<tr>
<td>Morphospecies code</td>
<td>Species</td>
<td>Family</td>
<td>Known host plant(s)</td>
<td>Life history</td>
<td>Other</td>
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<tr>
<td>MS08</td>
<td>Anoeconeossa communis Taylor, 1987</td>
<td>Psyllidae</td>
<td>Eucalyptus spp. in NSW, E. camaldulensis in NT &amp; SA.</td>
<td>commensal under abandoned lerp</td>
<td>My specimens are closest to this species. Distribution: [NSW], NT, QLD, SA, WA</td>
</tr>
<tr>
<td>MS09</td>
<td>Platyobria sp. 1</td>
<td>Psyllidae</td>
<td>Eucalyptus spp.</td>
<td>gall-inducers, free-living</td>
<td></td>
</tr>
<tr>
<td>MS10</td>
<td>Australopsylla sp. 2</td>
<td>Psyllidae</td>
<td>Eucalyptus spp. (The 2 described Australopsylla species have been collected on E. macrorhyncha, E. moluccana &amp; E. capitellata in NSW &amp; on other species in other states.)</td>
<td>lerp-former, leaf-curler or gall-inducer</td>
<td></td>
</tr>
<tr>
<td>MS11</td>
<td>Australopsylla sp. 3</td>
<td>Psyllidae</td>
<td>Eucalyptus spp. (The 2 described Australopsylla species have been collected on E. macrorhyncha, E. moluccana &amp; E. capitellata in NSW &amp; on other species in other states.)</td>
<td>lerp-former, leaf-curler or gall-inducer</td>
<td></td>
</tr>
<tr>
<td>MS12</td>
<td>Agelaeopsylla maculatae Taylor, 1990</td>
<td>Psyllidae</td>
<td>E. citriodora, E. maculate</td>
<td>free-living</td>
<td>Distribution: ACT, QLD</td>
</tr>
<tr>
<td>MS13</td>
<td>Schedotrioza distorta G.S. Taylor, 1990</td>
<td>Triozidae</td>
<td>Eucalyptus spp.</td>
<td>gall-former</td>
<td>Distribution: NSW, SA</td>
</tr>
<tr>
<td>MS14</td>
<td>Platyobria lewisi Taylor, 1987</td>
<td>Psyllidae</td>
<td>Eucalyptus blakelyi, E. camaldulensis</td>
<td>free-living</td>
<td>Distribution: ACT, SA, VIC</td>
</tr>
<tr>
<td>MS15</td>
<td>Creis sp.1</td>
<td>Psyllidae</td>
<td>Eucalyptus spp.</td>
<td>lerp formers</td>
<td>Eyes not ‘recessive’ as in Spondyliaaspis plicatuloides; very long antennae – longer than Creis sp.2; wings tinged yellow-brown; veins red.</td>
</tr>
<tr>
<td>MS16</td>
<td>Acizzia sp. 1</td>
<td>Psyllidae</td>
<td>Acacia spp.</td>
<td>free-living</td>
<td></td>
</tr>
<tr>
<td>Morphospecies code</td>
<td>Species</td>
<td>Family</td>
<td>Known host plant(s)</td>
<td>Life history</td>
<td>Other</td>
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<tr>
<td>MS17 (1st sampled in 2006)</td>
<td>Cryptoneossa sp.?</td>
<td>Psyllidae</td>
<td>Eucalyptus and Leptospermum spp.</td>
<td>Larvae of some species under deserted lerps.</td>
<td></td>
</tr>
<tr>
<td>MS18</td>
<td>Ctenarytaina sp.</td>
<td>Psyllidae</td>
<td>Eucalyptus spp. &amp; other Myrtaceous hosts</td>
<td>free-living</td>
<td>Ovipositor elongated and ‘saw like’. Male terminalia (claspers) longish. Wing venation distinct – straight veins. Head wider than body. Yellow body, without markings.</td>
</tr>
<tr>
<td>MS19 (in samples E23 &amp; M3)</td>
<td>Cardiaspina retator Taylor, 1962</td>
<td>Psyllidae</td>
<td>Eucalyptus spp.</td>
<td>Lerp-former</td>
<td>Distribution: ACT, NSW, SA, VIC Veins un-pigmented; genal cones about 1.5x longer than MS26, slightly convergent at apex.</td>
</tr>
<tr>
<td>MS20 (1st sampled in 2006, sample M82)</td>
<td>Protyora sterculiae Froggatt, 1901</td>
<td>Carsidaridae</td>
<td>Brachychiton populneus, Brachychiton sp. (i.e. Kurrajong)</td>
<td>Free-living larvae, in colonies</td>
<td>Distribution: ACT, NSW, QLD, SA</td>
</tr>
<tr>
<td>MS21</td>
<td>Glycaspis sp.</td>
<td>Psyllidae</td>
<td>Eucalyptus spp.</td>
<td>Lerp-formers</td>
<td>&gt;150 spp. described by Moore. Species are host specific to groups of related Eucalypts.</td>
</tr>
<tr>
<td>MS22</td>
<td>Hyalinaspis sp.</td>
<td>Psyllidae</td>
<td>Eucalyptus spp.</td>
<td>Lerp-formers</td>
<td></td>
</tr>
<tr>
<td>MS23</td>
<td>Blastopsylla sp.2 (near multisetulae Taylor, 1985)</td>
<td>Psyllidae</td>
<td>Eucalyptus spp., Melaleuca spp. (Known host of B. multisetulae is E. brachycalyx.)</td>
<td>Lerp-formers or free-living</td>
<td>This could be a new species. (Has setae on the ‘elbow’ of the paramere. Very small species.) Known distribution of B. multisetulae is SA.</td>
</tr>
<tr>
<td>Morphospecies code</td>
<td>Species</td>
<td>Family</td>
<td>Known host plant(s)</td>
<td>Life history</td>
<td>Other</td>
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<tr>
<td>MS24 (1st sampled in 2006, sample M102)</td>
<td><em>Acizzia</em> sp. 2</td>
<td>Psyllidae</td>
<td><em>Acacia</em> spp.</td>
<td>free-living</td>
<td></td>
</tr>
<tr>
<td>MS25 (1st sampled in 2006, sample M62)</td>
<td><em>Creiis</em> sp.2</td>
<td>Psyllidae</td>
<td><em>Eucalyptus</em> spp.</td>
<td>lerp formers</td>
<td>Eyes not ‘recessive’ as in <em>Spondyliaspis plicatuloides</em>, very long antennae, wings ‘glassy’, veins brown.</td>
</tr>
<tr>
<td>Not assigned</td>
<td><em>Orosius orientalis</em> (Matsumura) common brown leafhopper</td>
<td>Cicadellidae (subfamily Deltocephalinae)</td>
<td>Collected in this study from <em>Amyema miquelii</em> box mistletoe</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Not assigned</td>
<td><em>Orosius canberrensis</em> (Evans)</td>
<td>Cicadellidae (subfamily Deltocephalinae)</td>
<td>Collected in this study from <em>Amyema miquelii</em> box mistletoe</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Not assigned</td>
<td><em>Batracomorphus angustatus</em> (Osborn)</td>
<td>Cicadellidae (subfamily lassinae)</td>
<td>Collected in this study from <em>Amyema miquelii</em> box mistletoe</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>