Microhabitat Utilisation and the Spatial Distribution of Rainforest Canopy Invertebrate Communities

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Thesis submitted by

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Statement of the Contribution of Others

Nature of Assistance	Contribution	Name and Affiliation of Co-contributors
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Dedicated to the 40,374 invertebrates who

gave their lives for this research…

…lest we forget

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Go the Drunken Hellfish…

Abstract

The tropical rainforest is renowned for its high invertebrate species richness. Yet our understanding of the spatial distribution of the invertebrate communities inhabiting tropical rainforest canopies is very poor. Most mass-sampling invertebrate biodiversity studies from the rainforest canopy have either focussed on whole trees, via sampling methods such as canopy fogging, or on subsets of the invertebrate community (usually a particular herbivorous taxonomic group) inhabiting a single microhabitat type (usually the leaves), via hand collection and foliage beating techniques. Consequently, previous studies have been unable to examine the fine-scale spatial distribution of canopy invertebrates within individual trees, or establish where in the canopy different invertebrates are concentrated. This information is vital if we are to make accurate predictions about species and community level responses to disturbance and climate change, or make accurate calculations about ecosystem processes and species richness. I carried out a long-term mass-collecting effort from five canopy microhabitats (mature leaves, new leaves, flowers, fruit, and suspended dead wood) using hand collecting and beating techniques from a canopy crane to examine spatial differences in invertebrate density, diversity, community structure, host specificity, and body size in an Australian tropical rainforest.

First, I examined microhabitat differentiation in the invertebrate communities associated with each microhabitat. Specifically, I examined variation between microhabitats in invertebrate density, taxonomic composition and guild structure. I also focused on the beetle community to examine differences between microhabitats in species richness, overlap, abundance patterns, and guild structure. I focused on the beetle community since beetles are arguably the most species-rich taxon on Earth and are biologically diverse. Second, I examined the host specificity of beetles inhabiting different microhabitats to test the assumption that most host specific species are herbivores on the

leaves that interact antagonistically with the host tree. This assumption is the basis for many global biodiversity estimates and has resulted in the majority of studies in tropical rainforest canopies being restricted to herbivores on the leaves. Lastly, I investigate body size variation between microhabitats. Since microhabitats vary in a number of qualitative and quantitative factors, I examined whether microhabitat choice has influenced the evolution of the body sizes of the invertebrates that utilise them.

I collected 40,374 invertebrates from all five microhabitats, including 10,335 beetles which were sorted to 372 morphospecies. Per unit weight, invertebrate densities on flowers were 10 to 10,000 greater than on new or mature leaves. At the species level, flowers were utilised by an estimated 40% of canopy beetle species, despite constituting just 0.06% of crown biomass. Overlap between microhabitats in species composition was also very low, indicating that each microhabitat is utilised by a relatively unique assemblage. In terms of feeding guild structure, invertebrate communities varied between each microhabitat, largely in relation to the food sources provided. For example, herbivores were found predominantly on new leaves and flowers, but were underrepresented among the invertebrate communities inhabiting the other microhabitats. Fungivores and saprophages however, dominated the communities occupying suspended dead wood.

Contrary to expectation, host specificity was equally high between an assemblage of herbivorous beetles on the leaves that interact antagonistically with the host tree, and an assemblage of flower-visitors that interact mutualistically with the host plant. Indeed, both herbivores and non-herbivores on flowers were as host specific as herbivores on leaves. Only species that do not interact directly with the host tree (non-herbivores on the leaves) were significantly more generalised in host use. Consequently, the previous assumption that most host specialists on a tree are herbivores on the leaves is refuted, since half of the

host specific species were flower-visitors, and half of these belonged to beetle families that are not considered herbivores according to traditional guild assignments.

Mean body size of invertebrate taxonomic groups varied significantly between microhabitats. In particular, phylogenetically independent contrasts revealed that, in general, invertebrate taxonomic groups were significantly smaller on flowers compared to mature leaves and new leaves. Size differences between microhabitats were most pronounced among herbivorous taxa (Hemiptera, Lepidoptera), in particular the immature stages, which were significantly smaller than expected on flowers, and larger than expected on leaves. Taxonomic groups that complete larval development on resources other than flowers, especially those that contain a large proportion of strong flying species (Diptera, Hymenoptera, most Coleoptera) typically showed no differences in body size across microhabitats. Since body size variation was most pronounced among herbivores, and these differences occurred repeatedly in many unrelated lineages, it is apparent that microhabitat identity influences evolutionary changes in the body sizes of species that feed on the available resources.

These results indicate that invertebrate communities in the canopy are spatially partitioned between microhabitats, and that each microhabitat supports a unique community in terms of composition, guild structure, and abundance patterns. Variation between microhabitats in temporal and spatial availability, nutritional quality, chemical protection and other attributes may have resulted in species associated with different microhabitats being subject to different selective pressures. Evidence for this is shown in the differences in the level of host specificity and distribution of body sizes of invertebrates between foliage and flower samples. Furthermore, my results clearly indicate that extrapolations or assumptions about biodiversity patterns or ecosystem functions based only on knowledge of the spatial distribution of foliage-inhabiting invertebrates may

contain substantial error because this group is not representative of the wider canopy community. Based on my findings, I recommend that future canopy invertebrate biodiversity studies account for microhabitat differentiation in the planning stage, and experiments and sampling protocols be designed in an appropriate manner to account for any possible pre-existing bias that sampling only leaf material may introduce. In particular, the flower-visitor community is identified as an especially important (but previously neglected) assemblage. I suggest future studies focus on the spatial and temporal variation in canopy invertebrate abundance patterns and their influence on ecosystem processes such as nutrient cycling, energy flow and the pollination biology of rainforest trees.

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An introduction to rainforest canopy invertebrate biodiversity

Chapter 1: An introduction to rainforest canopy invertebrate biodiversity

1.1 Rainforests in Australia

As much as 90% of global terrestrial biomass exists in the world's forests (Ozanne *et al.* 2003), and plant-based terrestrial food webs include ~75% of global biodiversity (Price 2002). The highest concentrations of biodiversity exist in tropical rainforests, which may be home to more than half of all species on Earth (Stork 1988), despite covering just 6-7% of Earth's land area (Stork *et al.* 2008a). Tropical rainforests sit astride the equator, and are most expansive in South and Central America, West Africa, South East Asia, and New Guinea (Fig. 1.1). Smaller areas of rainforest also occur in Madagascar, Australia, and many island nations in the Pacific, Indian and Atlantic oceans (Corlett & Primack 2008). Throughout their range, tropical rainforests are under threat from legal and illegal logging, clearing for agriculture and mining, burning, road building, and climate change (Laurance 2003, 2008; Laurance *et al.* 2002, 2005, 2011; Corlett & Primack 2008). Today just half of the world's original rainforest cover still stands, and the only large tracts of intact rainforest left are in West Africa, New Guinea and the Amazon basin. However, at current rates of deforestation, even the largest remaining rainforests will be fragmented into small isolated pockets of habitat in the coming decades (Laurance *et al.* 2005).

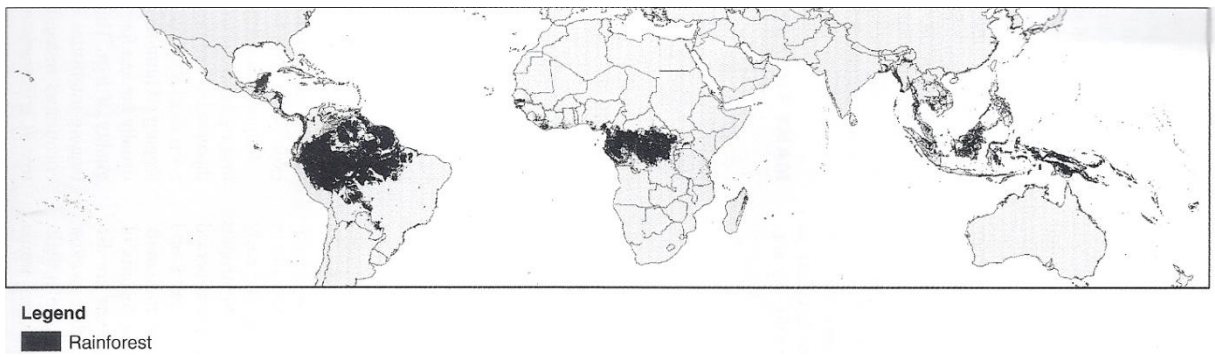


Figure 1.1: The global distribution of tropical rainforest. Source: from Corlett and Primack (2008), original figure provided by UNEP-WCMC.

In Australia most tropical rainforest is restricted to a small strip of land in north east Queensland called the Wet Tropics, an area of only about one million hectares, or less than 1% of the Australian landmass (Fig. 1.2). Australia rainforests are dynamic systems, and the area they occupy has expanded and shrunk repeatedly over geological time. At its peak, rainforest covered as much as one third of the Australian landmass (Bowman 2000), and some areas may have remained under continuous cover since the Cretaceous (Moritz 2008). Historical changes in rainforest cover have been driven by changes in climate, where dry periods resulted in a retraction of rainforest, while wetter periods facilitated rainforest expansion (Bowman 2000; Crisp *et al.* 2004; Kershaw *et al.* 2008). Since the Tertiary, expansion and retraction of the rainforest has followed the repeated glacial and interglacial periods (Hophins *et al.* 1993). During glacial maximums, tropical rainforest retreats to small refugia, and then expand again during warmer interglacial periods (Hilbert 2008). If left undisturbed by excessive burning and clearing, rainforest in north Queensland may still be expanding (Hopkins *et al.* 1996), although models predicting future rainforest distributions suggest that rainforest will contract in marginal areas due to a prediction of increasing seasonality in rainfall (Balston 2008).

Despite its small size, the Wet Tropics supports over 2,000 species of vascular plants, including many archaic lineages (Greenwood & Christophel 2008; Metcalfe & Ford 2008; Moritz 2008). Approximately 30% of Australia's terrestrial vertebrate fauna are also found in this small area (Williams *et al.* 2008). Among the insect fauna, over 50% of Australian species of dragonflies (Odonata), butterflies (Lepidoptera), and dung beetles (Scarabaeidae: Scarabaeinae) inhabit the Wet Tropics, and it is likely that a large proportion of species from less well known insect groups also exist in this area (Yeates *et al.* 2002). Like most forests, the Wet Tropics has suffered from logging and clearing for agriculture by early European settlers, especially the more accessible coastal lowlands

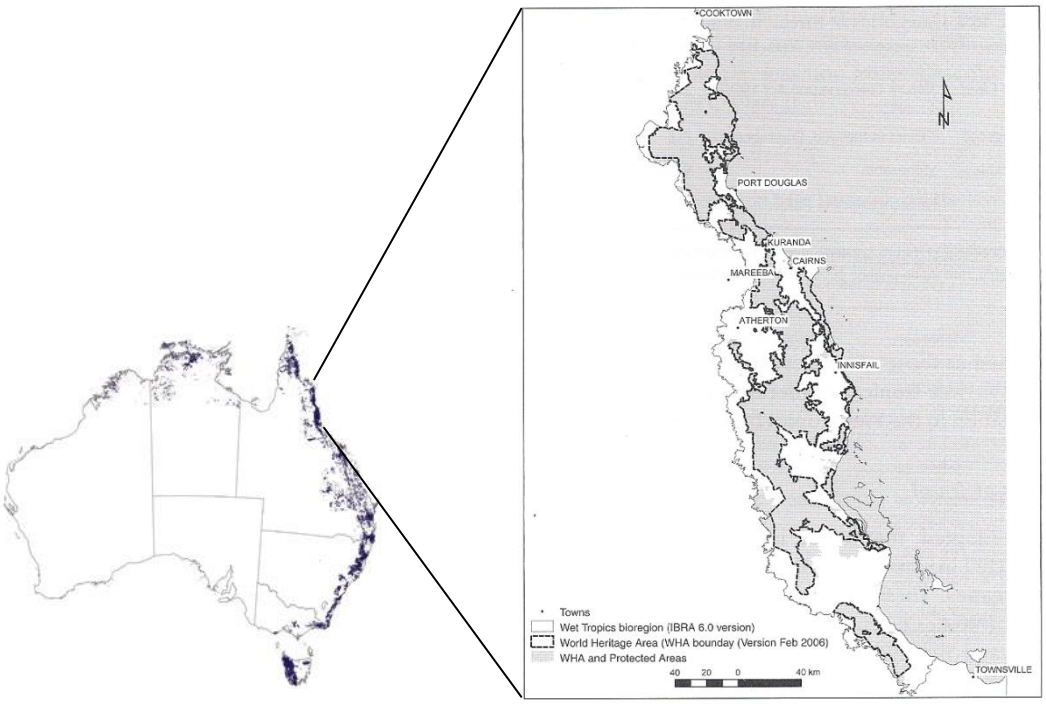


Figure 1.2: The extent of rainforest in Australia and (inset) the boundaries of the Wet tropics bioregion and World Heritage Area. Note that rainforest cover in the map of Australia is enhanced to more clearly show boundaries. Source: from Williams *et al.* (2008).

(Turton 2008). Throughout the 1980's public pressure mounted on local, state and federal governments to halt logging of Australia's tropical rainforests, resulting in most of the remaining rainforest of the Wet Tropics being declared a World Heritage Area in 1988 (Stork *et al.* 2008a; Valentine & Hill 2008).

1.2 The rainforest canopy and invertebrate research

The rainforest canopy is the site of a large but as yet unquantified proportion of terrestrial biodiversity (see Grimbacher & Stork 2006). Compared to the understorey, forest canopies have higher spatial heterogeneity and contain a wider range of habitats (Lowman & Moffett 1993; Ødegaard 2000a). However, despite being a centre for biodiversity and ecosystem function, very little is known about the distribution of organisms within forest canopies or the factors that regulate their spatial and temporal population dynamics (Ozanne *et al.* 2003). In fact, most canopy organisms remain undescribed, and based on

current rates of taxonomic description it will likely take centuries (if not millennia) just to identify and classify the majority of these species (see Tobin 1995; Grove & Stork 2000; May 2000; Stork *et al.* 2008b; Hamilton *et al.* 2010; Mora *et al.* 2011). Similar uncertainty exists in terms of understanding interactions between these species and the emergent phenomena they produce, and the importance of tropical rainforest canopy communities to biological processes and ecosystem functions (Ozanne *et al.* 2003).

The above limitations notwithstanding, important insights have been made in the study of canopy biology. In particular, studies on the distribution and abundances of arboreal insect communities occupy a prominent position in the history of canopy science (see Nadkarni & Parker 1994; Barker & Pinard 2001). Pioneering studies on canopy insects often involved collecting extremely large numbers of insects via relatively coarse collecting methods, such as light traps or canopy fogging, which were the principle sampling techniques for ground-based researchers (Wolda 1978a; Erwin 1982; Moran & Southwood 1982; Southwood *et al.* 1982a, b; Stork 1987a, b, 1991). Furthermore, insect samples from tropical rainforests (where insect assemblages are hyper-diverse (Barker & Pinard 2001)) contain a high proportion of undescribed species. The subsequent identification and/or classification of individuals within samples often took years, even though they may have only taken a few days to collect in the field (Stork 1991; Erwin 1995; Lawton *et al.* 1998; Kitching *et al.* 2001). This meant that early research was largely descriptive and dominated by studies examining insect community composition or ecologies either within a single tree species (Erwin 1982; Basset & Kitching 1991; Abbott *et al.* 1992), between tree species (Southwood 1961; Moran & Southwood 1982; Southwood *et al.* 1982a, b; Morse *et al.* 1988; Stork 1991; Moran *et al.* 1994) or between habitats (Stork & Blackburn 1993; Wagner 2001). This early work was, however, invaluable to the development of the field of canopy insect research because it established

that canopy insect communities were diverse and heterogeneous, and that canopies were thus highly important centres of biodiversity and ecosystem function.

Canopy insect research has now moved towards more hypothesis-driven research, aimed at interpreting the spatial and temporal dynamics of insect communities and their role in ecosystem functions and processes (see Ødegaard 2006). As a consequence, canopy entomologists have begun to focus on the mechanisms involved in determining canopy insect distribution in time and space (Stork *et al.* 1997b). A substantial amount of work has been carried out on host specificity, vertical stratification, diel activity and seasonal fluctuations in the abundance and composition of canopy insect communities (see Stork *et al.* 1997a; Basset 2001b; Basset *et al.* 2003a; Novotny & Basset 2005). There is also a burgeoning literature on the insect communities associated within specific microhabitats in host trees, especially the fauna inhabiting the foliage (Basset *et al.* 1996; Barone 1998; Novotny & Basset 1998; Novotny *et al.* 2002b, c, 2004a, b, 2006; Ødegaard *et al.* 2000, 2005; Ødegaard 2006).

1.3 The rainforest canopy and global biodiversity

Perhaps the most important driver of tropical rainforest canopy biodiversity research over the last 30 years is the central role of canopy insect species richness in generating estimates of the total number of living species. In 1982, Erwin published an estimate of >30 million species on Earth – some 10 times higher than previous estimates – based on extrapolations from beetles sampled from one species of canopy tree in Panama. In his calculation, Erwin (1982) estimated that 20 million of these species would be found in the canopies of rainforest trees, and 26 million would be herbivorous. If nothing else, Erwin's calculation succeeded in generating widespread interest in the study of insect communities inhabiting this highly important, but often neglected, environment (Godfray *et al.* 1999). Subsequent

research, largely in response to Erwin and also based on insect biodiversity in rainforest canopies, produced global estimates of the total number of extant species that ranged anywhere between 2 and 100 million species (Erwin 1988; Stork 1988, 1993; Thomas 1990a; Hodkinson & Casson 1991; Basset *et al.* 1996; Ødegaard 2000a; Ødegaard *et al.* 2000; Novotny *et al.* 2002a).

Although Erwin's (1982) original estimate of 30 million species is now considered too high by the majority of scientists in this field (Hamilton *et al.* 2010, 2011), the debate concerning global biodiversity is ongoing and the degree of uncertainty associated with these estimates exemplifies the lack of understanding about the distribution of arthropods in tropical rainforest canopies (Adis 1990; May 1990). Even after 30 years of data collection from numerous tropical locations around the world, global species richness estimates are still uncertain. Current estimates suggest anywhere between ~3 and 10 million species (Thomas 1990a; Gaston 1991, 1992; Hodkinson 1992; Stork 1993; Gaston & Hudson 1994; Basset *et al.* 1996; Ødegaard 2000a; Ødegaard *et al.* 2000; Novotny *et al.* 2002a; Hamilton *et al.* 2010; Mora *et al.* 2011).

1.4 Project objectives

The main objective of this study was to examine where in the canopy invertebrates are concentrated, and what mechanisms may determine differential distributions should they exist. I addressed this objective by testing the hypothesis that different rainforest canopy microhabitats support their own unique invertebrate communities in terms of community structure, as well as patterns of species richness and abundance. One of the most prominent gaps in current knowledge of the distribution of arboreal insects is how invertebrates are distributed among microhabitats (i.e., at the within-tree scale). Rainforest canopies contain many distinct microhabitats that arboreal invertebrates can exploit. The most obvious

resource is the foliage, which is often subdivided into two categories based on age (mature leaves and flush leaves) (e.g., Coley 1980; Basset 1991a; Aide 1993; Coley & Barone 1996), or categories based on relative position on the tree (e.g., sun leaves and shade leaves) (e.g., Moore *et al.* 1988; Bond *et al.* 1999). However, many insects are also associated with reproductive structures of host plants (flowers, fruit and seeds) (Janzen 1980; Frame 2003; Grimbacher *et al.* in prep), and/or dead and decomposing plant material (Grove & Stork 2000; Ødegaard 2004). However, to date few studies have compared the abundance, species richness, specialisation, guild structure or body size patterns of canopy invertebrate communities occupying distinct microhabitats within host trees. Instead, most have been restricted to the assemblages associated with the leaves (Novotny & Basset 2005). But information on the fine-scale distribution of arboreal invertebrates is vital for accurate analyses of food web structure, nutrient flow, and ecosystem function in tropical rainforest environments (Kitching 2006; Novotny *et al.* 2010). To achieve my objective and fill an important gap in our existing knowledge of the spatial distribution of arboreal invertebrates, I examined the abundance, diversity and specialisation of the canopy invertebrate community utilising 23 different host tree species and five microhabitats (mature leaves, new leaves, flowers, fruit and suspended dead wood) in an Australian tropical rainforest.

In this thesis, I first compile a comprehensive review of the mechanisms/factors that affect the distribution of arboreal invertebrates, and evaluate their individual and combined impacts on community structure (Chapter 2). The subsequent (7) results-based chapters are all based on one large-scale sampling program that involved collecting invertebrates directly from the canopy using the Australian Canopy Crane at the Daintree Rainforest Observatory. Analyses were conducted on the entire invertebrate community sorted into taxonomic groups (mostly orders) and feeding guilds. In addition, species-level

diversity, specialisation and body size analyses were conducted on the beetle fauna. Beetles were chosen for closer examination due to their high species richness and ecological diversity, which make them an ideal group to explore patterns in abundance, species richness and microhabitat differentiation.

Since microhabitats vary in availability, quantity and quality, I hypothesised that microhabitats should support their own unique communities that vary in density, diversity, and abundance patterns of their composite faunas. The first 4 results chapters (Chapters 3, 4, 5, and 6) examine different components of the invertebrate community to test this hypothesis. Specifically, Chapter 3 examines the density, diversity and uniqueness of the invertebrate communities inhabiting each focal microhabitat to determine where in the canopy invertebrates are concentrated and the degree of overlap in species composition between microhabitats. Chapter 4 contains an examination of the guild structure and taxonomic composition of the invertebrate communities inhabiting each microhabitat. In particular, I quantify the abundance distribution of each taxonomic group and feeding guild across the focal microhabitats to identify where particular invertebrate taxonomic groups are concentrated. Chapter 5 is a species-level examination of the distribution of beetles across microhabitats, where the relationships between species-richness and abundance patterns are examined. Chapter 6 focuses in detail on the guild structure of beetle communities inhabiting different canopy microhabitats, and assesses their distribution in relation to the distribution of their presumed food sources. In addition to testing the first hypothesis, the results of these four chapters are also used to assess the assumption that the mature leaf community (which is the basis for most biodiversity extrapolations) is representative of the canopy community as a whole in terms of abundance, species richness, and guild structure.

Chapter 7 is the first of two chapters on host specificity of beetles and tests the hypothesis that networks of antagonistic herbivores on the leaves are more host specific than mutualistic networks of flower-visitors. Due to the reciprocal evolution of defences and counter-defences between herbivores and host plants, antagonistic interactions often promote increased specialisation (Ehrlich & Raven 1964). In contrast, the structure of mutualistic pollination networks have been shown to promote increased generalisation (Fontaine *et al.* 2006, 2009). Chapter 7 tests this hypothesis by examining the level of host-tree specialisation among herbivorous and non-herbivorous beetles collected from leaves and flowers. This represents the first assessment of the expectation of this hypothesis undertaken using samples from a diverse topical rainforest. In Chapter 8, the host specificity of the beetle fauna is examined with respect to microhabitat utilisation and feeding guild. To date, most host specificity studies have focused on herbivores inhabiting the leaves, as this group is thought to comprise the vast majority of host specific species associated with trees (Erwin 1982). Chapter 8 tests this hypothesis by comparing host specialisation of herbivorous and non-herbivorous species on different microhabitats.

The final results-based chapter (Chapter 9) is an exploratory comparison of body size patterns on different microhabitats. The preceding chapters establish that there is great variation in community composition and structure between microhabitats. Since variation in microhabitat availability, quantity and quality can all influence abundance, diversity and compositional measures, there was an expectation that invertebrate body size may also vary between microhabitats. Chapter 9 therefore tests the hypothesis that the invertebrate communities inhabiting different microhabitats vary in body size. Finally, Chapter 10 contains a synthesis of the major results of each chapter to draw some principal conclusions on the effect of microhabitat use on the spatial dynamics of rainforest canopy invertebrates. I also identify future directions for research on rainforest canopy

invertebrates and highlight the importance of incorporating multiple microhabitats in any biodiversity study.

Chapter 2:

Literature review:

The spatial and temporal distribution of arthropods in forest canopies: the central importance of resource availability

Chapter 2: The spatial and temporal distribution of arthropods in forest canopies: the central importance of resource availability[1]

2.1 Introduction

Insect dominated plant-based food webs constitute an estimated 75% of global terrestrial biodiversity (Price 2002; Mora *et al.* 2011). In the Amazon rainforest, the biomass of invertebrates outweighs vertebrates by 10 to one (Wilson 1987). From an ecological and economical stand point, insects are the most important animals in terrestrial environments (Wilson 1987; Allen-Wardell *et al.* 1998; Robinson *et al.* 2011). They include the most diverse and important pollinators (Bawa *et al.* 1985, Bawa 1990; van Dulmen 2001; Ollerton *et al.* 2011), herbivores (Coley & Barone 1996), and predators (Floren *et al.* 2002) in the arboreal environment. Yet we have only a fragmented understanding of how most insect species are distributed in time and space, especially in tropical rainforests where a large proportion of species are unknown to science (Grove & Stork 2000; May 2000; Stork *et al.* 2008b; Hamilton *et al.* 2010; Mora *et al.* 2011). Even for the described species, we know very little regarding distribution patterns, habitat preferences, and the nature of the inter- and intra-specific interactions among them, or how any of these factors influence food web dynamics and ecosystem processes.

However, over the last few decades the amount of work investigating the spatial and temporal distribution of arboreal insect diversity has accumulated, and a number of distinct, recurrent patterns have emerged. In this review, the mechanisms involved in determining the spatial and temporal distribution and resource partitioning of arboreal insects are discussed, with a particular emphasis on insect communities in tropical rainforest canopies. The focus of this discussion is on the structure of insect communities

[1] A highy modified version of this chapter has been submitted (14 Apr 2013) as a single author review paper to *Biological Reviews* (Wardhaugh, C. W. in review: The spatial and temporal distributions of arthropods in forest canopies: uniting disparate patterns with hypotheses for specialisation.)

at the local scale only. Important mechanisms structuring insect assemblages at finer spatial scales, such as the effect of defensive phenotypes or nutritional quality of particular structures within individual host tree species (Greenfield *et al.* 1987; Strauss 1990; Mopper & Simberloff 1995; Preszler & Price 1995; Awmack & Leather 2002; Funk 2010) are beyond the scope of this review. Similarly, mechanisms driving the structure of insect assemblages at larger spatial scales (beta and gamma diversity), such as biogeography, geology and changes in climatic and environmental variables over geological time (Strong 1979; Kennedy & Southwood 1984; Ricklefs 1987; Gaston & Lawton 1988; Cornell & Lawton 1992; Kitching *et al.* 1997; Bartlett *et al.* 1999; Brändle & Brandl 2001; Gruner & Polhemus 2003; Novotny & Weiblen 2005; Novotny *et al.* 2007; Novotny 2009) are not addressed. Thus, the mechanisms that are examined here determine the structure of local arboreal insect communities on local host tree species.

Four fundamental mechanisms are examined; (i) resource specialisation, which determines the part of the tree or microhabitat that can be exploited; (ii) host specialisation, which determines the host species (plant, fungi, animal, etc.) that can be exploited; (iii) spatial specialisation, which determines the optimum point, both vertically and horizontally, to locate the resource and safely exploit it; and (iv) temporal specialisation, which determines when the resource is available and safe to utilise. These mechanisms are not mutually exclusive and each invariably influences different species of insects in different ways to determine the structure of resource division in arboreal insect communities.

It should be noted that the mechanisms listed here are resource-based (bottom-up) factors (Power 1992; Price 2002), and the top-down effects of competition, predation and parasitism are also continually acting on insect populations and affecting their spatial and temporal distributions (Holt 1977; Benson 1978; Lawton & Hassell 1981; Abrams 1987;

Fox & Eisenbach 1992; Hunter & Price 1992; Chesson 1994; Denno *et al.* 1995; Dial & Roughgarden 1995; Hawkins *et al.* 1997; Martin Waltz & Whitham 1997; Siemann *et al.* 1998; Schlindwein & Martins 2000; Ballabeni *et al.* 2001; Moon & Stiling 2006; Recher & Majer 2006; Viswanathan *et al.* 2008). For many species, biotic interactions, such as predation and competition (Denno *et al.* 1990, 1995; van Veen *et al.* 2006), will often confine insect populations to discrete subsets of potential habitat (Ehrlich & Murphy 1988; Murphy *et al.* 2004). However, the search for enemy- and competitor-free space involves avoiding host species, microhabitats, areas, or temporal periods that are enemy- or competitor-filled (e.g., Wolda 1988; Price 1992; Moon & Stiling 2006). Therefore, the restrictive effect of intra- and inter-specific interactions invariably manifests within the constraints of the four mechanisms that are the focus of this review, and will thus be discussed in the context of the focal resource-based mechanisms (see Denno *et al.* 2002).

2.2 Resource specialisation by insects

Most non-predatory (and many predatory, especially parasitoid) insects are feeding specialists. That is, they specialise on one kind or resource such as leaves, stems, nectar, pollen, seeds, phloem or xylem sap, fruit, live or dead wood, fungi, or meristematic tissues. Resource specialisation and host plant specialisation constitute the two facets of specialisation in herbivorous insects (Schoonhoven *et al.* 2005), but are equally applicable to fungivorous insect species. The interaction between these two mechanisms determines the maximum diet breadth of an insect species and facilitates the possible distribution of insect populations. But to date, most studies that have examined specialisation in canopy insects have been concerned with host tree specialisation (Basset *et al.* 1996; Barone 1998). And these have mostly been restricted to various subsets of the invertebrate community inhabiting single microhabitats, especially leaves (Basset & Arthington 1992;

Basset *et al.* 1996; Barone 1998; Novotny & Basset 1998; Basset 1999a, 2001a; Novotny & Basset 2000; Ødegaard *et al.* 2000, 2005; Wagner 2000; Novotny *et al.* 2002b, 2002c, 2004a, 2004b, 2006; Ødegaard 2006; Kitching *et al.* 2007)

One of the few studies that has compared insect assemblages on different resource types in forest canopies was carried out by Ødegaard (2004), who showed that the number of species associated with *Brosimum utile* (Moraceae) increased dramatically when dead wood habitats were sampled in addition to the foliage. The lack of faunal overlap between assemblages utilising these two microhabitats meant that they had an additive effect on species richness. Similar additive effects on host tree biodiversity are likely to be found when other microhabitats, such as fruit and flowers, are also sampled, or if insect samples collected from different microhabitats within tree crowns are kept discrete rather than pooled. For example, Morais *et al.* (2009) found that 65% of Brazilian Cerrado flower-feeding caterpillar species (90/138) were not recorded from the foliage during 17 years of sampling! At larger scales, the combined effect of several distinct, but previously unrecorded or unrecognised, assemblages within tropical rainforests could substantially alter or explain our current perceptions about specialisation, energy flow and global species richness (Colwell & Coddington 1994).

A number of factors probably contribute to the discrepancy between the number of host specialisation and resource specialisation studies, including the logistics of canopy access (Stork *et al.* 1997c) and the central importance of host specificity to global species estimates (Erwin 1982). It is a relatively simple exercise (and often the only possibility) to collect insects from within a tree crown through the use of canopy fogging, flight intercept traps, Malaise traps or indiscriminate hand collecting and beating from elevated walkways and towers. These techniques are adequate for ascertaining host specificity, assuming a relatively high number of trees are sampled, but provide little or no information relevant to

the spatial distribution or resource specialisation of arboreal insects. To circumvent this problem, sampled insects are often assigned to specific feeding guilds, such as leaf chewers, sap-suckers, predators and so on. Provided the phenology of the host tree is also recorded, patterns of resource use by canopy insects can potentially be detailed (e.g., Itioka *et al.* 2003).

In this way it is possible, for instance, to ascertain the relationship between flowering events and the number of insect species, individuals or biomass of flower visiting insects, which should respond to increased levels of nectar and pollen associated with flowering patterns (e.g., Armstrong 1997). Studies that have linked insect community patterns with the phenology of a host tree have been able to show insect community responses to the temporal dynamics of host tree phenology (Mendonça 2001; Southwood *et al.* 2004, 2005). For example, large increases in herbivore abundance have been linked with leaf production in Panama (Wolda 1978a; Barone 2000; Basset 2001a), Australia (Lowman 1985; Basset 1991a, b, c, 1992a; Steinbauer *et al.* 1998) New Guinea (Basset 1996, 1999a), Borneo (Itioka & Yamauti 2004), and Brazil (Price *et al.* 1995; Marquis *et al.* 2001).

The results of these studies are not surprising, since young leaves generally have higher nitrogen content per unit dry weight (Aide & Londoño 1989; Basset 1991a; Merritt 1996), which is necessary for insect growth (Mattson 1980; but see Faeth *et al.* 1981), and lower leaf toughness (Coley 1983; Aide & Londoño 1989; Sagers & Coley 1995), than mature leaves. Although new leaves are often better defended chemically than mature leaves (Crankshaw & Langenheim 1981; Cooke *et al.* 1984; Aerts *et al.* 1992; Iwasa *et al.* 1996; van Dam *et al.* 1994, 1996; Read *et al.* 2003), the general pattern of preference for new leaves among folivorous species (Coley 1980; Lieberman & Lieberman 1984; Aide & Zimmerman 1990; Basset 1992a, 1994; Coley & Barone 1996; Marquis *et al.* 2001)

suggests that the structural and nutritional defences of mature foliage are often more effective (Lowman & Box 1983; Cooke *et al.* 1984; Raupp 1985; Bernays 1991; Kursar & Coley 1992; Peeters 2002a; Lucas *et al.* 2000; Read *et al.* 2003; Ribeiro & Basset 2007). Indeed, ants (*Petalomyrmex phylax*) on the ant-plant *Leonardoxa africana* in Cameroon only patrolled new foliage for prey, as the mature foliage was structurally well protected and rarely attacked by herbivores (McKey 1984).

In addition, many rainforest trees produce red, white or purple flush leaves that are photosynthetically and nutritionally poor compared to typical green flush leaves (Moles *et al.* 2011). It has been reasonably proposed that this delayed greening is a defence against insect herbivores, where the host tree withholds resources from the leaves until they are fully expanded and structurally defended (Kursar & Coley 1992). Although, red colouration may also serve to protect shade leaves from photoinhibition (Gould *et al.* 1995). In addition to toughness, many plant species produce leaves that are covered in trichomes, which are thought to function in plant defence by preventing direct feeding or oviposition by herbivorous insects (Levin 1973; Ezcurra *et al.* 1987). The structural defences of some seeds are also better at preventing attack from insects than secondary chemicals (Kuprewicz & Garcia-Robledo 2010). Indeed, chemical defences may act more as deterrents than toxins (Bernays 1990; van Dam *et al.* 1995), or even attractants (Bowers 1983) to some herbivorous species. The production of chemical defences no doubt exacts a cost to the host tree (Coley 1986; Bazzaz *et al.* 1987; Herms & Mattson 1992; Han & Lincoln 1994; Yamamura & Tsuji 1995), perhaps so much so that competitive abilities become hindered if too many resources are invested in defence, resulting in most plants being palatable to at least some herbivores (Tuomi *et al.* 1994). In any case, determining the relative strength of host plant variables, competition, and natural enemies on herbivore population dynamics is not straightforward, with both plants and insects displaying several

tradeoffs and co-correlated variables that introduce uncertainty (see Harper 1989; Herms & Mattson 1992; Eichhorn *et al.* 2007).

In general, nitrogen content has been shown to be more important in the selection of feeding sites than chemical defences for many insect herbivores (Feeny 1970; Fox & Macauley 1977; but see Faeth *et al.* 1981; Strauss 1987; Peeters 2002a). In fact, Aide (1993), in a study of 32 tree species in Panama, showed that most leaf damage occurred during leaf expansion, suggesting a high concentration of leaf feeding insects on juvenile leaves. Many insects specialise on foliage of a particular developmental stage, suggesting that the leaves can be subdivided into distinct resources that are exploited by discrete subsets of the local insect community, and should be treated as such in studies of folivorous insects. Most commonly, divisions are drawn between expanding new leaves and fully expanded and toughened mature leaves. For example, the sap-sucking seed bug *Nicuesa speciosa* (Lygaeidae) preferred mature leaves of *Pentagonia donnell-smithii* (Rubiaceae) in Costa Rica, while the chewing leaf beetle *Phanaeta* sp. (Chrysomelidae) preferred new foliage (Ernest 1989). Further, Mauffette and Oechel (1989) suggest that the preference shown by *Phryganidia californica* (Lepidoptera) for mature *Quercus agrifolia* leaves over the nutritionally superior new leaves is the result of adaptations to overcome the quantitative defences of mature foliage. Adaptations in mandibular design that allow for efficient handling of mature or new leaf material are also prevalent among chewing Lepidoptera caterpillars in a Costa Rican dry forest (Bernays & Janzen 1988).

For many insect species, a simple association of feeding specialisation can be problematic, and potential uncertainty in assigning species to their correct trophic guild can significantly distort the relative proportions of species identified within particular feeding guilds (Stork 1987b). For instance, the adult stages of some species can belong in a different guild to their larval stages (Novotny & Basset 1999, 2005), or occupy completely

different habitats (Pokon *et al.* 2005). Many Hymenoptera, Lepidoptera and Diptera may only consume nectar or honeydew in adult life stages (if they feed at all), whereas their larvae could be parasitoids, phytophages, fungivores, or xylophages (Stork 1987b). The reliability of guild assignation also varies between different feeding guilds. Assigning sap-suckers to their appropriate guild is relatively straightforward, due to the restricted number of taxa that have the specialised feeding structures required to extract plant sap. In contrast, the broad range of species associated with dead and decaying wood, such as xylophages (wood eaters), fungivores (fungus eaters), and xylomycetophages (wood-boring fungus eaters), are often more difficult to discern (see Grimbacher & Stork 2007).

2.3 Host tree specialisation

While arboreal insects are generally restricted to feeding on discrete food sources within trees, most herbivorous species are also limited in the number of host tree species they are capable of utilising. Thus, the interaction between feeding specialisation and host tree specialisation provides a basis for high species diversity. Only a small proportion of insect species are strictly monophagous; i.e., specialising on only a single host plant species (Basset 1992b; Basset *et al.* 1996; Ødegaard *et al.* 2000; Novotny *et al.* 2002b, 2002c; Novotny & Basset 2005). In these situations however, host specialist insects are often the most important enemies of host trees and cause the most damage (Janzen 1988; Barone 1998).

Host specialisation has been attributed to insects adapting to overcome the chemical defences of a particular host tree species, and subsequently losing the ability to overcome the defences of other potential host trees (Ehrlich & Raven 1964). This hypothesis has even been extended to explain the host specificity of parasitoids that attack herbivores that have sequestered the chemical defences of their host plants in their tissues

(Gauld *et al.* 1992). Other factors such as predator avoidance (Bernays & Graham 1988; Dyer 1995), chemical affinities (Landolt & Phillips 1997), nutritional factors, local host plant abundance and plant community composition (Futuyma & Wasserman 1980) may play an important role in the initial selection of a host plant species, and may explain why many monophagous species do not utilise alternative hosts even though they are capable of feeding on them (Smiley 1978; Futuyma 1983, 1991; Barbosa 1988; Futuyma & Moreno 1988; but see Wee & Singer 2007).

Host tree specialisation has received a relatively large amount of attention from forest canopy researchers (e.g., Erwin 1982; Stork 1988; Jaenike 1990; Thomas 1990a; Basset 1992b, 1996; Mawdsley & Stork 1997; Barone 1998; Novotny & Basset 1999, 2005; Ødegaard 2000a, 2006; Ødegaard *et al.* 2000; Novotny *et al.* 2002a, b, 2004b). Primarily this has been because the number of species that are unique to a particular tree species was an important, and controversial, estimate in Erwin's (1982) original attempt to estimate global biodiversity (Stork 1988). Erwin (1982) sampled invertebrates from one tree species (*Luehea seemannii*) in Panama, and estimated that 163 species of beetles were host-specific. He then speculated that a similar proportion would also be host specific to every tropical tree species. Evidence for this figure, and other estimates in the original equation such as the proportion of arthropods that are beetles (0.4), the (implied) proportion of specialist beetles that are herbivores (0.83), and the proportion of species that are canopy specialists (0.67), is lacking, and there is now a general consensus that these figures were too high (Gaston 1991; Basset *et al.* 1996; Ødegaard 2000a; Ødegaard *et al.* 2000; Novotny *et al.* 2002a; Stork & Grimbacher 2006). In particular, the important figure of the number of host specific beetle species has been reduced considerably from Erwin's original estimate of 163 to just 1.4-4.4 and 2.3-5.8 from studies compiled by Gaston (1993)

and Ødegaard (2000a) respectively, and 7.9 from rainforest trees in New Guinea (Novotny *et al.* 2002a, b).

Despite the fact that most insect species are not monophagous and are capable of feeding on a number of different host species (Thomas 1990b), the identities of host tree species are not likely to be random plants from the local species pool (Benson *et al.* 1975; Becerra 1997; Symons & Beccaloni 1999; but see Hulcr *et al.* 2007), especially in tropical rainforests. Tropical rainforests typically contain a number of species-rich plant genera and families (see Novotny *et al.* 2002a). As a result, congeneric and con-familial host trees are often found in relatively high densities in rainforests, but individual tree species usually display a much patchier distribution. Furthermore, it has been reasonably proposed that closely related trees are more similar in their nutritional quality and defensive characteristics than trees that are distantly related (Ehrlich & Raven 1964; Kennedy & Southwood 1984; Futuyma 1991). In accordance with this, a greater proportion of insect species have been found to specialise on plants from within the same genus or family than on a single species (Mawdsley & Stork 1997; Barone 1998; Lepš *et al.* 2001; Novotny *et al.* 2002b, 2002c, 2004a, 2005; Kitching *et al.* 2003; Novotny & Basset 2005; Ødegaard *et al.* 2005; Weiblen *et al.* 2006), and only true generalists feed on host plants from different families (Barone 1998). Perhaps as a consequence, taxonomically isolated tree species have been found to support fewer insect species or a greater proportion of specialists than tree species that coexist with other congeneric or con-familial species (Moran *et al.* 1994; Kelly & Southwood 1999).

Host specificity is a relative measure that often varies at different spatial and temporal scales (Ødegaard 2000a). The geographic range of a particular tree rarely coincides with that of its insect fauna, and insects that feed exclusively on one tree species at one site, may feed on a completely different species at another (Fox & Morrow 1981;

Michaud 1990; Herrera 1988; Thomas 1990a; Novotny *et al.* 2005). In addition, ecological specialists (i.e., those that can feed on a number of host species but are monophagous due to factors other than adaptation to chemical defences, such as host plant location or mate acquisition (Smiley 1978)) could easily (compared to obligate specialists) switch host plants over evolutionary time (Futuyma & McCafferty 1990; Michaud 1990; Futuyma 1991; Radtkey & Singer 1995; Fox *et al.* 1997). Therefore, the host specialisation of the local insect fauna at a particular site is dependant on a number of factors, including the geographical range and local abundance of the host plants (Lawton & Schroder 1977; Moran *et al.* 1994; Kelly & Southwood 1999) and their close relatives (Barone 1998), and the temporal pattern of contraction and expansion of the host tree's range and that of the forest in general (Kennedy & Southwood 1984; Brändle & Brandl 2001).

The ability of herbivorous species to locate and discriminate between potential host plant species is a particularly important, but often overlooked, factor. It is not enough that an insect species can thrive on a particular plant species, it also has to be able to locate that species among many other, often unsuitable, species. The implied assumption is that the sensory systems [e.g., olfactory, visual, chemoreception (Rausher 1978; Wood 1982; Prokopy & Owens 1983; Visser 1986; Chapman 1988, 2003; Roseland *et al.* 1992; Dafni *et al.* 1997; Berkov *et al.* 2000; Campbell & Borden 2006; Powell *et al.* 2006; Heisswolf *et al.* 2007)] insects use to select host plants are perfect, and that all host plant and feeding records are indicative of the natural environment. However, regional variation in host plant use (Fox & Morrow 1981), as well as the omission of suitable host plants from an insect's diet (Stastny *et al.* 2006), or the inclusion of inferior plant species, suggests that insects can be confused during host selection (Fox & Lalonde 1993; Janz & Nylin 1997). Indeed, host selection confusion has been proposed as a possible evolutionary mechanism for the inclusion of novel tree species to an insect's diet (Fox & Lalonde 1993; Larsson & Ekbom

1995). Furthermore, it has been suggested that a shift towards specialisation is accompanied by a reduction in decision times for ovipositing on appropriate hosts for herbivorous insect species, which reduces host searching and time-based mortality factors (Bernays & Wcislo 1994; Janz & Nylin 1997; Bernays & Funk 1999; Bernays 2001; but see Wee & Singer 2007).

The prevalence of host plant specialisation among insect herbivores may be due to neural limitations and the inability to process large amounts of information (Bernays 2001; Janz 2003). Therefore, rather than being restricted to particular plant species via species-specific defensive characteristics, some herbivores may be adapted to locating and identifying a particular subset of potential hosts (Jermy 1984; Bernays *et al.* 2000). In support of this, the oviposition preferences of some adult insects are much narrower than the potential diet breadth of the larvae, suggesting that specialisation is often due to location choice rather than dietary restrictions (Mitchell 1981).

It should be noted that there are also benefits to being a generalist, and the fact that most insect herbivores are not monophagous suggests that a more generalised host range is often favoured by natural selection (Singer 2008). In particular, a broader diet increases the amount of available food in the environment, although this can be paradoxically more difficult to locate (see above). Since rainforest canopy herbivores typically feed on trees, an increase in diet breadth is effectively an increase in habitat area. Species that exhibit aggregated distributions can be vulnerable to high mortality, so avoiding high concentrations of conspecifics by expanding the host range could increase survival (see Williams *et al.* 2001). Consequently, generalists may display greater plasticity when selecting an optimal feeding site, with regard to competition, predation, or unfavourable abiotic conditions. Furthermore, polyphagy will be favoured by migratory species, since different suites of host plants are likely to be encountered in different locations (Michaud

1990). Diet mixing can also reduce the build up of defensive chemicals and counteract nutritional deficiencies that may arise from single host diets (Waldbauer & Friedman 1991; Held & Potter 2004; Franzke *et al.* 2010; Karban *et al.* 2010).

2.4 Spatial specialisation

The forest canopy is not a homogenous environment. Climatic conditions, such as light intensity, humidity, wind velocity, and temperature, vary from near ground level to the upper canopy and from the interior of tree crowns to the tips of the leaves, providing a series of often unique environments for plants and animals to exploit (Parker 1995; Nieder *et al.* 2000, 2001; Szarzynski & Anhuf 2001). For example, the upper canopy constitutes the interface between the biosphere and the atmosphere (Ozanne *et al.* 2003) and consequently experiences extreme temperature fluctuations and heavy rainfall compared to the understorey. Different abiotic conditions within forest canopies subsequently affect the distribution of plant resources and the spatial composition and structure of the plant community, which has flow on effects to insect consumers. Flowers, fruit, new leaves and areas of rapid growth such as vegetative and reproductive meristems are usually concentrated in the outer and upper canopy, (Basset *et al.* 1992a; Basset 2001a; Charles & Basset 2005), whereas the interior mid canopy harbours the highest concentrations of shade leaves and vascular epiphytes (Coxson & Nadkarni 1995; Nieder *et al.* 2000; Kelly *et al.* 2004), and the understorey is composed of saplings, detritus, and large amounts of living and dead wood. It should be expected then, that the distribution of insects exploiting different resources would predominantly follow that of the resources they are exploiting, which are spatially separated (Schulze *et al.* 2001; Lewinsohn *et al.* 2005). Spatial distribution patterns of arboreal insects therefore, could simply reflect a broad pattern of

resource availability, rather than be an independent mechanism influencing insect community dynamics.

2.4.1Vertical stratification

Most studies on the spatial distribution of arboreal insects have focussed on vertical stratification (Basset *et al.* 2003b). Changes in insect community composition are often pronounced with height above ground, as are abiotic conditions which are often concurrently measured and suggested as likely factors driving these patterns (Basset *et al.* 2003b). However, I would argue that stratified abiotic conditions are typically not the limiting factors restricting particular insect species to particular vertical strata, but rather insects display vertical distributional patterns as a function of resource availability. In many cases, species occupy the vertical stratum that contains the resources that they need for food, mate finding, or oviposition (Basset 2001a; Grimbacher & Stork 2007). Also, broad patterns in insect community composition are not consistent in different localities or host species. Many studies have found that herbivore densities or species richness are higher in the canopy [Cameroon (Basset *et al.* 1992), Gabon (Basset *et al.* 2001), Panama (Basset 2001a; Charles & Basset 2005)], whereas other researchers have found mixed results [subtropical and tropical Australia (Kitching *et al.* 1993; Grimbacher & Stork 2007), Panama (Barone 2000)]. It should also be noted that few rainforests are even in height, such that the height of the tallest trees can vary considerably at a scale of just a few metres (Laidlaw *et al.* 2007). Thus a stratum such as the upper canopy may vary from 15m to over 60m in height, depending on the tree species and disturbance history of the forest.

Biotic and chemical conditions can vary within the same plant structures on the same plant species within different vertical strata. Leaves exposed to full sunlight typically have higher levels of nitrogen, carbon and secondary metabolites than shade leaves (Mole

& Waterman 1988; Nichols-Orians 1991; Brooks *et al.* 1996; Bond *et al.* 1999). However, other studies have reported mixed results (Le Corff & Marquis 1999; Downum *et al.* 2001) and herbivory rates do not always correspond to leaf nutritional or defensive characteristics (Basset *et al.* 1992). The chemical composition of leaves does not have a definitive effect on the distribution of many phytophagous insects, and other factors, such as structural defences, abiotic conditions and predator or competitor avoidance, may also be important.

Detailed studies on the vertical stratification of insects utilising resources other than leaves are uncommon. Wardhaugh *et al.* (2006) studied the vertical stratification of the sessile bark-dwelling phloem-feeding scale insect *Ultracoelostoma assimile* (Margarodidae) in New Zealand. Population densities were higher on branches in the canopy than low on the trunk of *Nothofagus fusca* (Fagaceae) trees. The authors suggest that vertical stratification in *Ultracoelostoma* is probably a function of bark thickness, which is vital to locating an appropriate settlement site. Thin bark does not provide enough crevices, which are preferentially colonised (McAllum 1992), and if the bark is too thick, the insect's stylet cannot reach the phloem elements. Indeed, the lower trunks of smaller trees (10-30 cm diameter at breast height), which are approximately the same size as the heavily infested branches of large trees, also harboured high densities of *U. assimile* (Wardhaugh *et al.* 2006), indicating that vertical stratification was dependant upon resource accessibility.

Several studies have examined the fauna inhabiting the suspended soils associated with epiphytes at various heights in the canopy (Nadkarni & Longino 1990; Winchester & Behan-Pelletier 2003). For instance, the abundance of Thysanoptera, Formicidae, Nematoda, Collembola and Coleoptera in the suspended soils of a *Ongokea gore* tree in Gabon varied significantly with height (Winchester & Behan-Pelletier 2003). In contrast, Nadkarni and Longino (1990) found that the relative abundances of a number of insect taxa

were similar in the canopy and on the ground, although densities were higher in the canopy. However, care must be taken to discriminate between communities that are vertically stratified, and communities comprised of species that are simply either arboreal (i.e., found at any height above ground) or ground dwelling (see Simon *et al.* 2003; Sørensen 2003).

Some insect species are likely to be strata specialists in spite of appropriate resources being distributed across different strata, and will only search for food, mates or refuges in discrete vertical layers of the forest. For example, large euglossine bees forage in the upper canopy to maintain a high body temperature, whereas smaller bees that are not as susceptible to heat loss are found in lower strata (Roubik 1993). The very low insect species overlap found between the faunas inhabiting mature canopy trees and conspecific saplings (Barrios 2003) suggests that insects are not searching out a particular host species, but rather they are searching their preferred strata for appropriate host plants. However, seedlings may constitute a poor quality resource for herbivores because they rarely flush with new leaves (Basset 1999b, 2000). Seedlings also lack a number of other resources that canopy trees provide, such as flowers, fruit, suspended dead wood and associated canopy flora such as epiphytes, and lianas. Clearly, most resources are not confined to certain strata, but most will be more predictable, relatively plentiful or of a higher nutritional quality in certain vertical strata than others. Selection will thus favour those individuals that restrict their searching to the discrete vertical layer of the forest where they will most likely locate an appropriate food source, and not waste energy searching elsewhere (see Barrios 2003).

Several studies have proposed that factors other than, or in addition to, resource availability may play an important role in the vertical stratification of insect assemblages. Pressure from aerial predators on certain forest insects, in particular large flying species,

may be an important factor influencing the structure of canopy assemblages (Schulze *et al.* 2001; De Dijn 2003; Koike & Nagamitsu 2003).

Abiotic conditions, in addition to indirectly affecting insect assemblages via vertical changes in plant resource availability, can also directly affect the vertical stratification of insects via species-specific physiological tolerance limits. For instance, the flight activity of mosquitoes (Culicidae) has been shown to be dependent on relative humidity in Columbia (Bates 1944). Other insects may also take advantage of the abiotic conditions in vertical strata that they do not utilise for feeding. For example, many species may use the canopy as a 'highway' to move around the forest (Ødegaard 2004), possibly because of more favourable abiotic conditions for flying in the canopy, such as higher visibility, or temperatures (May 1979; Prokopy & Owens 1983; Théry 2001). The higher wind velocities in the upper canopy (Szarzynski & Anhuf 2001) can also aid in transporting small arthropods and locating potential mates or host plants via sex or aggregation pheromones and host plant volatiles (Schal 1982; van Klinken & Walter 2001). For instance, fig wasps (Agaonidae) in Borneo use the overstorey to locate their host fig trees, even though many trees do not produce figs in the canopy (Compton *et al.* 2000). Wasps use the higher wind velocity of the overstorey to detect the species-specific volatiles emitted by their respective host trees and to move quickly and efficiently over the forest. The authors suggest that when a wasp detects the volatiles from a receptive host fig tree, it drops down into the canopy, where the wind velocity is much lower, and flies upwind to the tree. To locate the appropriate resources the wasps must utilise a vertical strata that does not contain the desired resource, but does increase the chances of finding it. Therefore, this can still be considered an example of vertical stratification in response to resource availability.

Although abiotic conditions and predation have been shown to influence vertical distributions of insects, most studies conclude that resource availability is the most important variable influencing the observed distribution patterns (but see Rowe & Potter 1996). Even where it has been shown that abiotic factors correlate with the vertical stratification of certain species, it is difficult to prove that climatic variables caused this restriction. Among 14 vertically stratified arthropod taxonomic groups in Borneo, 13 were positively related to leaf area (resource availability), 11 were positively related to climatic variables (climate tracking), and three were positively related to height (height specialists) (Dial *et al.* 2006). It is feasible that insects have tracked the resources they use through evolutionary time, and adaptations or preferences to the climatic conditions within certain vertical strata simply reflect the adaptations for locating and utilising their preferred resources, which are vertically stratified (Rader & Krockenberger 2006).

One of the few examples of vertical stratification that cannot feasibly be explained by resource availability is the feeding patterns of Japanese beetles, *Popillia japonica* (Scarabaeidae) on linden trees (*Tilia cordata*). The beetles attack the uppermost foliage and defoliate the tree from the top down (Rowe & Potter 1996). However, this pattern appears to be unrelated to any defensive or nutritional variable in association with the leaves, or any factor linked to beetle performance. The authors suggest that the preference for attacking the upper part of host trees may be due to behavioural thermoregulation (i.e., tracking warmer temperatures in the upper crowns of trees) or even host tree identification via its silhouette.

Resource specialisation may also be more important than host specificity in the vertical structure of arthropod communities. For example, plant communities and pollination systems are generally more diverse in the understorey (Bawa *et al.* 1985), and emergent trees usually constitute a subset of the local plant species and utilise similar

suites of pollinators (often bees) (Bawa 1990). Yet the upper canopy in tropical rainforests usually harbours a greater diversity and density of insects (Basset *et al.* 1992, 2001; Charles & Basset 2005). This dichotomy can be explained by the greater number of microhabitats in the upper canopy compared to the understorey, which indicate that it is the number of discrete microhabitats, and not within microhabitat variation (i.e., host diversity), that is most important to the vertical stratification of arthropod diversity.

Not all species are vertically stratified (Intachat & Holloway 2000), and some studies have failed to demonstrate any strata specialisation in their focal organisms (Roubik *et al.* 1995), in particular adult Lepidoptera (Hill *et al.* 1992; Schulze & Fiedler 2003.). Thus, strata specialisation may be more likely in some lineages than others, and is probably influenced substantially by the mobility and resource requirements of the insect taxa in question. High mobility, such as in many Lepidoptera, may facilitate the use of a greater proportion of the forest canopy, since little more energy may be wasted searching a large vertical area than a small vertical area along the horizontal plane. Indeed, Thomas (1990b) found that monophagous Lepidoptera colonised isolated host plants as quickly as they colonised neighbouring host plants, suggesting that many strong flying Lepidoptera may forage over a much greater area than most other insects.

Vertical stratification also appears to be a phenomenon that is synonymous with complex tropical rainforests (Smith 1973; Terborgh 1985), and studies carried out in temperate forests have failed to replicate the findings of researchers in the tropics (Lowman 1985; Winchester 1997; Schowalter & Ganio 1998; LeCorff & Marquis 1999). Temperate forests appear to lack vertical gradients in microclimatic conditions within tree crowns, such as temperature and relative humidity, that are often pronounced in tropical rainforests (Parker 1995; Basset *et al.* 2003b). This lack of variation means that temperate insects cannot track or adapt to the abiotic conditions within particular vertical strata, but

some degree of population stratification could still occur due to variation in resource availability between the ground and the upper canopy.

Vertical stratification is the result of the interaction between resource availability, abiotic conditions, biotic influences and evolutionary history. Most strata specialists are probably restricted to particular strata simply because their food source is also restricted or concentrated to the same strata. For instance, Shanahan and Compton (2001) found that the vertical distribution of fig-eating vertebrates in Borneo was dependent on the characteristics (size, colour) of figs in different vertical strata. Conversely, other species may be restricted to particular strata due to intense competition or predation in other parts of the host tree. In particular, the ant fauna of tropical rainforest canopies is highly structured, resulting in ant mosaics where dominant species are spatially partitioned due to competition for food sources (Blüthgen & Stork 2007). The strength of the underlying forces responsible for the vertical stratification of insect communities have yet to be quantified, and it is possible that the influence of opposing abiotic and biotic interactions are forest type, site or host species specific.

2.4.2 Horizontal distributions

Compared to vertical stratification, much less work has been carried out on the spatial distribution of arboreal insects utilising the same resources and occupying the same vertical strata. Variation in the horizontal distributions of insect species or assemblages is usually explained by spatial variation in sunlight and/or temperature, which often induces variation in foliar chemistry (Maiorana 1981; Mole & Waterman 1988; Mole *et al.* 1988; Moore *et al.* 1988; Nichols-Orians 1991; Bond *et al.* 1999). However, results are variable, and there appears to be a lack of consistency across biomes in insect preferences for the sun or shade. While some have found higher densities of insects on the sunny side of trees

(Moore *et al.* 1988; Basset 1991e; Stork *et al.* 2001; Unsicker & Mody 2005), others have found higher densities in the shade (Maiorana 1981; Mole & Waterman 1988; Mole *et al.* 1988; Nichols-Orians 1991). Not surprisingly, studies that report higher insect abundances on sun leaves are typically undertaken in temperate (Moore *et al.* 1988; Stork *et al.* 2001) or subtropical (Basset 1991e) forests, while those that report higher abundances on shade leaves are situated in hotter tropical forests (Mole & Waterman 1988; Mole *et al.* 1988; Nichols-Orians 1991). Spatial variation in abundance for many species therefore, could be related more to differences in abiotic conditions than differences in chemical or nutritive components of the foliage. For instance, feeding trials showed that plants grown in full sunlight were preferred by generalist herbivores among several temperate plant species in North America, but shaded leaves suffered higher herbivore damage (Maiorana 1981).

2.5 Temporal changes in arthropod activity

In addition to dividing resources in space, adult insects will often only be active at certain times of the day or year, introducing a temporal aspect to insect community dynamics (Didham & Springate 2003). Supra-annual periodicity in arthropods is also possible. The most familiar example of this is the 13 and 17 year cycles of periodic cicadas (Karban 1997), but the phenomenon has been little investigated among less conspicuous insects, or those within highly diverse tropical rainforests where long-term seasonality studies are lacking (Didham & Springate 2003). Often, variation in temporal abundance patterns is related to the coordinated timing of adult emergence and dispersal. However, adult life-span is also an important factor. Short lived species may be more likely to display marked changes in abundance through time than long lived species, particularly if their phenologies are seasonally coordinated and non-overlapping. Information on insect life-spans is lacking for the majority of species, but some large beetles may live for several

years as adults. Although much of this time may be spent in either diapause or aestivation (Tauber & Tauber 1976, 1981), temporal peaks may occur in activity or dispersal throughout the lives of individual cohorts.

2.5.1 Seasonality

Insect seasonality is well known in temperate regions where food availability and tolerable climatic conditions are usually restricted to short, predictable windows (Feeny 1970: Lowman 1982; Niemelä & Haukioja 1982; Wolda 1988; Hunter 1992; Forkner *et al.* 2008), but temporal population dynamics are often disregarded in apparently aseasonal tropical forests. However, most tropical forests experience distinct seasons with respect to rainfall, usually referred to as the wet season (summer) and the dry season (winter), that many rainforest plants and their respective insect faunas track (Tauber & Tauber 1976; Denlinger 1986). Many insect species are highly sensitive to even small changes in photoperiod or temperature (Paarmann 1974). Studies that have documented the population dynamics of insects within tropical rainforests have found that the abundances of most species show strong seasonal changes (Wolda 1992; Novotny & Basset 1998; Wagner 2001; but see Novotny *et al.* 2002c). In addition to seasonal changes in abiotic conditions, rainforest trees typically produce new leaves, flowers and fruit during relatively short periods of time and continuous leaf production and/or reproduction is rare (Borchert 1983; Murali & Sukumar 1993; van Schaik *et al.* 1993; Toriola 1998; Chapman *et al.* 1999; Forget *et al.* 1999; Poulin *et al.* 1999).

Discerning the causal factor(s) driving insect seasonality in tropical rainforests is difficult, since insect abundance often correlates with temperature, rainfall and host tree growth and reproduction (Frith & Frith 1985; Intachat *et al.* 2001; Didham & Springate 2003). Accordingly, insect abundance has been shown to increase in the summer wet

season in Panama (Aide 1993; Barone 2000), Guyana (Basset 2000), New Guinea (Novotny & Basset 1998; Basset 1999a), subtropical Australia (Basset 1991b), Paluma in tropical Australia (Frith & Frith 1985), and at the end of the dry season at Cape Tribulation in tropical Australia (Grimbacher & Stork 2009a). These peaks in insect abundance also coincide with peaks in production of new leaves and/or flowers by many local tree species (Frith & Frith 1985; Hopkins & Graham 1989; Basset 1991b, c; Bawa *et al.* 2003; Boulter *et al.* 2006).

For many insect species in moist tropical forests, abiotic conditions, such as temperature, rainfall or photoperiodicity, probably do not govern the ability to grow or reproduce successfully, but rather act as reliable indicators of resource availability (Didham & Springate 2003). As such, seasonality in tropical rainforests is probably a function of the periodic nature of resource availability (Basset 1991b, c). Certainly, vertebrate seasonal migrations are invariably governed by changes in food availability (e.g., Kimura *et al.* 2001), and it should be expected that insects are also sensitive to such changes. Conversely, antagonistic and mutualistic insect species could also influence the phenological patterns of host plants through temporal changes in the population dynamics of herbivores, seed predators and pollinators (Elzinga *et al.* 2007).

The availability of water is probably the most important limiting abiotic factor for most species (Wolda 1978b, 1988; Borchert 1983; Lieberman & Lieberman 1984; Frith & Frith 1990; Kwok & Corlett 2002; Didham & Springate 2003), but there are exceptions (Wolda 1989, 1992). As such, seasonality would be expected to be more pronounced in forests that experience more marked dry seasons (Wagner 2001, 2003), and among invertebrate groups that are more susceptible to desiccation (Hurtado Guerrero *et al.* 2003; Palacios-Vargas & Castaño-Meneses 2003). Consequently, in tropical dry forests, where insect seasonality is increasingly under the influence of abiotic factors, plants often flush

new leaves during the dry months when herbivore abundance is lower (Aide 1992; Murali & Sukumar 1993; Sloan *et al.* 2006; but see Lieberman & Lieberman 1984). However, the dry season coincides with peak irradiance levels, which may also influence host tree phenology (Wright & van Schaik 1994), further confounding seasonal patterns in these forests.

While strict seasonality may be a function of resource or climatic tracking, many species will opportunistically respond to large influxes of ephemeral resources by prolifically reproducing. For example, high supra-annual levels of flowering and flushing in south-east Asian dipterocarp forests are typically followed by large increases in the abundances of insects (Intachat *et al.* 2001; Itioka *et al.* 2003; Itioka & Yamauti 2004). It should be noted however, that the dipterocarp forests of south-east Asia are unique among the world's rainforest ecosystems in their irregular periodic mass reproductive strategies, so patterns from these forests may not be applicable to other forest types.

2.5.2 Diel activity

Many insects will only feed or be active at certain times of the day (Takeda & Skopik 1997), allowing an even greater number of species to utilise particular resources (Kitching *et al.* 2007). There are a number of reasons that an insect will avoid feeding at certain times of the day, including minimising competitor interactions (Morris *et al.* 2005), predator avoidance (Basset & Springate 1992), avoiding adverse environmental conditions (Springate & Basset 1996; Basset *et al.* 2001, 2003c) and maximising resource quality and/or quantity (Herrera 1990; Armstrong 1997; Hernández-Conrique *et al.* 2007). However, there is a general lack of consensus among studies as to the factors driving diel activity patterns (Springate & Basset 1996), particularly the role of predator avoidance

where contrasting results have been found in different locations (Buckley 1990; Basset & Springate 1992; Novotny *et al.* 1999).

Other factors, such as tracking temporal changes in resource quality or quantity, could have a major influence on the diel activity of tropical insects. For example, capture rates of pollen-feeding beetles within the canopies of *Myristica insipida* (Myristicaceae) trees in a tropical rainforest in Australia were positively related to the number of open flowers, which varied throughout the day (Armstrong 1997). In Panama, two species of *Dalechampia* (Euphorbiaceae) flowered at different times of the day, thus reducing cross-pollination from their shared pollinator (Armbruster & Herzig 1984). However, for many species circadian rhythms may simply be the result of evolutionary constraints (Kronfeld-Schor & Dayan 2003; Boulter *et al.* 2005), such that diurnal species are unable to become nocturnal to avoid diurnal predators and competitors or utilise nocturnal resources and vice versa.

2.6 The strength of interacting mechanisms

The structure and distribution of insect assemblages in forests are likely to be influenced by more than one of the mechanisms discussed. Resource availability is at the root of insect distribution patterns, but the population dynamics of most species are also influenced by at least one of the other mechanisms. Few, if any, arboreal species are insensitive to host specificity, seasonality, inter- and intraspecific interactions, or the microclimatic conditions and resources that vary spatially and temporally in tropical forest canopies. Indeed, it has been shown that to adequately survey rainforest insect communities requires long-term sampling from multiple vertical strata at multiple sites using multiple sampling methods (Adis *et al.* 1984; DeVries *et al.* 1997; Kitching *et al.* 2001; Stork & Grimbacher 2006). Resource specialisation has been discussed above in

relation to vertical stratification and temporal population dynamics and activity, where it has been proposed to be the main driver of these patterns, but do any other mechanisms interact in a predictable way in structuring arboreal insect assemblages?

2.6.1 Resource specialisation and host specialisation

Host specialisation of herbivorous insects varies substantially depending on the resources being exploited (Novotny & Basset 2005; Novotny *et al.* 2010). Much of this variation may be due to the differential herbivore defences employed by host plants in different plant parts (Gould 1991; Merritt 1996; van Dam *et al.* 1996; Hoy *et al.* 1998; Veldman *et al.* 2007). Apparent, long lasting plant parts, such as wood, are characteristically protected via digestibility reducing compounds or extremely low nitrogen levels (Mattson 1980; Yamamura & Tsuji 1995), whereas ephemeral plants and plant parts, such as seeds, are often protected with toxins (Rhoades & Cates 1976; Veldman *et al.* 2007). Insects utilising low quality, apparent resources should be less specialised than insects feeding on high-quality, well defended resources because specialising on low quality food does not necessarily restrict an insect to one or a few related host trees. An insect capable of subsisting on a nutritionally poor diet can theoretically feed on any host species provided the material reaches some species-specific nutritional threshold (Mattson 1980), and additional structural or chemical defences are not employed. In contrast, insects feeding on well-defended plant parts must overcome the usually host specific chemical and structural defences, thereby reducing their ability to overcome the defences of other potential hosts (Ehrlich & Raven 1964). Variation in host specificity of insects utilising different resources was shown in a community of Lepidoptera, where monophagous and oligophagous species were restricted to feeding on flush foliage, which is often well-

defended chemically, while polyphagous species fed predominantly on mature foliage, which is better defended structurally (Cates 1980).

In general, host specificity should decline with decreasing levels of defence, which should in turn decline with the nutritional quality of the resources (Mattson 1980), or their importance to the host tree's reproduction and growth. Evidence for such a pattern in tropical rainforests was provided by Novotny and Basset (2005) who reported that the percentage of species in different feeding guilds that are host family specific decreased in the order: granivores (99%) > leaf miners (96%) > fructivores (83%) > leaf chewers = sap-suckers (56%) > xylophages (24%) > root feeders (10%). Or, in terms of the resources that these insect guilds predominantly feed on: seeds > leaf mesophyll > fruit > leaf segments = sap > wood > roots.

Compared to low quality, largely structural food sources such as wood or roots, reproductively important, highly nutritious plant parts such as seeds and fruit, are more likely to be well defended in time and space (Grubb *et al.* 1998; Schoonhoven *et al.* 2005; but see Gerber *et al.* 2007) because their loss has a greater direct impact on the reproductive output of the host plant (Louda & Potvin 1995; Winkler *et al.* 2005). Certainly, high abundances of insects attacking the wood, roots, sap or mature leaves can be highly detrimental (Rockwood 1973; Marquis 1984, 1992; Whitham & Mopper 1985; Lowman & Heatwole 1992; Strauss 1997; Vranjic & Ash 1997; Harrison *et al.* 2005; Pratt *et al.* 2005). However, insect outbreaks are rare in complex tropical rainforests (Wallner 1987; Lowman 1995), and these insects probably do not reduce the growth or reproductive potential of the host tree to the same extent as insects directly attacking areas of new growth and reproduction (see Gould 1991; English-Loeb & Karban 1992; but see Marquis 1992).

A good example of the relative importance of certain kinds of herbivory can be seen on host trees that provide extrafloral nectaries (EFN's) that function to attract ants or other predators (Blüthgen *et al.* 2004; Wäckers & Bonifay 2004), which prey upon detrimental chewing herbivores (Barton 1986, but see Koptur & Lawton 1988). The ants however, will often tend aggregations of sap-sucking herbivores, which exact a cost to the host tree. But the widespread occurrence of EFN's in ant-rich rainforest canopies indicates that the benefits of a reduction in chewing herbivores must be greater than the costs of an increase in sap-sucking herbivores (see Dejean & Corbara 2003). Alternatively, EFN's could function to lure ants away from flowers, where they could significantly reduce the reproductive fitness of host plants through the destruction of flowers or the repelling of pollinators (Del-Claro *et al.* 1996; Wagner & Kay 2002).

Due to a lack of empirical data, there are also several herbivorous guilds missing from the sequence compiled by Novotny and Basset (2005), in particular those insects associated with the flowers. The position of flower visitors in the host specificity sequence will vary depending on what resources insects are feeding on and the prevailing flowering strategies employed in different forests. Some plant-pollinator interactions are highly specialised, such as those between of fig trees (*Ficus*) and what is usually a single species of wasp (Agaonidae) that is capable of carrying out successful pollination (Janzen 1979; Wiebes 1979; Weiblen 2002; but see Ware & Compton 1992). However, fig trees are exceptional, and most rainforest trees are not limited to one or a small number of specialised pollinators (Bawa 1990; Pellmyr 1997). Perhaps because one-to-one plant-pollinator systems are inherently fragile (Allen-Wardell *et al.* 1998; Lindberg & Olesen 2001), many trees employ a generalist pollination system that attracts a broad range of local pollinators (Hopper 1980; Crome & Irvine 1986; Herrera 1988; House 1989; Waser *et al.* 1996; Roubik *et al.* 2003; Boulter *et al.* 2005). The large number of generalist

pollinators moving through the forest canopy may compensate for the reduction in pollinator efficiency and fidelity compared to trees relying on specialist pollinators (Aigner 2001). Although only a few species may be effective pollinators on any particular host species (Schemske & Horvitz 1984; Herrera 1987; Bawa 1990; Fenster *et al.* 2004), the contrasting selective pressures from even a small number of successful pollinators may also prevent specialisation (Herrera 1989).

Furthermore, a shift towards a generalist pollination system should involve an increase in the number of potential pollen vectors, which could have positive effects on resource allocation to flowering. For example, insect pollinated flowers typically remain open for no more than two or three days, and many last less than one day, whereas the flowers of bird pollinated trees in southern Australia remained open for 12 days on average (Primack 1985). Similarly, hummingbird-pollinated flowers in a Costa Rican cloud forest were larger and remained open longer than the flowers of other tree species (Stratton 1989). Floral resources such as nectar can be costly for a host plant to produce (Pyke 1991), so a reduction in the longevity of individual flowers or their size should coincide with a reduction in energy per flower (Primack 1985), which could lead to greater potential seed set for the same reproductive effort. Flower longevity is linked to pollinator visitation rates (Primack 1985), so it is feasible that generalist flowers are cheaper to produce because the increase in visitation rate from small insects allows for a reduction in longevity and size, and hence a reduction in resources to sustain flowering.

A further adaptation of trees that rely on generalist pollinators is to flower when other trees are not flowering, thereby reducing interspecific competition for pollinators. This could have the affect of increasing the relative host specificity of pollinators by reducing the diversity of available host trees. For instance, dipterocarp tree species in south-east Asia stagger their flowering, which maximises pollination efficiency by

reducing competition and avoiding cross-species pollen transfer (Ashton *et al.* 1988). Hummingbird pollinated plants in Costa Rica have also been shown to display a temporally staggered flowering pattern (Stiles 1975, 1978), as well as beetle pollinated *Annona* spp. (Annonaceae) in Brazil (Gottsberger 1989a). Alternatively, sequential flowering in some species may be due to a mutualistic sharing of obligate pollinators by providing a constant succession of flowers (Waser & Real 1979). However, these examples appear to be exceptional and little evidence has been found for competition or mutualisms among tree species for scarce pollinators that results in staggered flowering in other tropical (Boulter *et al.* 2006) or temperate (Kochmer & Handel 1986) forests.

Nectar robbers and pollen feeders are probably less specialised than pollinators in general because they feed on plant-provided food sources, which function to attract pollinators and as such are unlikely to be strongly defended (but see Wootton & Sun 1990). It is likely that they are closer to generalist pollinators in host specificity, since neither is likely to have evolved specialised mutualistic relationships with particular host plant species. Indeed, it is possible that most, if not all, pollinators have initially been nectar robbers or detrimental pollen-feeders, only for an increasingly specialised relationship to develop with the host tree over evolutionary time to the point where the insect species becomes a valuable pollinator (see Frame 2003). A generalist pollinator visiting a flower that requires a specialist pollinator effectively becomes a nectar robber or pollen feeder anyway, so the distinction between the two categories is obscure at best.

Shoot and flower borers and flower and leaf gallers are probably relatively specialised since they predominantly attack important, ephemeral centres of growth and reproduction on the host tree. Pollen and nectar may be freely available but developing seeds may be much better defended. Also, endophagic insects tend to be more specialised than ectophagic species, since the former usually must complete their larval development

in intimate contact with the host plant and its defensive compounds (Cornell 1989; Hespenheide 1991; Gaston *et al.* 1992), which can promote host specialisation. Indeed, Pipkin *et al.* (1966) recorded several species of host specific fruit flies (Diptera: Drosophilidae) that bred exclusively in flowers in Panama and Colombia. Boring insects must also adapt to the physical structure of the tissues they attack on their host species (Lucas *et al.* 2000; Peeters 2002b), further restricting host utilisation. Therefore, by feeding internally on reproductively important plant parts, borers and gallers may exhibit a similar level of host specificity to leaf miners.

2.6.2 Seasonality and host specialisation

A positive relationship between host specificity and seasonality has been identified in some canopy insect communities, where monophagous insects tend to show strong seasonal changes in abundance and polyphagous species are more aseasonal (Novotny & Basset 1998; Forkner *et al.* 2008) (Fig. 2.1). The degree of seasonality exhibited by an insect species is positively related to resource availability in time, which decreases with increasing host specificity. That is, highly seasonal insects tend to specialise on resources that are patchy in time, and patchiness in time increases with increasing host specificity. Indeed, the availability of ephemeral resources has been found to have a significant effect on the seasonal patterns of insect abundance (Basset 1991c; Basset 1997).

As an example of the importance of host specialisation to seasonality, consider the insect assemblage that specialises on feeding on new leaves in a complex tropical rainforest. Most rainforest trees do not continuously flush new leaves, but limit their new leaf growth to short temporal windows where abiotic conditions are most suitable (Frankie *et al.* 1974; Wright & van Schaik 1994; Angula-Sandoval & Aide 2000) or herbivore abundances are low (Aide 1988, 1992, 1993; Murali & Sukumar 1993). A monophagous

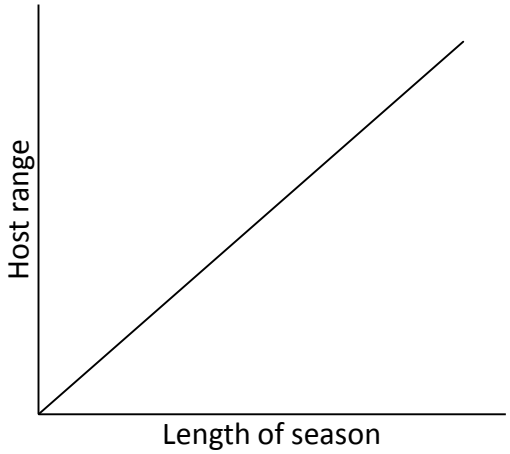


Figure 2.1: A hypothesised relationship between seasonality and host plant range where a shift up the continuum from monophagy to polyphagy corresponds to an increasing length in seasonality.

insect must time its reproduction to coincide with the flushing of new leaves on its host tree. The shorter the temporal window where the appropriate resources are available, the more seasonal the insect must be (Fig. 2.2a). This relationship can become so extreme that some monophagous insects have only a few days in which to oviposit on a suitable site for larval development (Hunter 1992; Komatsu & Akimoto 1995). Ovipositing too early or too late in such species can lead to complete reproductive failure (van Asch & Visser 2007). Consequently, polyphagy tends to increase with the increasing unpredictability of host plant availability, whereas monophagy is more common on predictable host plants or plant parts (Cates 1981; Forkner *et al.* 2008).

A polyphagous insect needs only to search, locate and move between trees in the local area that happen to be flushing with new leaves to feed and/or reproduce (Novotny & Basset 1998). Since resources are plentiful in time for a polyphagous insect, seasonality should be low or non-existent (Fig. 2.2c). Along the continuum from monophagy to extreme polyphagy, new leaves, and also flowers, fruit, and suspended dead wood, shift from being patchy to abundant in time (Fig. 2.3). As such, oligophagous species would be expected to show an intermediate level of seasonality (Fig. 2.2b), since the temporal

window where appropriate resources are available should be greater than for monophagous species, but may not be continuous as is the case for many polyphagous species (Fig. 2.2c).

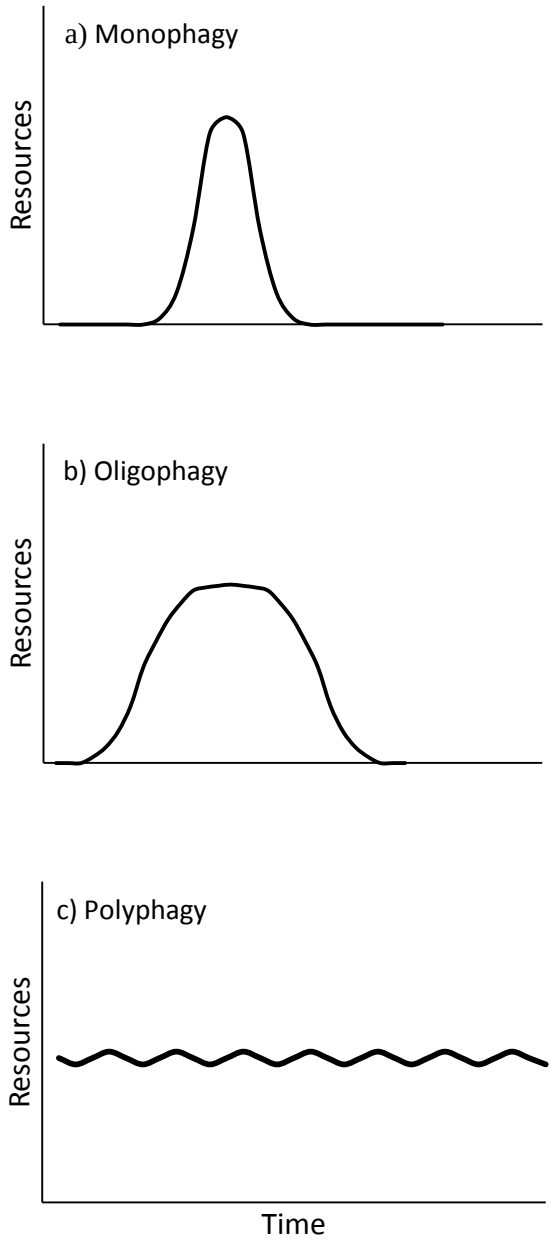


Figure 2.2: The changing availability of ephemeral resources through time for a) monophagous insect species, b) oligophagous insect species, and c) polyphagous insect species.

At the local forest scale, few resources are likely to be patchy in time (Frith & Frith 1985; Boulter *et al.* 2006), and only a few isolated examples of temporally patchy resources exist at larger spatial scales in tropical rainforests (Fig. 2.3). For example, the

mass flowering events in dipterocarp forests in South-east Asia. Flowers, fruit and seeds within these forests are rare most of the time, and then become extremely abundant during the intermittent periods when most of the trees in the local area reproduce simultaneously (Ashton *et al.* 1988; Brearley *et al.* 2007). In these forests, marked seasonality in polyphagous insects should be more prevalent than in other complex tropical rainforests,

a) Monophagous herbivore resources

	Patchy in time	Abundant in time
Patchy in space	Suspended dead wood	
Abundant in space	Flowers/fruit New Leaves	Mature leaves Live wood Roots Sap

b) Polyphagous herbivore resources

	Patchy in time	Abundant in time
Patchy in space		Suspended dead wood Flowers/fruit New leaves
Abundant in space	Mass flowering Mast seeding	Mature leaves Live wood Roots Sap

Figure 2.3: The distribution in time and space of plant resources at the local scale in tropical rainforest for a) monophagous herbivores and b) polyphagous herbivores.

since the resources available to polyphagous species display a similar patchiness in time as those available to monophagous species (see Ashton *et al.* 1988; Toy *et al.* 1992). Most other tropical rainforests exhibit temporal peaks in leaf and flower production, but these tend to be rather shallow peaks in abundance (Frith & Frith 1985; Boulter *et al.* 2006), and availability probably does not become so low during the troughs that polyphagous species will also be highly seasonal.

Insects specialised to feeding on resources that are abundant in both time and space within host tree species and at a local forest scale, such as mature leaves, wood and roots, should also show less seasonality, since they are always accessible. Because of their apparency, these resources tend to be either well defended or of relatively poor nutritional quality (Mattson 1980; Yamamura & Tsuji 1995) to avoid severe herbivore attacks and potential pest population outbreaks. Since many insects eventually circumvent plant defences, apparent resources such as wood and sap are invariably of low nutritional value (Mattson 1980). In addition, wood, roots and mature leaves are not centres of growth or reproduction, so they consequently lack the influxes of nutrients that are required for those tasks (Mooney & Gulman 1982; Raven *et al.* 1999). Developmental times of insect species that utilise these resources subsequently increase in order to extract enough nitrogenous compounds to facilitate growth (Novotny & Basset 2000), which increases the time that vulnerable larval stages are exposed to time-based mortality factors.

2.6.3 Temporal variability in spatial specialisation

Abiotic conditions are continually changing through time, so a mechanism like vertical stratification, which is often related to the climatic conditions in different vertical strata, either directly or via resource distribution, can also change through time (Fitzjarrald & Moore 1995). An extreme example of seasonal vertical migration in tropical rainforests

occurs in the seasonally inundated forests of the Amazon basin (Adis *et al.* 1984). In response to the flooding of the forest floor, ground strata arthropods, such as many spiders and beetles, move into the trees to avoid drowning (Marques *et al.* 2006).

In forests that do not experience seasonal flooding, temporal changes in vertical stratification are undoubtedly less extreme, but may still be widespread. Berkov and Tavakilian (1999) found that the xylophagous cerambycids of the genus *Palame* utilising Lecythidaceae trees in French Guiana reproduced exclusively in the canopy in the wet season, with reproduction at ground level restricted to the dry season. In the wet season, ovipositing beetles either avoid the ground because it is waterlogged, providing a rich medium for the growth of potentially harmful fungi, or because the high relative humidity at ground level masks the volatiles that beetles use to find an appropriate oviposition site (Berkov & Tavakilian 1999). In addition, the abundance of Blattaria, Heteroptera and Coleoptera shifted to higher vertical strata in response to general flowering in dipterocarp forests in Sarawak (Itioka *et al.* 2003). During the flowering period these insects moved into the canopy to take advantage of the increase in floral or associated resources. Thus, the insects in these examples exhibit temporally dependent vertical stratification based upon the availability of appropriate resources. This explanation was also given by Enders (1974) who found that the vertical stratification of two species of spiders (*Argiope aurantia* and *A. trifasciata*) in North Carolina was dependent on body size, with large mature individuals occurring higher than smaller immature individuals. The author proposed that this was due to differences in the size of potential prey in different vertical strata, where small prey items, and small spiders, were more plentiful among the herb layer than in the trees. Thus, there is a change in the vertical strata occupied by spiders over time as a function of growth. Stork *et al.* (2001) showed that some beetle species occupying the canopies of oak trees in Britain changed their preferred side of the tree throughout the year.

In one species, *Adalia decempunctata* (Coccinellidae), different colour morphs exhibited different spatial preferences.

Many species of insects will occupy different vertical strata at different times of the day. Some Diptera (Culucidae, Cecidomyiidae, Sciaridae, Chironomidae, and Ceratopogonidae) will swarm in the canopy at dawn and dusk, despite the fact that most of these species are associated with predominantly ground-based resources (Bates 1944; Stork 1991). This behavioural pattern may be associated with optimal climate tracking, where preferred abiotic conditions shift from the canopy to the ground and back to the canopy again during the day, or enemy avoidance (Stork 1991; Didham 1997). Basset *et al.* (2001, 2003c) showed that the species turnover between nocturnal and diurnal insects was greater in the canopy than in the understorey in Gabon. This pattern possibly reflects the relatively stable microclimate of the understorey which could facilitate the prolonged or temporally insensitive activity of low strata insects, whereas insects in the upper canopy may be adapted to the relatively extreme conditions of either the day or night. Conversely, some species display daily rhythms in stratification due to vertically separated feeding sites and refuges (Schal & Bell 1986).

2.6.4 Spatial specialisation and host specificity

There is little empirical evidence for any host specific spatial specialisation, where a polyphagous insect occupies a different spatial area in alternative host species. It is possible that some oligophagous or polyphagous species do occupy different vertical strata depending on the host species, but this would probably be the result of the differential vertical stratification of the resources being utilised, rather than variation in abiotic conditions in the same strata in different host species. If the reason is resource tracking, then the insect species in question is actually displaying an aggregated distribution on its

preferred food source, and is not specialised to that particular stratum. A true strata specialist should be unable to find or utilise resources in other strata, regardless of the palatability or availability of such resources.

Alternatively, vertical stratification could influence the host specificity of an insect species if it is restricted, because of physiological constraints, to a particular stratum that is occupied by only one or a small number of potential hosts. For example, consider a flower-boring insect that is unable to tolerate the abiotic conditions above ~10m in a rainforest. Few trees flower this low in the canopy so resources would be relatively scarce, and perhaps concentrated on the small number of trees that produce a reasonable number of flowers below 10 metres. Adapting to overcome the defensive characteristics of the available host species could result in a low strata flower-borer becoming increasingly specialised to the flowers it attacks over evolutionary time. As yet no published study has found any evidence for such a situation, and even if it has occurred, it is unlikely to be detected due to the difficulty of delimiting the causal factor (vertical stratification or host specialisation) behind the current distribution of an insect.

2.6.5 Resource specialisation varying in time

Many species exploit different resources as adults than they did as larvae, or during different larval instars (Waldbauer & Friedman 1991). However, this is a shift in resource use that is dependent on life stage, and is not an independent shift in resource specialisation in time. Similarly, omnivorous species do not strictly switch diets, since they consume food from more than one trophic level ad hoc, rather than changing food specialisation. Genuine changes in resource use should occur within life history stages, and not require certain feeding structures or size thresholds before a switch can occur. For example, Basset (1991c) showed that some species of psyllids (Hemiptera) switched from feeding on young

leaves to vegetative and reproductive meristems when the availability of young leaves was low. Also, Janssen *et al.* (2003) found that thrips consumed greater numbers of mite eggs when the quality of their usual plant diet was low.

Many different insect species from a wide range of taxonomic groups and feeding guilds have been recorded visiting flowers (Kevan & Baker 1983), but many of these species may be opportunistic, and do not require floral food sources for growth or reproduction. Switching to cannibalism or other suboptimal food sources has been recorded in some insect species, but is usually related to a lack of normal diet resources and the prospect of starvation (Via 1999; Spänhoff *et al.* 2005). Thus, substantial changes in diet usually fall into two categories; opportunistic utilisation of high quality resources, or the consumption of lower quality resources in response to normal food shortages (Diehl 2003).

2.7 Conclusions

The most important mechanisms structuring arboreal insect communities are resource specialisation, host tree specificity, and temporal variability. At the most basic level, an insect must feed on that which it is capable of finding and consuming. Thus the interaction between resource and host specialisation defines the limits of the resource base available to insect species. Vertical stratification, horizontal distribution and even some seasonal and diel activity patterns are largely functions of the interaction between resource specialisation and host specialisation and reflect where and when the appropriate resources are available. Together with biotic interactions such as competition and predation, spatial specialisation and temporal population dynamics function to further restrict the resource base available to different species of canopy insects. The strength of these restricting variables is species-specific, and individual insect species have adapted to the ‘path of least

resistance' among these interacting mechanisms to define the limits of the resources available to them in space and time (Schowalter *et al.* 1986).

Clearly, every species of tree in tropical rainforests (or any other forest type) will not harbour the same number of insect species or individuals. The structure, architecture, growth rate, successional status, growth pattern, size, abundance, phylogeny, distribution, phenology, chemical composition, and the diversity, abundance and predictability of resources on different host species directly and indirectly effects the size and composition of the respective insect faunas (Coley 1983; Lawton 1983; Marquis 1991). Coupled with the fact that many of these factors change through time, adding a temporal component to population dynamics, it is apparent that the arboreal insect fauna within tropical rainforests is an ever-changing, dynamic, mosaic of interacting species that are continually searching for and utilising the myriad resources available to them. Over evolutionary time, insects have adapted to the temporal and spatial heterogeneity in the availability of their required resources in order to maximise the chances of successfully locating an appropriate site for feeding and reproducing.

Chapter 3:

Cryptic biodiversity in flower-visiting invertebrates

"I went out collecting with Albert Way of Trinity, who in after years became a well-known archaeologist; also with H. Thompson, afterwards a leading agriculturalist, chairman of a great railway, and a Member of Parliament. It seems therefore that a taste for collecting beetles is some indication of future success in life."

Charles Darwin

Chapter 3: Cryptic biodiversity in flower-visiting invertebrates[2]

3.1 Abstract

Estimates suggest that perhaps 40% of all invertebrate species are found in tropical rainforest canopies. Extrapolations of total diversity, estimates of energy flow and nutrient cycles, and food web analyses have been based almost exclusively on species inhabiting the foliage, under the assumption that foliage samples are representative of the entire canopy. I test this assumption by comparing density and species richness measures across three microhabitats (mature leaves, new leaves and flowers) in an Australian tropical rainforest. I show that flowers in the canopy support invertebrate densities that are ten to ten thousand times greater than on the nearby foliage when expressed on a per-unit resource biomass basis. Furthermore, species-level analyses of the beetle fauna revealed that flowers support a unique and remarkably rich fauna compared to foliage, with very little species overlap between microhabitats. My results must lead to rejecting the hypothesis that the insect fauna on mature foliage is representative of the greater canopy community. The apparent importance of flowers as resources to tropical insects constitutes a substantial missing piece of the 'diversity jigsaw puzzle' and could alter our understanding of the evolution of plant-herbivore interactions, food web dynamics, and provide a better foundation for accurately estimating global species richness.

[2] This chapter has been published (19 Sept 2012) with little modification as a multi-authored paper in *PLoS ONE* (Wardhaugh, C. W., Stork, N. E., Edwards, W., and Grimbacher, P. S. 2012: The overlooked biodiversity of flower-visiting invertebrates. *PLoS ONE* 7: e45796).

3.2 Introduction

Current estimates suggest that approximately 40% of all invertebrate species utilise rainforest canopies (Ozanne *et al.* 2003). In these systems invertebrates typically represent the most diverse, abundant and effective pollinators (Bawa *et al.* 1985; Ollerton *et al.* 2011), herbivores (Coley & Barone 1996), and predators (Floren *et al.* 2002). High species richness and functional diversity of canopy plants and animals and the relationships that develop between them have been shown to be strongly influential in determining food web dynamics (Novotny et al. 2010), and have also been used to estimate global species richness (Erwin 1982, Stork 1993, Ødegaard 2000a, Novotny *et al.* 2002a, Hamilton *et al.* 2010, 2011).

While the high diversity of invertebrates in rainforest canopies has been recognized for some decades (Southwood 1961, Erwin 1982, Moran & Southwood 1982, Stork 1988), difficulties in accessing the canopy has limited previous biodiversity and ecological studies to techniques that indiscriminately sample all arboreal microhabitats together; such as insecticide fogging (Erwin 1982, Moran & Southwood 1982, Stork 1988) or flight interception/ Malaise traps (Stork & Grimbacher 2006). Sampling canopy invertebrates associated with specific microhabitats has also been largely restricted to mature foliage (Novotny & Basset 2005), since this represents the most abundant biomass in forest canopies. However, rainforest canopies contain a range of other resources, such as flowers, fruits, bark, and living and dead wood that may be exploited by invertebrates. The practical result of this sample bias is that it remains unknown whether samples taken from mature foliage accurately reflect abundances and diversity in the canopy as a whole. Consequently, generalisations about ecological processes such as nutrient cycling and energy flow are difficult to make since we know very little about habitat differentiation in rainforest canopies, or how species are divided across microhabitats.

There is a *prima facie* reason to expect that samples from a single resource type such as leaves are unlikely to represent the diversity or composition of all possible resources in rainforest canopies. First, resource differentiation and niche-based theories predict specialisation on different microhabitats (e.g., Condon *et al.* 2008). For example, feeding trials have shown that many herbivores are restricted to feeding on new leaves, and are unable to consume fully expanded mature foliage (Basset 2001a) suggesting they will be underrepresented (or undetected) in samples taken from mature foliage. Second, the very small amount of empirical evidence available is strongly in favour of different assemblages associated with different resources. For example, 90/138 (65%) flower-feeding caterpillar species from Brazilian Cerrado were not recorded from foliage during 17 years of sampling (Morais *et al.* 2009), indicating that different host plant microhabitats are inhabited by discrete, largely non-overlapping invertebrate communities. At present, there is only one study of which I am aware that has compared more than one microhabitat from tropical rainforest canopy trees. Ødegaard (2000b, 2004) examined the host specificity of the foliage, flower, and dead wood-inhabiting herbivorous beetle (Buprestoidea, Chrysomeloidea, and Curculionoidea) communities in Panama. He showed that the flower-visitor assemblage was diverse (flower-visitors made up ~20% of all beetle species collected), less host specific than folivores, and unique from the communities inhabiting the other focal microhabitats (Ødegaard 2000b). Furthermore, the beetle assemblage on suspended dead wood on one tree species, *Brosimum utile* (Moraceae), was complementary to that on the leaves, and even more diverse (Ødegaard 2004).

Results from studies in other fields also point to an expectation of differences in assemblage structure and diversity between microhabitats. For example, pollination studies have shown that flowers represent especially important sites of diversity (Frame 2003). Indeed, the evolution of insect pollination systems is thought to have been a major driver in

the diversification of angiosperms (Regal 1977; Grimaldi, 1999), and it is estimated that over 90% of tropical rainforest trees are pollinated by insects (Bawa *et al.* 1985, Bawa 1990, van Dulmen 2001). However, the hypothesis that angiosperm diversification was the result of specialist one-on-one pollination syndromes remains controversial, since plant species with generalised insect pollination systems that attract a suite of insect floral visitors outnumber specialist systems (Bawa *et al.* 1985; Bolmgren *et al.* 2003). Consequently, most pollination systems are weakly connected networks consisting of a large proportion of generalists, as opposed to specialised systems involving strong interactions between few species (Bascompte & Jordano 2007; Fontaine *et al.* 2009). Furthermore, numerous flower-visiting species are not actively involved in pollination (Frame 2003, Gribel *et al.* 1999), but may be associated with flowers because they consume nectar, pollen (Wäckers *et al.* 2007), oils (Simpson & Neff 1981), floral parts (Louda & Potvin 1995, McCall & Irwin 2006), or because they are predators of other flower-visitors (Louda 1982, Romero & Vasconcellos-Neto 2004). Flowers therefore, should be expected to support a large number of insect species. Unfortunately, difficulty accessing rainforest canopy flowers has meant that little collecting from this microhabitat has occurred, especially by those undertaking biodiversity studies, so this community has been largely ignored.

Understanding how biodiversity influences ecological processes requires a detailed understanding of how species are distributed (Taylor 1984). Although Ødegaard (2000b, 2004) examined the host specificity of beetles associated with different microhabitats and was able to tally total species counts, he did not record the biomass of each microhabitat. It was therefore not possible to determine the density of beetles on each microhabitat or whether species richness or abundance was proportional to resource availability. This knowledge is required for detailed examinations of rainforest food webs and the strength

and nature of intra- and inter-specific interactions, which have important implications for the evolution of insects and their host plants.

Despite the obvious importance that understanding the distribution and diversity of invertebrates in canopies has for quantifying nutrient and energy flow, beyond Ødegaard (2000b, 2004) there have been no studies that have quantified differences in tropical insect assemblages inhabiting multiple canopy microhabitats. Here, for the first time, I compare the abundance, density per unit dry weight, species richness and compositional overlap of the invertebrate communities between canopy microhabitats. Specifically, I examine the invertebrate assemblages on mature leaves, new leaves, and flowers from 23 species of rainforest canopy plants to determine the relative contribution of each microhabitat to canopy invertebrate diversity. I tested two hypotheses; 1) canopy invertebrate density and species richness are directly proportional to the amount of resource available; and 2) canopy microhabitats represent discrete resources that are utilised by their own specialised invertebrate communities. This approach allowed for an assessment of the validity of using leaf-based samples to capture representative canopy-wide patterns in invertebrate abundance, density and species richness. I propose a mechanism to explain differences in the abundance and diversity of invertebrates between the sampled microhabitats.

3.3 Methods

3.3.1 Study site

All fieldwork was conducted using the Australian Canopy Crane at the Daintree Rainforest Observatory (a Long-Term Ecological Research site www.jcu.edu.au/canopycrane/), near Cape Tribulation (16°17′S, 145°29′E) Queensland, Australia (Fig. 3.1) (Stork 2007). The crane is situated approximately 40 m a.s.l. and >300m from the forest edge in complex mesophyll vine forest (Tracey 1982) that is contiguous with the extensive lowland and

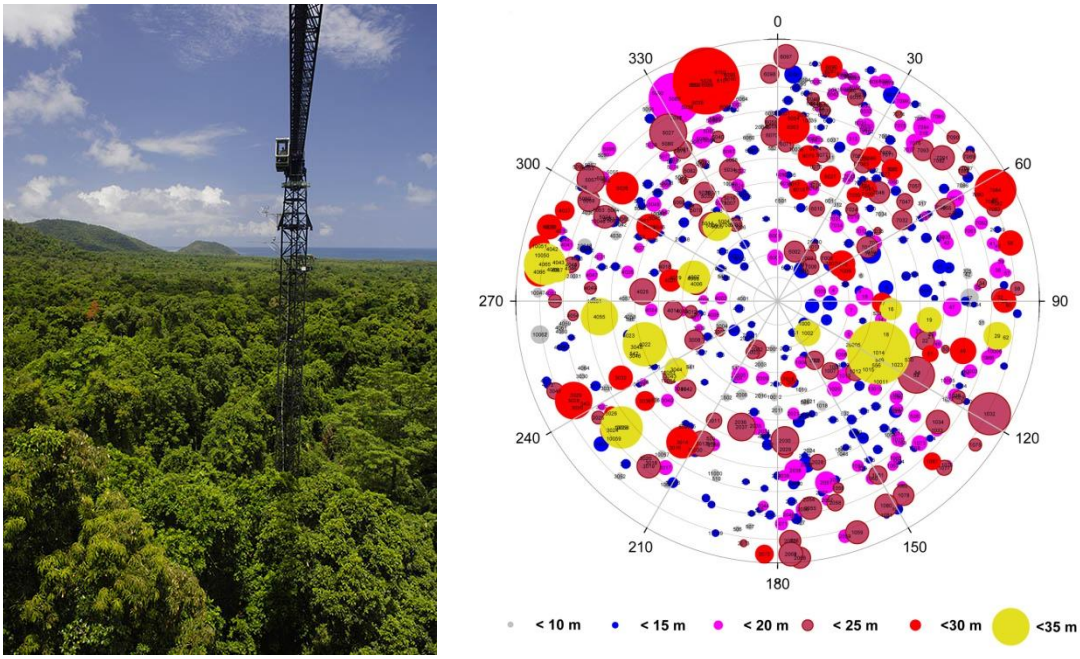


Figure 3.1: Left: view from the gondola of the Australian Canopy Crane. Right: map of the crane site showing the position of each tree over 10cm in d.b.h. (based on the 2005 survey). The different colours in the legend show the size of trees in height. The size of the circles representing each tree show relative size in d.b.h., where larger circles correspond to a larger d.b.h..

upland rainforests of the Daintree National Park and Wet Tropics World Heritage Area (0 m a.s.l. - >1300 m a.s.l.). Approximately1 ha of rainforest containing 745 individual trees (>10 cm d.b.h) (Fig. 3.1) from 82 species and 34 families is accessible from the crane gondola (based on a recent (2009) survey at the crane site which updates previously published data (Laidlaw *et al.* 2007)). The canopy is noticeably uneven in height, varying from 10 to 35 m. Although some rain does fall each month (the lowest average monthly rainfall occurs in August; 80mm), there is a distinctive wet season from November–April (the highest average monthly rainfall occurs in March; 550mm). The 50 year average annual precipitation at Cape Tribulation is 3996 mm (Hopkins *et al.* 1996). Coastal tropical rainforests in North-east Queensland are buffeted by moderate to severe tropical cyclones (category 3) about every 15 years, and a very severe storm (category 4-5) is a one in 75 year occurrence (Turton & Stork 2008). The invertebrate community can be affected by the change in available resources caused by cyclones (Grimbacher & Stork 2009b). The

lowland forests of North-east Queensland are therefore likely to be in a constant state of recovery due to these periodic disturbances (Laidlaw *et al.* 2007). The last cyclone to affect the crane site was Cyclone Rona (category 3), which passed 5 km south of the site in February 1999.

3.3.2 Sampling

Invertebrates were sampled initially from five microhabitats; mature leaves, new leaves, flowers, fruit and suspended dead wood from 23 locally common canopy plant species. The fruit and dead wood communities were omitted from this chapter since it was not possible to obtain accurate biomass measures for these microhabitats. Their insect assemblages are included in the subsequent chapters (4-8) where density measures are not required. The host tree species selected represent a broad range of taxonomic relatedness,

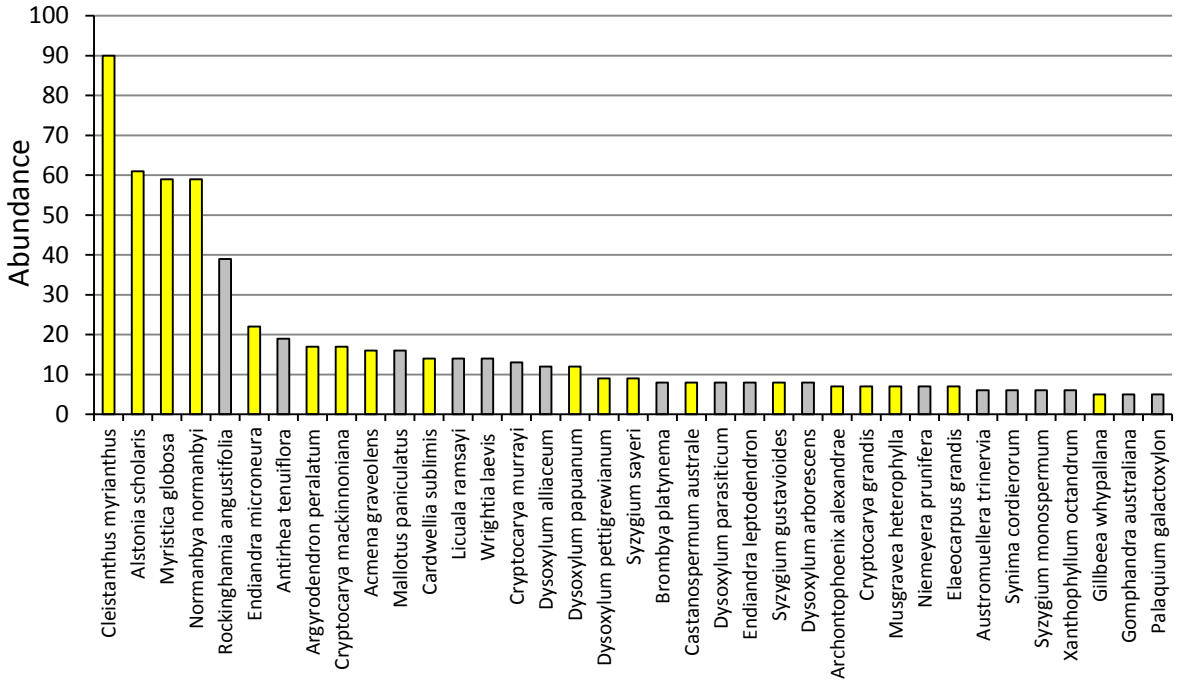


Figure 3.2: The abundances of the 37 most common tree species (≥5 individuals >10 cm d.b.h.) accessible to the canopy crane, based on a 2009 unpublished census of all trees under the crane (2005 census information available in Laidlaw *et al.* 2007). Species shown in yellow were selected for sampling in this study. Species shown in grey were not sampled because they failed to meet size and accessibility criteria (i.e., most are small subcanopy trees that are difficult to reach for adequate sampling from the crane gondola).

growth pattern, phenology, distribution, size, and abundance (Fig. 3.2). In addition to woody trees (19species), two species of palms and two species of lianas were sampled

Table 3.1: The plant species sampled and the number of individuals accessible to the canopy crane. Leaf flushing phenology for each species described as continuous, annual or intermediate, for those species that produced >1 flushing event annually. Flower diameter (mm) is listed for those species that flowered during the sampling period.

Habit	Species	Trees on site	Individuals sampled	Leaf flushing	Flower diam. mm
Trees	Lauraceae				
	Endiandra microneura	22	3	Intermediate	-
	Cryptocarya mackinnoniana	16	4	Intermediate	-
	Cryptocarya grandis	7	2	Intermediate	1.5
	Cryptocarya hypospodia	1	1	-	1.8
	Myrtaceae				
	Acmena graveolens	16	6	Intermediate	3.7
	Syzygium sayeri	9	5	Intermediate	7
	Syzygium gustavioides	8	4	Continuous	4.5
	Meliaceae				
	Dysoxylum papuanum	12	3	Intermediate	2
	Dysoxylum pettigrewianum	9	3	Intermediate	-
	Euphorbiaceae				
	Cleistanthus myrianthus	90	3	Intermediate	-
	Apocynaceae				
	Alstonia scholaris	61	4	Intermediate	-
	Elaeocarpaceae				
	Elaeocarpus grandis	7	4	Continuous	5
	Elaeocarpus bancrofti	1	1	Intermediate	8
	Cunoniaceae				
	Gillbeea whypallana	5	1	Intermediate	3.5
	Proteaceae				
	Cardwellia sublimis	14	4	Continuous	3
	Musgravia heterophylla	7	1	-	1
	Sterculiaceae				
	Argyrodendron peralatum	17	3	Intermediate	3
	Myristicaceae				
	Myristica globosa	59	3	Intermediate	2
	Fabaceae				
	Castanospermum australe	8	4	Intermediate	10
Lianas	*Entada phaseoloides*	-	5	Intermediate	2
	Convolvulaceae				
	Merremia peltata	-	9	Continuous	20
Palms	Arecaceae				
	Normanbya normanbyi	59	10	Continuous	5
	Archontophoenix alexandrae	7	2	Continuous	2.5

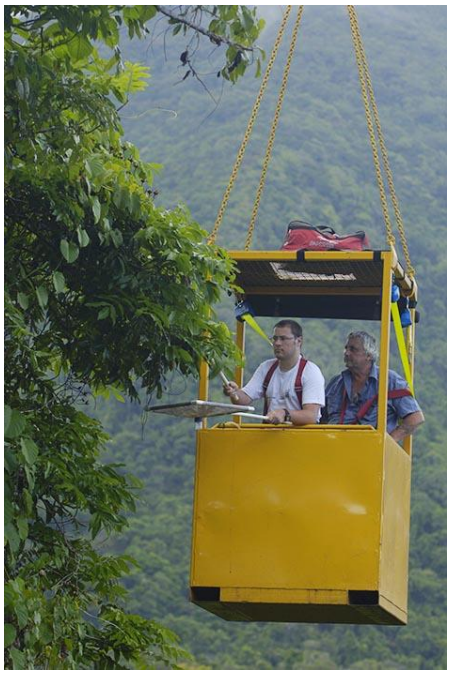


Figure 3.3: Using the canopy crane to sample insects using standardised beating techniques. The beating sheet is held under the microhabitat, which is then struck with a stick to dislodge insects.

(Table 3.1). These species comprise 435/745 individuals and >70% of the basal area of all trees >10 cm d.b.h. in the 0.95 ha area of forest directly under the crane (Laidlaw *et al.* 2007). One to three individuals of each host species were sampled each month for one year (May 2008 – May 2009). Sampling did not occur in October 2008 due to the temporary unavailability of the crane. Invertebrate sampling was carried out by hand collecting all observable individuals, as well as beating the microhabitat over a beating sheet to dislodge cryptic species (Fig. 3.3). Each microhabitat on each replicate tree was sampled for ten minutes. In general, trees that were flowering, fruiting and/or leaf flushing were selected wherever possible, to maximise the number and temporal distribution of samples from these more ephemeral microhabitats. Cross contamination between microhabitat samples was kept to a minimum by only sampling microhabitats that were discretely partitioned on host trees.

To examine patterns in species diversity between each microhabitat, all adult beetles (Coleoptera) were pinned or pointed and sorted to morphospecies (hereafter referred to as species). Species were compared with previous collections from the site (Stork & Grimbacher 2006) and were critically evaluated by myself, Nigel Stork and Peter Grimbacher. The beetle fauna was chosen because of its ecological diversity and high species richness (Grove & Stork 2000), which allowed me to make the comparisons necessary to test my hypotheses.

Microhabitat specialisation was calculated for each beetle species using *Sm* (Specificity to microhabitat *m*, analogous to the Host Specialization (*HS*) measure of

Novotny *et al.* (2004b) which is based on an earlier measure by Thomas (1990b). This technique is similar to the commonly used Lloyd's index. Indeed, the *Sm* measure and Lloyd's index for my data were closely correlated (r = 0.98). However, Lloyd's index is a relative measure of specialisation for each species in a community, which means that it can only show that species *a* is more or less specialised than species *b*. The *Sm* method was therefore chosen as it allowed for the identification of host specificity for each beetle species (e.g., species *a* is a specialist while species *b* is a generalist).

The *Sm* method involved assigning each beetle species to one of three groups based on the proportion of the total number of individuals collected from the microhabitat that supported the highest number of individuals. *Sm* accounts for variation in beetle abundance on different microhabitats, and reduces bias caused by increasing numbers of rare records that inevitably accumulate from large sample sizes. The categories were:

a) Specialists: species where $Sm > 0.9$.

b) Preferences (or oligophages): species where $0.5 < Sm < 0.9$, since most individuals were collected from a single microhabitat, indicating that they have a preference for it but are not necessarily specialised.

c) Generalists: species where $0.33 < Sm < 0.5$, since no microhabitat supported more than half of all individuals.

Assigning specialisation in this way is sensitive to absolute number of records per species. Specialisation analyses were therefore restricted to the 77 beetle species where at least 12 individuals were collected. The limit of 12 individuals was chosen as a compromise between including a maximum number of species and reducing errors arising from potential assignation of specialisation when none actually exists.

It should be noted that since mature leaf biomass constitutes >90% of the combined biomass of the focal microhabitats, a randomly distributed beetle species will be assigned

as a "mature leaf specialist" since >90% of its population should be found on mature leaves. It is therefore not possible to discern mature leaf specialists from randomly distributed microhabitat generalists, since both should be found predominately on mature foliage. However, for the sake of clarity, I refer to all beetles where *Sm* > 0.9 on mature leaves as specialists. This is not the case for flowers and new leaves, however. The spatially and temporally restricted distribution of flowers and new leaves means random distribution of individuals across microhabitats should produce (on average) less than 10% of all records for each species on these resources. Defining microhabitat specialisation using cut-off values of >90% and >50% as employed by the *Sm* method is therefore considered robust in determining specialisation or preference for flower and new leaf beetles.

Sorensen Index (*So*) was used to measure the similarity of the beetle community between each microhabitat across host tree species. The *So* coefficient is a pair-wise comparison that quantifies the proportion of beetle species common to two samples. *So* ranges from 0, where there is no species overlap occurs, to 1, where each beetle species is distributed equitably across microhabitats. The Chao 1 biodiversity indicator was used to estimate the number of beetle species that utilise each microhabitat on the tree species studied. Sorensen coefficients and Chao 1 biodiversity indicators were calculated using EstimateS 8.20 (Colwell 2009).

3.3.3 Microhabitat biomass estimation

Different microhabitats vary considerably in size and biomass both between tree species and within individual trees. As such, a time-based measure of collecting effort, where it is assumed that an equal amount of each microhabitat will be sampled during a set time period, is inappropriate to estimate invertebrate density as a function of biomass available.

Furthermore, an attempt to sample an equal amount (weight, surface area or volume) of each microhabitat on each tree was unfeasible, due to the large differences in biomass between microhabitats. Therefore, I combined my time-based sampling protocol (each microhabitat was sampled on each tree for ten minutes), with an estimate of the biomass of each microhabitat in each sample to produce densities of invertebrates/kg or resource.

To calculate the biomass of a unit of microhabitat (i.e., a single leaf or flower), mature leaves and flowers were collected from each plant species, dried at 60°C for 48 hours and weighed. Mature leaves (n = 9-40/species, mean 30.7) and flowers (n = 1-10, mean 8.2) were weighed and the mean used in subsequent calculations of biomass. New leaves were distinguished from mature leaves on the basis of colour and texture. Many new leaves on a flushing tree are still expanding, and will therefore weigh much less than fully expanded new foliage. Nevertheless, measurement of all new leaves is logistically impossible. Samples of fully expanded, but not yet toughened, new leaves weighed just 56.5% (± 6.7%) of conspecific mature leaves. I therefore estimated the biomass of a single new leaf to be 50% of the biomass of a conspecific mature leaf.

The amount of each microhabitat present on each tree was calculated following Chapman *et al.* (1992) and was based on visually estimating the number of units (leaves, flowers) of each microhabitat within tree crowns. Chapman *et al.* (1992) demonstrated this technique to be both quick and accurate, and ideal for studies attempting to assess change in the amount of available resources through time. Specifically, the number of resource units (i.e., leaves, flowers/inflorescences) within five, randomly located, $1m^3$ samples of tree crown were counted, and extrapolated to the total estimated volume (m^3) of tree crown sampled (Chapman *et al.* 1992). The estimated number of resource units sampled was then multiplied by the measured biomass of that particular resource unit to generate an estimated amount (kg) of microhabitat sampled. This provided a basis for a calculation of

the density of invertebrates and beetles per kilogram of resource within each tree species, making between- and within-microhabitat comparisons possible. Densities on each microhabitat were weighted for biomass/tree species each month, to avoid potential bias produced by high densities or high microhabitat biomass on single tree species. Differences in mean density among microhabitats were examined using ANOVA.

3.4 Results

Over one year a total of 39,276 invertebrates, including 10,185 beetles from 358 species, were collected from mature leaves, new leaves and flowers. Monthly assessments of the biomass of flowers and new leaves showed that these microhabitats constitute a mean (± 95% CI) of just 0.06% ± 0.05 and 1.8% ± 0.52 respectively of mature foliage biomass/ha. Expressed per unit biomass, a disproportionately large number of individuals were associated with new leaves and especially flowers, where invertebrate densities were 1-4 orders of magnitude greater than on the foliage; a pattern consistent across all 18 canopy plant species that flowered during the study (Fig. S3.1a-v). The density of invertebrates per unit biomass of resource varied significantly between microhabitats ($F_{2, 56} = 216.51$, $P < 0.0001$), with flowers supporting 11,055.9 ± 1,884.3 (weighted mean ± 1 SE) individuals per kilogram, and 105.0 ± 16.4/kg on new leaves compared to just 12.8 ± 0.7/kg on mature foliage (Fig. 3.4). Similar differences in density were also found among the beetle fauna ($F_{2, 56} = 181.27$, $P < 0.0001$), with flowers supporting 4,440.3 ± 1,020.1 individuals/kg, compared to 14.0 ± 5.0/kg on new leaves and 1.5 ± 0.1/kg on mature leaves (Fig. 3.4).

Species level analysis of the beetle community also showed a disproportionately high concentration of species on flowers. The majority of the estimated number of beetle species were found on mature leaves, reflecting the large proportion of canopy biomass this microhabitat constitutes (Fig. 3.5). However, the Chao 1 biodiversity indicator

Figure 3.4: The density of invertebrates and beetles on mature leaves, new leaves and flowers (per kg dry weight ± 2SE).

showed that 41% of beetle species utilise flowers and 23% utilise new leaves (Fig. 3.5), percentages far greater than the relative contributions of these microhabitats to total canopy biomass. The total number of beetle species associated with all five microhabitats combined was 596.54 ± 50.27, indicating that ~58-68% of the canopy beetle fauna associated with these microhabitats was sampled. The estimated total number of beetle species was lower than the accumulated totals for each microhabitat combined because

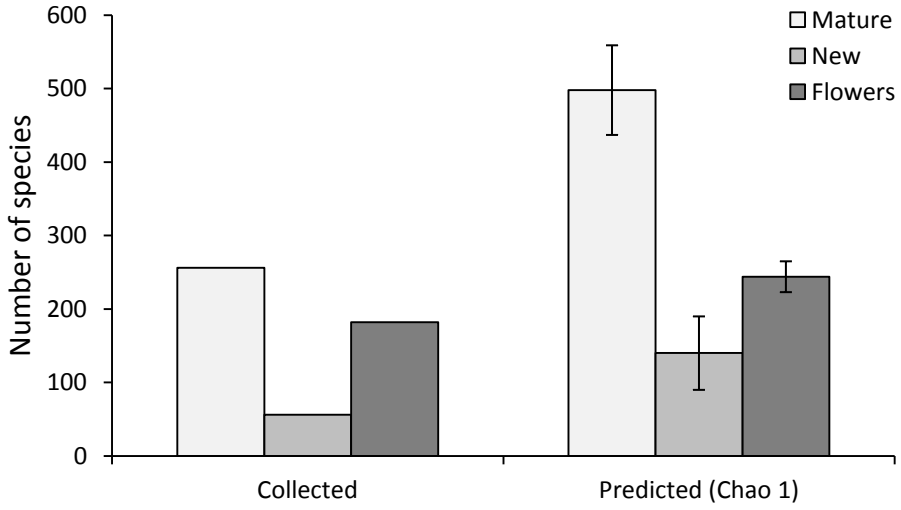


Figure 3.5: The total number of beetle species collected, and the estimated number of beetle species (Chao 1 (± 1SD) species richness estimator) utilising each microhabitat.

each respective community is not mutually exclusive and some beetle species utilise more than one microhabitat. Furthermore, flowers were utilised by a relatively specialised fauna, with 39% of the 77 most common beetle species collected identified as specialists (*Sm* >0.9) on this resource, compared to just 16% on mature leaves (Fig. 3.6).

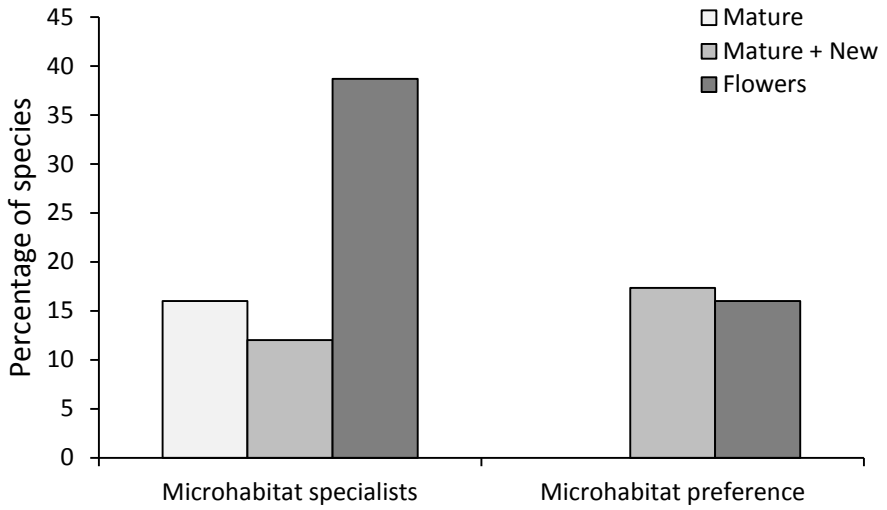


Figure 3.6: The percentage of the 75 most abundant beetle species (n ≥ 12) that are specialised to each microhabitat (*Sm* > 0.9) or showed a distributional preference for a microhabitat (0.5 < *Sm* < 0.9). Note that no species was specialised to new leaves, but some were specialised, or preferred, foliage in general (mature leaves and new leaves combined, identified as foliage specialists and foliage preferences).

Overlap in species composition was very low between microhabitats, with a mean Sorensen coefficient of 0.11 (± 0.004) for pair-wise comparisons between the beetle communities identified from flowers and mature leaves. There was also little overlap between the flower-visiting and new leaf beetle communities (*So* = 0.04 ± 0.003) or the mature leaf and new leaf beetles (*So* = 0.09 ± 0.004). No beetle species was identified as being specialised to new leaves. Rather, the new leaf beetle community was mostly a subset of the mature leaf beetle community, where 44/56 (78.6%) species representing 303/319 (95%) individuals collected from new leaves were also collected from mature leaves. Although 88/182 (48.4%) flower-visiting species were also recorded from mature

leaves, most of these (64) were represented on the less preferred microhabitat by just 1-3 individuals.

3.5 Discussion

Flowers clearly represent important resources for rainforest canopy invertebrates and my data clearly demonstrate that they are sites of very high concentrations of individuals and species. I show that despite constituting a tiny fraction of the biomass of mature foliage, flowers and to a lesser extent new leaves, harbour a large proportion of the abundance and diversity of canopy invertebrates. It is also shown that the communities associated with different microhabitats are unique, with flowers supporting a complementary fauna to that on leaves. As a result, the hypothesis that invertebrate abundance and species richness is proportional to microhabitat biomass is rejected, and the hypothesis that each microhabitat is inhabited by its own relatively discrete invertebrate community is accepted. I can therefore also reject the assumption that the foliage-inhabiting invertebrate community can be used as a proxy for communities inhabiting other canopy microhabitats, and suggest that insects associated with high quality flowers may be a neglected component of invertebrate diversity.

High concentrations of invertebrates on flowers may occur due to pollination rewards, floral herbivory, or because flowers act as aggregation sites for mate finding and/or because flowers attract prey for predatory species (Simpson & Neff 1981, Louda 1982, Louda & Potvin 1995, Frame 2003, Romero & Vasconcellos-Neto 2004, McCall & Irwin 2006, Wäckers *et al.* 2007). I suggest that one of the reasons why invertebrates are so hyper-abundant and diverse on flowers compared to leaves could be linked to the contrasting roles that these structures serve to the tree. Leaves are long-term photosynthetic structures whose loss impacts the growth, survival and/or reproduction of the parent tree

(Lowman & Heatwole 1992, Pratt *et al.* 2005), whereas flowers function to attract insect pollinators by providing food rewards in the form of highly nutritious and often easily digestible pollen and/or nectar (Roulston & Cane 2000). Although widespread comparative analyses of the chemical profiles of flowers and foliage are lacking (McCall & Irwin 2006), it is not unreasonable to assume that flowers are generally nutritionally superior to leaves for most herbivores (Irwin *et al.* 2004), since plants need to attract insect consumers to carry out pollination (Frame 2003 , but see Armbruster 1997). In fact, pollen-feeding is common among basal herbivorous beetle lineages and may have served as a nutritional and mechanical stepping stone towards folivory (Farrell 1998). Leaves in contrast, do not benefit from herbivores and are therefore protected structurally and chemically from insect attack, which renders them nutritionally poor.

In one of the few comparative studies, Carisey and Bauce (1997) showed that balsam fir (*Abies balsamea*) pollen contained lower concentrations of defensive compounds and higher levels of available nitrogen than either new or mature foliage. Indeed, it is unlikely that chemical defences should evolve to deter insect visitors from flowers, since reduction in insect floral attendants could have a detrimental impact on reproduction [but see Detzel & Wink 1993, Adler 2000). For example, *Brassica rapa* plant populations in Montana display variability in concentrations of the enzyme myrosinase. Potential pollinators spend more time foraging in populations with low myrosinase concentrations compared to populations in which flowers express high concentration of this enzyme, indicating that defensive compounds in floral tissues can negatively effect pollination (Strauss *et al.* 1999).

A number of studies have shown that the tough structure of leaves is an effective herbivore defence (Coley & Barone 1996). However, the ephemeral nature of flowers results in less structural defences such as lignified cell walls and fibre (Feinstein *et al.*

2007) compared to long lasting leaves. Insects that consume the lignified cell walls of leaves must typically consume large quantities of this material and pass the undigested cellulose in the excreta, even though it can constitute a high proportion of their food intake (Karasov & Martínez del Rio 2007). Flowers may therefore represent concentrations of high quality accessible food surrounded by lower quality and largely inedible foliage, resulting in spatially aggregated concentrations of diverse invertebrate consumers.

Several lines of evidence suggest that flowers are likely to support a similarly high proportion of the canopy insect community in other rainforests. First, other studies have also found that flower- and foliage-associated invertebrates represent distinct assemblages in both rainforests (Ødegaard 2004) and in other biomes (Morais *et al.* 2009). Second, 20 of the 23 plant species sampled in my study come from families that are pantropical in distribution; Arecaceae, Myristicaceae, Lauraceae, Proteaceae, Euphorbiaceae, Fabaceae, Myrtaceae, Sterculiaceae, Meliaceae, Apocynaceae, and Convolvulaceae. The remaining two families, Elaeocarpaceae and Cunonaceae, are also distributed beyond Australia. Third, beetle communities inhabiting rainforest canopies are remarkably similar across the tropics in terms of the rank order of families in species richness (Stork 1993, Hammond *et al.* 1996). Fourth, beetles are relatively conservative in their feeding biology at the family/subfamily level (Lawrence *et al.* 2000). All of these factors reduce the likelihood that the result reported here is a local phenomenon driven by host tree phylogeny or beetle assemblage composition, and suggest that my findings may be indicative of tropical rainforests in general.

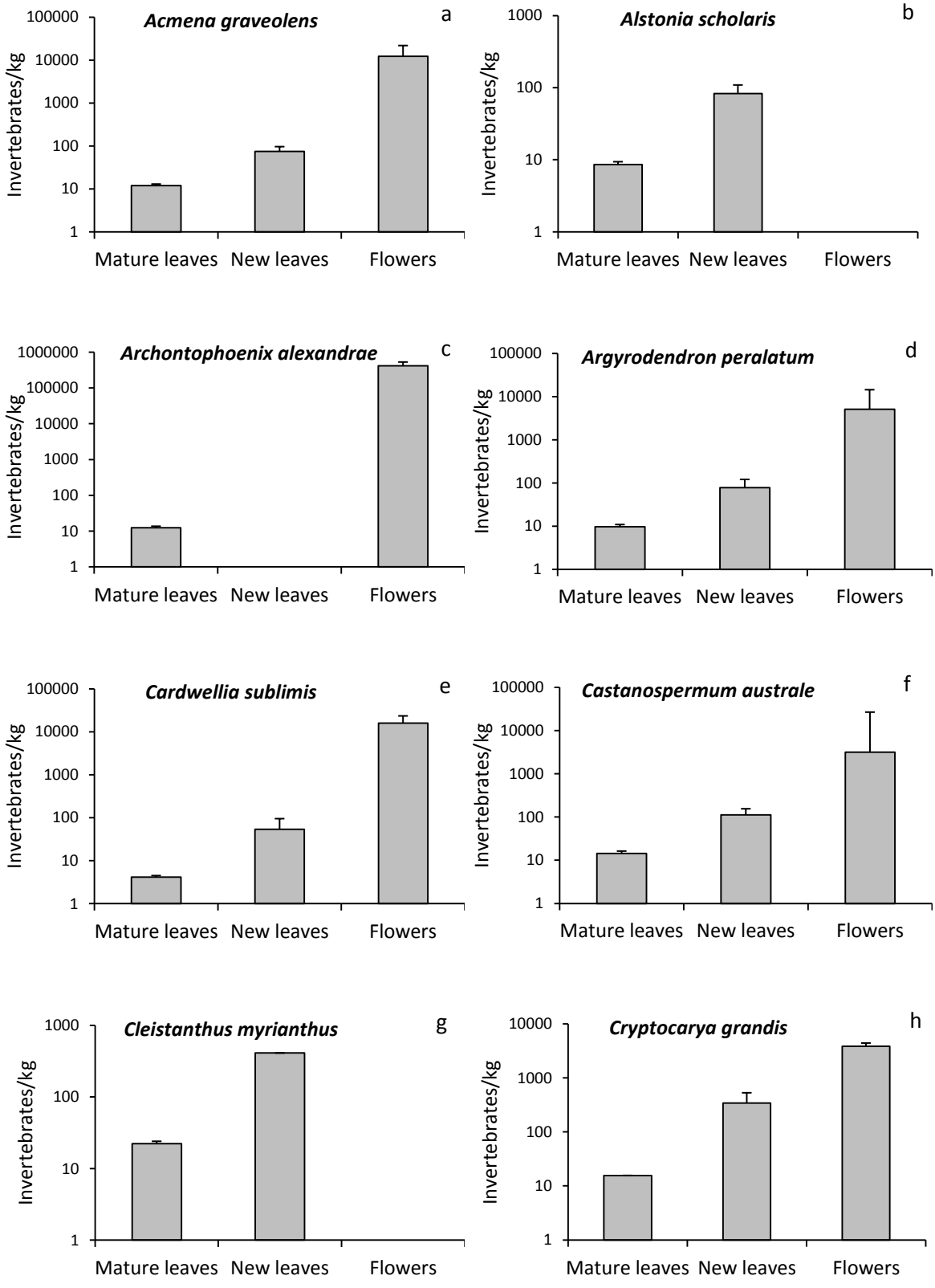
My results demonstrating the concentration of insects on the small biomass of flowers has wide-ranging implications for those attempting to further our understanding of plant-herbivore interactions and canopy food webs (Novotny *et al.* 2010). Recent attempts to quantify rainforest food webs have ignored flower-visiting insects. Kitching (2006)

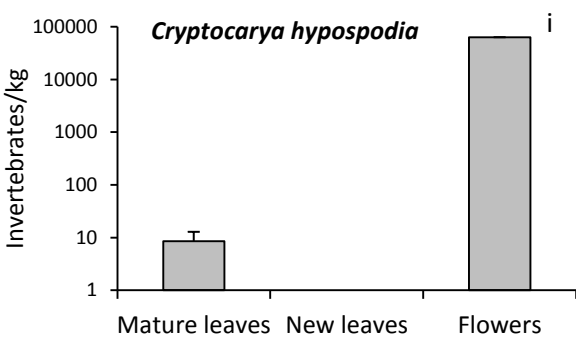
developed a simple rainforest food web in an attempt to identify components/linkages for which adequate information currently exists, and those that require further investigation. While Kitching's model incorporated plant, herbivore, predator/parasitoid, and detritivore diversity, the flower-visiting component was not addressed. Similarly, in one of the most comprehensive examinations of a rainforest food web to date, Novotny *et al.* (2010) examined the trophic links between 224 plant species and 1,490 species of herbivores from 11 distinct feeding guilds. Leaf feeders, xylem and phloem feeders, fruit feeders, and gall formers were studied, but flower-feeders were omitted from their analyses due to a lack of data. Spatial and temporal aggregations of very high densities of flower-visiting invertebrates could result in a high number of strong interactions, making flowers an ideal habitat to study intra- and interspecific interactions among a species-rich community. Flower-visiting invertebrate food webs, where resource availability and the resulting invertebrate abundances may fluctuate widely, are therefore likely to be more dynamic than those based on more widely available and reliable resources such as the leaves. Furthermore, since flowers and their components lack many of the defences typical of leaves, species from non-herbivorous feeding guilds often feed on floral resources. For example, many parasitoid wasps and flies consume nectar (Stork 1987b), blurring the line between herbivore and predator.

If flower-visiting insects do indeed represent a missing or under-represented component of rainforest biodiversity then we need to re-evaluate our current theories and estimates relating to the spatial and temporal distribution of insects in rainforest canopies. The exclusion of flowers from diversity studies in tropical rainforests could previously be justified by canopy access issues and the small biomass of flowers compared to the foliage. Furthermore, those studying herbivory generally dismiss flower-visitors as pollinators (Frame 2003), while pollination biologists typically focus on the few species in the

community that carry out successful pollination (Wäckers *et al.* 2007). The result has been the omission of many cryptic herbivores and an entire community from food web analyses and species richness estimates (Frame 2003). But, as I have shown, abundance and diversity estimates that do not include flower-visitors, or are derived from sampling the foliage-inhabiting community alone are unlikely to be indicative of the entire canopy fauna. Substantial microhabitat partitioning among arboreal invertebrate communities means that sampling mature leaves misses a large number of species altogether. The potential for the flower-visiting fauna to contribute significantly to global biodiversity and food web dynamics emphasises the need to account for this assemblage in future studies of rainforest biodiversity.

Figure S3.1a-v: The density/kg (± S. E. M.) of invertebrates on each of the 22 tree species for which at least two of the three focal microhabitats were sampled (all species except *Musgravia heterophylla*). Note that the data are presented on a log scale. Missing columns signify that no samples were taken from that microhabitat on that plant species.




i
Cryptocarya hypospodia
Invertebrates/kg
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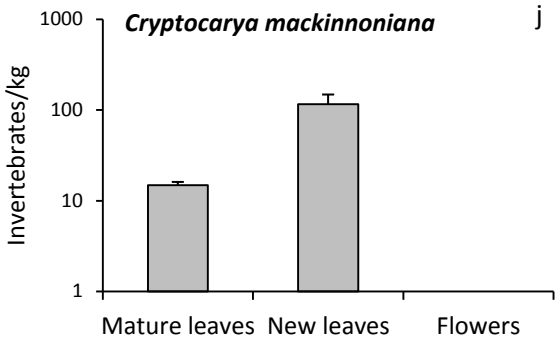
Mature leaves
New leaves
Flowers


j
Cryptocarya mackinnoniana
Invertebrates/kg
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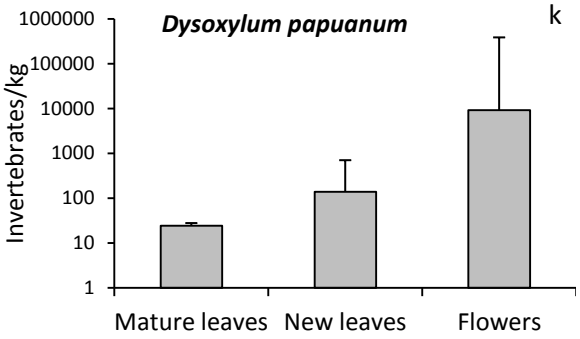
1
Mature leaves
New leaves
Flowers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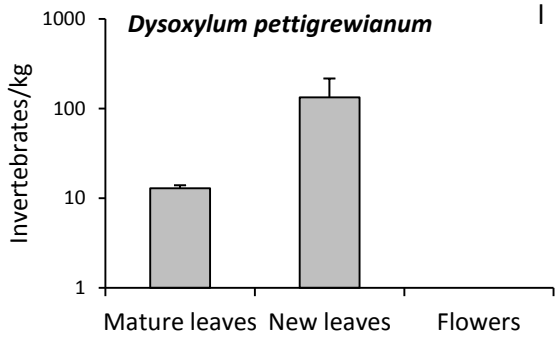
Mature leaves
New leaves
Flowers


l
Dysoxylum pettigrewianum
Invertebrates/kg
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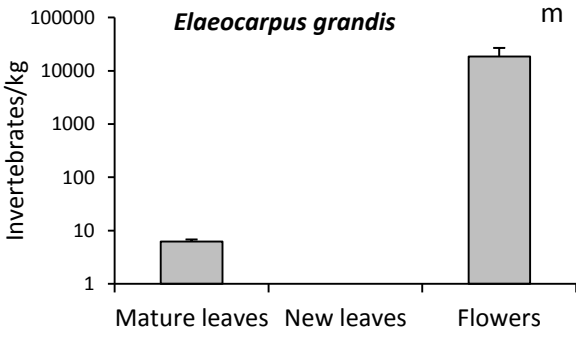
Mature leaves
New leaves
Flowers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Elaeocarpus grandis
Invertebrates/kg
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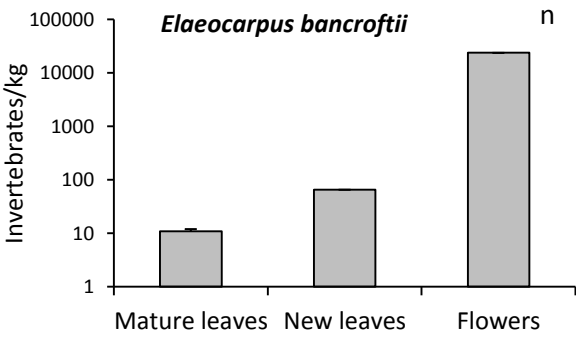
Mature leaves
New leaves
Flowers


n
Elaeocarpus bancroftii
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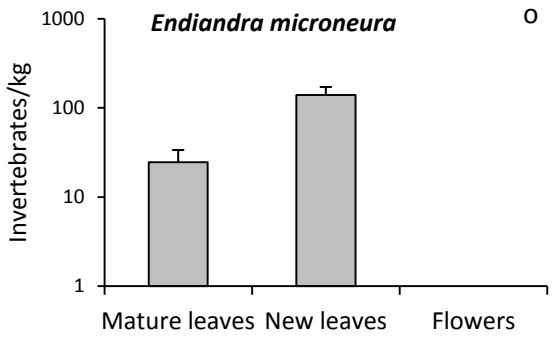
New leaves
Flowers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Invertebrates/kg
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New leaves
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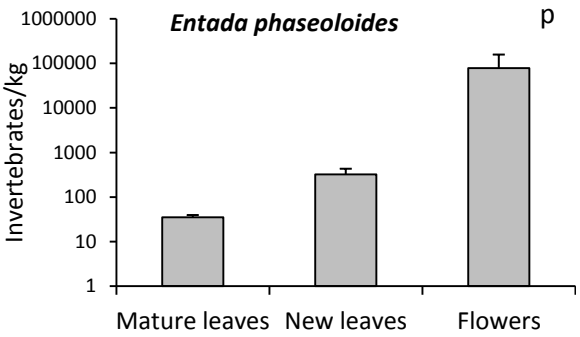
p
Entada phaseoloides
Invertebrates/kg
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Mature leaves
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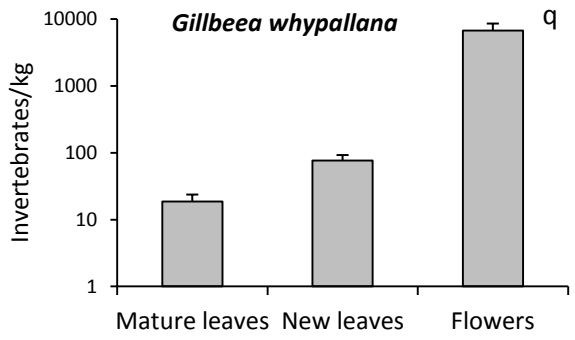
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Mature leaves
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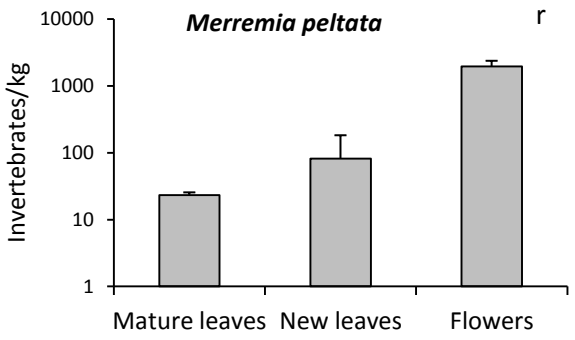
Flowers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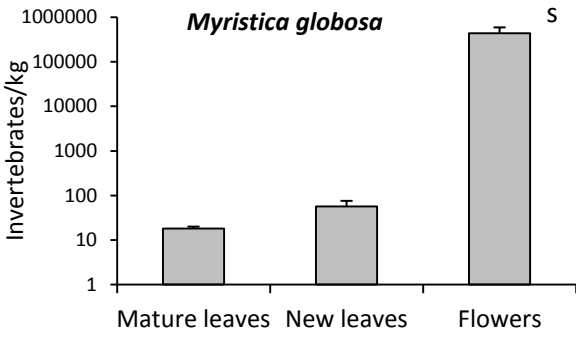
Myristica globosa
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Invertebrates/kg
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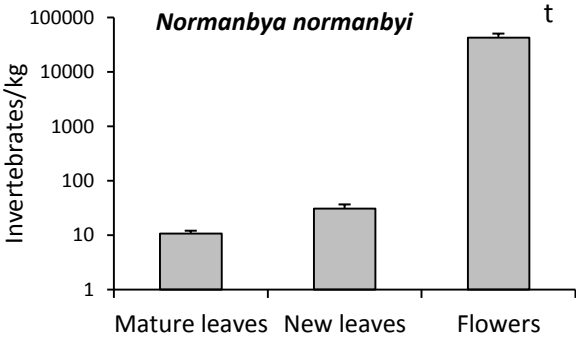
Mature leaves
New leaves
Flowers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Mature leaves
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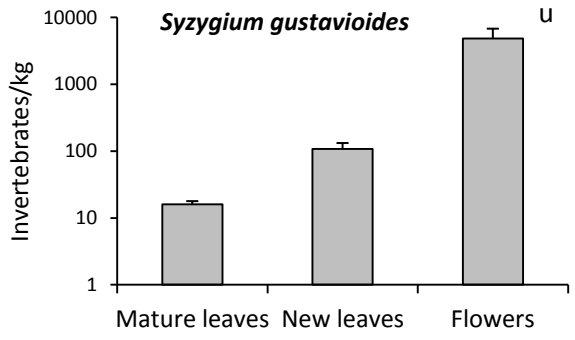
Flowers


Syzygium gustavioides
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Invertebrates/kg
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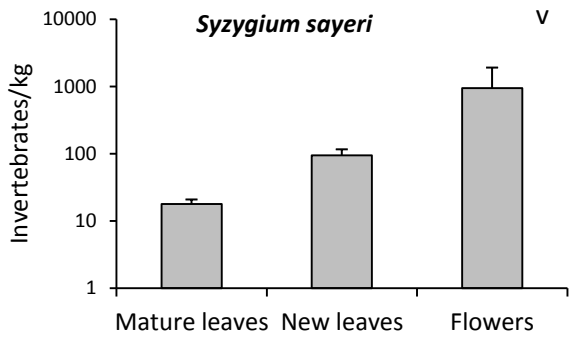
Mature leaves
New leaves
Flowers


Syzygium sayeri
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Invertebrates/kg
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Mature leaves
New leaves
Flowers

Chapter 4:

Canopy invertebrate community composition on rainforest trees: different microhabitats support very different invertebrate communities

Chapter 4: Canopy invertebrate community composition on rainforest trees: different microhabitats support very different invertebrate communities[3]

4.1 Abstract

Tropical rainforest canopies are renowned for their high invertebrate diversity and abundance. The tree canopy comprises a range of microhabitats representing very different food resources (including photosynthetic, reproductive, and structural tissues). Since these resources vary considerably in temporal and spatial availability, nutritional quality, chemical protection and other attributes, I hypothesised that microhabitats support structurally different invertebrate communities. To test this hypothesis I used the Australian Canopy Crane to simultaneously sample invertebrates from mature leaves, flush leaves, flowers, fruit and suspended dead wood from 23 plant species. Invertebrate faunas on different microhabitats varied in taxonomic composition and feeding guild structure in support of the microhabitat differentiation hypothesis. Herbivores were found predominantly on new leaves (Hemiptera, caterpillars) and especially flowers (Coleoptera, Thysanoptera), but were relatively uncommon on mature leaves. Instead, the mature foliage community was dominated by predators, especially spiders and ants, and supported high abundances of saprophages. Ripe fruit and dead wood were scarce canopy resources that were utilised by a relatively small number of invertebrates, mostly saprophages and fungivores. Flowers supported a more heterogeneous fauna than the leaves in terms of proportional abundances of taxonomic groups and feeding guilds both within tree species (evenness) and between tree species (non-uniformity). These results are the first quantification of microhabitat differentiation in a rainforest canopy and demonstrate differences in taxonomic composition, guild structure and abundance patterns between

[3] This chapter has been published (30 Mar 2013) with some modification as a multi-authored paper in *Austral Ecology* (Wardhaugh, C. W., Stork, N. E., Edwards, W. 2014: Canopy invertebrate community composition on rainforest trees: different microhabitats support very different invertebrate communities).

invertebrate assemblages within host trees. I conclude that previous canopy studies based only on sampling leaves may provide a distorted picture of invertebrate community structure.

4.2 Introduction

Understanding how biodiversity influences ecological processes requires an understanding of how species are distributed (Taylor 1984) and how they utilise available resources (Novotny *et al.* 2010). Both the spatial and temporal distribution of organisms determines food web dynamics, as well as rates and extents of nutrient cycles and energy flows (Montoya *et al.* 2006). For example, the canopies of tropical rainforests are the sites of essential ecosystem processes such as pollination and herbivory (Ozanne *et al.* 2003) and attempts to quantify and understand these processes, and to link diversity and ecosystem function has led to many studies of invertebrate biodiversity in rainforest canopies over the last 30 years (e.g., see papers presented in Stork *et al.* 1997a; Basset *et al.* 2003a; Lowman & Rinker 2004).

After woody structures, mature leaves make up most of the biomass of tree crowns (Chave *et al.* 2003; Liddell *et al.* 2007) and most rainforest canopy biodiversity and/or ecological studies have focused on insects inhabiting mature foliage (Novotny & Basset, 2005). Concentration of sampling within this most conspicuous element of tree canopies has meant that the taxonomic composition and (feeding) guild structure of invertebrate communities that exploit other microhabitats remain largely unknown. While there have been a few studies that have compared invertebrate communities between various forest components (i.e., between soil, leaf litter, tree trunks, ground vegetation and the forest canopy (Stork 1988; Nadkarni & Longino 1990; Stork & Blackburn 1993; Stork & Brendell 1993; Basset 2001a; Kitching *et al.* 2001; Beaulieu *et al.* 2010)) even fewer have

compared different microhabitats *within* the canopy (Ødegaard 2000b, 2004). It therefore remains uncertain whether analyses based on samples taken from mature foliage accurately reflect the abundance, diversity and guild structure of the invertebrate community in the canopy as a whole. Thus, assessing differences between tree species and between microhabitats is vital to understanding spatial variation in predation pressure, herbivory and decomposition that all underpin food web dynamics and nutrient and energy cycling.

While studies designed to result in strict comparison between canopy microhabitats are lacking, evidence does suggest that mature leaves are indeed unlikely to harbour similar abundances or species compositions as other canopy resources. For example, feeding trials have shown that many herbivores are restricted to feeding on new leaves, and are unable to consume fully expanded mature foliage (Bernays & Janzen 1988; Basset 2001a). Herbivore densities are also often much higher on flush foliage (Basset 1991a, 1996, 1999a; Steinbauer *et al.* 1998; Barone 2000; Marquis *et al.* 2001; Itioka & Yamauti 2004) and most lifetime herbivore damage on many plant species occurs during leaf expansion (Coley 1980, 1983; Aide 1993). I hypothesise that since resources such as flowers, leaves and dead wood in the canopy vary considerably in quality, composition and spatial and temporal availability, that the invertebrate communities associated with these microhabitats will likewise vary. Here, I compare the relative abundance, biomass, taxonomic and guild composition of the invertebrate communities on different canopy microhabitats by examining the invertebrate assemblages on mature leaves, new leaves, flowers, fruit and suspended dead wood from 23 species of rainforest canopy plants.

4.3 Methods

4.3.1 Study site

See Chapter 3, 3.3.1.

4.3.2 Sampling

See Chapter 3, 3.3.2.

4.3.3 Invertebrate sorting

All invertebrates were sorted to at least the level of order and then to feeding guild (Moran & Southwood 1982; Stork 1987b). Several groups were more finely sorted due to known intra-order variation in feeding mode. For example, the Hemiptera were divided into phloem feeders, mesophyll feeders, Cicadellidae, and predators, to reflect the different feeding modes within this order (Carver *et al.* 1991). Cicadellidae was placed in its own category due to the variety of feeding modes (phloem, mesophyll and xylem feeding species) within this family. Each hemipteran group was also divided between adults and nymphs, as the distribution of winged adults and flightless nymphs may differ. The Hymenoptera were divided into ants, parasitoids (hereafter referred to as Hymenoptera), and Symphyta (represented by a single individual). I separated out ants as an unspecified herbivore/predator guild (as did Moran & Southwood 1982 and Stork 1987b) since it is uncertain as to how much of their food is derived from plant sources (extra-floral nectaries or tending sap-sucking bugs) or from predation (see Blüthgen *et al*. 2003).

The ecologically diverse Coleoptera were sorted to family or subfamily level. Individual beetle families or subfamilies were then assigned to feeding guilds following Lawrence and Britton (1991) and Lawrence *et al.* (2000). Immature stages (larvae and nymphs) were sorted separately from adults for all endopterygote orders due to the often large differences in feeding biology and habitat choice between each life history stage

(Stork 1987b; Novotny & Basset 1999, 2005; Pokon *et al.* 2005). A summary of the taxa included in each feeding guild is: Ants (Formicidae adults and larvae), Predators (Acari, Hymenoptera, Araneae, various Coleoptera, predatory Hemiptera, Mantodea, Neuroptera, Pseudoscorpiones, Scorpiones), Saprophages (Blattodea, Collembola, various Coleoptera, Dermaptera, Diplopoda, Isopoda), Herbivores (sap-sucking Hemiptera, Lepidoptera, various Coleoptera, Gastropoda, Orthoptera, Thysanoptera), Fungivores (Psocoptera, various Coleoptera), Xylophages (various Coleoptera), Tourists (Diptera, Ephemeroptera, Trichoptera), Unknown (various adult and larval Coleoptera, larval Diptera, Symphyla, unidentified larvae) (Stork 1987b). Every individual invertebrate was measured from the front of the labrum to either the tip of the abdomen (excluding cerci or ovipositors) or the end of the elytra for some Coleoptera (which ever is longer) using a calibrated graticule. These measurements were used to calculate biomass using the formula:

equation 1

where L is the length of the invertebrate in millimetres (Rogers *et al*. 1976).

4.3.4 Statistical analyses

As a first approach I began by testing the overall hypothesis that community structure differed between microhabitats and host tree species via permutational multivariate analysis of variance (also called PERMANOVA (Anderson 2001); implemented in the Vegan library in R (Oksanen *et al.* 2010, R Development Core Team 2010)). This procedure tests the hypothesis of between-group differences by portioning variation into within- and between-group effects. The benefit of the approach is that significance tests use a pseudo- F statistic, and an R^2 value describing the proportion of the variation explained by the treatment effects is returned as in standard ANOVA. Unfortunately, at present there is no recourse to post-hoc pair-wise comparisons, and while PERMANOVA

(Anderson 2005) can implement post-hoc comparisons, the design must be balanced. This was not the case in my dataset. I performed the overall analyses including both main effects (tree species and microhabitat) as well as their interaction using a dissimilarity matrix based on Bray Curtis distances.

While PERMANOVA can provide a general answer to the question of between-group differences, I was also interested in identifying taxa and feeding guilds as being over- or under-represented on different microhabitats. To answer this question I employed a simple randomisation procedure that took the entire invertebrate dataset (40,374 individuals) and randomly assigned each taxa or feeding guild to microhabitat types in the exact proportions as they existed in the original data set. The procedure was iterated 1,000 times. After each iteration the number of individuals in each taxa and feeding guild was recorded to generate the frequency distributions of expected numbers under the hypothesis of randomness. To test over- or under-representation I compared the observed (true) number of individuals in each taxa or feeding guild against the 25^{th} and 975^{th} values in the ordered data set to ensure $\alpha = 0.05$ for all conclusions regarding significance. Invertebrate groups or feeding guilds with observed abundances under the 25^{th} value in the ordered randomisation data set on particular microhabitats were significantly under-represented, while observed abundances above the 975^{th} value were over-represented. Analyses were restricted to those taxonomic groups and feeding guilds where the total abundance was >40, chosen as a compromise between including a maximum number of groups while excluding those with insufficient abundances to detect significant differences, if they exist.

Evenness, the degree of equitability in the abundances of the component taxa in the community, is an important measure of invertebrate diversity patterns. For example, rare species are likely to be less important than common species in terms of interaction strength and community dynamics. To assess evenness in the abundance of invertebrate groups and

feeding guilds on each microhabitat on each tree species I used the Evenness index (*E*) of Bulla (1994): calculated as:

$$\frac{-}{-} \qquad \text{equation 2}$$

Where *S* is the number of species (in this case taxonomic groups or feeding guilds) and *N* is the number of individuals. *O* is an index of proportional similarity (Feinsinger *et al.* (1981), also called Schoener's niche overlap index (Bulla 1994). It is calculated as:

equation 3

where p*i* is the observed proportion of *i*th species, ρ*i* is the expected proportion under perfect evenness (1/*S*), and min is the minimum of the two values. Variation in mean evenness between microhabitats was explored with ANOVA. Where significant differences were detected, post-hoc pair-wise comparisons between microhabitats were performed using Tukey tests. Significant outcomes in these tests would reveal between-microhabitat variation in invertebrate community evenness. Conversely, non-significant outcomes are expected when proportional abundances of component taxa are similar on different microhabitats.

While evenness can assess the variation in abundance on each microhabitat within each tree species (i.e., within a single community), it cannot be used to measure variation in the relative abundances of individual taxonomic groups or feeding guilds across tree species (i.e., across multiple communities). To measure the uniformity of taxonomic groups and feeding guilds across tree species I used 2 x *k* contingency tables (where *k* is the number of tree species, = 14) (Moran & Southwood 1982; Stork 1987b). Analyses were restricted to those taxonomic groups (17/41) and feeding guilds (7/8) where n ≥ 14 as this was the number of tree species used in the analysis (i.e., this threshold is the minimum possible for perfect uniformity). Bonferroni corrections were made to significance levels (adjusted $P = 0.003$ for taxonomic groups, and $P = 0.006$ for feeding guilds) prior to pair-

wise analyses. Significant results would indicate variation in the relative abundances of taxonomic groups or feeding guilds across tree species on each microhabitat. Non-significant outcomes would indicate similar proportional abundances across tree species.

4.4 Results

4.4.1 Ordinal profiles

Across all tree species and microhabitats I collected a total of 40,374 invertebrates. Most (73.7%) of these were insects (29,764 individuals), but arachnids also made up a large proportion (25.4%) of total abundance (10,240 individuals). The most abundant insect groups were Coleoptera (10,335 individuals, or 34.7% of all insects), Thysanoptera (5,746, 19.3%), Hemiptera (4,628, 15.5%), Formicidae (3,292, 11.1%) and Blattodea (1,244, 4.2%). Among the arachnids, most individuals belonged to the two most abundant groups; Araneae (5,393, or 52.7% of all arachnids), and Acari (4,794, 46.8%). Total sample sizes and numbers of individuals sampled from different microhabitats were variable. The number of samples and the total number of invertebrates collected from each microhabitat were; mature leaves, 363 samples and 15,274 invertebrates; new leaves, 78 and 2,682; flowers, 82 and 21,320; fruit, 26 and 475; suspended dead wood, 23 and 623.

Figure 4.1a-f shows the contribution to total abundance of the nine most abundant orders in the pooled sample and the variation in proportional abundance of these orders on each of the five microhabitats. Mature leaf- and new leaf-inhabiting invertebrate communities are similar in proportional abundances of most invertebrate groups, while flowers support a larger proportion of Coleoptera and Thysanoptera. Fruit and dead wood invertebrate communities harbour relatively large numbers of Psocoptera, and fewer

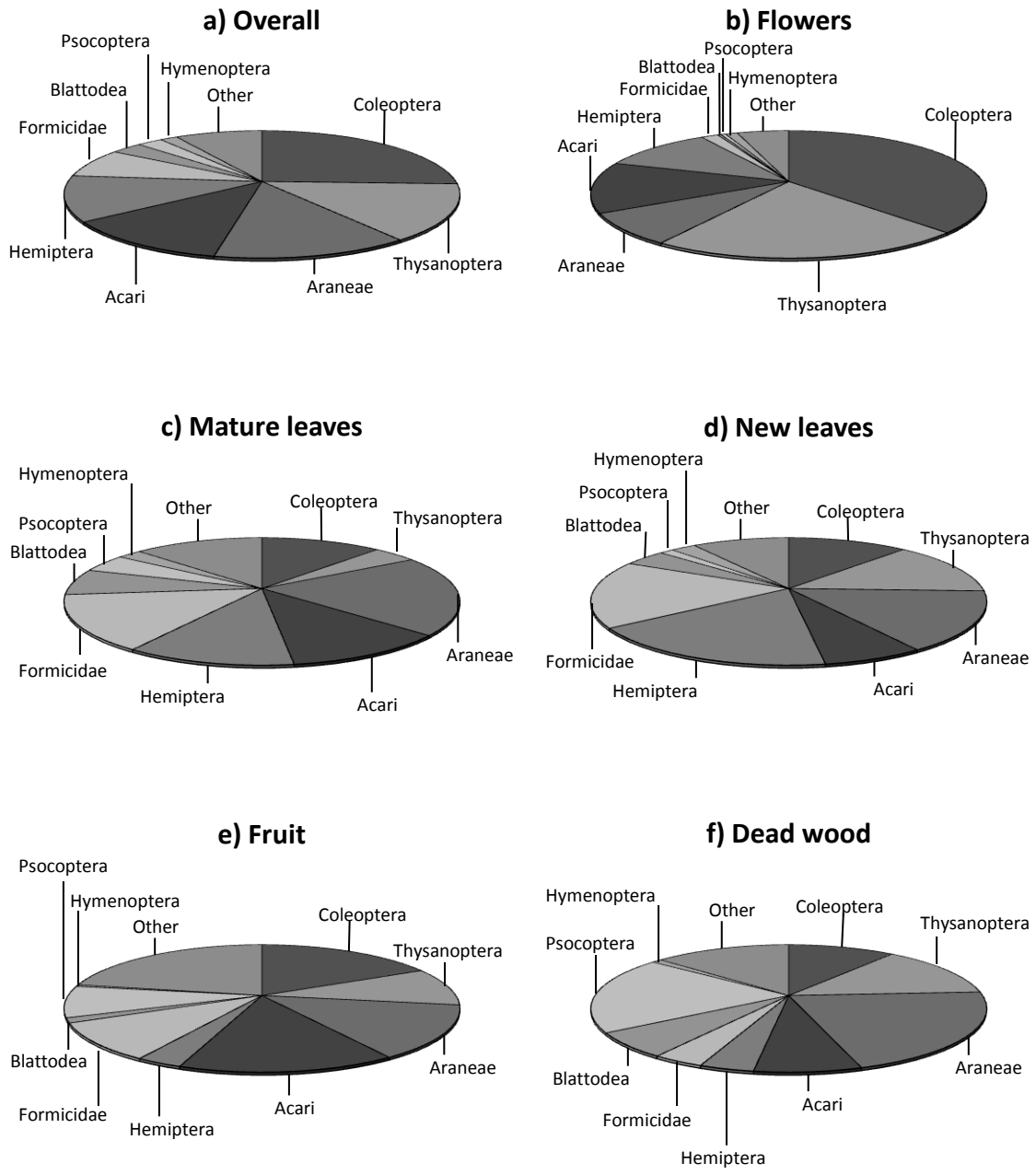

Figure 4.1: The relative abundances (%) of the nine most common invertebrate orders (plus all others combined) in the total sample on a) all microhabitats combined; b) flowers; c) mature leaves; d) new leaves; e) fruit, and; f) dead wood.

Hemiptera. When expressed as biomass however, invertebrate community structure is markedly different. Figure 4.2a-f shows that orders identified as relatively minor in terms of abundance (i.e., Phasmatodea, Orthoptera, Mantodea) constitute a large proportion of canopy invertebrate biomass, particularly on foliage habitats. Conversely, some small bodied orders, such as Thysanoptera and Acari, which are among the most abundant

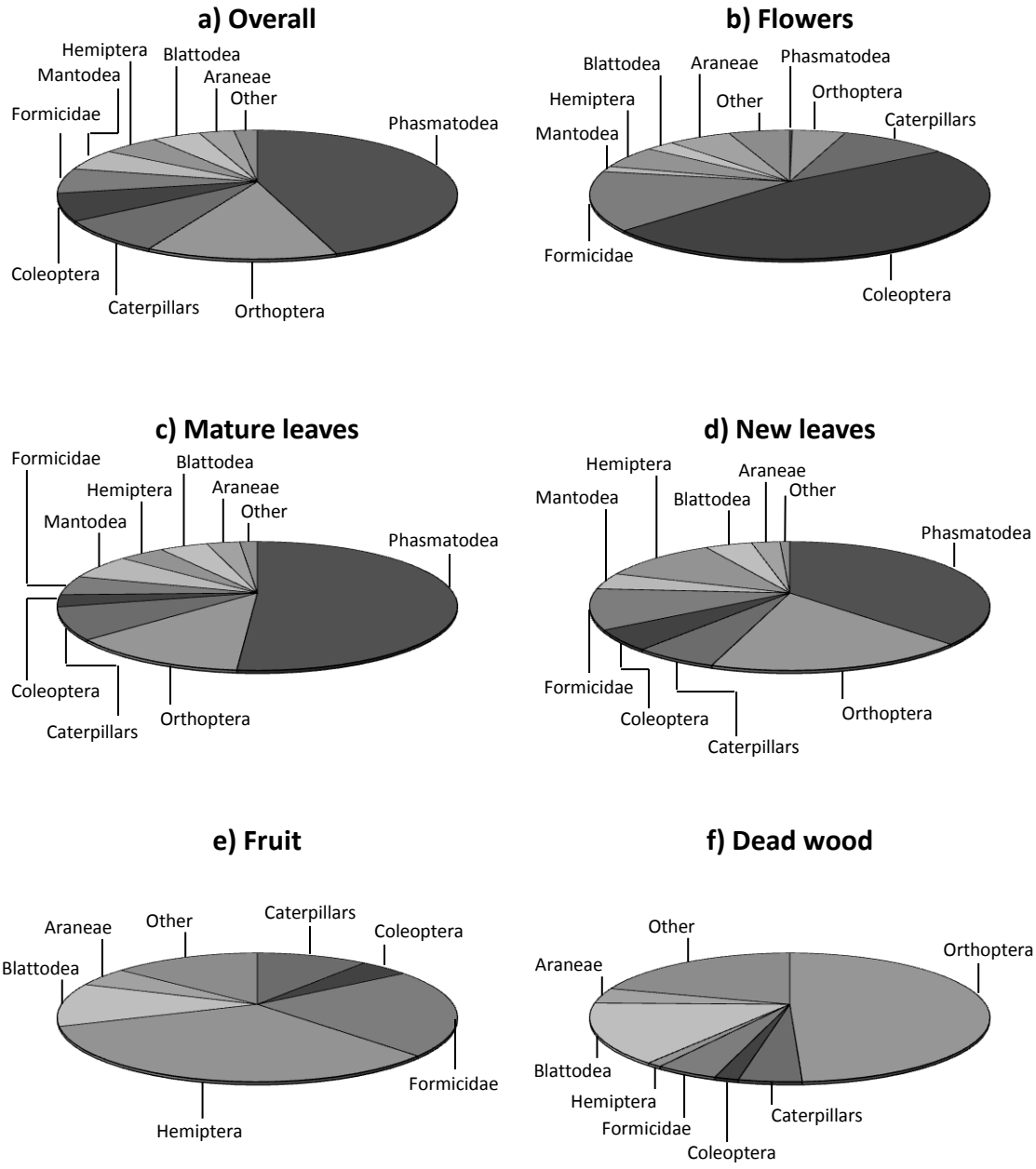

Figure 4.2: The relative biomass (%) for each of the nine orders in the total sample with the greatest cumulative biomass (plus all others combined) on a) all microhabitats combined; b) flowers; c) mature leaves; d) new leaves; e) fruit, and; f) dead wood. No Phasmatodea, Orthoptera, or Mantodea were collected from fruit, and no Phasmatodea or Mantodea were collected from dead wood. Note that these biomass measures are relative to the microhabitat in question, and that absolute biomasses can vary substantially between microhabitats.

invertebrate groups on every microhabitat, contribute very little to total canopy invertebrate biomass.

Overall, I found evidence for significant between-group differences in abundance between categories for both main effects (tree species, $F_{22,265} = 3.63$, $P < 0.001$;

microhabitat, $F_{4,265} = 6.06$, $P < 0.001$). Furthermore, PERMANOVA also returned a significant interaction term (tree species X microhabitat, $F_{42,265} = 1.67$, $P < 0.01$) indicating that community composition was not similar on the same microhabitat in different tree species.

The randomisation procedure identified all 25 invertebrate groups represented by >40 individuals and all eight feeding guilds to be non-randomly distributed among the five focal microhabitats (Tables 4.1, 4.2). Mature leaf invertebrate communities included higher than expected abundances of Blattodea, Psocoptera, Araneae, and Formicidae, and lower abundances of Thysanoptera, Coleoptera and Lepidoptera caterpillars. Samples from new leaves had higher than expected abundances of herbivorous Hemiptera, Formicidae and Araneae, and lower than expected abundances of Psocoptera and Acari. Samples from flowers revealed high abundances of Coleoptera, Thysanoptera, larval Coleoptera and Diptera, and Acari, and were notable for low abundances of Formicidae, Blattodea and Psocoptera. The decomposer community was abundant on dead wood, with higher than expected abundances of Psocoptera, Blattodea and Pseudoscorpiones. Dead wood also showed significantly fewer than expected Formicidae, Coleoptera and Hemiptera. Fruit was utilised by very few invertebrates in the canopy, but there were higher than expected abundances of Psocoptera and Lepidoptera caterpillars, and lower than expected abundances of Coleoptera and Thysanoptera. The high abundance of Formicidae larvae on fruit was due to the presence of a single ant nest within a *Cardwellia sublimis* seed case, and is therefore not reflective of the fruit community in general.

Differences between feeding guilds inhabiting each microhabitat were similar to the differences observed in the analyses based on taxonomic composition (Tables 4.1, 4.2). This similarity reflects the inclusion of whole orders in single feeding guilds, due to a lack in real or assumed variation in feeding biology at the ordinal or family level for most

Table 4.1: The number of individuals of each taxonomic group (n >40) (CSIRO 1991) collected from each canopy microhabitat. Invertebrate groups with higher and lower than expected abundances on particular microhabitats are indicated by colour coding (green for higher than expected, red for lower) and + and – signs after figures. Differences were determined by comparing the recorded abundances (± 95% confidence intervals) with the expected abundances (± 95% C.I.) generated from a randomisation procedure applied to the entire invertebrate community. A number in black with no sign signifies an abundance that does not differ significantly from random.

Taxa	Mature	New	Flowers	Fruit	Wood	Totals
Invertebrates	**15274**	**2682**	**21320**	**475**	**623**	**40374**
Arthropoda	15022	2665	21315	474	623	**40099**
Parainsecta						
Collembola	**391+**	27	**35-**	10	12	**475**
Insecta	10069	2068	16856	331	440	**29764**
Blattodea	**1017+**	**112+**	**70-**	**6-**	**39+**	**1244**
Orthoptera	**246+**	**37+**	**16-**	0	**20+**	**319**
Psocoptera	**711+**	**39-**	**102-**	**36+**	**123+**	**1011**
Hemiptera	1753	471	2366	15	23	**4628**
Phloem feeders						
Adults	**501-**	**104-**	**1043+**	**1-**	**7-**	**1656**
Nymphs	**777+**	**162+**	768-	**5-**	**5-**	**1717**
Mesophyll feeders						
Adults	**149-**	**70+**	257	8	4	**488**
Nymphs	**158-**	**46+**	254	1	7	**466**
Cicadellidae						
Adults	**26+**	**9+**	**6-**	0	0	**41**
Nymphs	**127+**	**79+**	**38-**	0	**0-**	**244**
Thysanoptera	**665-**	368	**4581+**	**48-**	84	**5746**
Coleoptera						
Adults	**1823-**	**319-**	**8043+**	**84-**	**66-**	**10335**
Larvae	**114-**	**22-**	**290+**	8	10	**444**
Diptera						
Adults	**256+**	38	**165-**	3	7	**469**
Larvae	**48-**	10	**188+**	0	1	**247**
Lepidoptera						
Adults	**77+**	4	**2-**	8	1	**92**
Larvae	**209-**	**74+**	359	**20+**	18	**680**
Hymenoptera						
Formicidae						
Adults	**2152+**	**459+**	**362-**	45	**22-**	**3040**
Larvae	**180+**	**15+**	**8-**	**46+**	3	**252**
Hymenoptera	**362+**	**66+**	**253-**	**2-**	6	**689**
Arachnida	4874	593	4458	134	181	**10240**
Araneae	**3110+**	**405+**	**1690-**	57	**131+**	**5393**
Acari	**1720-**	**186-**	**2766+**	77	**45-**	**4794**
Pseudoscorpiones	**42+**	2	**2-**	0	**5+**	**51**
Crustaceae						
Isopoda	**77+**	3	**1-**	**9+**	1	**91**
Mollusca						
Gastropoda	**252+**	17	**5-**	1	**0-**	**275**

Table 4.2: The number of individuals of each feeding guild (n >40) collected from each canopy microhabitat. Invertebrate feeding guilds with higher and lower than expected abundances on particular microhabitats are indicated by colour coding (green for higher than expected, red for lower) and + and – signs after figures. Differences were determined by comparing the recorded abundances (± 95% confidence intervals) with the expected abundances (± 95% C.I.) generated from a randomisation procedure applied to the entire invertebrate community. A number in black with no sign signifies an abundance that does not differ significantly from random.

Feeding guild	Mature	New	Flowers	Fruit	Wood	Totals
Ants	**2332+**	**488+**	**370-**	**91+**	**25-**	**3306**
Fungivores	1054	**55-**	1574	**53+**	**168+**	**2904**
Herbivores	**4025-**	**1233+**	**11784+**	**126-**	**155-**	**17323**
Predators	**5845+**	**698-**	**6387-**	143	193	**13266**
Saprophages	**1559+**	149	**522-**	**43+**	**60+**	**2333**
Tourists	**265+**	38	**165-**	3	7	**478**
Unknown	**165-**	**19-**	**500+**	8	13	**705**
Xylophages	29	2	**18-**	**8+**	2	**59**

groups (Stork 1987b). Herbivores were significantly more abundant than expected on new leaves and flowers, reflecting higher abundances of Hemiptera, Coleoptera, and Thysanoptera on these microhabitats. Fungivorous Psocoptera, in contrast, were significantly less abundant than expected on new leaves, and higher than expected on dead wood and fruit. The ant guild was, of course, similar to the taxonomic analysis above, with slight differences due to the inclusion of Formicidae larvae. The results remained similar though, with higher than expected abundances of ants on the foliage and lower than expected abundances on flowers and dead wood. Predators, saprophages and tourists were all over-represented on mature foliage. Dead wood and fruit also supported higher than expected abundances of saprophagous invertebrates. Over-representation of invertebrates in the unknown feeding guild category on flowers were due to the high numbers of beetle and fly larvae of unspecified guilds collected from this microhabitat compared to the other microhabitats. Xylophages were rare, but were significantly more abundant on fruit, due to several scolytine weevils (Curculionidae: Scolytinae) collected from *Cryptocarya mackinnoniana* fruit.

4.4.2 Evenness across microhabitats

Evenness varied significantly between microhabitats for taxonomic groups ($F_{4, 68} = 21.45$, $P < 0.0001$). Pair-wise comparisons revealed that the flower-visiting invertebrate community was significantly less even than the mature leaf, new leaf, fruit and dead wood communities (Fig. 4.3a). The mature leaf inhabiting community was also significantly less even than dead wood community. There was no difference in the evenness of invertebrate taxonomic group abundances on any other combinations of microhabitats. At the level of

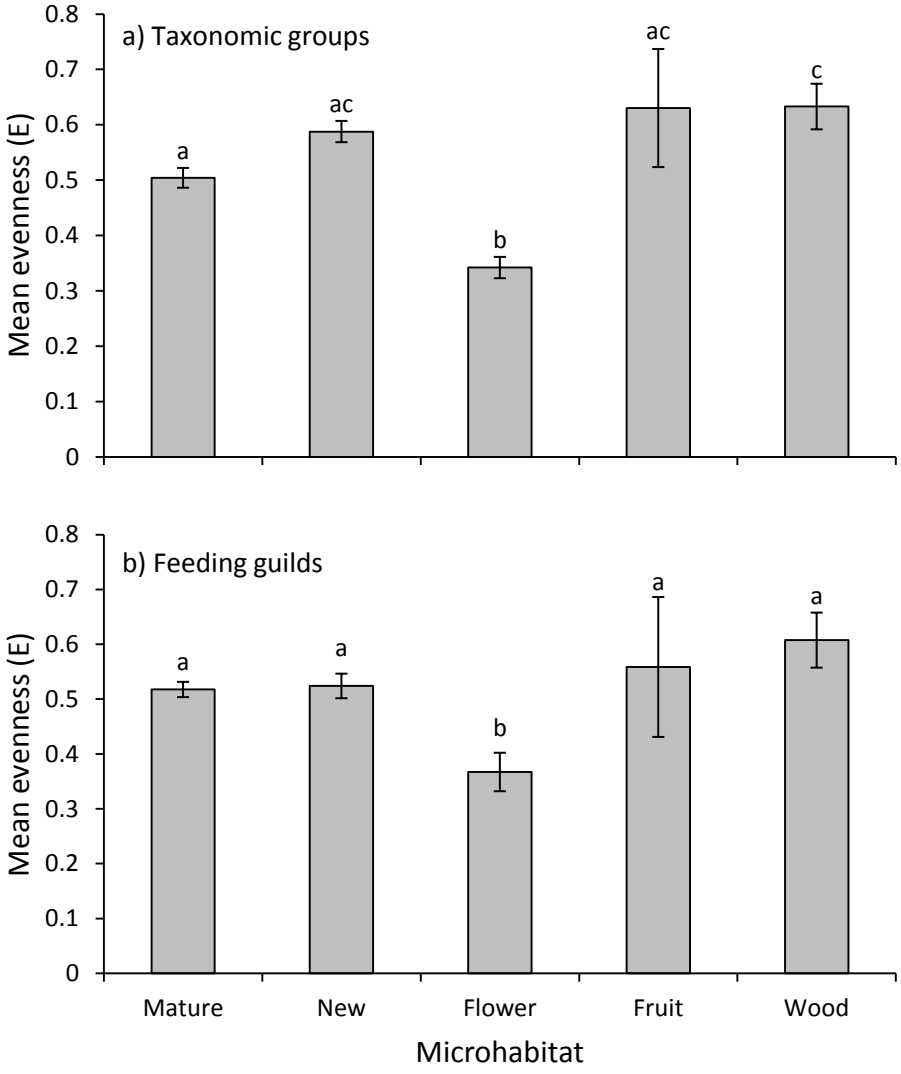

Figure 4.3: Mean evenness ($E \pm$ S.E.) for a) invertebrate taxonomic groups, and b) feeding guilds inhabiting mature leaves, new leaves, flowers, fruit and suspended dead wood. Higher numbers indicate more equitable (even) abundances across invertebrate taxa or feeding guilds, while lower numbers indicate increased heterogeneity in abundance within the microhabitat. Letters above the columns indicate significant differences in mean evenness scores.

feeding guild, evenness also varied significantly between microhabitats ($F_{4, 68} = 7.56$, $P < 0.0001$). As with the taxonomic groups, the flower-visiting invertebrate community was significantly less even in guild composition than the mature leaf, new leaf, fruit and dead wood invertebrate communities (Fig. 4.3b). There were no significant differences in the evenness of feeding guild abundances between any other combinations of microhabitats.

4.4.3 Uniformity across tree species

All 17 taxonomic groups analysed from flowers were non-uniformly distributed across tree species (Table 4.3). On mature leaves, only the Diptera and Hymenoptera were uniformly distributed across the 14 tree species examined. For the new leaf invertebrate fauna, lepidopteran caterpillars, Collembola, Diptera, Orthoptera and mesophyll feeding hemipteran nymphs were the only groups that were uniformly distributed across tree

Table 4.3: Tests of uniformity in the proportions of each taxonomic group across tree species for the invertebrates inhabiting mature leaves, new leaves and flowers. Each taxonomic group is tested against the sum of the remaining invertebrates using 2 x *k* contingency tables, where k is the number of tree species and d.f. = *k* – 1. Significant results indicate non-uniform distributions in proportional abundance.

Taxa	**Mature leaves**		**New leaves**		**Flowers**	
	X^2	*P*	X^2	*P*	X^2	*P*
Acari	453.42	<0.0001	95.17	<0.0001	5129.62	<0.0001
Ants	260.52	<0.0001	103.48	<0.0001	263.5	<0.0001
Blattodea	297.35	<0.0001	49.73	<0.0001	304.88	<0.0001
Caterpillars	80.37	<0.0001	18.99	ns	124.91	<0.0001
Cicadellidae nymph	64.86	<0.0001	88.16	<0.0001	52.1	<0.0001
Coleoptera	530.94	<0.0001	194.79	<0.0001	2268.37	<0.0001
Collembola	71.2	<0.0001	13.7	ns	41.99	<0.0001
Diptera	27.96	ns	16.03	ns	248.8	<0.0001
Hymenoptera	18.76	ns	16.67	<0.0001	225.84	<0.0001
Mesophyll	154.5	<0.0001	122.53	<0.0001	224.46	<0.0001
Mesophyll nymph	36.41	0.0005	25.9	ns	235.86	<0.0001
Orthoptera	32.91	0.0018	31.21	ns	34.6	0.001
Phloem	305.98	<0.0001	47.86	<0.0001	5828.15	<0.0001
Phloem nymph	129.74	<0.0001	360.06	<0.0001	3731.04	<0.0001
Psocoptera	180.14	<0.0001	33.8	0.001	97.48	<0.0001
Spiders	55.9	<0.0001	90.5	<0.0001	460.42	<0.0001
Thysanoptera	164.38	<0.0001	170.59	<0.0001	2398.9	<0.0001

species (Table 4.3). Among feeding guilds, ants, fungivores, herbivores, predators and saprophages were all non-uniformly distributed across tree species for the mature leaf, new leaf, and flower-visiting communities (Table 4.4). Tourists were uniformly distributed between tree species on mature and new leaves, but displayed a non-uniform distribution between tree species on flowers. Invertebrates within the unknown feeding guild were uniformly distributed across tree species on new leaves, but not on mature leaves or flowers.

Table 4.4: Tests of uniformity in the proportions of each feeding guild across tree species for the invertebrate communities inhabiting mature leaves, new leaves and flowers. Each feeding guild is tested against the sum of the individuals in the remaining feeding guilds using 2 x *k* contingency tables, where k is the number of tree species and d.f. = $k - 1$. Significant results indicate non-uniform distributions in proportional abundance.

Feeding guild	**Mature leaves**		**New leaves**		**Flowers**	
	X^2	*P*	X^2	*P*	X^2	*P*
Ants	303.21	<0.0001	122.72	<0.0001	253.85	<0.0001
Fungivores	116.09	<0.0001	35.34	0.0008	646.38	<0.0001
Herbivores	258.57	<0.0001	126.44	<0.0001	3556.58	<0.0001
Predators	262.69	<0.0001	112.36	<0.0001	2568.69	<0.0001
Saprophages	284.51	<0.0001	45.55	<0.0001	1181.35	<0.0001
Tourists	26.98	ns	15.05	ns	246.23	<0.0001
Unknown	46.98	<0.0001	12.21	ns	831.06	<0.0001

4.5 Discussion

My results support the hypothesis that the structure and abundance of invertebrate communities inhabiting different canopy microhabitats differ (e.g., Ødegaard 2000b, 2004; Condon *et al.* 2008). The dramatic differences in guild structure and taxonomic composition between microhabitats, between tree species, and within microhabitats between tree species that I report indicate that resource differentiation potentially has a very high role in determining the composition and functional diversity of the canopy invertebrate community. The data show that mature leaves support a more homogenous invertebrate community than new leaves or flowers. Indeed, the low density and broad range of invertebrates found on mature leaves suggests that many species may be transient

(Basset 1999a) and use the foliage, due to its ubiquity, as little more than a substrate on which to rest or hide. On the basis of these results, the relatively coarse approach of investigating invertebrate community structure using samples from entire trees (Erwin 1982; Moran & Southwood 1982; Stork 1987b, 1988; Moran *et al.* 1994; Marquis *et al.*, 2001; Charles & Basset 2005) does not appear capable of identifying subtleties of species habitat differentiation among microhabitats. Nor can samples using mature leaves alone (Basset & Arthington 1992; Basset 1999a, 2001a; Novotny & Basset 2000; Wagner 2000; Novotny *et al.* 2002a, b, 2004a, b, 2006) be considered reflective of the full complement, relative abundance, taxonomic composition or guild structure of the canopy invertebrate community as a whole. The composition of the invertebrate communities on different microhabitats suggests that biodiversity studies that focus on single microhabitats are only sampling a subset of the canopy assemblage.

4.5.1 Invertebrate assemblages on different microhabitats

The results support my hypothesis that variability in the composition of the invertebrate communities on different microhabitats likely reflects variation in resource availability and/or resource quality. For example, dead wood communities were characterised by high numbers of saprophagic and fungivorous invertebrates, while new leaves and flowers harboured high numbers of herbivores. These respective assemblages reflect concentrations of particular taxa on specialised food resources (Basset 2001a; Grove 2002a). The flowers especially attracted a specialised fauna, with particular taxonomic groups (Coleoptera, Thysanoptera, Acari) dominating the communities on this microhabitat. Equally, the identities of the taxa that are under-represented on particular resources also indicate differences in abundance based on the availability of food resources. For example, fungivorous Psocoptera were under-represented on flowers and

new leaves, which, due to their rapid growth and short temporal availability, are unlikely to support significant fungal growth. Spiders were also under-represented on flowers, but over-represented on mature and new leaves, and dead wood. However, while spiders comprise a large proportion of the foliage invertebrate community, in terms of invertebrate biomass, spiders constituted an equal or greater proportion of the invertebrate community on flowers than on any other microhabitat (Fig. 4.3a-f). Relative differences in abundance therefore may be nullified by relative differences in body size on different microhabitats.

Perhaps the most notable discrepancy was in the relative abundances of Formicidae between microhabitats. Ants are a ubiquitous part of the canopy community in tropical rainforests, often dominating all other invertebrate groups in terms of abundance, biomass, and community structure (Stork 1987b; Basset *et al.* 1992; Krüger & McGavin 1998; Simon & Linsenmair 2001; Floren *et al.* 2002; Dial *et al.* 2006). In my samples ants were predominantly foliage-inhabiting, with few individuals collected from flowers or dead wood. Although ants constitute a relatively high proportion of the biomass of invertebrates on flowers, these were mostly large-bodied green weaver ants, *Oecophylla smaragdina* (Fabricius), that were rarely observed carrying away invertebrate prey. Indeed, *O. smaragdina*, is the dominant ant species feeding on honeydew and extra-floral nectar sources at this site (Blüthgen *et al.* 2003), indicating that it derives a substantial amount of its nourishment from sources other than predation. However, the lack of ants, especially smaller species, attending high concentrations of potential invertebrate prey lends further support to the hypothesis that tropical arboreal ants are predominantly herbivorous, feeding on hemipteran honeydew or extra-floral nectar (Itino & Yamane 1995; Davidson 1997; Blüthgen & Reifenrath 2003; Blüthgen *et al.* 2003; Davidson *et al.* 2003). Furthermore, like the ants, most hemipteran groups were most abundant on foliage, particularly on new leaves, and less abundant on other microhabitats. Densities of ants were not however,

correlated with the density of Hemiptera on individual plant species, although higher densities of ants were recorded on plant species with extra-floral nectaries (unpublished data). But it should be noted that many Hemiptera tended by ants may not be recorded as they may be firmly attached to the host plant via their sucking mouthparts.

Why ants do not commonly feed on floral nectar or other flower resources (including the flower visitors), is not fully understood (see Beattie *et al.* 1984). There is some evidence that flowers exhibit chemical repellents or structural obstacles that act as deterrents to foraging ants (Feinsinger & Swarm 1978; Ghazoul 2001; Junker *et al.* 2008; Willmer *et al.* 2009). For example, ants may be particularly vulnerable to floral defensive volatiles, due to the widespread use of chemical scents among these social insects (Ghazoul 2001; Willmer *et al.* 2009). These same volatiles can also be used by other insects to locate flowers (Junker & Blüthgen 2010), which may explain why flowers can attract a wide spectrum of insect visitors, while repelling ants (Raguso 2008; Junker *et al.* 2010).

Herbivores in this study were over-represented on new leaves and under-represented on mature leaves. Previous studies have also noted that many insect folivores prefer young leaves over mature ones (Basset 2001a), and young leaves typically support much greater numbers of herbivorous insects (Lowman 1985; Basset 1991a, 1999a; Price *et al.* 1995; Steinbauer *et al.* 1998; Barone 2000; Marquis *et al.* 2001; Itioka & Yamauti 2004). This is because young leaves are not as tough (Coley 1983; Aide & Londoño 1989; Sagers & Coley 1995) and typically contain higher concentrations of available nitrogen (Mattson 1980; Aide & Londoño 1989; Basset 1991a; Merritt 1996) than older leaves. In support of this, most life time herbivore damage in tropical rainforests usually occurs during leaf expansion (Coley 1980, 1983; Aide 1993). Mature leaves, in contrast, support a wide range of orders and feeding guilds that often form loose communities that are not

well defined (Basset 1992c). My samples included higher than expected numbers of predators, saprophages, and tourists. These species are unlikely to feed directly on foliage and the exact reason for over-representation of these taxa on this microhabitat is unknown. One possible suggestion is that the vast quantity of mature leaves in the canopy act as locations for rest or refuge rather than as a food resource (Jermy 1984). Indeed, when expressed on a per unit biomass basis, invertebrates are found in very low densities on mature leaves (Chapter 3), further highlighting the possibility that recorded occurrences on mature leaves reflects the large proportional contribution to total canopy biomass this microhabitat represents, rather than active habitat differentiation on particular resources.

4.5.2 Variation in abundance between microhabitats and tree species

Heterogeneity in abundance patterns were significantly higher among the flower-visiting community compared to the foliage communities, both within and between tree species. Flowers attracted very high abundances of particular taxa (e.g., Coleoptera, Thysanoptera) and relatively low abundances of most other groups, which may explain why flower-visiting invertebrate communities were distinctly uneven in proportional abundances. Foliage samples in contrast, were not dominated to the same extent by high abundances of particular taxa, but generally consisted of relatively low abundances of most taxonomic groups, reducing the differences in population size (and thus proportional abundance) between each taxon. The greater heterogeneity in the abundances of invertebrate communities visiting flowers compared to leaves shows that flowers are intensively utilised by a subset of the canopy fauna, while leaves are utilised by a broader spectrum of visitors, many of which are unlikely to use leaves directly as a food source.

Moran and Southwood (1982) and Stork (1987b) showed that, at the level of species most arthropod guilds sampled by insecticide fogging were uniformly distributed

across tree species and that these proportions were remarkably similar between temperate and tropical trees. In contrast they found that for individuals, no invertebrate feeding guilds were uniformly distributed between host plants. As my samples were not sorted to species, I was unable to compare between-tree uniformity in the proportional number of species within each guild. But at the level of individuals, most feeding guilds and taxonomic groups in my samples were also non-uniformly distributed, corroborating these previous findings. However, Moran and Southwood (1982) and Stork (1987b) sampled entire trees using insecticide knockdown, which precluded comparisons between discrete canopy microhabitats. In my discrete samples, 2/17 and 5/17 taxonomic groups on mature and new leaves respectively were uniformly distributed between host tree species. Three of these groups, Collembola, Diptera, and Hymenoptera are unlikely to be feeding directly on the foliage. The remaining three groups that were uniformly distributed on new leaves are all herbivorous taxa: lepidopteran caterpillars, mesophyll feeding hemipteran nymphs and Orthoptera.

For feeding guilds, only tourists were uniformly distributed across tree species on mature and new leaves, while those invertebrates whose feeding guild could not be determined (unknown) were also uniformly distributed on new leaves. It is not unexpected that tourists should display a uniform distribution, since they are not associated with the host tree, but are simply collected by chance. The fact that tourists were not uniformly distributed across tree species on flowers may be due to the miss-assignment of species in this feeding guild for flowers. For example, although most, if not all, Diptera on the foliage are tourists, it is likely that many flies visiting flowers were doing so to feed and should thus have been included in another category.

Flower-visiting invertebrate communities lacked any uniformity in abundance across tree species for any taxonomic group or feeding guild. For some groups and guilds,

particular host plant species harboured very high numbers of individuals, while other host trees supported very low abundances. For example, *Argyrodendron peralatum* flowers supported a very high abundance of a specialist species of phloem feeding Psyllidae, resulting in high heterogeneity in abundance across all of the sampled trees. A similar situation occurred on flowers between host plant species for beetles, mites and thrips, where some tree species supported very high relative abundances of these taxa while other trees supported low relative abundances.

This study represents the first quantification of microhabitat differentiation in invertebrate community structure in a tropical rainforest canopy. The variation between microhabitats in invertebrate guild composition, abundance and biomass patterns I report have wide ranging implications, especially for those working in hyper-diverse, complex tropical rainforests. In particular, studies on the structure of invertebrate communities based only on samples taken from the leaves may contain substantial errors due to the inapplicability of the mature leaf community to the wider canopy community. The incorporation of multiple microhabitats in future canopy invertebrate biodiversity studies is likely to reveal a more accurate description of canopy invertebrate community structure and dynamics.

Chapter 5:

Variation in beetle community structure across five microhabitats in Australian tropical rainforest trees

Chapter 5: Variation in beetle community structure across five microhabitats in Australian tropical rainforest trees[4]

5.1 Abstract

Beetles (Coleoptera) are the most species rich and ecologically diverse group of organisms in tropical rainforest canopies. This study reports on the distribution of the beetle community on five discrete canopy microhabitats (mature leaves, new leaves, flowers, fruit, and suspended dead wood) on 23 tree species in an Australian tropical rainforest. Since these microhabitats vary in quantity, quality as a food resource, and availability, it was hypothesised that the beetle fauna would also vary in community structure. There was substantial variation in dominant beetle families in terms of species richness, abundance, and biomass between microhabitats. High dissimilarity in species overlap between microhabitats suggests that each microhabitat attracts a unique beetle assemblage which has an additive effect on canopy-wide species richness patterns. All communities were dominated by high numbers of rare species, with flowers supporting most of the more abundant species. Consequently, the flower-visitor community was more heterogeneous than the communities inhabiting the leaves or dead wood. The distribution of singletons was also non-random where flowers, which are spatially and temporally restricted, supported fewer singletons than expected by chance, while mature leaves and dead wood supported more. These differences were most likely related to variation in microhabitat distribution and availability, which influenced relative sampling efforts and the probability of random microhabitat/beetle associations. My results demonstrate that the structure of beetle communities, in terms of species composition and abundance patterns, varies

[4] This chapter has been published (22 Aug 2012) with little modification as a multi-authored paper in *Insect Conservation and Diversity* (Wardhaugh, C. W., Edwards, W., Stork, N. E., 2012: Variation in beetle community structure across five microhabitats in Australian tropical rainforest trees. *Insect Conservation and Diversity* 6: 463-472).

substantially between microhabitats in a tropical rainforest canopy. Consequently, biodiversity studies which focus on single microhabitats may inadvertently omit a large proportion of canopy species.

5.2 Introduction

Beetles are the most species rich group of organisms on Earth, with approximately one in five species belonging to the order Coleoptera (Hammond 1994). The ecological diversity of beetles is also unparalleled among insects, with beetles occupying almost every feeding guild and exploiting almost every terrestrial organic resource (Grove & Stork 2000). High species richness coupled with high functional diversity means that beetles are an ideal group to study community structure and distribution patterns. Beetle diversity peaks in tropical rainforests, and a large proportion of species utilise the diverse resources available in the canopy (Stork & Grimbacher 2006). The level of diversity in tropical rainforests is so great, and our knowledge so poor, that heated debate on the estimated number of beetle species in these forest canopies has continued unabated for 30 years (Erwin 1982; Gaston 1991; Ødegaard 2000a; Novotny *et al.* 2002a; Stork & Grimbacher 2006).

At the root of our problems deciphering species richness in arboreal environments is a lack of understanding regarding the distribution of insect species (Novotny *et al.* 2010). For most species, we do not know the identity of the canopy resources, if any, that they utilise (Stork 1987b). To date species abundance patterns have principally been assessed from collections made from single microhabitats, such as leaves (Basset & Kitching 1991; Basset 1992a, c, 1996; Novotny & Basset 2000; Novotny *et al.* 2002a), entire tree crowns (Erwin 1982; Hammond *et al.* 1996; Wagner 2000), or from activity-based trapping techniques (Stork & Grimbacher 2006; Grimbacher & Stork 2007, 2009a). Using indiscriminate trapping and collection techniques, such as insecticide fogging or

activity based traps, the most that can be concluded in many cases is an "association" between a particular insect species and its host tree. However, data from such methods give little indication of within tree variation in the distribution of species or individuals, which has important implications for species interactions and food web analyses (Novotny *et al.* 2010).

Based on studies of single microhabitats and entire tree crowns, tropical rainforest beetle communities are characterised by high numbers of rare species (Price *et al.* 1995; Wagner 2000; Coddington *et al.* 2009), and singletons (species recorded just once in collections) often make up >50% of species in even very large collections (Floren & Linsenmair 1998; Novotny & Basset 2000; Lucky *et al.* 2002). There are two broad reasons for finding high numbers of singletons: 1) sampling issues (Magurran 2005; Coddington *et al.* 2009), and 2) species rarity (Novotny & Basset 2000). Sampling issues include accumulating tourist species (i.e., species that are not associated with the host tree or microhabitat under investigation) and under sampling due to insufficient temporal and spatial replicates. Indeed, under sampling is perhaps the main reason why tropical invertebrate communities have been shown to be skewed heavily towards a high proportion of rare species (Magurran 2005; Coddington *et al.* 2009). However, some species may be rare in a collection because they occur naturally at very low densities on the tree species sampled. Usually this would be because the tree species sampled are marginal hosts or rarely utilised, while higher abundances would be recorded if optimal host species or habitats had been included in the sampling protocol (Novotny *et al.* 2004b). These issues are compounded in tropical rainforests, since the local diversity of host trees is usually much greater than the number of trees that can realistically be sampled (Novotny & Basset 2000). Distinguishing species that occur naturally at very low densities from those that

were missed due to insufficient sampling effort is therefore impossible without dramatically increasing sampling effort (Magurran 2005; Coddington *et al.* 2009).

While increasing the temporal and spatial scale of sampling efforts may ultimately reduce the number of species in a particular area that could be considered rare, the fact remains that insect communities within single trees or groups of trees at any point in time are comprised of a large number of rare species (Price *et al.* 1995; Novotny & Basset 2000). Therefore, the preponderance of rare species in rainforest canopies is a real phenomenon, at least at scales sufficiently small for most interspecific interactions to occur. Rather than ignore rare species, we need to incorporate them in analyses of community structure and distribution patterns (Novotny & Basset 2000). However, community diversity patterns that include large numbers of rare species pose a number of statistical problems, and interpretations or extrapolations from these communities are difficult (Vandermeer 1982; Mao & Colwell 2005). Indeed, it is very difficult to infer anything of the host specificity, seasonality, diel activity, population dynamics or distribution of a species that was collected only once. But this should not preclude rare species from analyses of species abundance patterns or guild structure.

Despite the lack of studies that have examined the abundance patterns of insect communities between microhabitats, variation in abundance patterns should be expected since each microhabitat varies in many structural, nutritional, and defensive characteristics. In this study, I tested the hypothesis that different microhabitats vary in species richness, abundance and biomass patterns by examining the abundance distribution of beetles on five canopy microhabitats; mature leaves, new leaves, flowers, fruit, and suspended dead wood, from 23 species of rainforest plants. To address rear speces directly, the distribution of singletons among microhabitats was also investigated. Since mature leaves comprise most of the biomass of tree crowns, and the other microhabitats are temporally and

spatially restricted (Chapter 3), mature leaves were relatively poorly sampled. It was hypothesised then that singletons comprise a greater proportion of species on mature leaves compared to the other microhabitats.

5.3 Methods

5.3.1 Study site

For study site description see Chapter 3, 3.3.1.

5.3.2 Sampling

For sampling procedures see Chapter 3, 3.3.2.

5.3.3 Statistical analyses

Species accumulation curves were calculated for the beetle communities inhabiting each microhabitat, as well as the entire pooled beetle assemblage using EstimateS (version 8.2, Colwell 2009). Cluster analysis was used to represent similarity patterns in beetle species composition between different microhabitats (Bray-Curtis similarity measures based on Log_{10} transformed abundance data). Evenness in the proportional abundances of species within microhabitats was measured using the Evenness index (E) of Bulla (1994). For details on the methodology of evenness calculations see Chapter 4, 4.3.4. Differences in mean evenness between microhabitats was explored with ANOVA. Where significant differences were detected, post-hoc pair-wise comparisons between microhabitats were performed using Tukey tests. Significant outcomes in these tests would reveal between-microhabitat variation in species abundance patterns. Conversely, non-significant outcomes are expected when variation in proportional abundances of species are similar on both microhabitats.

5.3.4 The distribution of singletons

A simple randomisation procedure was carried out that calculated the expected number of unique singletons (species collected just once in the pooled sample) that would be expected to be found on a particular microhabitat if unique singletons were randomly distributed across microhabitats. For technical details on the randomisation procedure and tests of significance see Chapter 4, 4.3.4.

The number of habitat singletons (species that were collected just once on a particular microhabitat but were also collected from other microhabitats) on each microhabitat was also examined. Unlike unique singletons, which may simply be very rare species associated with the microhabitat in question, habitat singletons are probably mostly transient species that are associated with another focal microhabitat. However, the number of habitat singletons on a particular microhabitat can be informative. For example, low numbers of habitat singletons could indicate active avoidance. In contrast, a high number of habitat singletons could be the result of colonisation by a large number of widely dispersed, opportunistic or generalist species that otherwise cannot effectively locate or aggregate on that microhabitat.

To test for the over- or under-representation of habitat singletons on each microhabitat, a similar randomisation procedure as that described in Chapter 4 (4.3.4) and above for unique singletons was undertaken. The output of this procedure generated a frequency distribution of the expected number of species with total $n \geq 2$ that would be recorded just once on each microhabitat. Significant over- and under-representation of habitat singletons on each microhabitat were tested using the same procedures as described above for unique singletons. Numbers of habitat singletons that do not differ from random

indicate that these species are a random selection of species spilling over from other microhabitats.

5.4 Results

5.4.1 Beetle distribution patterns

Overall 10,335 beetles were collected from 372 species (Table 5.1). The most species rich families were Curculionidae (111 species, or 30% of the total), Chrysomelidae (32, 9%), Coccinellidae (24, 6%), Nitidulidae (20, 5%) and Phalacridae (19, 5%) (Fig. 5.1a), while the most abundant families were Curculionidae (4,658 individuals, or 45% of the total), Staphylinidae (1,677, 16%), Nitidulidae (933, 9%), Chrysomelidae (857, 8%), and Coccinellidae (456, 4%) (Fig. 5.2a). In terms of biomass, the highly abundant

Table 5.1: The number of species, individuals and total biomass (mg) of each beetle family in the pooled sample.

Family	Spp.	Ind.	Biomass	Family	Spp.	Ind.	Biomass
Carabidae	2	3	11	Languriidae	4	93	29.7
Hydrophilidae	2	3	2.1	Coccinellidae	24	456	166.9
Ptiliidae	2	3	0.01	Corylophidae	15	436	18.2
Leiodidae	1	1	0.16	Latridiidae	2	140	6.9
Staphylinidae	17	1677	231.5	Mycetophagidae	1	28	4
Scirtidae	3	4	0.89	Ciidae	1	1	0.09
Scarabaeidae	7	38	1334	Mordellidae	3	13	5.9
Buprestidae	2	2	0.64	Rhipiphoridae	2	7	67.3
Psephenidae	1	1	0.59	Zopheridae	3	6	2.2
Elateridae	9	27	52.4	Tenebrionidae	7	9	294
Cantharidae	1	19	7.8	Salpingidae	2	2	0.2
Dermestidae	6	22	8	Anthicidae	1	2	0.67
Anobiidae	4	10	1.3	Aderidae	7	20	1.8
Cleridae	2	22	5.7	Scraptiidae	1	6	0.98
Melyridae	11	68	92.9	Cerambycidae	14	20	393.8
Nitidulidae	20	933	160.2	Chrysomelidae	32	857	361.3
Monotomidae	3	7	1.4	Anthribidae	12	41	17.8
Boganiidae	2	4	0.7	Attelabidae	1	1	0.37
Silvanidae	2	442	54.4	Brentidae	7	35	273.2
Laemophloeidae	1	2	0.21	Curculionidae	117	4658	4295.8
Phalacridae	19	216	31.9				

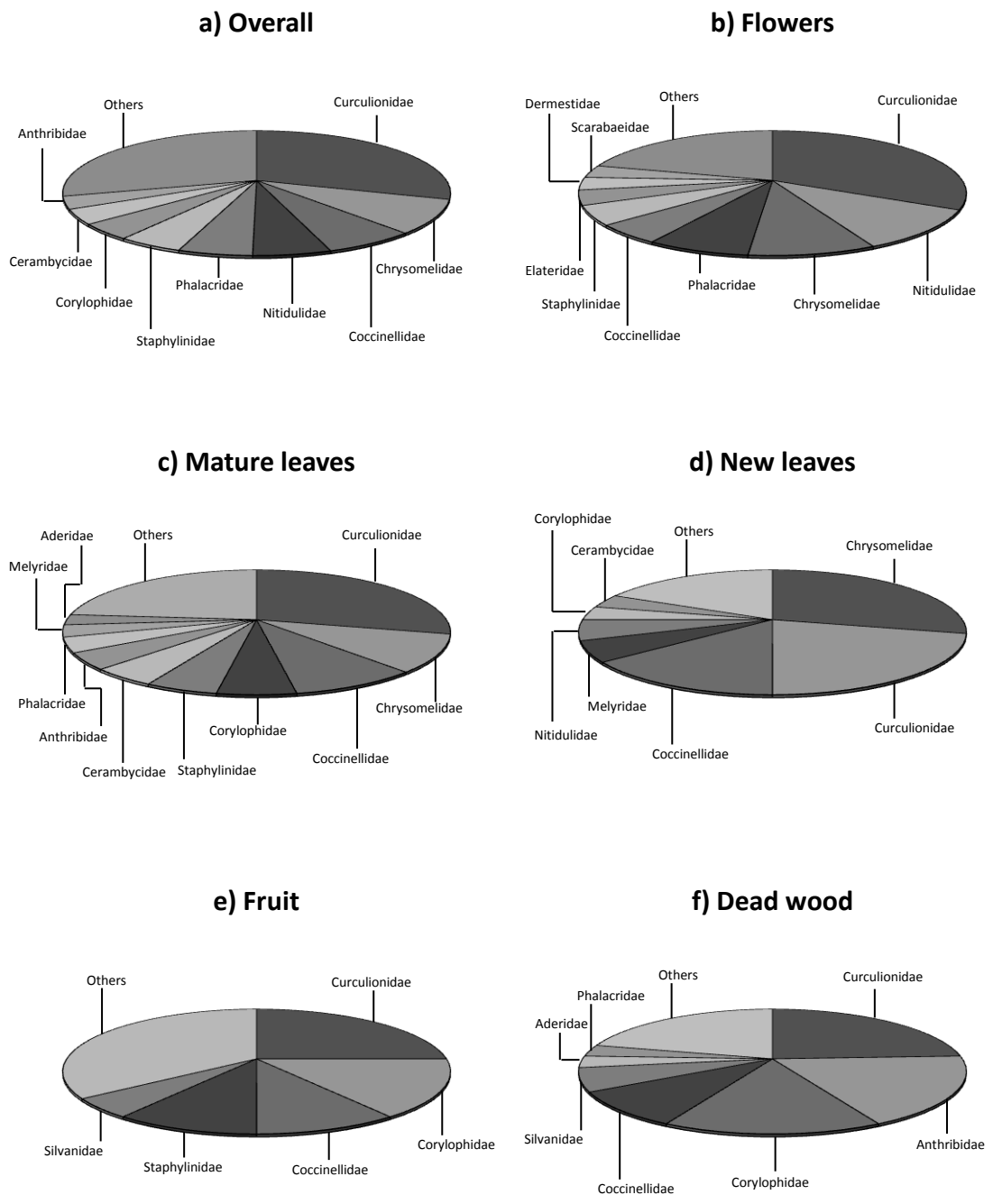

Figure 5.1: The proportion of beetle species belonging to the most species rich families in a) the entire pooled sample, and for each microhabitat; b) flowers, c) mature leaves, d) new leaves, e) fruit, and f) dead wood.

Curculionidae dominated, but relatively rare families that include many large bodied species, such as Scarabaeidae, Cerambycidae, Tenebrionidae and Brentidae, also made substantial contributions to overall biomass (Fig. 5.3a).

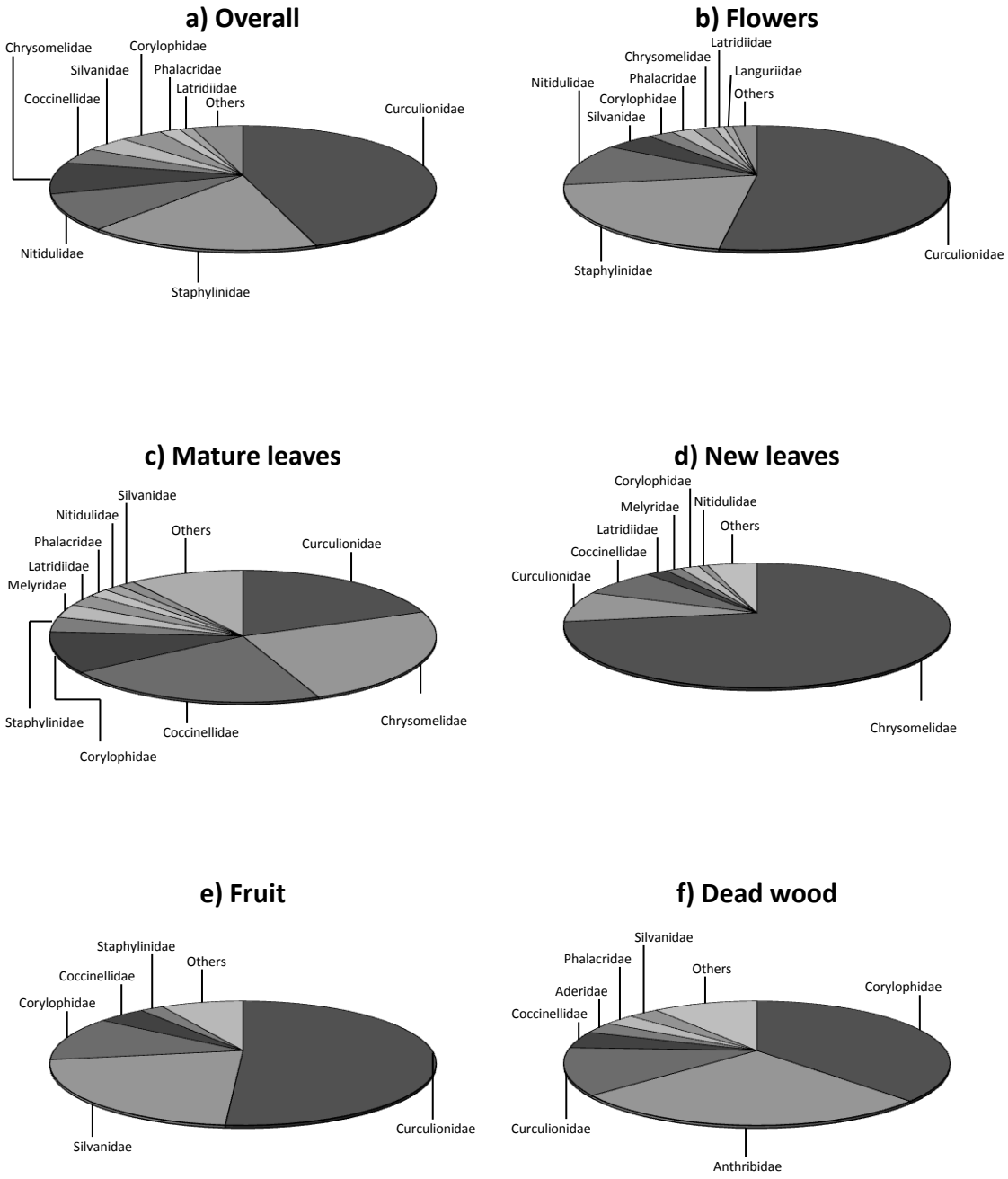

Figure 5.2: The proportional abundances of the most abundant beetle families in a) the entire pooled sample, and for each microhabitat; b) flowers, c) mature leaves, d) new leaves, e) fruit, and f) dead wood.

There was considerable variation in the identities of the most species rich families on each microhabitat. On mature and new leaves, Curculionidae, Chrysomelidae and Coccinellidae (Fig. 5.1c, d) contained the largest number of species, whereas flowers also supported many species of Nitidulidae and Phalacridae (Fig. 5.1b). Fruit and dead wood

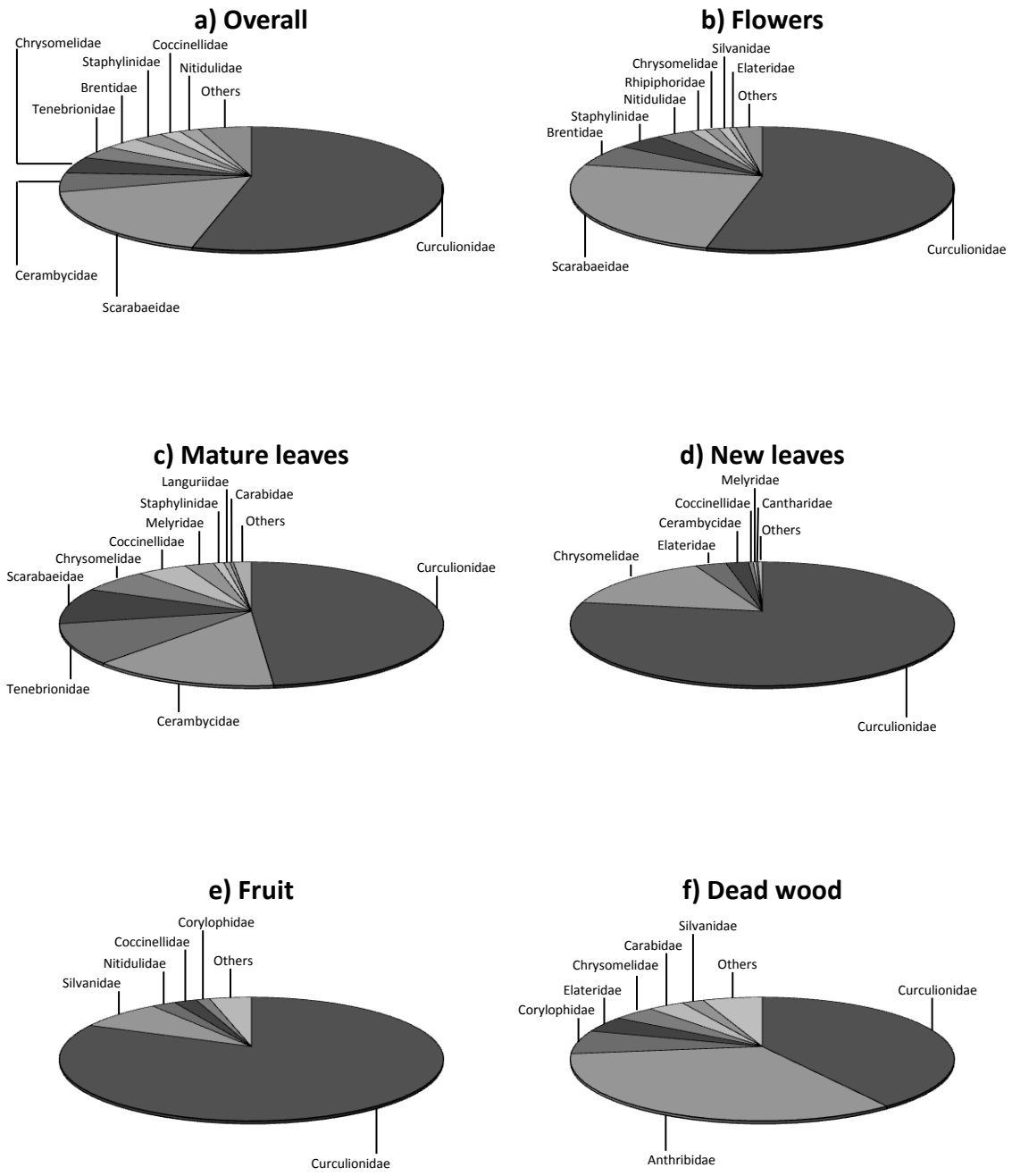

Figure 5.3: The proportional biomass of the beetle families that contributed the greatest proportions to total community biomass in a) the entire pooled sample, and on each microhabitat; b) flowers, c) mature leaves, d) new leaves, e) fruit, and f) dead wood.

communities were utilised by many species of fungivorous Corylophidae and Anthribidae respectively. Relative abundances of families differed markedly from the relative species richness of families on flowers, where Curculionidae and Staphylinidae were disproportionately abundant (Fig. 5.2b). On new leaves, Chrysomelidae dominated in

terms of the number of individuals within the community (Fig. 5.2d). Dead wood habitats in contrast were dominated by high abundances of Corylophidae and Anthribidae (Fig. 5.2f). Community dominance patterns change once again when the contribution of each beetle family to community biomass is examined. New leaves, which were numerically dominated by Chrysomelidae, are dominated by Curculionidae in terms of biomass. Several large bodied species from the families Scarabaeidae and Brentidae on flowers, and Cerambycidae and Tenebrionidae on mature leaves, increase the contribution of these otherwise rare families to the total biomass of beetles on these microhabitats (Fig. 5.3b, c).

The dendrogram in Figure 5.4 shows that different microhabitats are very dissimilar in species composition (Fig. 5.4), with only mature and new leaf beetle communities showing any noticeable similarity. The species accumulation curves in Figure 5.5 did not reach asymptotes for any microhabitats or for the total pooled sample, indicating that the assemblages associated with each microhabitat have not been exhaustively sampled. Species abundance distributions were skewed towards rare species (Fig. 5.6a-f), where most species on each microhabitat were collected in small numbers. Only on flowers were

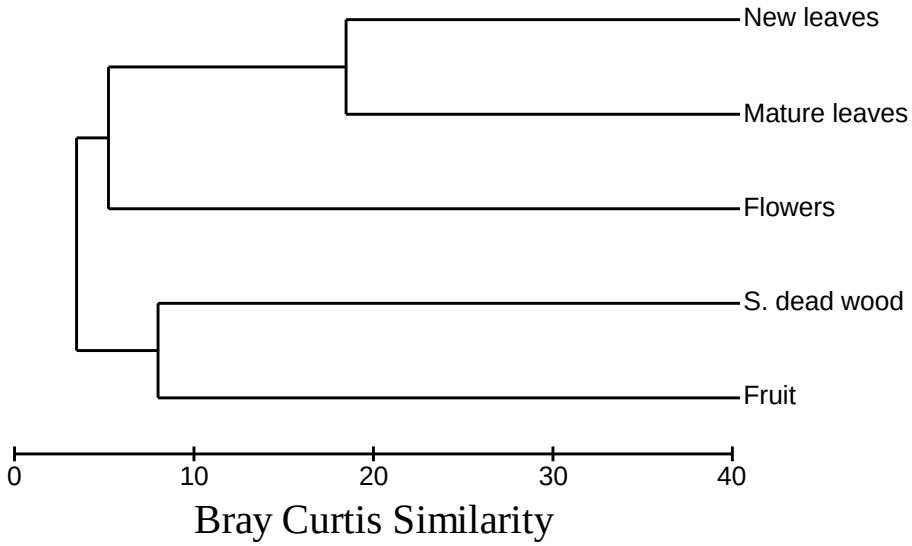

Figure 5.4: Dendrogram representing results of a cluster analysis of beetle community composition showing the Bray Curtis similarity among the five microhabitats sampled.

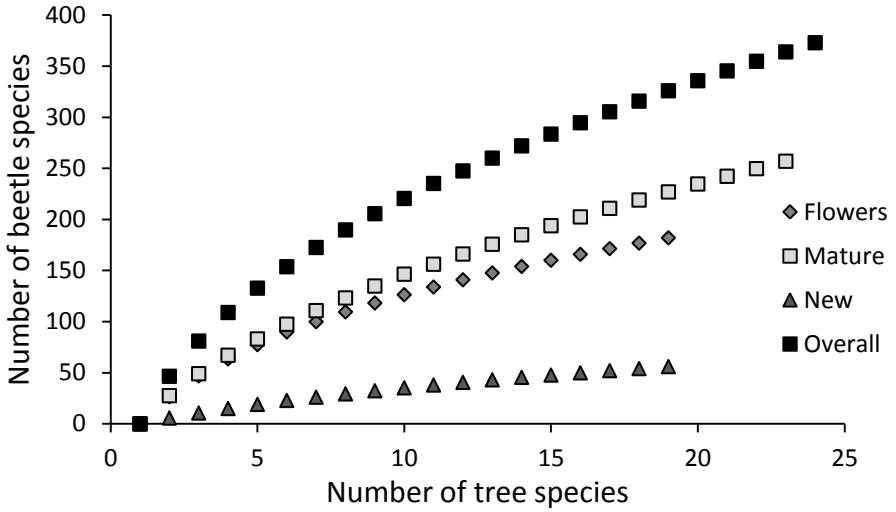

Figure 5.5: Species accumulation curves (Sobs – Mao Tau) of beetle species associated with mature leaves, new leaves, and flowers, as well as for the pooled sample including fruit and dead wood beetles. Separate accumulation curves for fruit and dead wood communities were omitted for the sake of clarity and because few species were collected from these microhabitats.

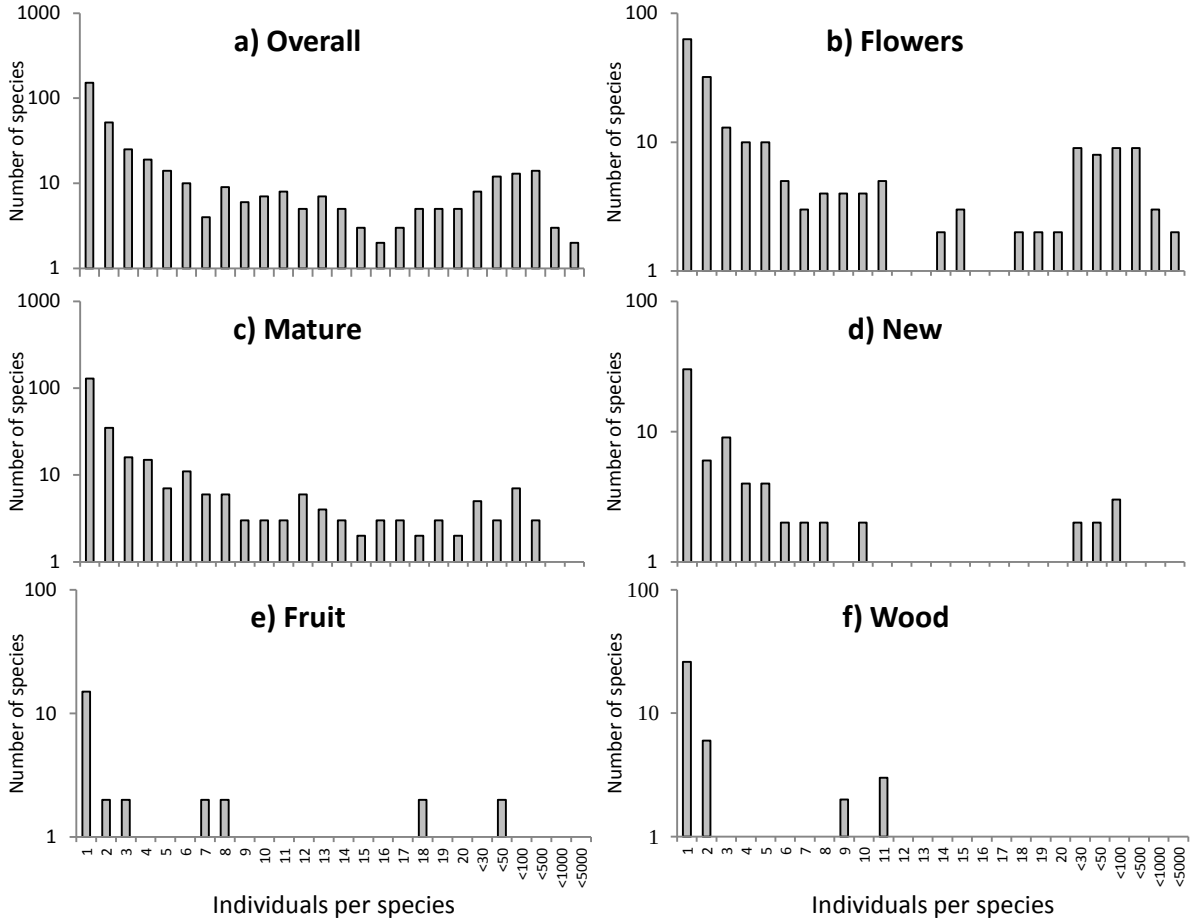

Figure 5.6: Species abundance distribution of beetles in the a) overall pooled sample, and on each microhabitat; b) flowers, c) mature leaves, d) new leaves, e) fruit, and f) dead wood. Note that at higher abundances (>20 individuals), abundance categories are used for the sake of clarity. Also note that the data on the y axis are presented on a log scale.

there a relatively large number of abundant species (>20 individuals), with a few species collected in very high abundances (>500 individuals) (Fig. 5.6b). Mean evenness varied significantly between microhabitats ($F_{4, 58} = 9.24$, $P < 0.0001$). The very abundant species on flowers increased heterogeneity, where evenness in the proportional abundances of beetle species was significantly lower for the flower-visiting community compared to the mature leaf, new leaf, and dead wood communities (Fig. 5.7). There were no significant differences in evenness between any other combinations of microhabitats.

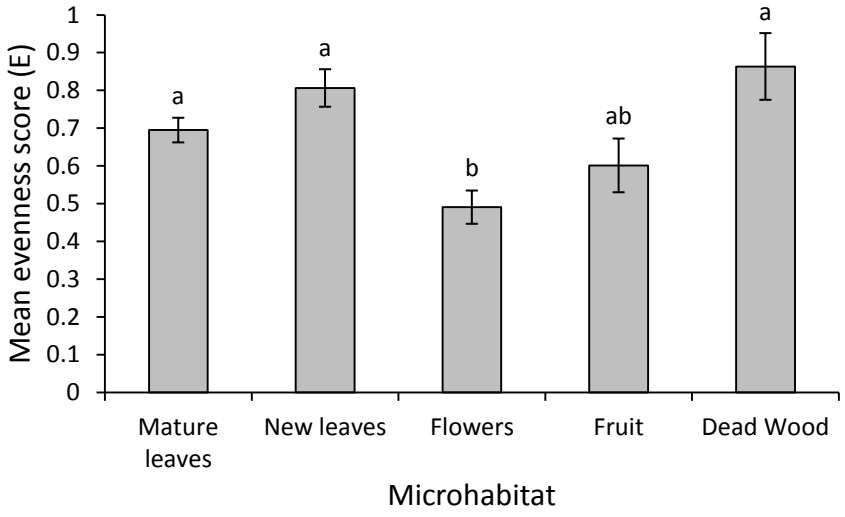

Figure 5.7: Mean evenness (± S.E.) in species abundance distributions on each microhabitat. *E* ranges between 0 and 1, with higher numbers indicating greater evenness in proportional abundances, and lower numbers indicating greater variation in proportional abundances, of species or individuals across feeding guilds. Letters above columns indicate significant differences between microhabitats in mean evenness.

5.4.2 Singletons

The number of unique singletons was not randomly or evenly distributed among the microhabitats sampled ($X^2 = 28.41$, df = 4, $P < 0.0001$). Mature leaves and dead wood supported significantly higher numbers of unique singletons (37.4% and 33.3% of species respectively) than would be expected under randomness, while flowers (18.7%) supported

significantly fewer unique singletons than expected (Fig. 5.8). The number of unique singletons on fruit (10%) and new leaves (14.3%) did not differ from random expectation.

The number of habitat singletons also differed significantly between microhabitats (X^2 = 53.33, df = 4, P <0.0001) (Fig. 5.8). A large percentage of the species collected from new leaves (37.5%), fruit (60%) and dead wood (42.4%) were collected once on these habitats, but also on other microhabitats. However, the number of habitat singletons found on dead wood did not differ from random expectation, while the number of habitat singletons was significantly less than expected on new leaves (P = 0.002) and fruit (P = 0.04). The number of habitat singletons collected from mature leaves was also significantly less than expected (P < 0.001), while the number collected from flowers did not differ from random expectation.

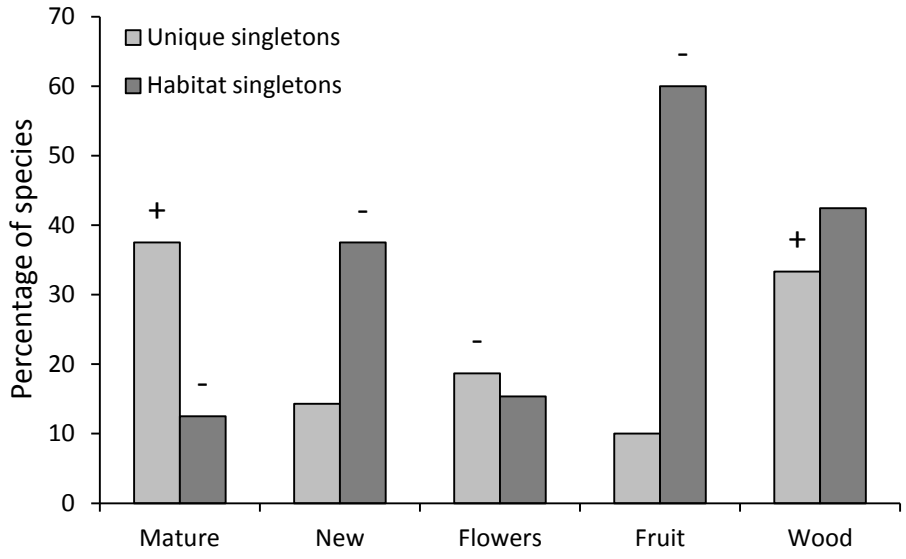

Figure 5.8: The percentage of the total number of beetle species on each microhabitat that were represented by single individuals in the entire collection (unique singletons) and single individuals on each microhabitat, but also recorded on other microhabitats (habitat singletons). + and – signs above columns indicate instances where significantly more or less unique or habitat singletons were collected than were expected by chance. Columns with no adjoining signs indicate instances where the number of singletons did not differ from random.

5.5 Discussion

Each canopy microhabitat supported unique beetle assemblages and were characterised by different beetle families that dominated their respective communities in terms of species richness, abundance and biomass. Although proportional species richness of beetle families was similar between mature leaves and the overall pooled sample (Fig. 5.1a, c), species overlap between microhabitats was very low (Fig. 5.4), indicating that few species are insensitive to microhabitat identity. The hypothesis that different microhabitats support their own distinctive beetle assemblages is therefore accepted. Furthermore, these results indicate that the mature leaf community is not representative of other canopy microhabitats in beetle community structure, especially in the distribution of the abundance and biomass of arboreal beetle families.

The abundance distribution of beetle species was similar on every microhabitat, in that rare species constituted the majority of species. The major difference was in the distribution of the very abundant species, which were predominantly found on flowers. This was largely a product of sampling effort. Flowers make up just 0.06% of crown biomass and support very large congregations of beetles (see Chapter 3). Flower-visiting species therefore, were relatively well sampled due to their highly clumped distribution. Foliage-inhabiting species in contrast, are spread over the remaining 99% of the canopy, such that the leaves need to be exhaustively sampled to collect any species in high abundances (Coddington *et al.* 2009). To illustrate this difference, nearly 1.2 tonnes of mature leaves were sampled in this study, yielding 1,823 beetles, compared to just over four kilograms of flowers, which produced 8,043 beetles. At this rate, one kilogram of flowers supports as many beetles as 1.25 tonnes of mature foliage. The low number of singletons collected combined with a relatively high sampling effort on flowers provides support for the hypothesis that the proportion of singletons decreases with increasing

sampling effort. However, the species accumulation curve for flower-visitors did not reach an asymptote, and the Chao 1 biodiversity measure estimated that an additional 41-83 species of beetles should be found on the flowers of the sampled tree species (Chapter 3). Therefore, as sampling intensity is increased, a reduction in the proportion of singletons may occur well before most species in the community are sampled.

A further, but not mutually exclusive, explanation for the low number of unique singletons collected from flowers is the distribution of floral resources in the rainforest canopy and the identities of many singletons. The accumulation of singletons on the foliage of host trees has been attributed to a 'mass effect' (Shmida & Wilson 1985; Novotny & Basset 2000), whereby the number of rare species on a particular host tree is inflated by the random influx of species associated with neighbouring tree species. In support of this effect on leaves, a high proportion of singletons on foliage in previous studies have been identified as tourists, and even if they are herbivorous, these species do not feed on the host tree under investigation (Basset 1997). While a mass effect may explain the higher than expected number of unique singletons on mature foliage (due to its large biomass), the isolated distribution of flowers means that congregations of genuine host associated flower-visiting species are common, while the accumulation of large numbers of tourist singletons through a random mass effect is unlikely since they occur at extremely low densities.

However, there is some evidence of a mass effect between microhabitats in this study. Mature leaves appear to be the source of most habitat singletons on other microhabitats, since they supported individuals from the majority (64/75, or 85.3%) of species identified as habitat singletons on all the other microhabitats. In turn, the lower than expected numbers of habitat singletons on mature leaves suggests there is little influx from the other focal microhabitats onto mature foliage. The disparity in microhabitat

biomass may explain the uneven exchange of transient species observed between mature leaves and the other microhabitats. As explained above, microhabitats with lower overall total biomass (such as flowers), were more thoroughly sampled, resulting in a higher capture rate of transient species from mature leaves, which is the dominant surrounding microhabitat.

Previous studies have also examined other characteristics of singletons in an attempt to ascertain whether singletons differ in predictable ways from more abundant species in the community (Novotny & Basset 2000; Coddington *et al.* 2009; Grove & Forster 2011a, b). Principal among these are body size patterns. Since it is difficult for very small insects to maintain strong directional flight in even a light breeze, it has been proposed that small-bodied species could be more randomly distributed, and hence constitute a greater proportion of singletons, than large-bodied strong flying species. Evidence for this is equivocal. For example, Noyes (1984) collected 437 singletons from 739 species and just 1,455 individuals of parasitoid wasps from rainforest trees fogged with insecticide in Borneo. Most of these species were rare and most were also weak fliers less than one millimetre in length, suggesting that small body size may be related to abundance and distribution patterns. However, comparisons in body size between singletons and more abundant species in studies where the body size distribution of the focal organisms is much greater, have not shown consistent results. In some cases singletons are smaller than common species (Gaston *et al.* 1993), which corroborates the proposition, while other studies report that singletons are larger than common species (Coddington *et al.* 2009). Using my data, unique singletons were slightly, but not significantly, larger than more abundant species (data not shown). This is not entirely surprising, since body size is generally inversely related to abundance (Blackburn *et al.* 1993a; Stork & Blackburn 1993; Blackburn & Gaston 1994). Therefore singletons, as rare

species in communities, may be expected to be larger than abundant species. The overall effect is likely to be weak though, since other studies have shown that body size explains very little of the variance in abundance patterns (Blackburn *et al.* 1993a).

Fruit and dead wood in the canopy supported small numbers of beetles, but probably for different reasons. While fruit was relatively common in the canopy, it was poorly utilised by external feeding beetles, whereas dead wood was particularly scarce, but supported a relatively rich, but under sampled, fauna when present. The higher than expected numbers of unique singletons on dead wood support this supposition (Coddington *et al.* 2009), as does previous work at this study site that identified over 600 species of dead wood associated beetle species (Grove & Stork 2000). Fruit in the canopy is mostly unripe and undamaged, which precluded externally feeding beetles. Indeed, most species on fruit appeared to be a random selection of species from other microhabitats, since 70% of beetle species collected from fruit were unique or habitat singletons. In contrast, fruit on the forest floor at this study site can support large numbers of externally feeding beetles (Grimbacher *et al.* in prep), but only after the fruit is damaged and begins to decompose. Rotting fruit in the canopy is rare, and few fruits could be found that were not unripe and intact. Furthermore, in the only large scale predispersal seed predator study carried out on tropical plants, Janzen (1980) found that a total of 110 beetle species attacked only 100/975 (10.3%) plant species, while the remaining 875 plant species did not support any predispersal beetle seed predators. Therefore few externally or internally feeding species may utilise fruit in the canopy. Both fruit and dead wood could thus be considered minor resources in the canopy due to the very small quantities that can be utilised by the beetle fauna compared to the forest floor.

Community evenness scores showed that flower visiting species were more heterogeneous in abundance than species inhabiting the other microhabitats (Fig. 5.7). The

foliage, fruit and dead wood all supported species at relatively low abundances, resulting in similar high evenness scores. Conversely, flowers supported large aggregations of some species, which reduced community evenness measures. This pattern may be common for insect assemblages on spatially and temporally isolated resources. For instance, fruit falls, animal dung, and cadavers can attract large numbers of insect consumers, but often only a few species reach high abundances on these resources (Zalucki *et al.* 1984; Paarmann *et al.* 2002; Feer & Pincebourde 2005; Scheffler 2005; Vernes *et al.* 2005; Grimbacher *et al.* in prep). Investigating the possible linkage between variation in spatial and temporal availability of resources and evenness in community structure should be considered in future studies.

In conclusion, beetle communities inhabiting different canopy microhabitats varied considerably in species richness, abundance, and biomass patterns, as well as in community heterogeneity. The differences were so great that each microhabitat supported their own unique assemblages. This means that individual microhabitats will have an additive affect on estimates of total species richness in the rainforest canopy. Differences in the spatial and temporal distribution and biomass of microhabitats affected community composition by altering the distribution and density of beetle species. This was most pronounced for flowers, where the comparatively small biomass of floral resources appears ti result in aggregations of very high numbers of individuals in some species, while few species that have not sought out flowers are likely to randomly utilise them for rest or refuge.

Chapter 6:

Feeding guild structure of beetles on Australian tropical rainforest trees reflects microhabitat resource availability

Chapter 6: Feeding guild structure of beetles on Australian tropical rainforest trees reflects microhabitat resource availability[5]

6.1 Abstract

The rainforest canopy is renowned for its extraordinary richness in arthropods. Most attempts to date to quantify and explain the diversity of canopy arthropods have been at the whole tree level. The canopy is comprised of many distinct microhabitats and resources suggesting that whole canopy studies cannot resolve issues of microhabitat differentiation. I tested the hypotheses that feeding guild structure of beetle assemblages changed with different arboreal microhabitats and that these differences are consistent across tree species. Hand collection and beating techniques were used from the gondola of the Australian Canopy Crane to collect beetles from five microhabitats (mature leaves, flush leaves, flowers, fruit and suspended dead wood) within the rainforest canopy. A simple randomisation procedure was implemented to test whether the abundances of each feeding guild on each microhabitat was different from that expected based on a null hypothesis of random distribution of individuals across microhabitats. Beetles from different feeding guilds were not randomly distributed, but rather congregated on those microhabitats that are likely to provide the highest concentrations of their preferred food sources. Herbivorous beetles in particular, were over-represented on flowers and flush foliage, and under-represented on mature leaves and dead wood compared to random expectation. Proportional numbers of species within each feeding guild were remarkably uniform across tree species for each microhabitat, but proportional abundances of feeding guilds were all significantly non-uniformly distributed between host tree species, regardless of

[5] This chapter has been published (14 Mar 2012) with little modification as a multi-authored paper to the Journal of Animal Ecology (Wardhaugh, C. W., Stork, N. E., Edwards, W. 2012: Feeding guild structure of beetles on Australian tropical rainforest trees reflects microhabitat resource availability. *Journal of Animal Ecology* 81: 1086-1094).

microhabitat, confirming patterns previously found for arthropods in trees in temperate and tropical forests. These results show that canopy beetle communities are partitioned into discrete assemblages between microhabitats with their own unique feeding guild structure as a function of the resources found on each microhabitat and the temporal and spatial availability of these resources.

6.2 Introduction

The guild concept has been widely applied in both aquatic and terrestrial environments to describe the spatial and temporal structure of animal and plant communities, usually with respect to the different ways in which animals feed (Root 1967; Hawkins & McMahon 1989; Simberloff & Dayan 1991; Wilson *et al.* 1995; Posey *et al.* 1998; Krüger & McGavin 2001; Blondel 2003; Petchey & Gaston 2006; Elliot *et al.* 2007). Many studies of guild structure involve analyses of temporal changes in single communities (e.g., Posey *et al.* 1998), while others investigate differences between geographically isolated but fundamentally similar habitats, such as aquatic habitats on different coastlines (e.g., Vermeij *et al.* 2008). In comparison, few studies have investigated differences in guild structure between different microhabitats at single sites (e.g., Joern & Lawlor 1981; Stork & Blackburn 1993).

High species richness, in particular among arthropod communities within forest canopies, is facilitated by the concentration of large quantities of diverse resources (Lowman & Moffett 1993). Although the positive relationship between resource diversity and biodiversity is a simple prediction, assessments of the feeding guild structure of insect communities inhabiting different microhabitats are lacking, and have either been carried out on the mature leaf community only (Basset 1992c), or at the scale of the whole tree, with little consideration for host tree phenology (Moran & Southwood 1982; Stork 1987b;

Basset 1991b; Krüger & McGavin 2001). However, it is a reasonable assumption that the distribution of the insect community reflects that of the resources they exploit (Hawkins & McMahon 1989). For example, foliage feeding insects are expected to be concentrated on the leaves, whereas pollen feeding insects should be concentrated on the flowers.

The specialised diets of most insect species suggest that insect communities inhabiting the forest canopy are likely to comprise a series of relatively distinct assemblages within particular microhabitats (Basset 2001a; Ødegaard 2004; Kitching *et al.* 2007). The structure of the communities exploiting each microhabitat is therefore likely to vary according to the nature of the resources available, as well as their quality. For example, a number of studies have noted that herbivores increase in abundance during leaf flushing (Lowman 1985; Basset 1991a, b, c, 1992a, 1996, 1999a; Price *et al.* 1995; Steinbauer *et al.* 1998; Barone 2000; Marquis *et al.* 2001; Itioka & Yamauti 2004), indicating that new leaves provide superior resources for folivorous insects than do mature leaves. Further, Southwood *et al.* (2004) found that within the herbivore guild the abundance of different sub-guilds, such as chewers, sap-suckers, and leaf miners were temporally separated on oaks in accordance with the temporal availability of food resources that they utilise (Stork & Hammond unpublished).

However, not every insect associated with new leaves is likely to be feeding directly on foliage (e.g., McKey 1984), nor is every insect on flowers likely to be there to feed on pollen or nectar (Simpson & Neff 1981; Louda 1982; Louda & Potvin 1995; Wolfe 1997; Frame 2003; Romero & Vasconcellos-neto 2004; Boulter *et al.* 2005; McCall & Erwin 2006; Kitching *et al.,* 2007). Instead, each microhabitat will contain a suite of visitors from multiple feeding guilds, many of which may not be attracted for the purposes of feeding, but rather occur there due to mate finding, resting, or avoiding unfavourable abiotic or biotic conditions experienced elsewhere (Bates 1944; Schal 1982; Stork 1987b;

Mawdsley & Stork 1997; van Klinken & Walter 2001). The structure of these assemblages can provide valuable information on the distribution of both insects and resources, which is vital for assessing nutrient flow (Reynolds & Hunter 2004) or food web dynamics in tropical rainforest systems (Kitching 2006; Novotny *et al.* 2010).

The paucity of fine-scale within-tree studies that have examined the spatial dynamics of insect abundance and diversity has not been due to a lack of interest, rather it is primarily due to the logistical restraints of canopy access and the inability to discretely sample different microhabitats within a single tree (Stork *et al.* 1997c; Sutton 2001). Thus, very little is known about the distribution of rainforest canopy insects within individual trees. To overcome this problem, I used the Australian Canopy Crane at the Daintree Rainforest Observatory in tropical Australia to directly access canopy microhabitats on a regular basis. In particular, I sampled the beetle faunas inhabiting mature leaves, new leaves, flowers, fruit and suspended dead wood from 23 species of trees, lianas, and palms over the course of one year to investigate the relative abundances of feeding guilds from assemblages associated with each microhabitat. I sampled beetles because they represent a large proportion of canopy insects, are trophically diverse and are taxonomically and biologically well-known at the study site, since they have been the focus of a number of related earlier studies (Stork & Grimbacher 2006; Stork *et al.* 2008; Grimbacher & Stork 2007, 2009a). Although a broad range of feeding guilds are expected to be found inhabiting each microhabitat, it is predicted that relative abundances of different feeding guilds on different microhabitats will reflect distribution of the resources on which they feed. Moran and Southwood (1982) and Stork (1987b) found that there was a remarkable consistency in the feeding guild structure for arthropods at the species level (but not at the individual level of relative abundances) across different tree species and that this was the same in both temperate and tropical forest. I compared the compositional uniformity of

feeding guilds on different microhabitats to test the assumption that arthropod feeding guilds are equally distributed at the species level, but not the individual level, across different habitats.

6.3 Methods

6.3.1 Study site

For study site description see Chapter 3, 3.3.1.

6.3.2 Sampling

For sampling procedures see Chapter 3, 3.3.2. Beetle families and subfamilies were placed in feeding guilds (Table 6.1); herbivores, predators, fungivores, saprophages, and xylophages (Lawrence & Britton 1991; Lawrence *et al.* 2000; Grimbacher & Stork 2007). Families or subfamilies that could not be assigned a feeding guild due to a lack of definitive data or a broad range of feeding guilds were placed in an 'unknown' group. All samples are stored at James Cook University, Cairns.

6.3.3 Statistical analyses

For all analyses temporal data were pooled. A randomization procedure was employed to identify feeding guilds as being over- or under-represented on different microhabitats. The procedure took the entire beetle sample (10,335 individuals) and randomly assigned them to microhabitat types in exact proportions as existed in the original data set. For technical details on the randomisation procedure and tests of significance see Chapter 4, 4.3.4.

The abundance patterns of feeding guilds between microhabitats were assessed using the Evenness index (*E*) of Bulla (1994). For technical details on the calculation of *E* see Chapter 4, 4.3.4. Cases where only a single feeding guild was recorded from a particular host tree/microhabitat combination were omitted. Evenness scores were

calculated for both the proportional number of species and the proportional abundances of each feeding guild on each host tree/microhabitat combination. Variation in mean evenness between microhabitats was explored with ANOVA. Where significant differences were detected, post-hoc pair-wise comparisons between microhabitats were performed using Tukey tests. Significant outcomes in these tests would reveal between-microhabitat variation in guild structure. Conversely, non-significant outcomes are expected when proportional abundances of feeding guilds are similar on different microhabitats.

While evenness can assess the variation in abundance on each microhabitat within each tree species (i.e., within a single community), it cannot be used to measure variation in the relative abundances of feeding guilds across tree species (i.e., across multiple communities). To measure the uniformity of feeding guilds across tree species I used 2 x *k* contingency tables (where *k* is the number of tree species, 13 as this was the number of species for which samples were taken from mature leaves, new leaves, and flowers) (Moran & Southwood 1982; Stork 1987b). Fruit and dead wood communities were omitted from uniformity analyses due to the low numbers of tree species that these microhabitats were sampled from. Analyses were also restricted to those feeding guilds where $n \geq 13$ as this was the number of tree species used in the analysis (i.e., this threshold is the minimum possible for perfect uniformity). Consequently, saprophages and xylophages on new leaves were omitted from this analysis, as was the unknown group on mature and new leaves. Bonferroni corrections were made to significance levels (adjusted $P = 0.008$) prior to pair-wise analyses. Significant results would indicate variation in the relative abundances of feeding guilds across tree species on each microhabitat. Non-significant outcomes would indicate similar proportional abundances across tree species.

6.4 Results

A total of 372 species of beetles comprising 10,335 individuals were collected from the five microhabitats combined. Herbivores dominated in terms of abundance (5,580 individuals, or 54% of the total), but there were also large numbers of predators (2,266, 22%), fungivores (1,893, 18%), and saprophages (508, 5%) (Tables 6.1, 6.2). The three most abundant feeding guilds also dominated in terms of species richness, with 161 species

Table 6.1: Feeding guild assignations for beetle families and subfamilies based on Lawrence and Britton (1991) and Lawrence et al. (2000).

Family	No. species	No. individuals
Predators		
Cantharidae	1	19
Carabidae	2	3
Cleridae	2	22
Coccinellidae	24	456
Melyridae	10	68
Rhipiphoridae	2	7
Pselaphinae	1	1
Aleocharinae	7	1029
Omaliinae	1	596
Tachyporinae	3	22
Paederinae	5	29
Cybocephalinae	2	14
Herbivores		
Apioninae	2	20
Attelabidae	1	1
Buprestidae	2	2
Chrysomelidae	32	857
Curculionidae (gen.)	111	4644
Mordellidae	3	13
Psephenidae	1	1
Cetoniinae	3	26
Melolonthinae	3	11
Rutelinae	1	1
Boganiidae	2	4
Fungivores		
Anthribidae	12	41
Ciidae	1	1
Corylophidae	15	436
Laemophloeidae	1	2
Latridiidae	2	140
Leiodidae	1	1
Mycetophagidae	1	28
Ptiliidae	2	3
Zopheridae	3	6
Languriidae	4	93
Nitidulidae (gen.)	18	919
Phalacridae	19	216
Monotomidae	3	7
Xylophages		
Anobiidae	4	10
Brentidae (gen.)	5	15
Cerambycidae	14	20
Scolytinae	6	14
Saprophages		
Anthicidae	1	2
Dermestidae	6	22
Hydrophilidae	2	3
Silvanidae	2	442
Tenebrionidae	7	9
Aderidae	7	20
Scraptiidae	1	6
Scirtidae	3	4
Unknown		
Salpingidae	2	2
Elateridae	9	27

of herbivores (43% of the total), 60 species of predators (16%) and 82 fungivorous species (22%) (Table 6.1).

The abundances of every beetle feeding guild deviated significantly from random expectation on at least one microhabitat (summarised in Table 6.2). Flower-visiting beetle communities were composed of higher than expected abundances of herbivores and saprophages, with lower than expected abundances of predators and xylophages. The new leaf beetle community was dominated by herbivores, which constituted higher than expected abundances, while fungivores, predators and saprophages were significantly less abundant on new leaves than expected under randomness. Mature leaf beetle communities in contrast supported lower than expected abundances of herbivores and saprophages, with higher than expected abundances of predators and xylophages. Fruit and dead wood communities were dominated by the decomposer community, with higher than expected abundances of fungivores on dead wood and saprophages and xylophages on fruit.

Table 6.2: The number of individuals from each feeding guild collected from each canopy microhabitat. Guilds with higher and lower than expected abundances on particular microhabitats are indicated by colour coding (green for higher than expected, red for lower) and + and – signs after figures. Differences were determined by comparing the recorded abundances (± 95% confidence intervals) with the expected abundances (± 95% C.I.) generated from a randomisation procedure applied to the entire beetle community. A number in black with no sign signifies an abundance that does not differ significantly from random.

Guild	Mature leaves	New leaves	Flowers	Fruit	Wood	**Totals**
Fungivores	343	**18-**	1472	15	**45+**	**1893**
Herbivores	**825-**	**260+**	**4450+**	36	**9-**	**5580**
Predators	**558+**	**35-**	**1662-**	**7-**	**4-**	**2266**
Saprophages	**67-**	**3-**	**416+**	**18+**	4	**508**
Xylophages	**29+**	2	**18-**	**8+**	2	**59**
Unknown	1	1	25	0	**2+**	**29**
Totals	**1823**	**319**	**8043**	**84**	**66**	**10335**

6.4.1 Community evenness

The proportional number of species within each feeding guild varied significantly between microhabitats ($F_{4, 57} = 3.94$, $P = 0.0068$). Post-hoc pair-wise comparisons revealed that flowers were significantly less even new leaf and fruit communities in the proportional

number of species within guilds (Fig. 6.1a). That is, flower-visitor communities displayed significantly greater heterogeneity in the number of species within each feeding guild than fruit-inhabiting communities. There were no significant differences in mean evenness scores between any other combinations of microhabitats.

Proportional abundances (i.e., number of individuals) of feeding guilds also varied significantly between microhabitats ($F_{4, 57} = 3.99$, $P = 0.0064$). Flower-visitor

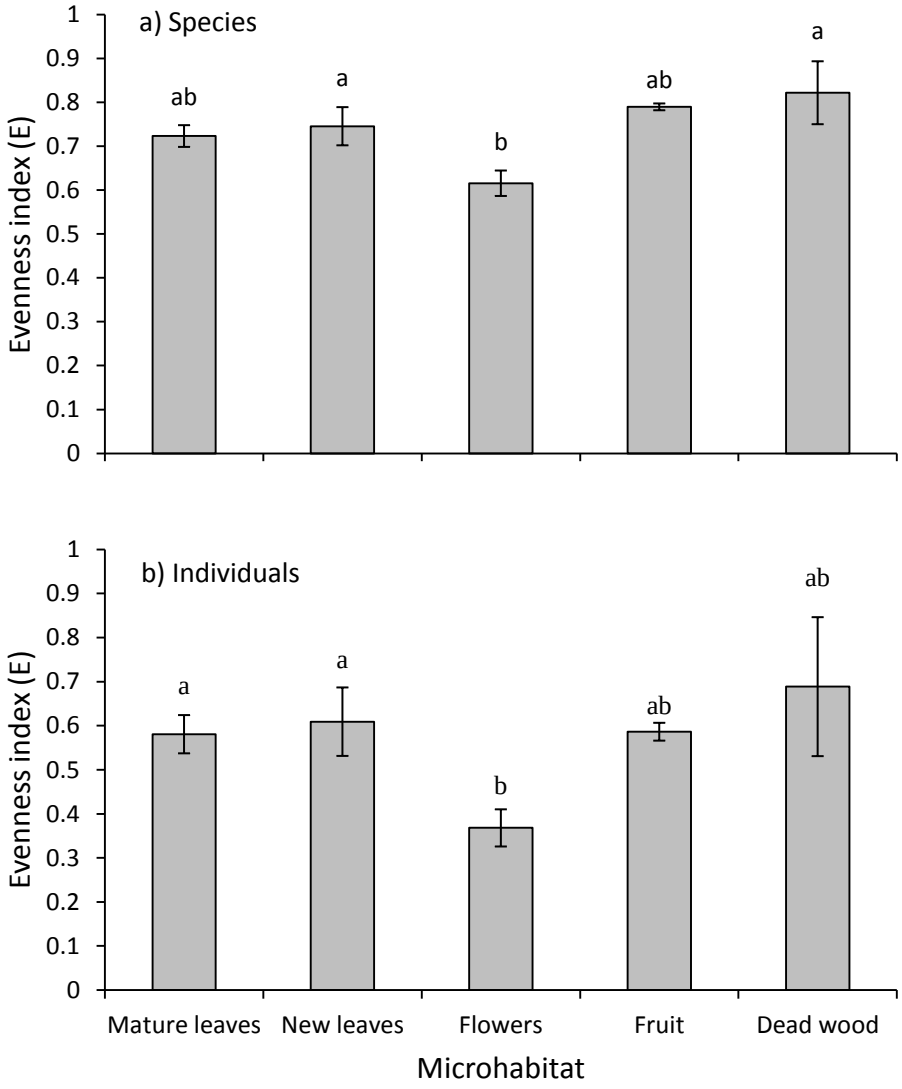

Figure 6.1: Mean evenness in the proportional abundances of feeding guilds on each microhabitat measured by the evenness index *E*. Mean *E* (± S.E.) are shown for a) the number of species within each feeding guild, and b) the number of individuals within each feeding guild. *E* ranges between 0 and 1, with higher numbers indicating greater evenness in proportional abundances, and lower numbers indicating greater variation in proportional abundances, of species or individuals across feeding guilds. Letters above columns indicate significant differences.

communities were significantly less even in proportional abundances of guilds than mature leaf and new leaf communities (Fig. 6.1b). There were no significant differences in mean evenness scores between any other combinations of microhabitats.

6.4.2 Uniformity in guild structure

Between tree species, the proportional number of species on each microhabitat within each feeding guild was remarkably uniform, with only fungivores and herbivores on flowers displaying a non-uniform distribution (Table 6.3) across the 13 host tree species. When all microhabitats were pooled, only the herbivores and predators were significantly non-uniformly distributed. The significant result for predators was due to a high proportion of predators on *Dysoxylum pettigrewianum* and disappeared when this tree was omitted from the analyses (X^2 = 29.5, P = 0.13). Conversely, at the individual level no feeding guild was uniformly distributed across tree species on any microhabitat or when the samples were pooled (Table 6.4).

Table 6.3: Tests of uniformity in the proportions of the number of beetle species in each feeding guild across the 13 tree species. Each feeding guild is tested against the sum of the species from the other feeding guilds on the host tree. Significant results indicate non-uniformity in proportional species richness between tree species and are marked in bold. Bonferroni adjusted P = 0.008.

Species	Mature		New		Flowers		All	
	X^2	P	X^2	P	X^2	P	X^2	P
Fungivores	19.98	0.52	26.39	0.07	42.95	**0.0005**	31.1	0.09
Herbivores	33.1	0.045	19.39	0.31	40.24	**0.0012**	50.38	**0.0005**
Predators	17.37	0.69	17.69	0.41	23.33	0.14	44.93	**0.0027**
Saprophages	11.35	0.96			5.19	0.998	10.64	0.98
Unknown					24.95	0.1	23.41	0.38
Xylophages	27.4	0.16			18.74	0.34	21.77	0.47

Table 6.4: Tests of uniformity in the proportions of the number of beetle individuals in each feeding guild across the 13 tree species. Each feeding guild is tested against the sum of the individuals from the other feeding guilds on the host tree. Significant results indicate non-uniformity in proportional abundance between tree species and are marked in bold. Bonferroni adjusted $P = 0.008$.

Individuals	Mature		New		Flowers		All	
	X^2	P	X^2	P	X^2	P	X^2	P
Fungivores	265.27	**<0.0001**	82.63	**<0.0001**	1725.6	**<0.0001**	1385	**<0.0001**
Herbivores	466.73	**<0.0001**	83.34	**<0.0001**	4003.4	**<0.0001**	3728.2	**<0.0001**
Predators	214.8	**<0.0001**	44.64	**0.0003**	3344.4	**<0.0001**	3013.7	**<0.0001**
Saprophages	71.66	**<0.0001**			792.7	**<0.0001**	723.7	**<0.0001**
Unknown					167.69	**<0.0001**	91.1	**<0.0001**
Xylophages	56.23	**<0.0001**			54.39	**<0.0001**	176	**<0.0001**

6.5 Discussion

As predicted, the feeding guild structure of the beetle communities differed substantially between microhabitats, and these differences were consistent across tree species. This variation largely reflected the presumed differences in food resources available on each microhabitat. New leaves, for instance, harbour higher than expected abundances of herbivores, which is consistent with previous studies that have identified new leaves as preferred food sources for folivorous insects (Coley 1980, 1983; Lowman 1985; Basset 1991a, b, c, 1992a, 1996, 1999a, 2001a; Aide 1993; Price *et al.* 1995; Steinbauer *et al.* 1998; Barone 2000; Marquis *et al.* 2001; Itioka & Yamauti 2004). Indeed, the availability of flush foliage was the best predictor of herbivore abundance in the subtropical Australian tree *Argyrodendron actinophyllum* (Basset 1991a). New leaves, due to their young age, are also unlikely to support fungal growths or accumulated dead material. Consequently, fewer fungivorous or saprophagic species were collected from this microhabitat than expected. Dead wood, in contrast, supported higher than expected abundances of fungivores, which are presumably feeding on fungi growing on the dead wood, and lower than expected abundances of herbivores, since this microhabitat lacks live plant material. Mature foliage also supported fewer herbivores than expected, indicating that it is not a particularly high quality food source compared to new leaves and flowers for herbivorous species (see

Mattson 1980; Carisey & Bauce 1997). The higher than expected numbers of predators on mature leaves were mostly ladybirds (Coccinellidae). Many of these species feed on sap-sucking Hemiptera nymphs that are common on the foliage of trees, but were not often collected from flowers.

Flowers attracted higher than expected numbers of herbivores. These speceis are presumably either flower specialists or have switched from feeding on other vegetative structures to take advantage of the high quality food available from flowers (Wäckers *et al.* 2007). The higher than expected numbers of saprophages on flowers were mostly individuals from one species of Silvanidae. This species was a broad host generalist and was recorded from the flowers of 12 plant species. A relatively large number of fungivores were also attracted to flowers, and it is likely that at least some of these species are feeding on pollen (Cook *et al.* 2004), nectar or other floral resources (Teichert *et al.* 2011) since these resources are often easily digestible, even to species that do not typically consume them (Roulston & Cane 2000). This could also be the case with flower-visiting predatory beetles (Opitz 2002; van Rijn *et al.* 2002), although they could be attracted by the high concentrations of herbivorous insects that attend flowers. However, two species of aleocharine and one omaliine (Staphylinidae) are flower specialists (>97% of individuals of all three species were collected from flowers, Chapter 8) and made up the majority (96.3%) of flower-visiting predatory beetles. They three species also show varying degrees of host specificity, with >95% of the individuals of the most common aleocharine species collected exclusively from *Syzygium gustavioides*. Furthermore, most of the fungivorous and predatory beetles I collected from flowers belong to families (Nitidulidae, Phalacridae, Mycetophagidae, Staphylinidae, Cleridae) that have previously been identified as common flower-visitors and even successful pollinators in other systems (Gottsberger 1989b; Blanche & Cunningham 2005; Teichert *et al.* 2011). High population densities on plants

and high host specificity are uncommon traits for non-herbivores and it is feasible that these beetles are may be supplementing their diets with plant resources. The disputable trophic level of these species also highlight the underlying problems with assigning entire families or subfamilies of insects to particular trophic guilds due to a lack of species level information (Stork 1987b; Hammond 1994).

Although many groups were congregated on particular canopy microhabitats in a predictable way, the distributions across microhabitats for other feeding guilds did not differ from random expectation. Most cases involved feeding guilds that were recorded in relatively low abundances (xylophages, unknown) or microhabitats from which relatively few beetles were collected (fruit, suspended dead wood). The notable exception was the fungivore guild, that showed abundances on mature leaves and flowers that were not different from random expectation, despite relatively high abundances on both microhabitats (Table 2). The obvious conclusion to draw is that mature leaves and flowers are similar in the resources they provide to fungivorous beetles. However, few fungivorous species were common to both mature leaves and flowers (Chapter 8), indicating substantial differentiation in, and specialisation on, the resources that flower-visiting and leaf-inhabiting fungivores seek.

6.5.1 Heterogeneity in abundance

Low evenness scores for proportional abundances and species richness of feeding guilds were characteristic of the flower-visiting community. This level of heterogeneity in communities attending flowers may be due to the very high numbers of herbivores on flowers compared to species from other feeding guilds. Flowers are thus important food sources for large aggregations of species. Higher evenness scores among the other

microhabitats suggest that they provide a broader range of resources that are utilised by species that do not form large feeding aggregations.

The results presented here confirm those of Moran and Southwood (1982) on temperate trees in Europe and Africa and Stork (1987b) on tropical rainforest trees in Borneo. In both of these studies feeding guilds were remarkably uniform in the proportional number of beetle species, and distinctly non-uniform in abundance, across tree species. Stable guild composition has also been noted at larger spatial scales in comparison between geographically isolated, but similar, habitats (e.g., Vermeij *et al.* 2008). My results showed that this pattern holds true even at the level of microhabitats within host trees, indicating that guild structure can be a predictable trait of ecological communities across a broad range of spatial scales and taxonomic groups. The expression of uniformity in the proportional number of species within feeding guilds at multiple spatial scales may be linked to the common pattern of abundance seen in almost all assemblages, including arboreal beetles, where the community consists of a large proportion of rare species and few common species (Floren & Linsenmair 1998; Novotny & Basset 2000; Lucky *et al.* 2002). Common species have little effect on proportional uniformity in species richness, because they are weighted the same as rare species. But if most species are rare and rare species are randomly distributed with respect to tree species, as they tend to be (Novotny & Basset 2000), uniformity in species number across tree species is to be expected. Proportional abundances of feeding guilds in contrast, are disproportionately affected by the few common species, since common species contribute a greater number of individuals to total abundance and are typically not randomly distributed across host tree species (Novotny *et al.* 2004b).

The majority of canopy biodiversity studies have been limited to insects inhabiting the leaves (Novotny & Basset 2005). This study has shown that mature foliage supports a

very different beetle community from other canopy microhabitats. The abundance distribution of beetles from each feeding guild on the microhabitats examined matched that of the resources for which they have most likely searched (see Southwood *et al.* 2004). For instance, the high abundances of herbivores on new leaves and flowers indicate that beetles search for and select these microhabitats as substrates and food sources. Since ephemeral resources such as flowers and new leaves are always available at the local scale in most tropical rainforests (Chapman *et al.* 1999; Boulter *et al.* 2006), in particular those that do not experience extended and relatively severe dry seasons (Frankie *et al.* 1974; van Schaik *et al.* 1993; Wright & van Schaik 1994), they should be considered key resources to the maintenance of high levels of beetle biodiversity in the canopy (Ødegaard & Frame 2007).

Chapter 7:

Mutualistic and antagonistic interactions and host specialisation: rainforest canopy beetles are equally specialised on flowers and leaves

Chapter 7: Mutualistic and antagonistic interactions and host specialisation: rainforest canopy beetles are equally specialised on flowers and leaves

7.1 Abstract

Host specialisation is of central importance to understanding food web dynamics, biodiversity patterns and the structure of natural communities. It is generally assumed that antagonistic interactions (such as between herbivores and host plants) favour increasing host specificity, whereas mutualistic interactions (such as in pollination networks) are associated with higher levels of generalisation. To examine this assumption I compared the host specificity of the beetle communities between antagonistic networks of herbivores, non-antagonistic networks of non-herbivores and mutualistic networks of flower-visitors (both herbivores and non-herbivores) inhabiting the foliage and flowers of 23 canopy plant species in a tropical rainforest in north Queensland, Australia. Contrary to expectation, mutualistic herbivore and non-herbivore communities on flowers showed similar levels of host specificity as the antagonistic herbivore community on leaves. As expected, (antagonistic) herbivores were significantly more specialised than (non-antagonistic) non-herbivores on leaves. These results demonstrate that both antagonistic and mutualistic interactions can result in high levels of host specialisation among beetle communities in tropical rainforests. The patchy distribution of flowering trees in time and space in tropical rainforests may promote greater specialisation of flower-visitors in these systems via selection favouring host finding abilities which may override the expectations based on antagonism or mutualism previously proposed. Plant communities in temperate systems in contrast, are typically less diverse, individuals within plant species occur at greater densities, and flowering is often co-ordinated at the community level within brief temporal episodes (flowering periods). Spatial and temporal flowering patterns may thus be a

mechanism that promotes generalisation in temperate systems, but may not be relevant in tropical rainforests where flowers are often available over larger parts of the year.

7.2 Introduction

Ecological communities are comprised of networks of interacting species (Bacompte *et al.* 2003, 2006; Tylianakis *et al.* 2010). The types of interactions that occur between species within ecological communities have important implications for the evolution of species and the generation of biodiversity (Montoya *et al.* 2006; Bascompte & Jordano 2007; Bastolla *et al.* 2009; Fontaine *et al.* 2006, 2009).

Antagonistic interactions, such as those between plants and herbivores or hosts and parasites, are thought to be strong drivers of specialisation because they involve continuous reciprocal co-evolutionary processes of defences and counter defences between interacting species (Ehrlich & Raven 1964; Freeland & Boulton 1992; Barker 1994; Becerra 1997; Tripet *et al.* 2002; Dick 2007; Tylianakis *et al.* 2007; Roslin & Salminen 2008; Ballhorn *et al.* 2010; Funk 2010). Leaves typically contain unique compositions of secondary chemicals, often at relatively high concentrations (Cates & Rhoades 1977; Jones & Fern 1991) that are thought to function as deterrents against herbivore attack (Feeny 1970; Coley 1986; Schultz 1988; Karban & Myers 1989; van Dam *et al.* 1995; Coley & Barone 1996; Gatehouse 2002; Ode 2006). As a consequence, herbivorous species are expected to become specialised on leaf material they are able to process. On the other hand, non-herbivorous species do not consume foliage, and thus should be less host plant specific because they do not ingest chemically defended plant material and are thus not involved in same co-evolutionary process (Erwin 1982; May 1988; Stork 1988; Basset *et al.* 1996; Ødegaard 2000a; Novotny *et al.* 2002a, 2006; Novotny & Basset 2005; but see Futuyma &

Wasserman 1980; Bernays & Graham 1988; Beard & Walter 2001; Bernays 2001; Janz 2003).

In contrast, studies have shown that mutualistic networks, such as those between host plants and their animal seed dispersers and pollinators, contain many species that are more generalist in host use than would be expected under randomness (Bascompte & Jordano 2007). Generalisation among mutualistic networks may be favoured because dependence on single specialist species for pollination or seed dispersal increases the risk of extinction of both species if one partner in the mutualism is removed from the system. Highly specialised pollination syndromes are therefore inherently fragile, which may explain why they are rare (Waser *et al.* 1996; Lindberg & Olesen 2001; Tripp & Manos 2008). Consequently, mutualistic interaction networks have a nested structure and typically contain many weakly interacting species and higher levels of generalisation (Bascompte & Jordano 2007; Aizen *et al.* 2008; Bastolla *et al.* 2009; Fontaine *et al.* 2009). Evidence for this was recently produced by Fontaine *et al.* (2009) who showed that mutualistic pollination networks were more generalist than antagonistic networks of herbivores on other plant parts among 43 datasets of plant-pollinator and plant-herbivore networks. They argued that greater generalisation among pollinators compared to herbivores could be due to both ecological and evolutionary factors. In particular, a high density of pollinators could promote generalisation by increasing the strength of competitive interactions, thus favouring individuals that utilise a greater number of plant species (Fontaine *et al.* 2008). Conservatism in flower morphology may also promote generalisation, since many disparate plant lineages have converged into a relatively small number of floral types that attract distinct pollinator groups (Fenster *et al.* 2004; Stang *et al.* 2006).

Fontaine *et al.*'s (2009) analysis contained no studies that examined pollinator and herbivore networks simultaneously or on the same plant species. To date, the only study of

which I am aware that has simultaneously examined the host specificity of insects on leaves and flowers in a rainforest canopy is Ødegaard (2000b). He found that the foliage-inhabiting herbivorous beetle (Curculionoidea, Chrysomeloidea, and Buprestoidea) community displayed a higher level of host specificity than the flower-visiting community, supporting Fontaine and co-workers' hypothesis that host specificity is more pronounced among antagonistic rather than mutualistic networks. Here I test the hypotheses; (i) that host specificity is higher among antagonistic networks of herbivores than non-antagonistic networks of non-herbivores on the foliage, and (ii) that antagonistic herbivore communities on leaves are more host specific than either antagonistic or mutualistic interaction networks on flowers.

7.3 Methods

7.3.1 Study site

For study site description see Chapter 3, 3.3.1.

7.3.2 Sampling

Beetles were sampled from mature leaves and flowers within the upper canopies of 23 locally common canopy plant species. For further details on sampling methodology see Chapter 3, 3.3.2. Beetle families were assigned as either herbivores (Curculionidae, Chrysomelidae, some Scarabaeidae) or non-herbivores (all other collected families). On the leaves, herbivores constituted what was considered a community for which the underlying interaction was antagonistic, while non-herbivores were considered a non-antagonistic (neutrally interacting) community. All species on flowers were considered mutualists, although herbivores and non-herbivores were both identified and these categories were used in subsequent analyses.

Host specificity

Lloyd's index was used to measure host tree specificity of each beetle species. This index accounts for variation in abundance between host plant species, which renders it sensitive to sample size (Lepš 1993). Analyses were therefore restricted to beetle species where at least 12 individuals were collected as a compromise between including a maximum number of species and reducing errors arising from small sample sizes.

Lloyd's index is calculated as:

$$\frac{S_x^2}{\bar{x}} \qquad \text{equation 1}$$

where S_x^2 is the variance and $\bar{x}$ is the mean number of individuals per tree species. Lloyd's index increases with increasing specificity and is minimum for an equitable distribution (Lepš 1993). Variation in mean host specificity of herbivores and non-herbivores on flowers and leaves was tested using ANOVA. Post-hoc pair-wise comparisons in mean host specificity were performed using Tukey tests. Lloyd's index was $Log_{10}(x+1)$ transformed prior to analyses to normalize the data.

Results

A total of 9,866 beetles from 350 species were collected from leaves and flowers. Seventy one species had an abundance of ≥12 (41 on flowers and 30 on leaves) and were included in host specificity analyses. The interaction between microhabitat and feeding guild was significant ($F_{1, 67} = 11.50$, $P = 0.001$) (Fig. 7.1) indicating that feeding guilds did not exhibit similar levels of host specificity on both microhabitats. Mean host specificity varied significantly between feeding guilds ($F_{1, 67} = 9.30$, $P = 0.003$), but not microhabitats ($F_{1, 67} = 3.70$, $P = 0.067$). There was no difference in host specificity, mean Lloyd's index (± S.E.), between herbivores and non-herbivores on flowers (10.21 ± 1.39 and 10.44 ± 1.27 respectively) and herbivores on leaves (13.15 ± 2.42). Only non-herbivores on leaves were

more generalised (i.e., lower overall Lloyd's index) in host use than all other groups (4.83 ± 0.90).

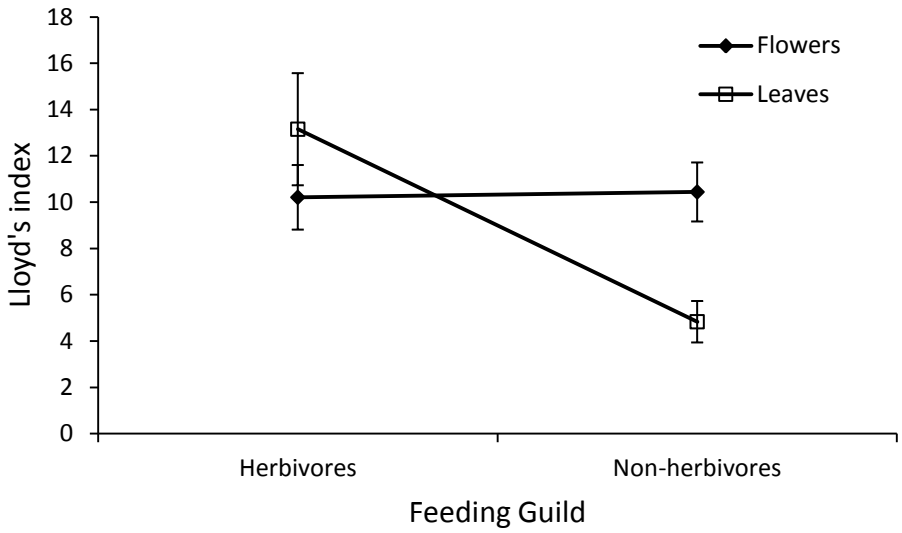

Figure 7.1: Interaction plot of mean host specificity (± S.E.), as measured by Lloyd's index, of herbivorous and non-herbivorous beetles on flowers and leaves. The plot shows no difference in host specificity for herbivores and non-herbivores on flowers, and herbivores on leaves. Non-herbivores on leaves are significantly more generalised in host use.

Discussion

In this study I tested the hypothesis that host plant specificity should be higher within assemblages in which relationships are underpinned by antagonistic interactions (i.e., foliage-feeding herbivores), than in assemblages where interactions between species are underpinned by mutualistic or neutral interactions (i.e., mutualistic networks of flower-visitors and non-herbivores on leaves) (Fontaine *et al.* 2009). In contrast to expectation, the mutualistic network of flower-visitors showed levels of host specificity that were equal to host specificity in the antagonistic network of herbivores on leaves. In fact, non-herbivorous floral visitors were equally as host specific as herbivores on both leaves and flowers. It thus seems that both mutualistic and antagonistic interactions can promote high levels of specialisation. Only non-herbivores on leaves were significantly more generalised than any of the other communities, suggesting that neutral interactions (i.e., non-

antagonistic and non-mutualistic) do not promote high levels of specialisation. Consequently, only species that interact directly with the host plant (either leaf material or floral resources) are likely to be under selective pressure to specialise upon particular host tree species.

My results contrast with the meta-analysis of Fontaine *et al.* (2009) who showed that mutualistic networks were more generalist than antagonistic networks. One possible explanation for this is that Fontaine *et al.* (2009) used pollination datasets from mostly temperate systems, including alpine and boreal communities, and their analyses included no studies from tropical rainforests. It is possible therefore, that their conclusions are applicable to temperate communities, but may not be representative of tropical rainforests. Temperate and tropical rainforest systems differ in many abiotic (e.g., temperature, rainfall, humidity) and biotic (species richness and abundance patterns, growth periods) factors, which could alter specialisation and the strength of interactions (see Wolda 1988; Novotny *et al.* 2006; Dyer *et al.* 2007). If this is the case, we are left with the question: why would specialisation among flower-visitors be higher in tropical rainforests than in temperate systems? It is possible that factors suggested to promote generalisation among flower-visitors in temperate systems may not exert a similarly strong effect in topical rainforests. Firstly, high densities of competing pollinators have been proposed as a mechanism increasing generalisation of individual insects (Fontaine *et al.* 2008). Densities of flower-visitors in my study were incredibly high, and were up to four orders of magnitude greater than densities of invertebrates on the leaves (Chapter 3). Since this was not coupled with greater generalisation in my comparisons, specialisation due to weak competitive interactions seems unlikely in this study. Second, convergent evolution in floral morphology to attract particular pollinator groups has been suggested as another possible reason why flower-visitors in temperate systems may be relatively generalised

(Stang *et al.* 2006; Fontaine *et al.* 2006; 2009). For example, flowers can be categorised into a limited number of pollination syndromes, which differ in flower morphology and the identity of pollinator taxa (Fenster *et al.* 2004; Hermann & Kuhlemeier 2011). Flower-visitors may therefore be relatively generalised because they can use any host plant exhibiting a particular floral morphology. However, whether or not variation in the diversity of floral morphology differs between assemblages of plants occurring in temperate and tropical rainforest systems has never been quantified. This represents a potential extension of the hypothesis that the main driver of local species richness among herbivorous insects on leaves is host plant diversity (Novotny *et al.* 2006). Future work could focus on the role of floral functional diversity as a potential driver of host specificity and species richness of flower-visiting insects between communties.

One other possibility exists. Local plant diversity is much higher in most tropical rainforests than most temperate ecosystems (Novotny *et al.* 2006). As a result tropical plant species often occur at very low local densities (Janzen 1970). Locating and moving between individuals of a particular host plant in a rainforest is difficult, requiring an ability for host identification coupled with long-range movement. Flowers are also always available at the local scale in moist tropical rainforests due to overlapping flowering times of different tree species (van Schaik *et al.* 1993; Chapman *et al.* 1999; Boulter *et al.* 2006). An unbound flowering period coupled with high plant diversity (i.e., low individual species density), results in flowers being very patchily available in space and time in tropical rainforests (Bawa *et al.* 2003). In contrast, floral resources are typically more spatially abundant and temporally predictable in temperate systems where plant diversity is usually comparatively low, individual plant species usually occur at higher abundances, and community-level flowering is restricted to the spring and summer months when abiotic conditions are favourable (Wolda 1988). Greater specialisation of flower-visitors in my

study could therefore be due to the lack of spatially and temporally concentrated flowering at the community scale, which are more common in temperate systems where generalisation is more prevalent. Indeed, the lack of tropical rainforest pollination networks in Fontaine *et al.'s* (2009) meta-analysis means that it is uncertain that the results they reported are applicable to all plant-pollinator communities. Therefore, it is feasible that the results reported here are applicable to rainforests in general, while Fontaine *et al's* (2009) results are applicable only to temperate systems.

I believe that my results support the hypothesis that specialisation is the result of adaptations that increase the ability to locate particular preferred host plants at the expense of locating other potentially inferior hosts (Waser *et al.* 1996). Others have previously suggested that a similar process may promote specialisation among some herbivorous insects (Jermy 1984; Bernays *et al.* 2000; Bernays 2001; Janz 2003; Singer 2008). The neural constraints hypothesis states that host specificity arises as a result of the inability for insects to process large amounts of information (Bernays 2001; Janz 2003; Singer 2008). Therefore, specialisation may be favoured because specialisation imposes limits on cognitive requirements to identify and locate true hosts from the many possible co-existing plant species (Jermy 1984; Bernays *et al.* 2000; Janz 2003). Further, unlike hypotheses that are concerned with the host specificity of herbivores (such as adaptations to overcome enemy defences), the neural constraints hypothesis can be applied to any species, regardless of feeding guild, which must locate a patchy resource. As a result, this hypothesis may explain why both herbivores and non-herbivores were equally host specific on flowers in this study, since neural constraints should exert similar selective pressures in both groups.

7.5.1 Conclusions

My data show that host specificity among non-herbivorous insects associated with flowers is as high as that of flower-visiting or leaf inhabiting herbivores. This result does not support the hypothesis that species that interact antagonistically with the host plant are more specialised than species that interact mutualistically with the host plant. While there is an extensive literature concerning the ecological and evolutionary drivers of specialisation for herbivores (see Jermy 1984; Strong *et al.* 1984; Lewinsohn *et al.* 2005; Novotny & Basset 2005), few studies to date have examined the drivers of specialisation among mutualistic pollinator networks. Indeed, previous studies of host specialisation of pollinators are dominated by examples of extreme morphological adaptations in one-to-one interactions, such as those between figs and fig wasps (Janzen 1979; Wiebes 1979; Weiblen 2002), and yuccas and yucca moths (Pellmyr & Huth 1994; Pellmyr *et al.* 1996). Future work should explore the possible mechanisms giving rise to equally high levels of specialisation among flower visitors in tropical rainforests. In particular manipulative and comparative studies to fully explore the possible limits in identification abilities that underlie the neural constraints hypothesis should be encouraged.

Chapter 8:

Host tree and microhabitat specificity of rainforest canopy beetles

Chapter 8: Host tree and microhabitat specificity of rainforest canopy beetles[6]

8.1 Abstract

The host specificity of tropical rainforest beetles is of central importance to understanding food web dynamics and biodiversity patterns. However, the widespread assumption that most host specific species are folivorous has concentrated studies of host specialisation on foliage inhabiting herbivores. I tested the generality of this assumption by comparing both plant host- and microhabitat-specificity between beetle communities inhabiting the foliage (flush and mature), flowers, fruit and suspended dead wood from 23 canopy plant species in a tropical rainforest in north Queensland, Australia. Independent of host tree identity, 76/77 of the most abundant beetle species (n ≥ 12 individuals) were aggregated on a particular microhabitat. The degree of microhabitat specialisation (measured by the indices *Sm* and Lloyd's) did not differ between beetle communities on flowers and foliage. In accordance with previous studies, host specificity of foliage-inhabiting beetles was most pronounced among herbivorous families (Curculionidae, Chrysomelidae). Host specificity among flower-visitors in contrast, was equally high among herbivorous and non-herbivorous (e.g., Nitidulidae, Staphylinidae, Cleridae) families. Species overlap between communities inhabiting mature leaves and flowers was also very low (Sorensen's coefficient, *So* = 0.11) suggesting that each newly-sampled microhabitat will have an additive effect on species richness. Effective specialisation (F_T) measures showed that traditional non-herbivore correction factors used in extrapolative biodiversity estimates are not applicable to the flower-visiting beetle fauna. These results demonstrate that host specialisation is not concentrated within folivores as previously assumed and has wide-

[6] This chapter has been published (22 Nov 2012) with little modification as a multi-authored paper in the *Biological Journal of the Linnean Society* (Wardhaugh, C. W., Stork, N. E. & Edwards, W. 2013: Specialization of rainforest canopy beetles to host trees and mocrohabitats: not all specialistis are leaf-feeding herbivores. *Biological Journal of the Linnean Society* 109: 215-228.)

ranging implications for understanding the evolution of plant-insect interactions, food web dynamics and global species richness estimates.

8.2 Introduction

The interactions between plants and the insects that live and feed on them is of central importance in ecology (Southwood 1961; Ehrlich & Raven 1964; Feeny 1970; Crawley 1983; Jermy 1984; Strong *et al.* 1984). These intimate relationships have greatly influenced the evolution of both groups, resulting in wide-spread inter-dependence and specialisation between plants and insects (Ehrlich & Raven 1964; Benson *et al.* 1975; Atsatt & O'Dowd 1976; Regal 1977; Crepet 1984; Farrell 1998; Ren 1998; Grimaldi, 1999; Frame 2003). The level of host plant specificity exhibited by insects in particular is an important component of rainforest food web analyses (May 1988; Novotny *et al.* 2010) and global biodiversity calculations (Erwin 1982; Stork 1988; Ødegaard 2000a: Novotny *et al.* 2002a; Hamilton *et al.* 2010, 2011). Host specificity is not the only facet of specialisation, however. Most herbivorous insects are also resource specific; that is they are restricted to feeding upon particular plant materials. The interaction between resource- and host-specificity thus defines the broad limits of insect diet breadth (Schoonhoven *et al.* 2005).

Specialisation has long been thought to be characteristic of foliage-feeding herbivorous insects (Erwin 1982). Leaves typically contain unique compositions of secondary chemicals often at relatively high concentrations (Cates & Rhoades 1977; Jones & Fern 1991) that are thought to function as deterrents against herbivore attack (Feeny 1970; Coley 1986; Schultz 1988; Karban & Myers 1989; van Dam *et al.* 1995; Coley & Barone 1996; Gatehouse 2002; Ode 2006). The argument for high levels of specialisation on leaves is based on the expected outcome of the reciprocal co-evolutionary process of the

evolution of novel chemical defences in plants, followed by adaptations to counter these defences in insect herbivores (Ehrlich & Raven 1964; Bowers 1983; Becerra 1997; Roslin & Salminen 2008; Ballhorn *et al.* 2010). Other plant parts, such as wood or flowers, generally contain lower concentrations of defensive chemicals (Carisey & Bauce 1997; Irwin *et al.* 2004), and thus may not strongly promote specialisation through antagonistic co-evolutionary mechanisms. As a consequence, non-herbivorous species are assumed to be less host plant specific than herbivores (Erwin 1982; May 1988; Stork 1988; Basset *et al.* 1996; Ødegaard 2000a; Novotny *et al.* 2002a, 2006; Novotny & Basset 2005; Fontaine *et al.* 2009; but see Futuyma & Wasserman 1980; Bernays & Graham 1988; Mawdsley & Stork 1997; Beard & Walter 2001; Bernays 2001; Janz 2003).

The widely accepted assumption that leaf-eating herbivores are more specialised than species using other canopy resources has resulted in most host specificity studies being concentrated on folivores. For example, of the 36 tropical invertebrate studies cited in a review of host specificity by Novotny and Basset (2005: data from Table 1), only eight involved feeding guilds other than herbivores on leaves: three studies investigated host specificity of wood boring insects, three seed predators, and one each on fruit and root feeders. In contrast, all 26 canopy-based studies focused on foliage inhabiting species.

Although the majority of host specialisation studies have focused exclusively on folivores, the few studies carried out on other host plant structures show that specialisation rates vary substantially between microhabitats and/or feeding modes. In Novotny and Basset's (2005) review the percentage of species in different feeding guilds that were host specific (at the plant family level) decreased in the order: granivores (99%) > leaf miners (96%) > frugivores (83%) > leaf chewers = sap-suckers (56%) > xylophages (24%) > root feeders (10%). Or, expressed in terms of the resources that these insect guilds predominantly feed on: seeds > leaf mesophyll > fruit > entire leaf segments = sap > wood

> roots. Even so, the generality of these findings is unknown at present since Novotny and Basset's (2005) review included results from single microhabitat studies undertaken in a variety of different forest systems. To date, the only study of which I am aware that has simultaneously examined the host specificity of insects on different rainforest canopy microhabitats is Ødegaard (2000b). He found that the foliage-inhabiting herbivorous beetle (Curculionoidea, Chrysomeloidea, and Buprestoidea) community displayed a higher level of host specificity than the flower-visiting community, in support of the assumption that host specificity is most pronounced among folivores, while specialisation rates for wood feeders varied considerably depending on the plant taxa under examination.

The degree of host specialisation among taxa and feeding guilds has generated great debate over the last 30 years, mostly because it is a fundamental measure in Erwin's (1982) global biodiversity calculation, and is associated with a high degree of uncertainty (Hamilton *et al.* 2010, 2011). Erwin's (1982) estimate was based on a number of extrapolative measures from samples of rainforest canopy beetles. Many of these figures have been refined based on newer information attempting to reduce uncertainty in the estimates for each measure used in the overall extrapolation (see Ødegaard 2000a). Such studies have provided more precise descriptions of the host specificity rates of folivores (Basset *et al.* 1996; Novotny *et al.* 2002a), the relative species richness of canopy versus ground dwelling invertebrates (Stork & Grimbacher 2006), the proportion of all beetles that are herbivorous (Basset 1991d; Stork 1991), and the proportion of all insects that are beetles (Stork 1988; Basset 1991d). These modifications have reduced Erwin's original estimate of 30 million species, to a probably range of 3-10 million. Nevertheless, estimates of host specificity still remain the measure with the greatest degree of uncertainty (Hamilton *et al.* 2010; 2011).

The one estimate of Erwin's calculation that has gone untested and unchanged is the proportion of host specific species that are herbivores, which is assumed to be ~83% (Stork 1988). The lack of studies on entire insect assemblages also means we have little idea of the host specificity of non-herbivorous insects. In response to this, some authors have applied a correction factor (x 1.2) when extrapolating to account for host specific non-herbivorous species based on Erwin's original assumption that folivorous herbivores constitute 83% of all host specific species (see Novotny *et al.* 2002a). Furthermore, the concentration of host specialisation studies to insects on foliage means we do not know how applicable the results of these studies are to assemblages inhabiting other canopy microhabitats. One further consequence of limited information about specificity in non-folivorous taxa is that we have little understanding of the outcome of processes that may promote specialisation via paths other than adaptation to defensive chemicals, such as predator avoidance (Bernays & Graham 1988), host tree abundance (Futuyma & Wasserman 1980) or host identification (Bernays 2001; Janz 2003). For example, flowers are ephemeral resources that often possess intricate visual and olfactory displays to attract potential pollinators. Selection operating on host finding and recognition abilities for flower-visiting species could lead to a reduction in the ability to locate other potential hosts, thus promoting host specialisation (see Jermy 1984; Bernays *et al.* 2000; Bernays 2001; Janz 2003).

In this study, the host specificity of all beetles collected from five different canopy microhabitats (mature leaves, flush leaves, flowers, fruit and suspended dead wood) were examined across 23 species of canopy plants in the tropical rainforest of north Queensland, Australia. I tested the hypothesis that herbivores on the foliage constitute the great majority of host specific species on a tree, as assumed in all previous work. If previous assumptions are correct, I expect two main results; 1) host specificity will be greater among herbivorous

beetle families (e.g., Curculionidae, Chrysomelidae) than beetles from other feeding groups; and 2) host specificity will be greatest among leaf-inhabiting species, with lower host specificity on other microhabitats.

8.3 Methods

8.3.1 Study site

For study site description see Chapter 3, 3.3.1.

8.3.2 Sampling

For sampling procedures see Chapter 3, 3.3.2, and Chapter 6, 6.3.2.

8.3.3 Host and microhabitat specificity

Specialisation can be assessed using a variety of different statistical measures, each of which has its own intrinsic strengths and weaknesses. Although most measures deliver similar results for the same data set, no single measure of population variation is considered superior (Lepš 1993). It was therefore deemed appropriate to utilise a number of measures as this constituted a more rigorous and conservative approach. Specifically, I used Lloyd's index and *HSk* (Host Specificity to plant species *k*; Novotny *et al.* 2004b) to measure host specificity; Lloyd's index and *Sm* (Specificity to microhabitat *m*) to measure microhabitat specificity; effective specialisation (F_T) (May 1990) to calculate mean host specialisation and the number of herbivorous and non-herbivorous beetle species specialised to each plant species within each microhabitat; and Sorensen's similarity coefficient to assess the overlap in beetle species composition between host species and microhabitats.

Lloyd's index, *HSk* and *Sm* account for variation in abundance between host plant species or microhabitats, which renders them sensitive to sample size. Analyses using these indices were therefore restricted to species where at least 12 individuals were collected as a compromise between including a maximum number of species and reducing errors arising from potential assignation of specialisation when none actually exists.

Lloyd's index is caculated as:

$$\frac{S_x^2}{\bar{x}} \qquad \text{equation 1}$$

where S_x^2 is the variance and $\bar{x}$ is the mean number of individuals per tree species or microhabitat. Its value increases with increasing specificity and is minimum for an equitable distribution.

HSk and *Sm* were used to categorise beetle species as host or microhabitat specialists, which is not possible using Lloyd's index which can only provide a relative measure of specialisation. The *HSk/Sm* method involves assigning each beetle species to one of three groups (specialist, preference (or oligophagous), and generalist) based on the proportion of the total number of individuals collected from the host tree species (*HSk*) or microhabitat (*Sm*) that supported the highest number of individuals. Note that the preferred host tree species or microhabitat does not have to support a majority (>50%) of individuals, just the greatest proportion within the sample. *HSk/Sm* is calculated for each species as:

$$\frac{\text{number of individuals collected from preferred host tree species or microhabitat}}{\text{total number of individuals collected}} \qquad \text{equation 2}$$

Like Lloyd's index, *HSk/Sm* accounts for variation in beetle abundance on different host trees or microhabitats, and reduces bias caused by increasing numbers of rare host records that inevitably accumulate from large sample sizes. The categories were:

a) Specialists: species where *HSk/Sm* > 0.9.

b) Preferences (or oligophages): species where $0.5 < HSk/Sm < 0.9$, since most individuals were collected from single host species or microhabitats, indicating that they have a preference for it but are not necessarily specialised.

c) Generalists: species where $HSk/Sm < 0.5$, since no host species or microhabitat supported more than half of the individuals.

It should be noted that since mature leaf biomass constitutes >90% of the combined biomass of all samples, a species that is randomly distributed across microhabitats will be found to be a "mature leaf specialist" since >90% of its population are expected to be found on mature leaves. It is not possible therefore to discern mature leaf specialists from microhabitat generalists, since both should be found predominantly on mature foliage. Nevertheless, for the sake of clarity, I classify all beetles where $Sm > 0.9$ on mature leaves as specialists. This is not the case for flowers and new leaves, however. The spatially and temporally restricted distribution of flowers and new leaves means random distribution of individuals across microhabitats should produce (on average) less than 10% of all records for each species on these resources. Thus, defining specialisation for these microhabitats using cut-off values of >90% and >50% of total abundance should reflect true deviations from randomness. Comparisons of the mean microhabitat and host specificity (mean *Sm*, *HSk* and Lloyd's index across all species that were clumped on those microhabitats (i.e., $Sm > 0.5$)) of beetle communities inhabiting different microhabitats were carried out using Student's t-tests. Comparisons of mean host specialisation (Lloyd's) were also examined for herbivorous (Curculionoidea, Chrysomeloidea) and non-herbivorous beetles, both overall and within microhabitats, using Student's t-tests. Prior to analysis, Lloyd's index was Log_{10} transformed, *Sm* measures were arcsin square root transformed, and *HSk* measures were square root transformed to normalise the data.

A key weakness of the two host specificity measures described above is that they can only be applied to a subset of the total beetle community (i.e., the most abundant species), and give no information as to the total number of species or specialists inhabiting a given host tree species. May (1990) developed a metric (effective specialisation) for calculating tree- and community-level host specialisation based on all available species presence/absence data independent of total abundance. This measure is a key component of many global arthropod biodiversity extrapolations because it produces an estimate of the total number of host specialists per tree species (May 1990; Novotny *et al.* 2002a). Effective specialisation was used to determine the number of herbivorous and non-herbivorous species effectively specialised to each tree species. If previous assumptions are correct, herbivorous species should comprise ~83% of the total number of host specialist species on each tree. This was tested for the mature leaf, new leaf, and flower-visiting beetle community, as well as for the entire pooled sample. Fruit and dead wood communities were omitted from these analyses due to the small number of beetles collected from these microhabitats.

The strength of effective specialisation is also a weakness, in that while the measure incorporates the entire community, it does not account for variation in abundance between host tree species. As opposed to Lloyd's index and *HSk*, effective specialisation is reduced for every transient individual collected from non-host trees, as these are considered equally valid host records and contribute equal weight to the calculation. These facts reaffirm the need to use more than one measure of host tree specialisation. For a plant species *k*, in a community of *T* plant species, the proportion of species that are effectively specialised on *k* (f_k), is given by:

equation 3

where $p_k(i)$ is the proportion of beetles associated with plant species *k*, that are also associated with *i* other plant species. The number of beetle species that are effectively specialised on each plant species (*k*) is given as S_f:

equation 4

where S_k is the number of beetle species found on plant species *k*. The weighted average effective specialisation across *T* plant species is given as F_T:

equation 5

where S_T is the total number of beetle species found on *T* plant species and is the total number of host observations (= mean beetle species per tree) (May 1990).

While Lloyd's index, HSk and effective specialisation measure host specificity, they give little indication of microhabitat fidelity. For example, if most beetle species utilise several microhabitats then sampling additional microhabitats will not reveal many new host specialists. But if the overlap in species composition is very low between microhabitats, then additional microhabitats could potentially contribute a large number of previously unaccounted for host specific beetle species. The Sorensen index (*So*) was therefore used to measure the similarity of the beetle community across host tree species within and between each microhabitat. The *So* coefficient is a pair-wise comparison that quantifies the proportion of species common to two samples. The mean *So* coefficients for each microhabitat are averaged across all pair-wise comparisons of host tree species. Sorensen coefficients were calculated using EstimateS 8.20 (Colwell 2009).

8.4 Results

8.4.1 Host specificity

Seventy seven out of a total of 372 beetle species had abundances of at least 12 individuals and were used in host and microhabitat specificity analyses involving Lloyd's index and

HSk/Sm. Due to their similar traits, Lloyd's index and *HSk* for my data were closely correlated (Pearson, r = 0.982, n = 77, $P < 0.001$). The median number of host tree species per beetle species was 6 (Fig. 8.1a), while the median number of tree species sampled in order to collect 90% of individuals of each species was 4 (Fig. 8.1b). Each of these

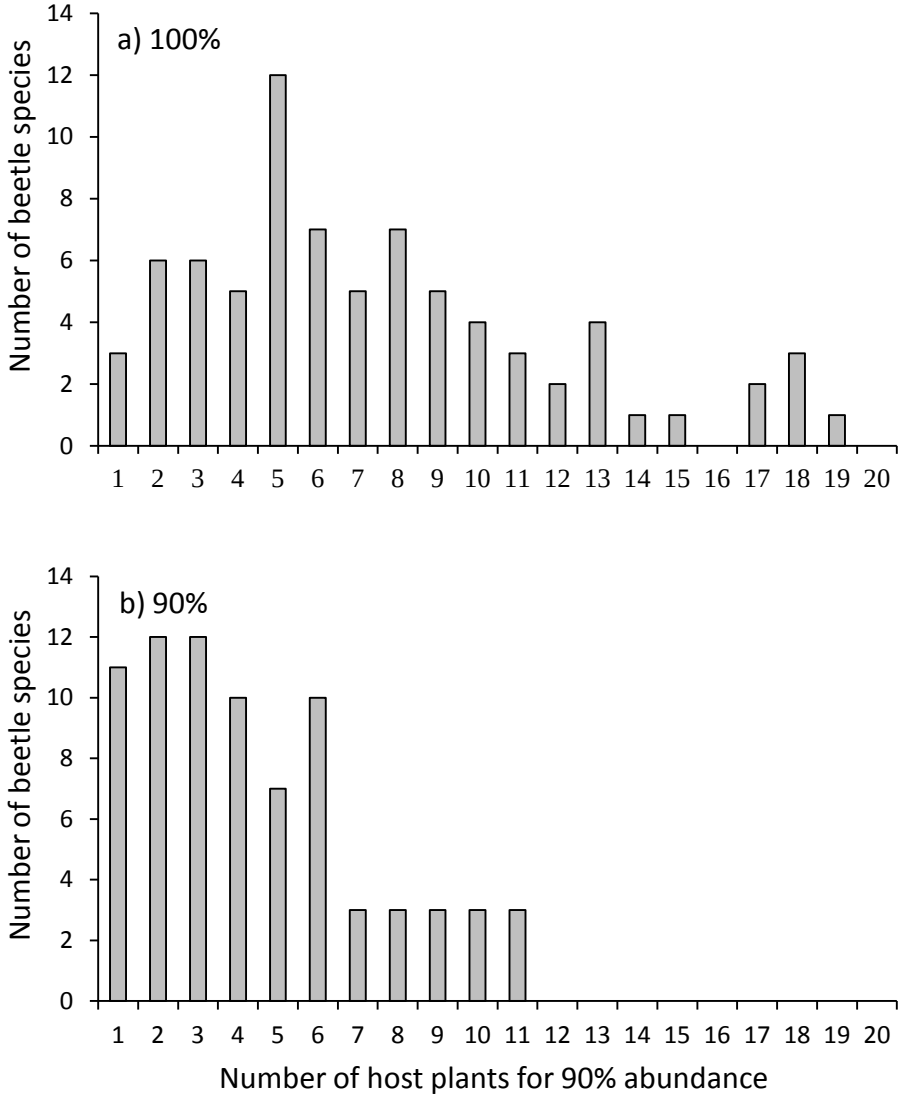

Figure 8.1: The number of host plants utilised by, a) all individuals of each beetle species, and b) the minimum number of host plant species that support ≥90% of the individuals collected.

distributions was right skewed, indicating that most beetle species utilise a relatively small number of host tree species. Mean host specificity and the median number of host plant species varied according to feeding guild on mature leaves where herbivores were

significantly more specialised than fungivores (t_{18} = 3.00, P = 0.0077) and predators (t_{31} = 3.19, P = 0.0032), and utilised more host species than (Fig. 8.2a, b). In contrast, herbivorous on flowers did not differ significantly in host specificity from fungivorous and predatory species (Fig. 8.2a), and all three guilds utilised similar numbers of host trees

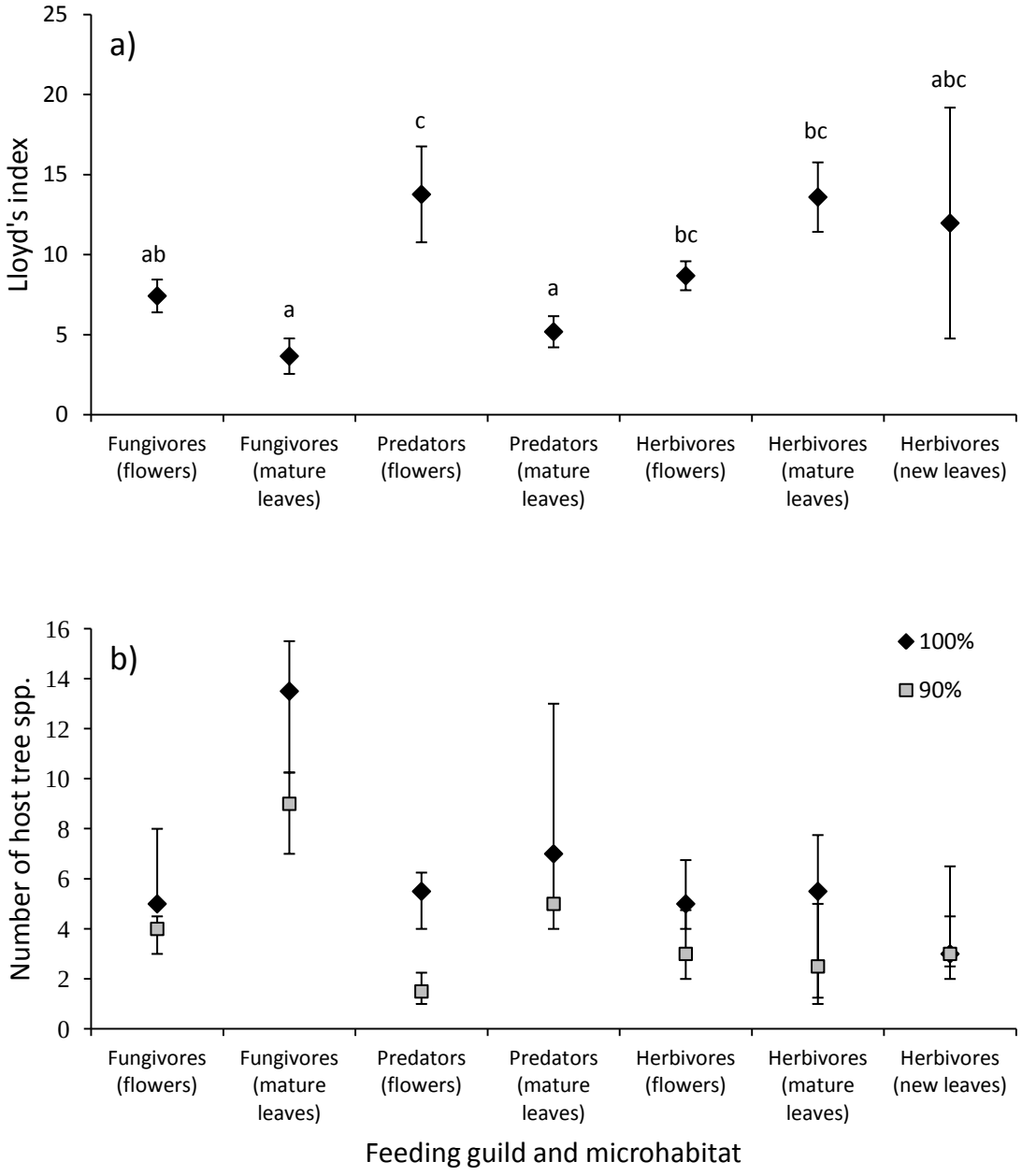

Figure 8.2: a) Mean (± S.E.) host specificity of beetles from each feeding guild on mature leaves new leaves and flowers. Letters denote significant differences in host specificity. b) The median (± upper and lower quartiles) number of host plants for fungivorous and predatory beetles on flowers and mature leaves, and herbivorous beetles from flowers, mature leaves and new leaves. The median number of host trees are shown for 100% and the median for the minimum number of host trees to collect 90% of all individuals of each species in the analysis.

(Fig. 8.2b). There was no significant difference in host specificity between herbivores on flowers, mature leaves and new leaves (Fig. 8.2a), and all three groups utilised similar numbers of host tree species (Fig. 8.2b). Predators on flowers were significantly more host specific than fungivores ($t_8 = 3.50$, $P = 0.0081$) and predators ($t_{21} = 3.51$, $P = 0.0021$) on mature leaves (Fig. 8.2a). Figure 8.3 shows that a large number of species are host generalists (<50% of individuals inhabiting the preferred host species), and then the number of species declines with increasing host preference to a low point at 80-90%. A second peak is then reached at 90-100%, which are all of the host specific beetle species (i.e., *HSk* > 0.9).

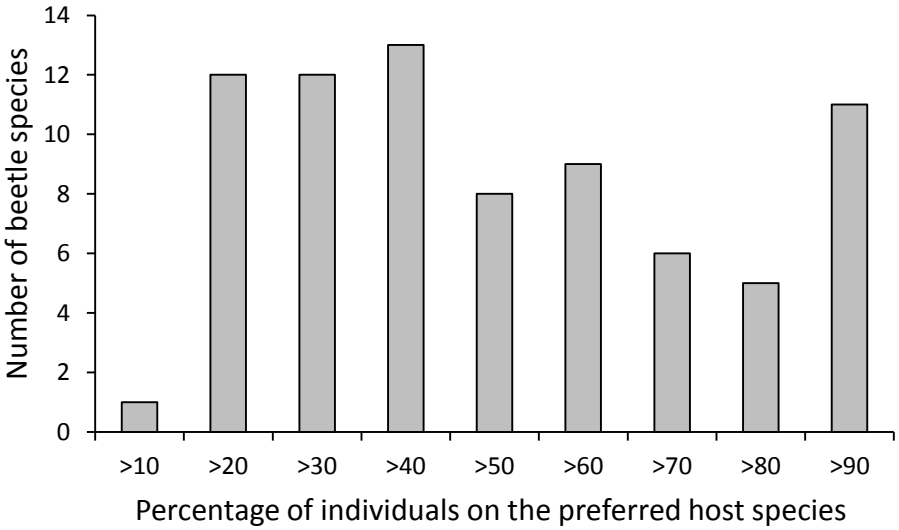

Figure 8.3: The percentage of each beetle species' population that was collected from the most preferred host (the host species that supported the greatest proportion of individuals).

Of the 77 most abundant beetle species, 38 (49.4%) showed no preferences for single host species (*HSk* < 0.5), while thirty nine (50.6%) showed a preference for a single host species (*HSk* > 0.5). The 39 species that showed some level of host preference included 11 host specialists (14.3%) (*HSk* > 0.9), and these were identified from only 8/23 host tree species; *Myristica globosa* (Myristicaceae) hosted three specialists, while *Cryptocarya mackinnoniana* (Lauraceae) supported two host specific beetle species. A

further six host plants, *Merremia peltata* (Convulvulaceae), *Castanospermum australe* (Fabaceae), *Syzygium gustivioides* (Myrtaceae), *Archontophoenix alexandrae* (Arecaceae), *Elaeocarpus grandis* (Elaeocarpaceae), and *Entada phaseoides* (Fabaceae), each supported one specialist beetle species. In terms of feeding guilds, the 11 host specific species included seven species of herbivores (five Curculionidae, two Chrysomelidae), two species of fungivores (one Nitidulidae and one Anthribidae) and two predators (one Staphylinidae: Aleocharinae, and one Cleridae). One additional beetle species (Curculionidae: Baradinae) from the host preference category was found to be specific to one plant genus (*Cryptocarya*), while three other species were specific to single plant families (a Curculionidae: Derelomini on Arecaceae, a Chrysomelidae: Eumolpinae on Myrtaceae, and a Nitidulidae on Myrtaceae).

8.4.2 Microhabitat specificity

The median number of microhabitats that each common beetle species was collected from was 2 (Fig. 8.4a), whereas the median for reaching 90% of the individuals collected was 1 (Fig. 8.4b). Microhabitat specificity measured by Lloyd's index and *Sm* were also closely correlated (Pearson, r = 0.976, n = 77, $P < 0.001$). All but one of the 77 beetle species (98.7%) exhibited *Sm* values > 0.5, indicating aggregation upon specific microhabitats (Fig. 8.4b). Of these, 41 species (53.2%) were microhabitat specialists (*Sm* values > 0.9). Most of these (29, or 70.7%) were flower specialists, while the remaining 12 species (29.3%) were collected almost exclusively from mature leaves. Thirty five of the remaining 36 species that were not classified as specialists were, nevertheless, classified as showing a preference to a single microhabitat ($0.9 > Sm > 0.5$). Twelve (33.3%) of these were associated with flowers and 18 species (50%) were from mature leaves. Three species (8.3%) displayed a preference for new foliage, and two species (5.6%) for suspended dead

wood. No species were associated predominantly with fruit. Nine species within the preference category achieved *Sm* > 0.9 when individuals collected from new and mature leaves were combined, indicating that they are foliage specialists. The single microhabitat

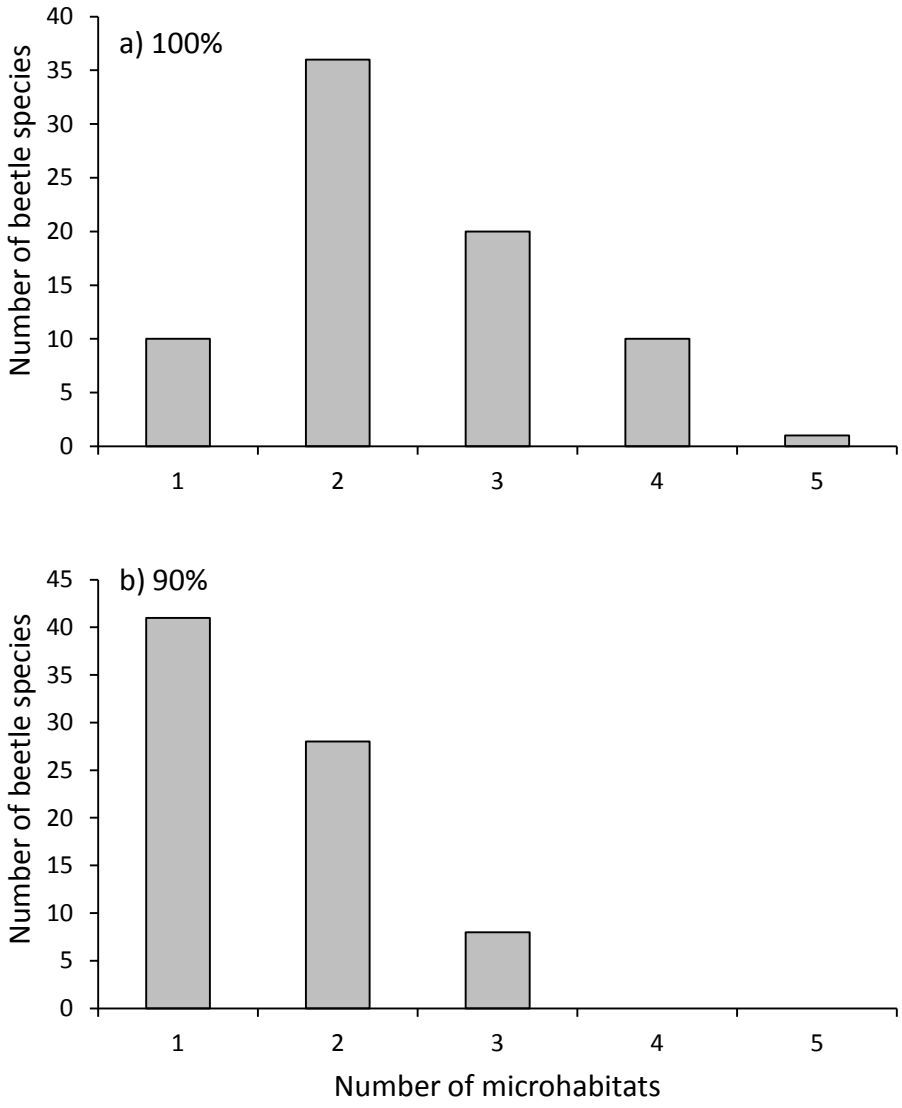

Figure 8.4: The number of microhabitats utilised by, a) all individuals of each beetle species, and b) the minimum number of microhabitats that support ≥90% of the individuals collected.

generalist (*Sm* < 0.5) also showed a preference for leaves (i.e., *Sm* > 0.5) when new and mature leaf samples were combined.

Overall, microhabitat specialisation was very high. Mean *Sm* (± S.E.) for all 77 beetle species combined was 0.87 (± 0.02) (Fig. 8.5). Microhabitat specificity was

significantly higher among the flower-visiting community than the mature leaf community (0.92 ± 0.01 and 0.83 ± 0.03 respectively, $t_{69} = 3.67$, $P = 0.0005$). *Sm* for mature and new leaves combined (i.e., foliage specialisation) was 0.9 (± 0.02), which did not differ significantly from the *Sm* of flower-visitors ($t_{73} = 0.96$, $P = 0.34$).

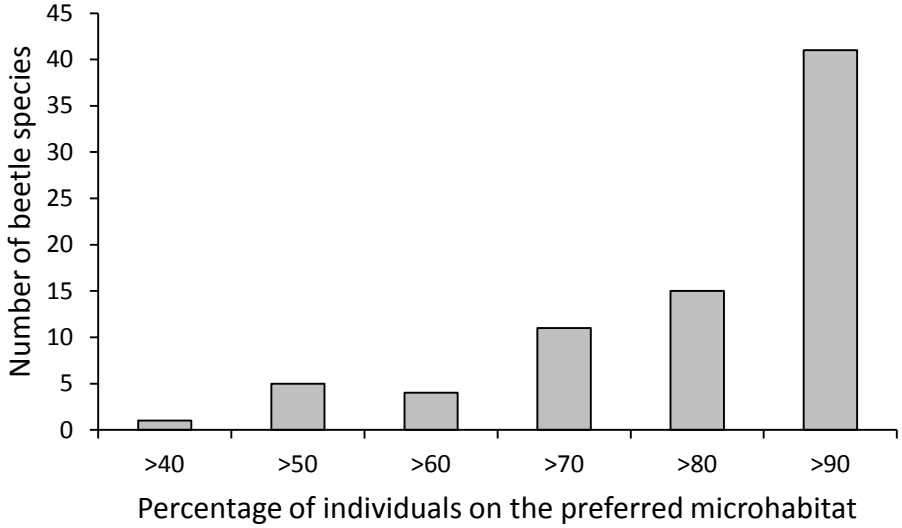

Figure 8.5: The percentage of each beetle species' population that was collected from the most preferred microhabitat (the microhabitat that supported the greatest proportion of individuals).

Flower specialist beetle species included 12 herbivores (10 Curculionidae, one Chrysomelidae, one Scarabaeidae), four predators (three Staphylinidae, one Cleridae), and 13 fungivores (seven Nitidulidae, four Phalacridae, one Languriidae, and one Latridiidae). Conversely, mature leaf specialists were either herbivores (four Curculionidae, one Brentidae: Apioninae), or predators (two Coccinellidae). The foliage specialists that were collected predominantly from new and mature leaves combined included four herbivores (Chrysomelidae), four predators (two Coccinellidae, one Cantharidae, and one Melyridae), and one fungivorous species (Corylophidae).

8.4.3 Interactions between microhabitat and host specificity

Regression analysis showed no relationship between host specificity and microhabitat specificity as determined by Lloyd's index ($F_{1, 75} = 2.509$, $R^2 = 0.0324$, $P = 0.12$). Flowers did however, support a relatively large number of species from within the preference category, while the foliage supported a higher proportion of host generalists (Table 8.1).

Table 8.1: The number of beetle species from each of the host specificity categories recognised using HSk that were specialised to, or displayed a preference for, flowers, foliage (mature and new leaves combined) and suspended dead wood (as measured by Sm).

	Host specific	Host preference	Host generalist
Flower specialist	4	16	9
Flower preference	1	5	6
Foliage specialist	5	4	12
Foliage preference	0	3	10
Dead wood specialist	0	0	0
Dead wood preference	1	0	1

Of the 11 host specific beetle species (*HSk* > 0.9), five were flower-visitors (*Sm* > 0.5), five were foliage-visitors, while the remaining species showed a preference for dead wood (Table 8.1). Most beetle species that showed a preference for a single host plant species were found on flowers (21/28, or 75%), while the foliage (mature and new combined) supported the majority of host generalists (22/38, or 57.9%). Of the four species identified as specific to a particular plant genus or family, three were flower specialists, while the fourth displayed a preference for the foliage. Eight of the 15 (53.3%) host-, genus- or family-specific species therefore, were either specialist flower-visitors or displayed a preference for flowers, while six of the remaining seven host- genus- or family-specific species (40%) were found predominantly on the leaves. Overall, mean host specificity of flower-visitors was significantly higher than that of the mature leaf beetle community (mean *HSk* = 0.6 (± 004) and 0.51 (± 005) respectively, $t_{69} = 2.36$, $P = 0.02$);

mean Lloyd's index = 10.3 (± 0.9) and 7.9 (± 1.2) respectively, $t_{69} = 2.53$, $P = 0.01$) (Table 8.2).

Table 8.2: A comparison of the host specificity of the beetle communities inhabiting flowers, mature leaves, and new leaves. Mean *HSk*, Lloyd's index and Sorensen similarity coefficients (± S.E.) are shown for each microhabitat. F_T is the effective specialisation of the beetle faunas inhabiting each microhabitat, while the last column shows the total number of beetle species on each tree species for each microhabitat (± S.E.). Totals displayed in the bottom row are calculated for data pooled across all microhabitats. The total in the last column differs from the cumulative total due to overlap in microhabitat use by some beetle species, and issues related to abundance characteristics of the beetle fauna (see text).

Microhabitat	HSk	Lloyd's	Sorensen	F_T	No. of spp.
Flowers	0.6 ± 0.04	10.3 ± 0.9	0.2 ± 0.03	0.38	10.1 ± 2.1
Mature leaves	0.51 ± 0.05	7.9 ± 1.2	0.2 ± 0.02	0.42	11.6 ± 1.5
New leaves	0.6 ± 0.27	12 ± 7.2	0.11 ± 0.04	0.55	3.1 ± 0.6
Total	0.56 ± 0.03	9.5 ± 0.7	0.25 ± 0.02	0.35	16.2 ± 1.9

Mean Sorensen similarity measures (± SE) between host plant species were virtually identical for the beetle communities inhabiting mature leaves (0.203 ± 0.02) and flowers (0.201 ± 0.03) ($t_{382} = 0.25$, $P = 0.8$), but overlap in species composition between the mature leaf and flower beetle communities was very low (mean $So = 0.113$ (± 0.004)), indicating that each of these microhabitats supports a largely unique fauna. The mean Sorensen coefficient of the new leaf beetle community was also low (0.112 ± 0.05), while the similarity across host plants for the canopy community as a whole (i.e., all microhabitats combined, including fruit and dead wood beetles) was relatively high (0.249 ± 0.02). There was little overlap between the flower-visiting and new leaf beetle communities ($So = 0.04 \pm 0.003$) or the mature leaf and new leaf beetles ($So = 0.09 \pm 0.004$). However, the new leaf beetle community was comprised mostly of species that were also collected from mature leaves, since 44/56 (78.6%) species representing 303/319 (95%) individuals collected from new leaves were also collected from mature leaves. The low similarity of the new leaf beetle community between tree species and other

microhabitats possibly reflects the lower total number of beetles collected from this microhabitat and the concomitant reduction in species overlap between host plant species.

8.4.4 Effective specialisation

For the three focal microhabitats (mature leaves, new leaves and flowers) combined on 23 plant species, average effective specialisation (F_T) was 0.345. F_T was slightly higher on flowers (0.38), and higher still on mature leaves (0.42) (Fig. 8.6). On new leaves, F_T was particularly high (0.55), possibly reflecting the low number of beetles collected from this microhabitat and the subsequent small number of host records per species, to which presence/absence measures like F_T are sensitive (Fig. 8.6). There were on average (± S.E.), 16.2 ± 1.9 beetle species on each tree species (Table 8.2). Mature leaves supported 11.64 ± 1.51 beetle species while new leaves supported just 3.11 ± 0.64 species. Flowers supported as many species as mature leaves, with 10.11 ± 2.11 beetle species on each tree species. The total number of beetle species (16.2) on each tree species is considerably less than the cumulative total calculated by adding each microhabitat community (24.8), indicating an overlap in microhabitat use by many species. However, since F_T is a presence/absence measure, rare host or microhabitat records will also increase the disparity between these numbers.

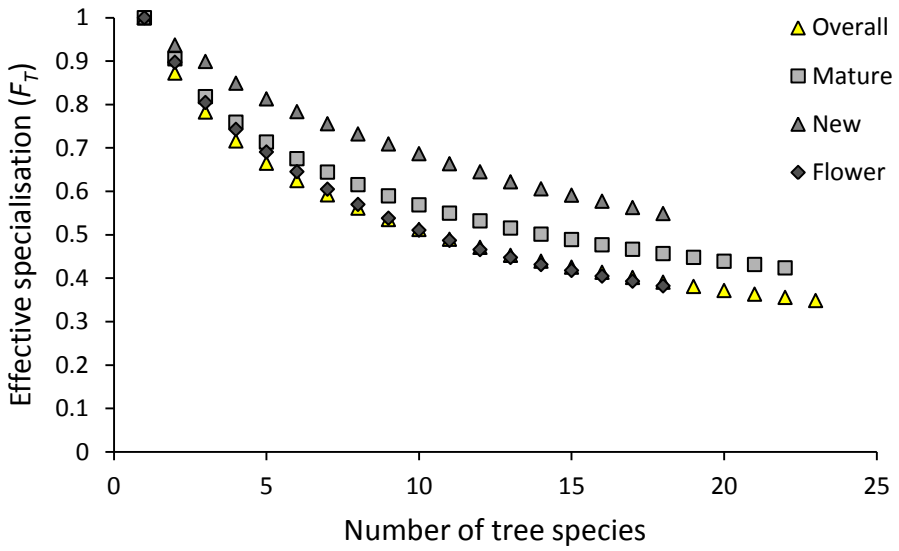

Figure 8.6: Effective specialisation F_T as a function of the number of host tree species sampled for the pooled beetle communities, as well as those inhabiting mature leaves, new leaves and flowers. Data points represent the mean F_T from 100 randomised combinations of the tree species sampled.

The mean number of species effectively specialised to each tree from all feeding guilds combined was 5.64 (± 0.9). The number of herbivorous species in the pooled sample effectively specialised to each tree was 2.57 (± 0.37), while the number of non-herbivorous host specialists per tree was 2.83 (± 0.65). Therefore, just 47.6% of host specific species were herbivores, which is considerably less than the 83% that has previously been assumed. The slight difference in the total number of effectively specialised species (5.64) and the cumulative total from herbivores and non-herbivores (5.4) are due to slight differences in mean specificity measures on each tree species when the data set is divided in the latter analysis.

When broken down into microhabitats, flowers supported 1.91 (± 0.52) herbivorous host specialists, and 1.97 (± 0.59) non-herbivorous host specialists per tree species. Herbivores on flowers thus constituted 49% of all host specialists on this microhabitat. Similar results were found on mature leaves, (2.56 ± 0.42 herbivorous versus 2.51 ± 0.68 non-herbivorous), and new leaves (0.83 ± 0.27 herbivores, and 1.01 ± 0.16 species of non-herbivores) effectively specialised to each tree species. Herbivores therefore constituted

just 50% and 45% of the total number of effectively specialised beetle species per tree species on mature and new leaves respectively.

8.5 Discussion

In this study I tested the prevailing assumption that both host plant specificity and microhabitat specificity of the beetle fauna was higher in foliage-feeding herbivores than non-herbivores or beetles using other microhabitats in rainforest canopies. I found that by every measure, the flower-visiting beetle community was as diverse, unique and host specific as that inhabiting mature leaves. In fact, the flower-visiting beetle community displayed significantly higher levels of plant species host specificity than the foliage-inhabiting community as measured by *HSk* and Lloyd's index. The flower- and mature foliage-inhabiting beetle communities also showed identical community similarity across tree species as measured by the Sorensen index. And the number of host specific beetle species identified using *HSk* was equal between the flower-visiting and foliage-visiting assemblages, with five species each. Overwhelmingly, the evidence suggests that the assumption that host specificity is largely a characteristic of foliage-inhabiting insects must be rejected.

In my samples, the host specific beetle fauna on foliage was similar in guild composition to previous studies, where most specialised beetle species were from families that are predominantly herbivorous. In contrast, host specific flower-visitors included species from predominantly fungivorous and predatory families that were as host specific as species from herbivorous families. Most species on the flowers showed some level of host tree preference (classified as either host specialists or as displaying preference to single host species, genera or families) (Table 8.1). In contrast, few foliage-inhabiting species showed any preferences for particular host plants. This is due to the differences in

host specificity of non-herbivorous species on each microhabitat. On flowers non-herbivores were as host specific as the herbivores, but non-herbivorous species on leaves were distinctly generalised in host use (see Chapter 7). Furthermore, the effective specialisation analyses showed that herbivores only constituted 45-50% of the total number of host specific beetle species per tree species, substantially less than the 83% assumed by Erwin (1982). The second assumption, that host specificity is predominantly associated with herbivorous insects, is therefore also rejected.

The only previous study that has simultaneously examined the host specificity of foliage- and flower-visiting species was carried out in Panama by Ødegaard (2000b). He found that flower-visiting beetles were less host specific than foliage-inhabiting beetles. However, Ødegaard (2000b) focussed only on three herbivorous superfamilies; Buprestoidea, Chrysomeloidea, and Curculionoidea. My results are similar, showing that foliage preferring herbivorous beetles that were specific to single plant species, genera or families, also belonged to the herbivorous superfamilies (Curculionidae and Chrysomelidae) included in Ødegaard's study. Where my results differ from previous work is in the demonstration that non-herbivorous (predatory and fungivorous) flower-visiting species as host specific as herbivorous foliage-inhabiting species. Indeed, 50% of the host-, genus- and family-specific flower-visitors belonged to predominantly non-herbivorous families (Nitidulidae, Staphylinidae, and Cleridae). The implications of this finding are obvious. Had this study also been restricted to these herbivorous superfamilies, the results I found would be largely in agreement with Ødegaard's conclusions. I expect then, that host specificity in Panama would also be greater among flower-visitors if the entire beetle community was examined.

The preponderance of herbivores among the host specific foliage-inhabiting beetle community has been hypothesised to result from co-evolutionary processes involving the

evolution of defensive chemistry by host plants, followed by counter adaptations to overcome those defences by herbivores (Ehrlich & Raven 1964; Bowers 1983; Becerra 1997; Roslin & Salminen 2008; Ballhorn *et al.* 2010). The high proportion of non-herbivorous specialists among flower-visitors, however, suggests that host specificity in this community is not solely the result of an antagonistic co-evolutionary arms race between plants and their natural enemies. Flowers are patchy in space and time (Bawa *et al.* 2003), and many flower-visitors need to travel relatively large distances between floral resources (Gathmann & Tscharntke 2002). They also must be able to locate and orientate themselves towards often isolated flowering trees (Hubbell & Johnson 1978). It has been suggested that host specificity in some insect species may be due to neural limitations and the inability to process large amounts of information (Bernays 2001; Janz 2003). Therefore, rather than being restricted to particular plant species via species-specific defensive characteristics, specialisation may arise because of limits set on locating and identifying a small number of potential hosts from many possible plant species (Jermy 1984; Bernays *et al.* 2000; Janz 2003). If true, host specialisation among many flower-visitors could be the result of adaptation for improved host finding abilities. Moreover, this hypothesis could be applicable to flower-visitors because, unlike co-evolutionary arms race hypotheses, host-specialisation via host finding abilities may be less sensitive to feeding guild, and all flower-visitors must ultimately locate floral resources.

One possible alternative explanation might be that flower-visiting species that I identified and assumed to be non-herbivorous based on family or subfamily level generalisations may in fact be incorrect. We know virtually nothing of the feeding ecology of most tropical insect species, and the assignation of feeding guilds is often based on knowledge of a few well-known species, applied to the entire family (Stork 1987b; Hawkins & MacMahon 1989). This will be a particular problem if well-known species are

not representative of the entire family (Hawkins & MacMahon 1989). Even so, if it is the case that the majority of flower-visitors are miss-identified herbivores, then these species constitute an unrecognised herbivore fauna that has not been accounted for in previous rainforest food web and biodiversity studies, and does not detract from the finding of high microhabitat and host specialisation of flower-visitors that I report.

8.5.1 Host specificity and sample size

Like all studies that examine host-specificity, some caveats must be placed in association with sample size. First, a relatively large number of individuals need to be collected to accurately determine host or microhabitat specificity for a particular beetle species. Indeed, when a small total number of individuals are collected, only two or three individuals need to be recorded from non-hosts or alternative microhabitats to obscure correct assignation of specialist or generalist. Increasing the lower limit for inclusion in analyses should be accompanied by an increase in the ability to identify true habitat and host plant specialisation. Some evidence for this effect exists in my dataset. For example, just 56% of species (27/48) with an abundance between 12 and 49 were identified as microhabitat specialists, whereas 79% of species (23/29) with an abundance of >50 were classified as microhabitat specialists. It is likely then that the true proportion of species that specialise on particular canopy microhabitats is closer to the higher values reported for species with abundances >50.

It is difficult to speculate on how or if the host specialisation results would change with an increase in sample size, as there was no difference in host specificity when analyses were restricted to species with higher abundances (mean (± S.E.) Lloyd's for species represented by > 50 individuals = 9.0 (± 1.1), versus 9.9 (± 1.0) for those with an abundance between 12 and 49). Invariably, an increase in sampling effort increases the

number of host records for particular insect species. This can happen for two reasons. Firstly, an increase in the number of plant species sampled could lead to the inclusion of legitimate host species that were omitted in the original sampling protocol, resulting in a legitimate reduction in host specificity (see Novotny *et al.* 2002a). Secondly, an increase in sampling effort within tree species (i.e., more samples per tree species) leads to an increasing number of spurious host records, thus increasing the number of insect-host associations, resulting in a largely artificial reduction in host specificity (Novotny & Basset 2005; Dyer *et al.* 2007). Provided that indices are used that take account of abundance, the issue of accumulated spurious host records should not be very important, as the number of genuine host records should increase at a greater rate than tourist records on non-hosts (Novotny & Basset 2000), assuming equal sampling effort. Indeed, the median number of host records per beetle species increased disproportionately from 90% abundance (4 hosts) to 100% (6 hosts), as most individuals of most species were only found on a small subset of the total number of host plants sampled.

The measure that was perhaps the most affected by sample size was effective specialisation. This measure incorporates the entire community and can be exaggerated by rare species and underestimated by rare host records for abundant species. Both of these problems appear to have occurred in this study. Firstly, the high proportion of non-herbivorous host specialists identified using effective specialisation on the foliage (45-50% of all host specific species) are at contrast with the results measuring host specificity with Lloyd's index, which showed non-herbivorous foliage beetles were significantly more generalised in host use than herbivores. This is because Lloyd's index was only applied to the most abundant species ($n \geq 12$), while effective specialisation was applied to the entire assemblage, and rare species cannot possibly be distributed across all or a majority of the host tree species. It is therefore unlikely that the foliage supports as many host specific

non-herbivorous species as the effective specialisation measures suggest, since Lloyd's index revealed that the abundant non-herbivores on leaves were not particularly specialised. On flowers however, the effective specialisation measures are more applicable, since there was no difference in the host specificity of abundant herbivores and non-herbivores as measured by Lloyd's index. By combining the results from effective specialisation and Lloyd's index, I suggest that any significant deviation from Erwin's estimate of 83% of host specific species being herbivores will only occur on flowers, where ~50% of host specialists are expected to be non-herbivorous species.

Abundant species can reduce F_T via the accumulation of rare host records. This was especially the case on flowers, where the average number of individuals per beetle species was 44.2, compared to 7.1 on mature leaves and 5.5 on new leaves. While an increase in the number of individuals per species does not automatically result in an increase in host plant records, it does raise the potential for this to occur. Indeed, Figure 8.6 shows that F_T is highest on new leaves, which supported the smallest number of beetle species and individuals, and lowest on flowers, which supported the greatest abundances of beetles, with mature leaves intermediate. For example, the most abundant species in my samples was a flower-visiting weevil that was recorded from 11 different host plant species. Using a presence/absence measure like effective specialisation, this species would be classified as being particularly generalised in host use. However, 99.6% of those individuals came from two species of palms, indicating that they are specialised to the family Arecaceae and do not commonly, or intentionally, utilise the other nine recorded host tree species. These results demonstrate that using more than one measure of host specialisation is imperative. Of particular importance is the use of measures that incorporate variation in abundance between host tree species (Novotny *et al.* 2004b), as those indices using presence/absence data are subject to greater potential errors.

8.5.2 Implications of more host specialists

The immediate conclusion that a higher than expected level of host specificity among presumed non-herbivorous insects associated with flowers is that global biodiversity estimates might be required to be revised upward. Recall that Erwin suggested 83% of host specific species were herbivores. My data suggest that the correction factor based on Erwin's estimate that is commonly used to account for host specific non-herbivores is not applicable to the flower-visitor community, since only 50% of the host specific beetle species on this microhabitat were herbivorous. The original correction factor (x 1.2) should only be applied to foliage inhabiting assemblages, with a correction factor of x 2 used to extrapolate from the number of herbivorous host specific beetle species to all host specific beetle species on flowers.

The degree to which estimates will be revised upward also depend on another important component of global biodiversity estimates; the turnover in species (beta diversity) from the local scale to the regional scale. Currently there are no data on the beta diversity of flower-visitors, or their host specificity in other tropical rainforests. Only if their beta diversity is relatively high, and the host specificity results reported here are found to be generally applicable, is it likely that flower-visitors will substantially increase global species richness estimates. For example, if flower-visiting species are widely distributed, and the folivores are more localised, then flower-visitors will contribute fewer species to the regional (and global) species pool (see Thomas 1990a; Novotny *et al.* 2007). To date flower-visitors have not been accounted for in biodiversity estimates derived from mass sampling of tropical rainforest canopies, so regardless of their beta diversity and host specificity at other locations, flower-visitors constitute a largely under-represented or unrecorded fauna.

In conclusion, host specificity was much higher than previously assumed for beetle communities inhabiting flowers. Previous studies have assumed that host specificity is largely restricted to folivores. However, this study shows that specialisation rates among families that are traditionally considered non-herbivorous is much higher on flowers than on the foliage. In contrast, host specific beetles on the foliage were almost entirely herbivorous. The assumption that host specialisation is largely a phenomenon associated with foliage feeding herbivores is therefore refuted, since flowers support a high proportion of host specific non-herbivorous species. These results emphasise the need for future canopy insect studies to not be restricted to the foliage, since a substantial proportion of the community is located on, and specialised to, other microhabitats, especially the flowers.

Chapter 9:

Body size variation among invertebrates inhabiting different canopy microhabitats: why are flower-visitors small?

Chapter 9: Body size variation among invertebrates inhabiting different canopy microhabitat: why are flower-visitors small?[7]

9.1 Abstract

Factors such as reproductive fitness, climatic tolerance, predation pressure, energetic requirements and the quality and quantity of food sources all interact to influence invertebrate body sizes. This study examines body size variation across an invertebrate community inhabiting five microhabitats (mature leaves, new leaves, flowers, fruit and suspended dead wood) that are thought to differ in quality, quantity, availability, and invertebrate community composition in the canopy of an Australian tropical rainforest. Mean body size varied significantly between invertebrate and beetle feeding guilds and microhabitats. Phylogenetically independent contrasts revealed that invertebrate taxonomic groups were significantly smaller on flowers compared to mature leaves and new leaves. Size differences between microhabitats were most pronounced among herbivorous taxa (Hemiptera, Lepidoptera), in particular the immature stages or those groups that develop on flowers, which were significantly smaller than expected on flowers and larger than expected on leaves. Taxonomic groups with many strong flying species, especially those that complete larval development on resources other than flowers, typically showed no differences in body size across microhabitats. There are a number of potential explanations for the smaller body sizes of flower-visitors presented here, including the physical sizes of the microhabitats (flowers are smaller than leaves), time-dependent mortality factors that promote short development times (flowers harbour higher densities of potential predators and competitors), or differences in the nutritional quality of the microhabitats, all of which

[7] This chapter has been published (18 Oct 2012) with little modification as a multi-authored paper in *Ecological Entomology* (Wardhaugh, C. E., Edwards, W., & Stork, N. E. 2013: Body size variation among invertebrates inhabiting different canopy microhabitat:flower-visitors are smaller. *Ecological Entomology* 38: 101-111.)

can influence minimum body size limits via the relationship between body size and metabolism.

9.2 Introduction

Body size is a fundamental species trait. Development times (Klingenberg & Spence 1997; Blanckenhorn 2000), fecundity (Honěk 1993; Wardhaugh & Didham 2005), dispersal ability (Forkner *et al.* 2008), physiology (Wasserman & Mitter 1978; May 1979; Willmer & Unwin 1981), competitiveness and vulnerability to predation (Connor & Taverner 1997; Beckerman *et al.* 2010) are all strongly influenced by body size. Body size patterns also show distinctive relationships with species richness and abundance in multispecies assemblages (Blackburn *et al.* 1990, 1993a; Stork & Blackburn 1993; Siemann *et al.* 1996, 1999), and have an important influence on community structure (Damuth 1981; Morse *et al.* 1988; Blackburn *et al.* 1990, 1993a, b; Stork & Blackburn 1993; Blackburn & Gaston 1994; Lindström *et al.* 1994; Nylin & Gotthard 1998; Novotny & Basset 1999; Savage *et al.* 2004).

Within species, large individuals often achieve higher reproductive fitness and have greater environmental tolerances than smaller individuals (Shine 1989; but see McLachlan 1986; Ohgushi 1996; Klingenberg & Spence 1997; Nylin & Gotthard 1998), so some directional selection should operate toward larger body sizes. Indeed, it is generally accepted that sexual selection in males and fecundity selection in females primarily act to promote increased body size (Blanckenhorn 2000). However, selection against larger body sizes also exists. Development times usually increase with body size, potentially increasing exposure of vulnerable immature stages to time-dependent mortality factors, such as predation, adverse weather conditions or food shortages (Häggström & Larsson 1995; Bernays 1997; Williams 1999; Blanckenhorn 2000; but see Clancy & Price 1987; Leather

& Walsh 1993; Nylin & Gotthard 1998). Further, habitat constraints can also limit body size. For example, endoparasitic species are constrained by the physical size of their hosts (Fox *et al.* 1996). Bonal and Muñoz (2009) showed that body size of the seed weevil, *Curculio elephas* (Coleoptera: Curculionidae), was limited by the size of the acorns within which their larvae develop. Resource limitation may also exert influence at scale of host plant size. Small plants in general tend to result in reduced adult sizes among insects that complete development on them (Thompson 1983; Dixon *et al.* 1995).

For particular taxonomic groups, locomotion, energy requirements, feeding ecologies, and respiration impose the upper and lower limits in body size (Blackburn & Gaston 1994). For example, the lower limit to body size in endothermic birds and mammals is set by the energetic requirements for maintaining internal body temperatures (Pough *et al.* 1999), while upper size in terrestrial arthropods is limited by diffusion efficiencies of tracheal respiratory systems under given atmospheric O_2 concentrations (Schmidt-Neilsen 1992, cited in Blackburn & Gaston 1994). Novotny and Wilson (1997) proposed that the minimum body sizes of xylem feeding Hemiptera were constrained by the energetic cost of feeding on xylem fluid that is under negative tension and must be physically pumped from the plant. Xylem feeding insects therefore, need to be large enough that the work required to extract xylem fluid is negligible compared to the nutritive benefits gained by consuming it. Xylem fluid is also nutritionally poor (Mattson 1980) and must be consumed in large quantities in order to extract enough nitrogenous compounds to facilitate growth, which may also favour larger insects with longer digestive tracts that can absorb all of the available nutrients. Furthermore, metabolic rate is inversely related to body size (weight) (Elgar & Harvey 1987; Nagy 1987; West *et al.* 2002; Brown *et al.* 2004), resulting in a general requirement for small species to feed on more nutritionally

concentrated food sources than larger species (Horsfield 1977; Augner 1995; Behmer 2009).

The quality, quantity and availability of food may ultimately be responsible for the body size range exhibited within and between many species (Ergon *et al.* 2004; Pfenning *et al.* 2007). As such, there is an expectation that body size distributions should differ between habitat types. Substantial differences in the body size distributions for species inhabiting different broad habitat types (soil, leaf litter, herb layer, tree trunks, and canopy) have been reported in tropical rainforest in Indonesian (Stork & Blackburn 1993). However, as far as I am aware, no published data has examined body size variation at a scale as fine as between microhabitats within single trees. There is reason to suspect differences at this resolution. First, species abundances are negatively related to body size (Damuth 1981, 2007; Blackburn *et al.* 1990, 1993a; Stork & Blackburn 1993; Brown *et al.* 2004). Previous work examining the invertebrate community in an Australian rainforest canopy has shown that abundance varies considerably between different microhabitats (mature and new leaves, flowers, fruit and suspended dead wood) (Chapters 3, 4, 5, and 6). In particular, flowers support densities of invertebrates that are orders of magnitude greater than other microhabitats. Thus, if the abundance-body size relationship holds true within microhabitats on a single tree species, I expect that body size distributions would be very much smaller on flowers in comparison to the other microhabitats. Here, I test this hypothesis by examining body size variation within and between different invertebrate taxonomic groups and feeding guilds collected from each microhabitat, and explore this in more detail using beetle taxa alone in separate analysis. I discuss possible hypotheses for why taxa or feeding guilds vary in body size between microhabitats, including habitat size constraints, predation pressure, and the nutritional quality of the microhabitats.

9.3 Methods

9.3.1 Study site

For study site description see Chapter 3, 3.3.1.

9.3.2 Sampling

For sampling procedures see Chapter 3, 3.3.2.

9.3.3 Invertebrate sorting

For sorting procedures see Chapter 3, 3.3.4.

9.3.4 Body size measurements

A representative of each beetle species and every other individual invertebrate was measured from the front of the labrum to either the tip of the abdomen (excluding cerci or ovipositors) or the end of the elytra for some Coleoptera (which ever is longer) using a calibrated graticule. For most beetle species there was little variation in body size, therefore a single individual was selected at random. For the few species in which individuals varied noticeably in size (~10% of species, mostly Curculionidae), the mean size was calculated from a sample of up to five individuals. All samples are stored at James Cook University, Cairns.

9.3.5 Statistical analyses

Since different food sources can influence invertebrate body sizes, I first tested whether invertebrate and beetle feeding guilds differed in body size between each other and on different microhabitats using two-way ANOVA and $Log_{10}(x+1)$ transformations. Different microhabitats also differ in the physical size of habitat units (i.e., individual leaves or

flowers). To test for the influence of microhabitat size, the relationships between flower and leaf size (dry weight biomass) and the body sizes of each of the 26 taxonomic groups and eight feeding guilds where n ≥ 10 individuals on at least two microhabitats were explored using linear regression. The minimum abundance limit of 10 individuals on at least two microhabitats was chosen as a compromise between including a maximum number of groups for comparisons while excluding those with insufficient abundances to detect significant differences in body size, if they exist.

Next I tested whether individual taxonomic groups differed in body size between microhabitats. Whereas the initial two-way ANOVA described above tests for broad differences in body size between microhabitats and feeding guilds, this analysis identified which taxonomic groups, if any, are significantly smaller or larger on each microhabitat. For this I carried out a randomisation procedure to identify significant deviations from random expectation in body size of invertebrate taxonomic groups inhabiting different canopy microhabitats. This process involved taking the entire invertebrate sample (40,374 individuals) and randomly assigning each individual to microhabitat types to generate an expected mean body size of each taxonomic group on each microhabitat. See Chapter 4 (section 4.3.4) for details on the randomisation procedure and how comparisons were made between expected measures and true measures. Analyses were again restricted to those taxonomic groups where abundance was ≥10 on at least two microhabitats.

Lastly, since broad comparisons of body size distributions between microhabitats that group taxa into a single mean estimate will be confounded by phylogeny, I also attempted to correct for this using phylogenetically independent contrasts (PIC's) (Felsenstein 1985). PIC's were used to test for coordinated changes in body size and microhabitat utilisation across multiple independent divergences. The null hypothesis for the test is that divergences in one aspect (microhabitat usage) are not associated with

divergences in another (body size). The mean difference in body size between different microhabitats was thus tested against a null hypothesis of zero using a paired t-test. Fruit and dead wood invertebrate communities were omitted from this analysis due to the low numbers of invertebrates collected from these microhabitats.

Because beetle taxa were categorised at a much finer resolution (Family and sub-family) than all other groups, I used a similar procedure of a set of phylogenetically independent contrasts using data for beetles. Due to low species richness and family level diversity on new leaves, fruit and dead wood, only the single contrast comparing flower-visiting species and mature leaf-inhabiting species was possible. All body size measurements were $Log_{10}(x+1)$ transformed prior to analyses to normalise the data.

9.4 Results

9.4.1 Body size variation between feeding guilds and microhabitats

A two way ANOVA showed a significant interaction between microhabitat identity and invertebrate feeding guild ($F_{22, 422} = 3.69$, $P < 0.0001$). Body size varied significantly between invertebrate feeding guilds ($F_{7, 422} = 52.22$, $P < 0.0001$) but not significantly

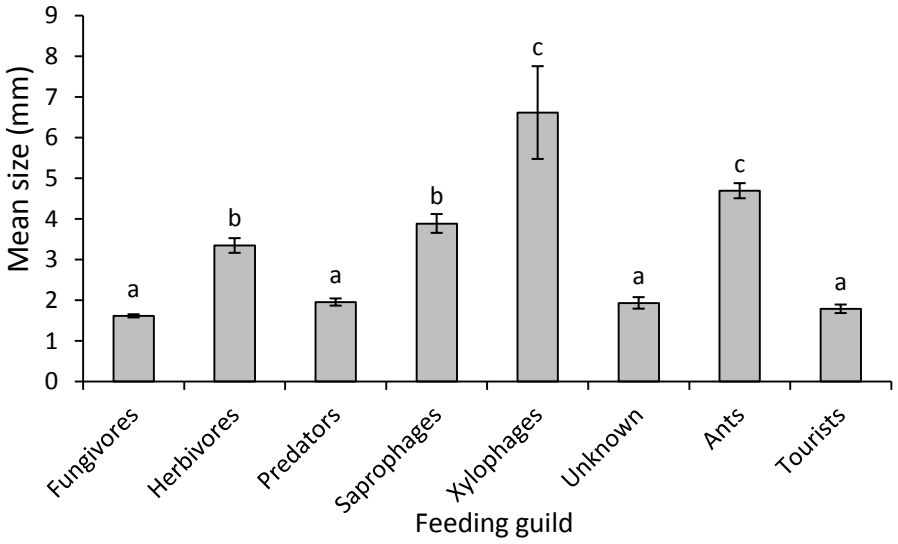

Figure 9.1: The mean body size (± S.E.) of each invertebrate guild in the pooled sample. Letters indicate significant differences in size between feeding guilds.

between microhabitats $F_{4, 422} = 2.39$, $P = 0.0505$). Mean body size (± SE) decreased in the order Xylophages (6.61 ± 1.18) = Ants (4.69 ± 0.19) > Saprophages (3.89 ± 0.23) = Herbivores (3.34 ± 0.18) > Fungivores (1.61 ± 0.04) = Tourists (1.79 ± 0.1) = Predators (1.95 ± 0.09) = Unknown (1.93 ± 0.14) (Fig. 9.1).

At the level of beetle species, there was a significant interaction between feeding guild and microhabitat on body size of beetles ($F_{19, 214} = 2.183$, $P = 0.0039$). Body size of beetle species varied significantly between microhabitats ($F_{4, 214} = 4.498$, $P = 0.0016$) and feeding guilds ($F_{5, 214} = 14.681$, $P < 0.0001$) (Fig. 9.2a). When analysed at the individual

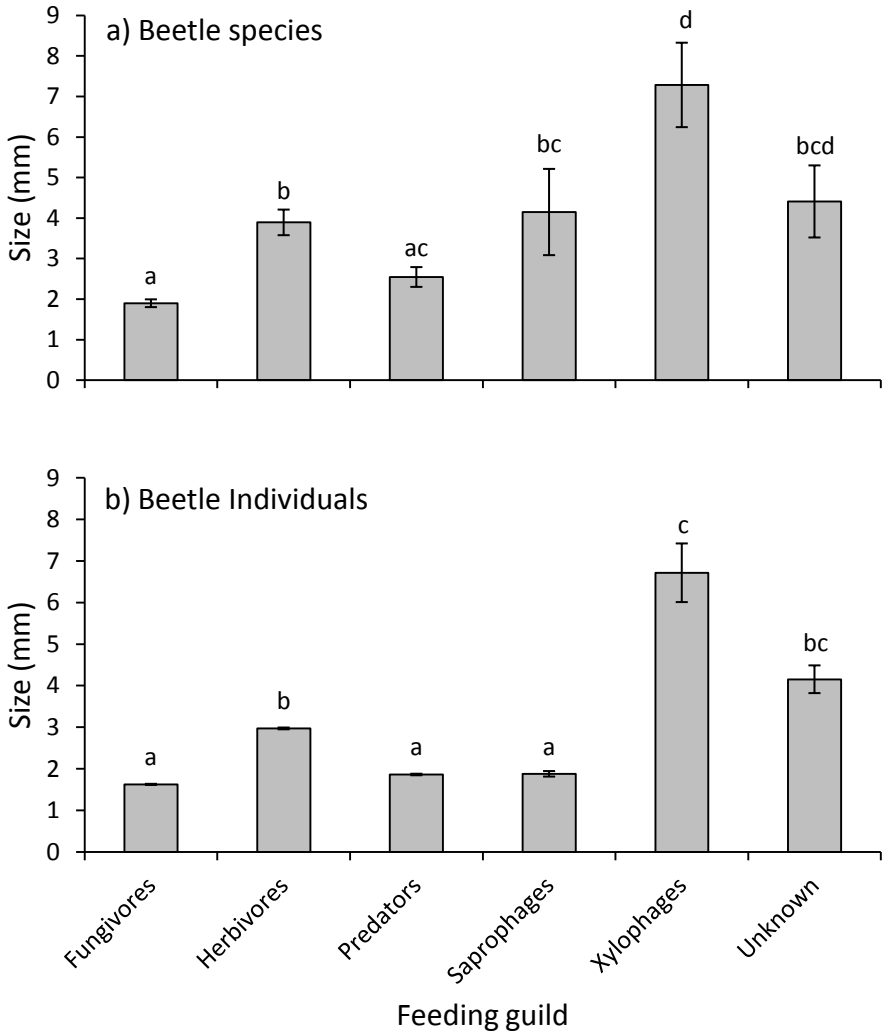

Figure 9.2: The mean body size (± S.E.) of each feeding guild at the level of a) beetle species and b) individual beetles. Letters indicate significant differences in size between feeding guilds.

abundance level, there was a significant interaction between feeding guild and microhabitat in beetle body size ($F_{19, 214} = 2.043$, $P = 0.0078$). Body size varied between microhabitats ($F_{4, 214} = 4.399$, $P = 0.0019$) and feeding guilds ($F_{5, 214} = 9.694$, $P < 0.0001$) (Fig. 2b). Mean body size (± SE) of beetle species decreased in the order Xylophages (7.28 ± 1.04) > Herbivores (3.89 ± 0.32) > Predators (2.55 ± 0.24) = Fungivores (1.9 ± 0.1) (Fig. 9.2a).Similar differences in the body sizes of feeding guilds were found when analysed at the individual level (Fig. 9.2b).

9.4.2 Body size variation of taxonomic groups between microhabitats

There was an overall trend for taxa to be smaller on flowers, especially among herbivores. Six of the ten herbivorous taxonomic groups were significantly smaller on flowers than expected based on the randomisation model (summarised in Table 9.1). Within the herbivores, a number of immature groups (Lepidoptera caterpillars, mesophyll-feeding and phloem-feeding Hemiptera nymphs) were significantly smaller than expected on flowers. Three of the five predatory groups (Acari, Araneae and predatory Coleoptera) were also significantly smaller than expected on flowers. In contrast, herbivores (Lepidoptera caterpillars, mesophyll feeding adult Hemiptera, and phloem feeding adult and nymphal Hemiptera) and two predator groups (Acari and Coleoptera) were significantly larger on mature leaves than expected. Adult Formicidae were the only group for which body size was significantly larger than expected on flowers. No taxonomic groups differed significantly in body size on fruit and suspended dead wood, with the exception of Thysanoptera on suspended dead wood, which were larger than expected. Most remaining taxonomic groups, including saprophagic groups, Hymenoptera, Diptera and most Coleoptera guilds, showed no significant deviations from random expectation in body size on different microhabitats (Table 9.1).

Table 9.1: The mean body size (mm) of invertebrates within each taxonomic group across the five microhabitats. Measurements are shown only for those groups where at least 10 individuals were collected from that particular microhabitat. Numbers in red with – signs signify those taxonomic groups that are smaller than expected under randomness on that particular microhabitat, while numbers in green with + signs signify those groups that are larger than expected. Numbers in black did not differ from random expectation in mean body size.

	Flowers	Mature leaf	New leaf	Fruit	Wood
Predators					
Acari	**0.37-**	**0.45+**	0.40	0.41	0.43
Hymenoptera	1.52	1.31	1.37		
Araneae	**2.12-**	2.49	**2.90+**	2.30	2.18
Larvae (Neuroptera)	4.21	2.88			
Coleoptera	**1.74-**	**2.24+**	1.81		
Formicidae					
Adults	**5.58+**	**4.32-**	**5.24+**	5.11	5.30
Larvae		3.00	3.27	2.97	
Saprophages					
Blattodea	5.02	5.39	6.34		6.23
Collembola	1.20	1.30	1.14	1.50	1.21
Coleoptera	1.77	2.63		1.7	
Herbivores					
Larvae (Lepidoptera)	**4.24-**	**9.36+**	7.19	3.98	4.93
Cicadellidae nymph	2.59	3.56	2.79		
Gastropoda		3.57	3.86		
Mesophyll feeders	**3.39-**	**7.38+**	6.49		
Mesophyll nymph	**1.88-**	3.06	5.29		
Orthoptera	7.85	8.93	12.71		8.59
Phloem feeders	**1.62-**	**3.85+**	3.01		
Phloem nymph	**0.61-**	**1.87+**	**1.69+**		
Thysanoptera	**1.03-**	1.03	**0.79-**	1.14	**4.69+**
Coleoptera	2.95	3.02	3.15	3.03	
Fungivores					
Psocoptera	1.54	1.73	1.69	1.70	1.64
Coleoptera	1.66	**1.44-**	1.43	1.29	1.94
Xylophages					
Coleoptera	9.75	6.37			
Tourists					
Diptera	1.76	1.67	1.64		
Unknown					
Larvae (Coleoptera)	1.50	**2.27+**			1.43
Larvae (Diptera)	1.63	**1.18-**	**0.93-**		
Total Invertebrates	**1.79-**	**2.96+**	**3.29+**	2.50	**2.92+**

9.4.3 Body size and microhabitat biomass

Mean body size among flower-visitors was not related to flower size (dry weight biomass) on different tree species for any of the 26 invertebrate groups or eight feeding guilds (all $P > 0.1$) with the exception of fungivorous beetles which showed a positive relationship ($F_{1, 16} = 11.8793$, $R^2 = 0.4261$, $P = 0.0033$). Leaf size (dry weight biomass) also had no effect on the body sizes of the foliage invertebrate community either as a whole ($F_{1, 20} = 0.3273$, $R^2 = 0.016$, $P = 0.57$), or when different taxonomic groups or feeding guilds were analysed separately (all $P > 0.05$).

9.4.4 Phylogenetically independent contrasts

Phylogenetically independent contrasts revealed a coordinated and repeated change in body size with microhabitat for invertebrate taxonomic groups, which were significantly smaller on flowers compared to mature leaves ($t_{19} = 2.36$, $P = 0.03$) (Fig. 9.3a), and new leaves ($t_{18} = 2.64$, $P = 0.017$) (Fig. 9.3b). PCI's revealed no difference in body size between invertebrate taxonomic groups inhabiting mature and new leaves ($t_{19} = 0.35$, $P = 0.73$) (Fig. 9.3c). Between beetle species within the same families, PIC's showed no difference in body size between flowers and mature leaves ($t_{19} = 1.24$, $P = 0.23$) (Fig. 9.4).

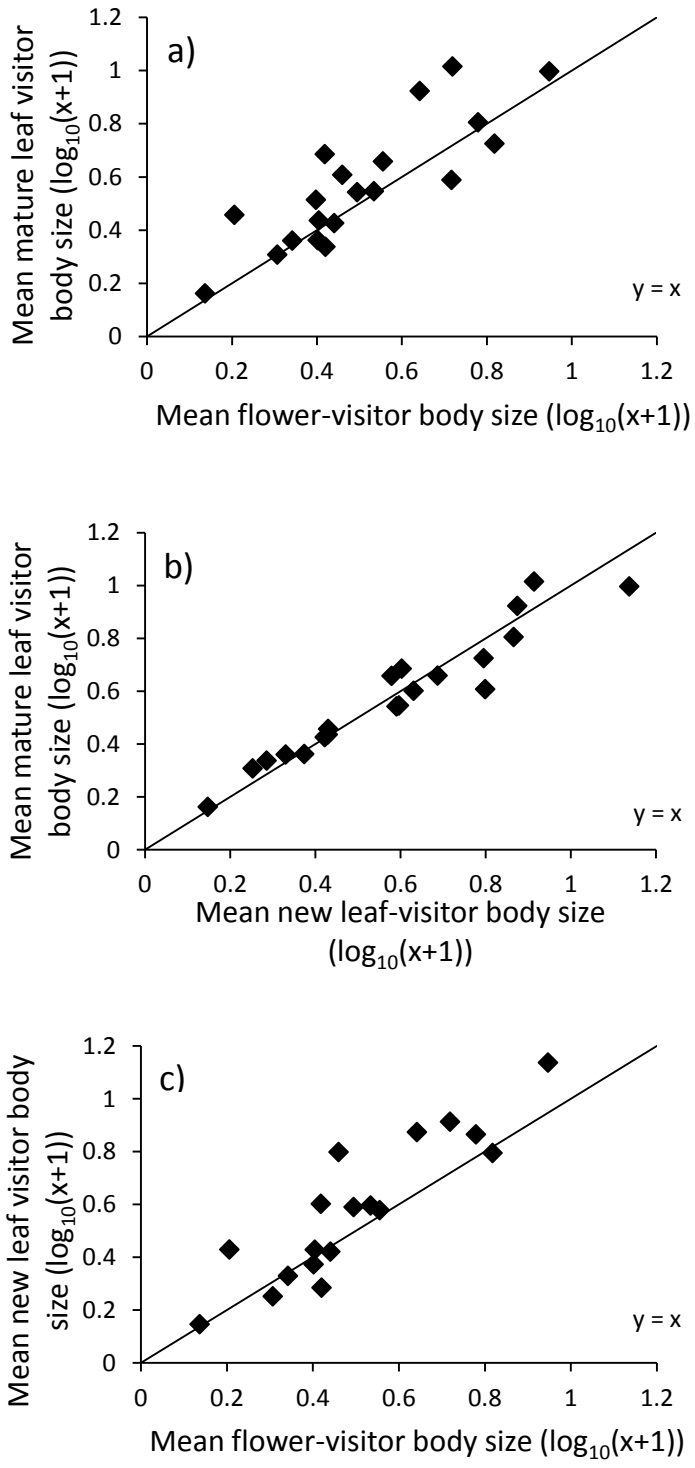

Figure 9.3: The mean body size ($\log_{10}(x + 1)$) of invertebrate taxonomic groups in phylogenetically independent contrasts between a) mature leaf and flower-visiting taxa, b) mature leaf and new leaf taxa, and c) new leaf and flower-visiting taxa. The trend lines in each graph represent the null hypothesis of no difference in mean body size between microhabitats (y = x). Points above the line represent taxonomic groups that are larger on the microhabitat represented on the y axis, while points below the line represent groups that are larger on the microhabitat on the x axis.

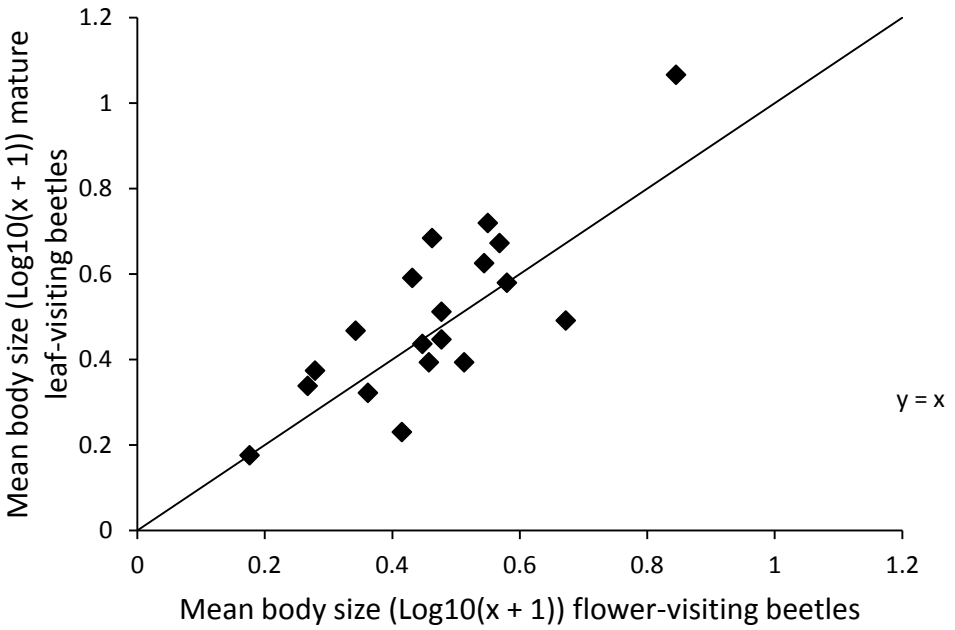

Figure 9.4: Phylogenetically independent contrasts in mean body size ($\log_{10}(x + 1)$) of flower visiting beetle species and confamilial species inhabiting mature leaves. The trend line represents the null hypothesis of no difference in mean body size between microhabitats (y = x). Points above the line represent beetle families that are larger on the microhabitat represented on the y axis (mature leaves), while points below the line represent families that are larger on the microhabitat on the x axis (flowers).

9.5 Discussion

The distribution of body sizes for invertebrates differed significantly between microhabitats, and PIC's showed that invertebrates collected from flowers were (on average) smaller than those collected from other microhabitats. These results support the hypotheses that body size varies between canopy microhabitats and that invertebrates on flowers are smaller than invertebrates inhabiting the other focal microhabitats. PIC's carried out between beetle species on flowers and mature leaves showed no differences in body size associated with microhabitat identity. Half of the taxonomic groups (6 out of 12) for which mean body size was identified as being significantly different from that expected under randomness were herbivorous, and half of these (3 out of 6) were immature stages (larvae and nymphs). All of the herbivorous taxa that differed significantly from random

expectation in mean body size were smaller on flowers are larger on other microhabitats. This pattern suggests that size differences among many invertebrate groups could be linked to factors associated with larval growth, while those same selective forces may have less effect on those species that develop elsewhere and only visit the focal microhabitats as adults (e.g., Hymenoptera, Diptera, various Coleoptera). Body size also varied significantly between different invertebrate and beetle feeding guilds. The general pattern found in both sets of analyses was for a decrease in body size of feeding guilds in the order; xylophages > herbivores > fungivores = predators, with only the saprophages varying markedly in body size between the analyses of invertebrate feeding guilds and beetle feeding guilds.

9.5.1 Why are flower-visitors small?

Body size in invertebrates is often influenced by diet during the larval stages (Scriber & Slansky 1981). During juvenile development, increased nutritional quality of food often result in increased growth rates (Heisswolf *et al.* 2005; Cornelissen & Stiling 2006) and larger adult body sizes (but see Cornelissen & Stiling 2006), which usually have positive effects on survival and reproduction (Ohgushi 1996; Awmack & Leather 2002). But immature stages of invertebrates are typically less mobile than adults and are exposed to high mortality rates due to predation or food shortages (Häggström & Larsson 1995; Bernays 1997; Williams 1999; Blanckenhorn 2000; but see Clancy & Price 1987; Leather & Walsh 1993; Nylin & Gotthard 1998). Under these conditions, selection should favour rapid growth in order to minimise time spent in the vulnerable larval stage (Nylin & Gotthard 1998). This creates conflict between the advantages of prolonging the larval stage and thereby attaining a larger adult size, and the presumed reproductive benefits that larger size confers, and shortening the larval period to minimise juvenile mortality risks. Life histories (including developmental periods) of individual species represent the outcome of

the compromise between these extremes. The following sections discuss potential hypotheses to explain the differences in body size found between canopy microhabitats, and in particular why flower-associated invertebrates are smaller than their relatives on leaves. Each of these hypotheses, with the exception of *Nutritive and metabolic explanations*, is primarily concerned with larval development, and are thus unlikely to apply to all adult invertebrates. However, it should be noted that taxonomic groups that include adults (phloem and mesophyll feeding Hemiptera, Thysanoptera, Araneae, Acari) likely all develop on flowers, and their final adult body sizes could be the result of processes operating on immature stages.

9.5.2 Time-dependent mortality factors

Since significant deviations in body size were prevalent among the same immature and adult insect groups (e.g., Hemiptera groups), it is possible that differences in body size between microhabitats are driven by the necessity for rapid development of insects on flowers in response to increased vulnerability to juvenile mortality. Flowers harboured high densities of predators (mites, spiders, see Chapter 4), which could make flowers a particularly dangerous place for developing herbivorous insects. Romero and Vasconcellos-Neto (2004) provide tangenital evidence for the strength of predation pressure that may exist on flowers. They showed that predation of herbivorous insects due to flower-dwelling spiders on *Trichogoniopsis adenanther* (Asteraceae) was great enough to exert positive effects on seed production by reducing herbivore numbers and thus damage to reproductive structures. Insects that develop on flowers may therefore experience very high rates of predation, and thus short development times may be advantageous. A similar argument could be made for competition. Flowers are locations of very high densities of invertebrates (Chapter 3), so resource competition could also be

intense. In this case, rapid development could reduce time spent competing for limited resources.

The ephemeral nature of flowers could also impose limits on development time for florivorous insects. Most trees do not flower continuously, or even for prolonged periods (Bawa *et al.* 2003). In this study most trees were recorded as flowering during a single sampling period (32/44 individuals), and just five trees flowered on more than two consecutive sampling periods (i.e., for more than 8 weeks; a *Syzygium sayeri*, an *Argyrodendron peralatum*, and an *Acmena graveolens* for three consecutive months and two *Syzygium gustavioides* trees which flowered almost continuously). Single inflorescences last for shorter time periods, and individual flowers last little more than one day for most generalist insect-pollinated plant species (Primack 1985). Developing on flowers could thus constrain development as a function of resource availability, especially since flowers supported very high densities of potential competitors. Insects that develop on flowers may therefore have short larval or nymphal stages, resulting in small body sizes as adults. In contrast, individual leaves on tropical rainforest trees last from several months to several years (Coley 1988). Consequently, foliage-feeding species, even those that develop on a single leaf (e.g., leaf miners), may not be subject to the same temporal constraints to development time as flower-feeding species.

9.5.3 Nutritive and metabolic explanations

Small species cannot survive on poor quality food because the energetic costs of obtaining the meal outweigh the nutritional benefits (see Novotny & Wilson 1997). Flowers are generally a more nutritious food source than leaves (Carisey & Bauce 1997; Irwin *et al.* 2004), which may allow for the maintenance of very small body sizes. This could explain why many herbivorous groups were smallest on flowers, and the overall pattern in changes

in mean body size among feeding guilds supports this hypothesis (Mattson 1980). For example, in the analyses using the entire invertebrate assemblage and those using just beetle species, I found mean body size to decrease across feeding guilds in the order xylophages > herbivores > fungivores = predators. This order represents decreases in nutritional quality of the resources used by each group; wood < living plant material < animal prey = fungi. Similar patterns in body size were found by Grimbacher and Stork (2007) who showed that xylophagous and herbivorous beetle species captured at the same site (Daintree Rainforest Observatory) were larger than predaceous or fungivorous species.

9.5.4 The physical size of microhabitats

While ecological factors can affect body sizes as discussed above, it is possible that differences in body size between microhabitats simply reflect differences in the physical sizes of those microhabitats (Dixon *et al.* 1995). For all tree species examined in this study, flower sizes were very small compared to leaf sizes (only *Merremia peltata* flowers were larger in dry weight biomass than the smallest mature leaves). I found little support for this proposition. There was no relationship between flower size and the body size of any invertebrate group except fungivorous beetles, which showed a positive relationship between flower size and body size as predicted. Leaf size also had no effect on the body size of foliage-inhabiting invertebrates.

Most tree species sampled produced dense inflorescences, which greatly increases the amount of flowers available in the immediate area, despite the small size of individual flowers. Thus, it is not necessarily the case that individual flowers are the appropriate level to consider habitat size/body size relationships, since aggregations of individual flowers within inflorescences results in a large total biomass in a small local area. The physical size of flowers may thus only restrict the maximum sizes of endophagous species, with little

affect on externally feeding flower-visiting species, which constituted the majority of the invertebrates collected in this study. For example, I found that there were no differences in body size between microhabitats among strong flying groups such as Diptera, Hymenoptera and many Coleoptera feeding guilds. However, spiders were also significantly smaller than expected on flowers, which could be the result of selection favouring the ability to hide among or within small flowers. Indeed, most spiders on flowers were sit-and-wait hunting crab spiders (Thomisidae), which rely on camouflage to hunt flower-visitors (Llandres *et al.* 2011). It is possible therefore, that spiders and perhaps some other invertebrate groups may be smaller on flowers because flowers are physically small.

9.5.5 Life history stage and microhabitat switching

Lastly, differences in body size of immature taxa between microhabitats could be due to the use of different resources during larval or nymphal development. For instance, small early instars may be more vulnerable to chemical defences that are prevalent within the foliage (van Dam *et al.* 2001), but not within floral tissues (e.g., Carisey & Bauce 1997). Variation in susceptibility to chemical defences dependent on life history stage could therefore facilitate diet switching. Immature chewing herbivores (such as caterpillars) may also need to attain a given size before their mouthparts and related muscles are physically able to process toughened leaf material (Bernays 1986; Bernays & Janzen 1988). Early instars may therefore feed on flowers before switching to foliage once large enough to mechanically handle leaf material (see Bernays 1986). However, if habitat switching does occur in this system, it is likely to be restricted to chewing herbivores, and thus have little effect on community level differences in body size identified between microhabitats.

Indeed, body size differences between microhabitats are more likely to be the result of different microhabitats supporting different species of invertebrates. For example, for phloem and mesophyll feeding Hemiptera, both adults and nymphs were significantly smaller than expected on flowers, indicating that the differences are due to true differences in body sizes between species that occur on flowers and those that occur on other microhabitats. These differences are also responsible for the significantly larger body sizes of Thysanoptera on dead wood compared to flowers and leaves, and the smaller than expected body sizes of spiders on flowers. Dead branches supported a large and distinctive species of Thysanoptera (adults were typically over 10mm in length, compared to 0.5 to 2 mm for most other species) that was not found on any other microhabitat (*personal observation*), and was likely the main driver of body size differences between microhabitats for Thysanoptera. In the case of spiders, flowers supported large numbers of small crab spiders, while the foliage supported a wide variety of larger actively hunting species (*personal observation*).

9.5.6 Conclusions

This exploratory study represents the first demonstration of body size differences of invertebrate taxonomic groups between different canopy microhabitats. In particular, I showed that invertebrates sampled from flowers were significantly smaller in body size than invertebrates collected from other microhabitats. This pattern was demonstrated across a number of mostly herbivorous taxonomic groups, indicating that size differences may be related to feeding biology. There are a number of potential (and not necessarily exclusive) hypotheses for this that require further investigation. The first include factors that promote rapid development via high rates of mortality associated with inhabiting flowers, such as predation and competition, or temporal changes in resource availability

which are particularly pronounced on flowers. Invertebrate size variation is often related to diet quality, but whether nutritional quality is the proximate or ultimate cause of the observed size differences is unresolved. Small size may also arise as a function of the physically smaller habitat size that flowers present in comparison to leaves, which may account for the smaller body sizes of some predatory groups (spiders, mites) on flowers. Finally, it is also possible that some species switch microhabitats as they grow. My data do not discount the feasibility of either time-dependent mortality factors or nutritional variation as drivers of body size differences between microhabitats. Nutritional variation and metabolic rates in particular are promising, since they can be applied to both adult and immature life history stages. My data do not lend support to the hypotheses that invertebrates are smaller on flowers than leaves due to differences in the physical size of microhabitat units (with the possible exception of one or two predatory groups), or because species switch microhabitats during development. The challenge now is to thoroughly test these hypotheses using manipulative experiments to separate and identify the relative strengths of the effects of these possible causative factors.

Chapter 10:

General discussion

Chapter 10: General discussion

The principal conclusion from my thesis is that discrete microhabitats support unique invertebrate faunas in tropical rainforest canopies. I have argued in Chapter 2 that resource diversity is the most important driver of high total biodiversity at the local scale in tropical rainforests, while the subsequent data chapters have demonstrated marked differentiation in community composition between adjacent microhabitats. The main conclusions from each component of this thesis are as follows:

1. The density/kg of invertebrates varies widely (by up to four orders of magnitude) between microhabitats. In particular, flowers support densities per unit biomass of microhabitat that are up to 10,000 times higher than on mature leaves, and 1,000 times higher than on new leaves (Chapter 3).

2. Species richness of beetles is not proportional to microhabitat biomass. New leaves and flowers supported a disproportionately high number of species on the trees sampled (23.5% and 40.9% respectively), despite constituting just 2.5% and 0.06% of crown biomass respectively (Chapter 3).

3. Microhabitats varied widely in beetle species composition, and virtually no species were insensitive to microhabitat identity in terms of abundance. Even mature leaves and new leaves, which are relatively similar resources compared to other combinations of the other microhabitats, were still very dissimilar in community composition (Chapters 3 & 5).

4. Each microhabitat supported a unique community in terms of guild structure. Community composition was broadly related to the distribution of preferred food sources. For instance, herbivores were concentrated on new leaves and flowers, while fungivores and saprophages were particularly abundant on dead wood (Chapters 4 & 6).

5. Heterogeneity in abundance of beetles, invertebrate taxonomic groups and feeding guilds between tree species varied significantly between microhabitats. In particular, the abundances of flower-visitors varied more between different tree species than the abundances of foliage-inhabitants, which were more even across tree species (Chapters 4, 5 & 6). This was largely due to the fact that flower-visitors achieved greater abundances than invertebrates on other microhabitats, resulting in a greater potential for variation in abundance.

6. Host specificity was equally high among the mutualistic flower-visitor community and the antagonistic foliage-inhabiting herbivore community (Chapter 7). While host specificity among leaf-inhabitants is largely restricted to herbivores, non-herbivorous beetle species on flowers are as host specific as herbivores on both flowers and leaves. The previous assumption that most host specialists on a tree are herbivores on the leaves is refuted since flowers supported many host specific species from other feeding guilds (Chapter 8).

7. Chapter 9 constitutes the first demonstration of body size variation between arboreal microhabitats. Phylogenetically independent contrasts revealed that flower-visitors tend to be smaller than their relatives on the other microhabitats, suggesting that there is selective pressure on either flower-visitors to be small, and/or species on other microhabitats to grow larger.

10.1 Trees are more than their leaves

Over the last 30 years many studies on the spatial and temporal patterns in the diversity and abundance of rainforest invertebrates have been carried out, theories postulated, and hypotheses tested. Central to many of these hypotheses and theories are numerous assumptions; some based on large amounts of evidence; some on very little; and some that

have progressed from educated guesswork to dogma with little scrutiny (see Erwin 1982; Stork 1988; Ødegaard 2000a; Basset 2001b; Novotny & Basset 2005). Some of these assumptions have been overturned in light of more recent evidence. In particular, many of the numerical values that Erwin (1982) assumed or estimated to calculate 30 million species of arthropods have been altered or revised (see Chapter 2). However, almost all of our current hypotheses, estimates, predictions, and theories have been based on a subset of the canopy fauna inhabiting a single microhabitat; namely herbivores (or more precisely various subgroups of herbivores) on mature foliage. The primary result of this thesis is the recognition that the invertebrate assemblage inhabiting the leaves is *not* representative of the wider canopy community, and that each microhabitat supports a unique assemblages in terms of guild structure, composition, relative abundances, species richness, host specificity, and density. In particular, my results show that flowers constitute a very important, but until now under appreciated, microhabitat for species richness and abundance.

It is clear from the results presented here (and from previous work in other rainforest locales (Stork & Blackburn 1993; Ødegaard 2000b, 2004)) that canopy insect communities are made up of relatively discrete subsets of species that have an additive effect on species richness. Indeed, despite making up just 0.06% of mature leaf biomass/ha, flowers supported a rich beetle community (~250 species across the 18 tree species that flowered). These species were as host specific as the foliage community resulting in little overlap in species composition between tree species (Chapters 3, 7 & 8). Especially notable is the fact that many host specific beetle species that visit flowers are from families that have not been included in other studies that have focused on herbivores. The high densities and specialisation of "fungivores" and some "predators" such as nitidulids, phalacrids, and staphylinids constitute a missing or ignored plant-associated

fauna. These families were recorded in very low numbers from the foliage, and traditional methods of guild assignment remove these species from estimates of herbivore species richness.

My results have also confirmed the importance of new leaves to rainforest herbivores, by corroborating the findings of previous studies that have found higher densities of folivores on flush foliage (Murali & Sukumar 1993; Barone 2000). Guild assessments also showed that few non-herbivorous taxa were attracted to new leaves (Chapters 4 & 6), reinforcing the idea that this resource is predominantly associated with folivores. Dead wood attracted few invertebrates, but this was mainly through scarcity of the resource rather than being underutilised. When present, dead wood did support a relatively rich fauna, but the higher than expected numbers of singletons found on dead wood suggest that it was not thoroughly sampled (Chapter 5). Previous work in Panama showed that dead trees can attract a high diversity of beetle species (Ødegaard 2004), and there are many diverse beetle families that are found predominantly in or under decomposing wood (Lawrence & Britton 1991; Lawrence *et al.* 2000; Grove 2002a). The one microhabitat that was poorly utilised in the canopy was fruit. Fruit supported very few invertebrates and this was true when expressed either as the total number of individuals or the number of beetle species. Species level analyses suggest that the fruit fauna in the canopy was comprised mostly of transient species "spilling over" from adjacent microhabitats (Chapter 5), and that few externally feeding species actually utilise this resource while in the canopy (Grimbacher *et al.* in prep).

10.2 Future work

As this is one of the few studies to examine the fauna attracted to flowers in tropical rainforests, it is difficult to conclude that the patterns reported here are applicable to other

tropical forests. This is because flower attending insects are very poorly understood at the present. Indeed, the pollination biology of less than 1% of the plant species in the Australian Wet Tropics has been studied, and the Australian flora is much better known than most tropical rainforest areas (Gross 2005). Some information is available for some areas or plant groups (Bawa *et al.* 1985; Gottsberger 1986, 1988). For instance, Ødegaard (2004) has shown that flowers attract a species rich and relatively unique community of herbivorous beetles within the canopy in Panama, but little work has been carried out in other parts of the neotropics. In South-east Asian dipterocarp forests it is becoming apparent that beetle pollination is more important than previously thought (Momose *et al.* 1998). Indeed, it was long assumed that thrips were the dominate pollinators in these forests, but recent evidence suggests that it was wrong to apply this assumption to all dipterocarp species (Momose *et al.* 1998). Furthermore, Hansman (2001) found that 88% of 141 plant species in a dry rainforest in Australia were pollinated by insects, including 22% by beetles and a further 25% by generalist insects. Only 3% were pollinated by vertebrates, and just 13% were pollinated exclusively be bees, which are usually the dominant pollinators in most other locations (Bawa *et al.* 1985). Almost nothing is known of flower-visitors or pollinators within the rainforests of Africa, India, Madagascar, New Guinea or the islands of the Pacific (but see Frame & Dorou 2001). Future studies that incorporate a standardised examination of the pollination syndromes and flower-visitor profiles from multiple plant species in multiple rainforest locales is needed (Renner & Feil 1993).

The ability of forests to recover from disturbance relies on the ability of trees to reproduce (see Lamb & Erskine 2008). Equally, the ability of animal species to recover and/or survive relies on the availability of their food sources. With tropical forests under threat from logging and land clearing for agriculture (Laurance 2003, 2008; Laurance *et al.*

2002, 2005, 2011; Corlett & Primack 2008), it is of paramount importance to identify pollinators and flower-visitors of rainforest plants, how they interact, their distributions, and their requirements for maintaining a viable long-term population (e.g., House 1993). Only with this knowledge is it possible to definitively protect intact, functioning ecosystems for the long-term (Terborgh 1992; Gathmann & Tscharntke 2002; Fontaine *et al.* 2006; Potts *et al.* 2010; Tylianakis *et al.* 2010).

While my work has identified flowers as a particularly important microhabitat for the maintenance of species richness and abundance of canopy insects, other microhabitats also warrant more research. Resources such as fruit and dead wood were scarce in the canopy and were subsequently utilised by few canopy invertebrates (Chapters 4, 5, & 6). However, these resources are much more plentiful on the forest floor (Grove 2001), where they are utilised by a wide diversity of beetle species that often occur at relatively high densities (Grove 2002b; Grimbacher *et al.* in prep). Future work could focus on comparing the canopy and ground level fruit and dead wood faunas to establish whether the canopy fauna is merely a subset of the more substantial ground fauna. This could best be achieved through experimental manipulations where fresh fruit and cut branches are placed in the canopy and on the ground in a pair-wise arrangement and monitored over time. It is also likely that these resources attract a large proportion of internally feeding species (e.g., pre-dispersal seed predators, and wood borers), so an investigation of the fauna that feed on all fruit components is also warranted. Determining the vertical stratification of fruit and dead wood associated species has implications for global biodiversity estimates, since the proportion of canopy to ground species is an important assumption used in multiplicative calculations (Erwin 1982).

The preceding section advocates an extension of the overall aim of this project to examine where invertebrates are in the canopy. But beyond establishing where canopy

insects are distributed, there are also questions about how insects find, move between and utilise canopy resources. For example, what cues (e.g., olfactory, visual) do insects use to find fruit, flowers, new leaves, a particular host species, or a dead branch? Furthermore, in Chapter 8 I show that fungivorous and predatory beetles display high levels of host specificity on flowers. However, it is unknown what resources these species are utilising, or even if they really are fungivores and predators. Important future work on canopy insect communities therefore should focus on what these species are doing in the canopy, since this will have important implications for food web and interaction network analyses (see Kitching 2006; Lewinsohn *et al.* 2006; Fontaine *et al.* 2009; Novotny *et al.* 2010).

Information on canopy ecology is required for future planning under climate change (Stork 2001). Flowering often occurs in response to climatic cues (Chapman *et al.* 2005), especially in mass-flowering species such as the Dipterocarpaceae (Brearley *et al.* 2007). These climatic cues can also be tracked by flower-visiting insects and other species, resulting in temporal synchronisation of floral resources and flower-visitors (Hegland *et al.* 2009). Similar tracking can also occur for insect species that utilise fruit or flush leaves (van Asch & Visser 2007). Since many trees rely on climatic cues to initiate growth and/or reproduction, changes in the intensity, frequency, and timing of phenological events are likely under a changing climate (Graham *et al.* 2003; Chapman *et al.* 2005; Visser & Both 2005; Körner & Basler 2010). These changes will flow-on to the insects that utilise those resources, potentially altering rates of pollination, herbivory, seed predation and seed dispersal (Coley 1998; Memmott *et al.* 2007; van Asch & Visser 2007; Hegland *et al.* 2009; Potts *et al.* 2010). Predicted changes in precipitation, cloud cover and CO_2 concentrations could also affect plant-insect interactions (Louda & Collinge 1992; Reich 1995; Coley 1998; Graham *et al.* 2003; Thomas *et al.* 2004; Stork *et al.* 2007; van Asch & Visser 2007; Balston 2008). Work on how the predicted effects of climate change will

impact the phenology of both plants and insects are needed to identify species at risk of temporal and spatial mismatching between interacting partners.

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