IMPACTS OF CLIMATE CHANGE ON PLANT-INSECT INTERACTIONS

Sabine Nooten, Dipl. Biol.

Department of Biological Sciences
Macquarie University

Submitted May 2013

This thesis is presented for the degree of Doctor of Philosophy

‘*Tempora mutantur, nos et mutamur in illis*’

– Anon

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SUMMARY

Current and future climate change will have profound impacts on species interactions and communities. This thesis investigates the community structure and composition of insect communities on Australian native plant species, with the ultimate aim of predicting possible impacts of climate change. To this end, three topics were investigated: firstly the Coleoptera and Hemiptera fauna associated with several host plant species from three important Australian plant families were assessed across the plant species' native range, in terms of morphospecies composition and feeding guild structure. Secondly, possible impacts of climate change on these communities were investigated using a multispecies transplant experiment, in which plants were planted into sites that are approximately 3°C warmer, in terms of mean annual temperature. Thirdly, levels of total leaf herbivory and damage types were assessed on plant species, both across the current range and within the transplant experiment. Assessments of the Coleoptera and Hemiptera fauna across the plant species native range revealed little commonality, in terms of morphospecies composition and feeding guild structure, among plant species within each family. This was reflected by herbivory patterns, which were species-specific and characterised by changes in dominant feeding types among plant species. The assessment of potential impacts of a warmer climate on these plant-insect communities via the transplant experiment showed that for each individual plant species, Coleoptera and Hemiptera community composition may undergo significant turnover, whereas herbivore feeding guild structure may remain relatively unchanged. This relative stability between host plants and their phytophagous guilds was reflected by largely consistent patterns of leaf herbivory between native and warmer sites. We conclude that transplant experiments provide a powerful means of exploring the impacts on natural systems of a rapidly changing climate.

DECLARATION

I certify that the work in this thesis entitled ‘Impacts of Climate Change on Plant-Insect Interactions’ has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research work and the preparation of the thesis itself have been appropriately acknowledged.

In addition, I certify that all information sources and literature used are indicated in the thesis.

Sabine Nooten (Student ID: 41608755)
May 8th , 2013

ACKNOWLEDGEMENTS

Many people have helped and supported me during my PhD candidature, and without them this thesis would be quite different, if it would be at all.

First, I would like to thank my supervisor Lesley Hughes for the opportunity to work on this amazing project. Her continued support, guidance and knowledge have been invaluable. Lesley managed to keep me focused and stay on track. I am also grateful to my associate supervisor, Mariella Herberstein.

I am most grateful to my adjunct co-supervisor Nigel Andrew. He was very helpful throughout my whole thesis, especially in disentangling my insect data and getting the analyses going. Nigel gave valuable moral support whenever I felt crushed by the immenseness of the project. Nigel and his partner Sarah were most accommodating during my time in Armidale, thanks for the fish.

My partner Patrick Schultheiss has been, and continues to be, wonderful. I thank him with all my heart for his love, patience and support (and food). Patrick has helped me so much with fieldwork, collecting insects, clearing transplant sites, and reading manuscripts. Huge hug for you! Whichever country we are living in, he simply manages to bring more joy into my heart.

From the very first day, Katherine McClellan and Nola Hancock have been not only colleagues but great friends. I am most grateful for the joint fieldtrip with Kath exploring the deep south of the continent and collecting insects and leaves on the way. It was great fun, thank you! I am very thankful to Nola, for her generous help with transplanting 480 plants into the sites at Minnie Water and Wooli. It was a fantastic time, …bog in!

I would like to thank Kerinne Harvey for her good company during the endless hours of insect sorting (which we both had to do) and valuable ideas about reducing neck tension. She also was a great help in exploring herbivory types and reading manuscripts.

I would also like to thank Abigail Cabrelli for inspiring discussions and feedback on manuscripts, Alex Bush and David Nipperess for interesting conversations and help with statistics.

Many thanks to several more people for their help during field and lab work: Cornelia Bühlmann, Claudia Schlegel, Manuel Nagel, Neville O'Loughlin.

At Macquarie University, I would like to thank all those who have made my time in Sydney very enjoyable. Thanks to Fernando, Felipe, Mayra, Julia, Marianne, Marco, Seppi, Antoine, Dan, Dani, … oh this is hopeless. All others: Thank you, [insert name here]!

Lastly, I would like to thank my parents Margrit and Wolfgang Nooten for putting up with a daughter they rarely see, and for letting me do my thing. Thanks.

CHAPTER I

INTRODUCTION

Global climate change

Human-induced climate change is already affecting species and ecosystems, chiefly through rising air and ocean temperatures, higher frequencies of warm days and nights, decreases in cold days and nights, heavier precipitation events, and more intense and longer droughts (IPCC 2012). Over the last century, mean global surface temperatures have increased by ~0.7°C (Allison et al. 2009; Braganza & Church 2011). In the last 25 years, the rate of global warming has increased by 0.2°C per decade (Allison et al. 2009; Burrows et al. 2011). These climatic changes are now confidently attributed to higher levels of atmospheric greenhouse gases due to human activities (IPCC 2011). The current concentration of atmospheric CO_2 is just over 400 ppm, an increase of nearly 40% above pre-industrial levels (IPCC 2011). The key drivers of CO_2 emissions are fossil fuel combustion and land use changes (Raupach et al. 2007; Le Quere et al. 2009). Emission rates continue to accelerate, with a rate of +3% per year during the first decade of this century compared to the rate of +1% at the end of last century (Raupach et al. 2007; Le Quere et al. 2009; Friedlingstein et al. 2010). In 2010, global greenhouse gas emissions rose at a record rate of 5.9%, which was the highest annual growth recorded, eclipsing previous records in 1979 and 2003 (Peters et al. 2012). Current emission rates are tracking the highest-emission scenario (A1FI), described by the Intergovernmental Panel on Climate Change (IPCC) in their last assessment report (AR4) (Raupach et al. 2007; Allison et al. 2009; Le Quere et al. 2009; Peters et al. 2012).

Climate change in Australia

Recent climate trends in Australia are consistent with those recorded globally. Average air temperatures have increased by ca. 0.9°C over the past 100 years, with an accelerated rate of warming during the last 50 years (Braganza & Church 2011;

CSIRO 2012). Although warming in Australia is consistent with the global average, there are regional variations across the continent, with the weakest warming in the northwest and the strongest across the eastern part of the continent (Braganza & Church 2011; CSIRO 2012). Since 1910, annual daily maximum temperatures have warmed by 0.75°C and minimum temperatures by more than 1.1°C (Steffen et al. 2009; CSIRO 2012). During the past ten years, the average temperature has been more than 0.5°C warmer than the 1961-1990 average, with each decade being warmer than the previous one (CSIRO 2012). 2011 was the warmest year on record during a La Niña event (CSIRO 2012). Precipitation patterns in Australia are highly variable in space and time, but there has been a general trend during recent decades towards an increase in spring and summer monsoon rainfall in the north, more rainfall than usual across the central regions, and a decrease in late winter and autumn rainfall in the south (Braganza & Church 2011; CSIRO 2012). Severe weather events such as droughts and floods have become more frequent, with higher frequency and duration of heat waves, and lower frequency of cold days and frosts (Braganza & Church 2011; CSIRO 2012).

Projections for global and Australian future climates

Future climates are dependent on the amount of emitted greenhouse gases (Allison et al. 2009; Le Quere et al. 2009; Solomon et al. 2009; Friedlingstein et al. 2011; Raupach et al. 2011). Globally, temperatures are projected to rise by 4-7°C until 2100 under high emission scenarios, and by 2-3°C under more conservative scenarios (Allison et al. 2009; IPCC 2007). The frequency of warm temperature extremes is projected to increase and the frequency of cold daily temperature extremes to decline (IPCC 2012). Globally, precipitation patterns are expected to change (increasing or decreasing depending on the region), and the frequency and intensity of extreme weather events such as heat waves, floods, droughts, and cyclones, will likely increase (IPCC 2012).

In Australia, temperatures are projected to rise 0.6-1.5°C by 2030, compared to the climate of the late 20th century. Further warming by 2070 is projected to be in the range of 1-5°C if global greenhouse gas emissions lie within the range of projected emission scenarios considered by the IPCC (Steffen et al. 2009; Lambeck

2010; CSIRO 2012). Warming is projected to be greater inland compared to coastal regions (Suppiah et al. 2007). The frequency of hot days and warm nights is likely to increase and the number of cold days and nights is projected to decline (CSIRO 2012). Rainfall is predicted to decline in the southern part of the continent and increase in the north, and it is very likely that locally intense rainfall events will become more extreme (CSIRO 2012). In the south, a long-term drying trend over southern areas during winter and in southern and eastern areas during spring is projected (Frederiksen et al. 2011; CSIRO 2012). Severe weather events such as heat waves, droughts, flooding and bushfires are expected to become more frequent (CSIRO 2012).

Many features of the Australian landscape and its biota suggest that Australian species and ecosystems will be particularly vulnerable to the impacts of rapid climate change. A large proportion of Australian species are endemic with narrow geographic and climatic ranges (Orians & Milewski 2007; Steffen et al. 2009; Thomas 2010; Hughes 2011; Laurance et al. 2011; Ohlemueller 2011). The lack of topographic relief (Augee & Fox 2000; Orians & Milewski 2007) across much of the continent means that most species have a limited capacity for altitudinal migration to adjust to shifting climate zones (Loarie et al. 2009; Steffen et al. 2009; Hughes 2011; Laurance et al. 2011). This means that species will have to move considerably further latitudinally than altitudinally to track climate change (Parmesan & Yohe 2003; Burrows et al. 2011). Such latitudinal shifts may not be possible for many species, chiefly because habitat loss and degradation in many regions, due to clearing for agricultural and urban development, will limit opportunities for dispersal and establishment in new habitats. Furthermore, Australian ecosystems are subject to a range of other existing stresses such as invasive species, nutrient-enrichment of soils and waterways, and dryland salinity (Steffen et al. 2009); these stresses will reduce the resilience of species to the ‘new stress’ of climate change.

Climate change impacts on species - general

Over the last half century (1960-2009) the mean velocity of climate change across global land surfaces was 27.3 km per decade (Burrows et al. 2011). The highest velocity was estimated to be in flat land areas such as low lying grasslands and forests, mangroves and deserts, and the lowest velocity in mountainous areas

(Loarie et al. 2009; Burrows et al. 2011). Climate change is now considered a major threat to global biodiversity, next to habitat destruction and invasive species (Thomas et al. 2004; Maclean & Wilson 2011).

Profound impacts are expected on the distribution, abundance and ecology of virtually all species (Hughes 2000; Walther et al. 2002; Parmesan & Yohe 2003; Root et al. 2003; Parmesan 2006; Rosenzweig et al. 2008). Many species are predicted to be at greater risk of extinction (Thomas et al. 2004; Hannah 2012). Adaptive responses include genetic change, and changes in physiology, behaviour, distribution and/or phenology (Hughes 2000; Root et al. 2003; Parmesan 2006; Rosenzweig et al. 2008; Visser 2008; Hoffmann & Sgro 2011; Parmesan et al. 2011). Many species have already responded by shifting their geographic ranges either polewards, with an average of 6.1 km per decade, or to high elevations - by 6.1 m per decade (Parmesan & Yohe 2003). Shifts in phenology are already apparent with an overall spring advancement in life cycle events of 2.8 days per decade (Root et al. 2003; Parmesan 2007; Rosenzweig et al. 2008). A meta-analysis conducted across many taxa showed that the magnitude of spring advancements is variable and that amphibians, birds and butterflies showed the greatest spring advancement, whereas herbs, grasses and shrubs showed the least (Parmesan 2007).

Climate change impacts on species - insects

Arthropods, and especially insects, are by far the most diverse group of organisms on earth, contributing substantially to global biodiversity (Wilson 1988; May 1990; Chapman 2009) and they are critical components of many terrestrial food chains. The proportion of phytophagous insects alone is approximately one quarter of all described species and about half the number of species of the global insect fauna (Strong et al. 1984). Insects have detrimental as well as beneficial effects on ecosystems: they can be pests and devastate large areas, but also perform crucial ecosystem services such as pollination; these ecosystem services may be severely altered under a changing climate (Harrington et al. 2001).

Recent studies have identified insects as particularly vulnerable to warming temperatures (Deutsch et al. 2008; Netherer & Schopf 2010; Wilson & Maclean 2011), because many stages within insect life cycles are cued by environmental

factors such as temperature (Bale et al. 2002). High sensitivity to climatic changes also make insects potentially useful indicators of a changing climate (Hodkinson & Bird 1998). Climate change impacts on insects may be direct, via effects on their physiology and behaviour, or indirect, via climate-induced changes in species with which they interact, such as host plants (Bale et al. 2002). Some insects have already responded to climate change with changes in phenology, especially with the advancement of spring events such as first spring flights (e.g. Forister & Shapiro 2003; Kearney et al. 2010). Many insects have also responded with changes in distribution, either latitudinal (e.g. Parmesan et al. 1999; Musolin 2007), or altitudinal (e.g. Wilson et al. 2007; Merrill et al. 2008). Increased numbers of generations per year have been observed in some species, leading to increased population sizes (Altermatt 2010). These types of responses may result in a higher frequency of insect outbreaks, with potential threats to agriculture and forestry (Coley 1998; Harrington et al. 2001; Logan et al. 2003; Cornelissen 2011).

Climate change impacts on communities

Individualistic species responses to climate change will affect interactions (competition, predator-prey, host-parasite etc.), with some existing relationships becoming increasingly decoupled (Tylianakis et al. 2008; Thackeray et al. 2010; Hughes 2012). Present day plant-insect interactions may be disrupted because the greater mobility and climate sensitivity of many insects means they have greater capacity to adapt to climate change than their hosts, either through range shifts or changes in phenology. These differences in responses may lead to pronounced mismatches in trophic interactions; e.g. differential changes in phenology leading to temporal mismatches in interactions between plants and herbivores (Visser & Both 2005; Parmesan 2007), or between plants and insect pollinators (Memmott et al. 2007; Hegland et al. 2009). Differential shifts in distribution and phenology of interacting species within communities have already resulted in pronounced changes in community composition and structure (reviewed in Walther 2010). For example, the disassembly of communities due to climate driven range shifts are already apparent across various ectotherm and endotherm species in temperate and tropical communities (Sheldon et al. 2011). These same range shifts can also lead to the establishment of new communities (Gonzalez-Megias et al. 2008; Thomas 2010).

Temperature increases in particular, have been found to have profound impacts on community composition. Studies have reported compositional changes in detrital arthropod communities (Lessard et al. 2011) and herbivore insect communities (Musolin 2007; Villalpando et al. 2009) associated with warming. In some cases, entire herbivore communities have responded to climate change with uphill range shifts of the component species, while retaining a similar composition (Wilson et al. 2007).

Climate change impacts on herbivory

Particularly strong associations exist between plants and their phytophagous insect community (Strong et al. 1984; Cornelissen 2011). The impacts of climate change on herbivore communities raise several questions. For example, how might current climate change affect the herbivore community a host plant harbours? To what extent might herbivore damage change in the near future, and how might this affect the host plants' performance? Metabolic rates increase with temperature, potentially leading to an increase in consumption rates (Dillon et al. 2010). Based on changed herbivory patterns during past warming periods (Wilf & Labandeira 1999; Wilf et al. 2001), and the hypothesis that there is more herbivore damage at lower latitudes (Coley & Barone 1996), it has been suggested that climate change may lead to intensified herbivore pressure on host plants (Coley 1998; Bale et al. 2002). Intensified herbivore pressure, with negative consequences for the host plant, due to recent climate change has been reported (Kozlov 2007; Cornelissen 2011; Garibaldi et al. 2011). Comparisons of herbivory rates at different latitudes, however, provide contrasting results, with some studies finding an increase of herbivore damage towards lower, warmer latitudes (Morrow & Fox 1989; Pennings et al. 2007; Pennings et al. 2009), others finding the opposite trend (Adams & Zhang 2009; del-Val & Armesto 2010), and still others finding no effect of latitude at all (Andrew & Hughes 2005c; Andrew & Hughes 2007; Sinclair & Hughes 2008; Moles et al. 2011).

How can we predict climate change impacts?

Many predictions about climate change impacts on individual species are derived from species distribution models (SDMs), which are based on the statistical relationship between species' occurrences and environmental variables (e.g. Berry et al. 2002; Pearson et al. 2002; Beaumont et al. 2007; Roubicek et al. 2010). These models are useful tools for understanding relative species' vulnerabilities to climate change but they have well known limitations, including the fact that they typically do not incorporate the effects of species interactions into their predictions (reviewed by Guisan & Thuiller 2005; Van der Putten et al. 2010). Manipulative experiments in controlled environments have also been used to assess the potential impacts of factors such as increased temperature and elevated atmospheric CO_2 (e.g. Johns et al. 2003; Coll & Hughes 2008) but tend to be limited in replication and the numbers of factors tested. Other studies have used thermal tolerance curves of insects to predict impacts of warming on insect populations (Deutsch et al. 2008).

The challenges of predicting future impacts of climate change for individual species are significant. At the community level, however, these challenges are orders of magnitude greater. General predictions about plant communities have been made using large-scale dynamic vegetation models (e.g. Malcolm et al. 2002; Keenan et al. 2012; Murray et al. 2012). On a more local scale, potential changes in communities have been assessed using field surveys along latitudinal (e.g. Andrew & Hughes 2004; Andrew & Hughes 2005a, b), and altitudinal gradients (e.g. Colwell et al. 2008; Chen et al. 2009; Garibaldi et al. 2011). A few studies have also related long term changes in communities to environmental changes (e.g. Voigt et al. 2003), but such data sets are relatively rare. Other studies have used warming experiments in the field to assess impacts of increased temperature on communities (Barton et al. 2009; Pelini et al. 2011). One of the most powerful techniques to predict the future is to transplant species or groups of species to new climatic habitats and measure their response. Despite their potential as predictive tools, relatively few such studies have been performed in relation to climate change. Those that have been performed have mainly focused on plant communities (e.g. Bruelheide 2003; Egli et al. 2004; Ibanez et al. 2008; de Frenne et al. 2011; Haggerty & Galloway 2011; van der Veken et al. 2012) with only a few focused on plant-insect assemblages (e.g. Andrew & Hughes 2007; Marsico & Hellmann 2009; Pelini et al. 2009).

The research described in this thesis investigated potential changes in plant-insect communities using a multi-species transplant experiment. In addition to investigating potential changes in community composition, I also assessed community structure by grouping species into feeding guilds (Root 1973; Simberloff & Dayan 1991). The results of this study, in addition to building predictions about the potential future impacts of climate change, also offer some fundamental insights into the factors that shape the structure of present-day insect communities on plants.

What factors drive community structure?

The factors that shape the structure of insect communities on plants have long been an area of interest in community ecology (Lawton 1982; Southwood et al. 1982; Kennedy et al. 1984; Strong et al. 1984), though many questions remain unresolved (Lewinsohn et al. 2005). Numerous possible drivers for community structure have been discussed, such as the regional and local species pool (Cornell & Lawton 1992; Ricklefs 2004; Harrison & Cornell 2008), species traits (Weiher & Keddy 1995; McGill et al. 2006) or stochastic processes (Bell 2001; Hubell 2001). A better understanding of the fundamental drivers of community assembly will significantly improve our predictions as to how these communities will respond in the future to climate change. In this study I test two hypotheses about possible drivers of community assembly: climatic factors and plant characteristics.

Hypothesis 1: *Species assemblages in a particular location are largely a product of the local environment, including the climate.*

MacArthur (1972) proposed that climatic factors are the main drivers of community composition and structure. He based this idea on observations of the convergence of species traits, i.e. organisms from different ancestral lines occupying similar environments tend to have similar morphological characteristics. MacArthur extended this observation to conclude that there must be a similar pattern for community properties, namely community convergence. He suggested that the main mechanism by which climate affects species ranges and communities is probably through the impact on species interactions. Species interactions, such as competition and predation, are thus considered the main drivers of communities (Hutchinson

1959; MacArthur 1972). Consequently, alteration in climatic variables, for example temperature increase and/or elevated CO_2, might differentially affect species interaction strengths and thus the characteristics of assemblages (Petchey et al. 1999; Emmerson et al. 2005). Studies investigating changes to trophic interactions between plants, herbivores and predators have revealed that increased temperature strengthens the indirect top down effects on plants (e.g. Barton et al. 2009; O'Connor 2009). More recently, Thomas (2010) found that anthropogenic climate change strongly affected the position of range boundaries of terrestrial animal species, with climate contributing indirectly through alterations to species interactions. These included positive effects, such as changes in mutualistic interactions and availability of resources, and negative effects, including alterations of competitive interactions.

Climatic factors have been found to affect the composition and structure of numerous arthropod communities; for example, temperature influences the structure of detrital arthropod communities along an elevation gradient (Lessard et al. 2011). Precipitation has also been found to be associated with the structure of canopy arthropods in Douglas fir forests (Progar & Schowalter 2002). When multiple climatic drivers were investigated in relation to the insect community in an old-field experiment, increases in temperature were found to have the strongest effect, with particularly profound impacts on the herbivore guild (Villalpando et al. 2009).

Hypothesis 2: *The major determinant of herbivore community structure is the host plant (Strong et al.1984).*

There are two principal, though not mutually exclusive, ways that host plants might affect the structure and composition of the insect communities that use them as habitat: the characteristics of their general abundance and distribution, and the characteristics of the individual plant species.

Firstly, widespread and common plant species are generally associated with more diverse insect communities; the number of species has been found to decrease with smaller patch size, which can be explained by the species-area relationship (see Strong et al. 1984). Several studies have found evidence for the importance of the hosts' abundance in shaping the associated insect community (e.g. Southwood 1961; Kennedy et al. 1984; Novotny et al. 2012).

Secondly, there is strong evidence that the chemical and physical characteristics of individual host plants can drive the structure of insect communities; insect communities tend to be more similar on closely related plant species (Novotny et al. 2002; Ødegaard et al. 2005; Weiblen et al. 2006; Nipperess et al. 2011). Chemical properties in particular, especially secondary metabolites, have been found to affect both the composition and structure of herbivore insect communities (Jones & Lawton 1991; Ricklefs & Marquis 2012). The influences of the host plants' physical traits on insect communities have received far less attention. The term 'plant architecture' was introduced to describe a variety of plant attributes, such as size, growth form, as well as the seasonal development, persistence and variety of above ground parts (Schroder & Lawton 1977; Lawton 1983). Various plant architectural attributes have been found to affect the phytophagous insect community (Moran 1980; Moran & Southwood 1982; Basset 1996; Campos et al. 2006). More recent studies also provide evidence that host plant identity may be a major driver for insect assemblages, regardless of environmental factors. Arthropod communities along an extensive climatic and latitudinal gradient show consistency in trophic structure and the distribution of feeding guilds (Andrew & Hughes 2004, 2005a, b).

There is an urgent need to identify the principal drivers of insect community composition and structure and to assess the effects of global climate change on plant-insect associations (Lewinsohn et al. 2005; Cornelissen 2011). Studies along environmental gradients are particularly revealing. For example, a survey along a latitudinal gradient spanning 1500 km showed that although the composition of the herbivore community displayed significant spatial turnover, community structure in terms of the feeding guild distribution, stayed remarkably constant (Andrew & Hughes 2004, 2005a, b). These results support best the hypothesis proposed by Strong et al. (1984) that herbivore community structure may be principally driven by characteristics of the host plant. Given that this study, however, used only a single host plant species, the question remains as to whether these results are generalisable.

The overarching aim of the work described in this thesis was to conduct both field surveys and a large-scale manipulative (transplant) experiment to understand the factors driving insect community structure on a range of host plant species in eastern Australia. I have specifically expanded the work and methods of Andrew & Hughes (2007) to encompass multiple host plants in three of the most important plant families in Australia. The ultimate goal of this work is to provide a basis for predicting how such insect communities will be affected as the climate changes rapidly over the next century.

Thesis organisation

Chapter 2

In this chapter I characterised the insect fauna on three host plant species from each of three major Australian plant families, the Fabaceae, Myrtaceae and Proteaceae. The insects were collected, using pyrethrum knockdown, across each host species' native distribution in southeast Australia. I focused on the highly speciose orders Coleoptera and Hemiptera. Species in these orders can be reliably identified to family/subfamily level and feeding guilds can be assigned to families. The Coleoptera and Hemiptera communities were assessed in terms of species richness, density, composition and structure. These measures were determined for the orders as a whole, and also for the subset of phytophagous species.

My aim was (i) to compare species richness and (ii) community composition among host plant species, both within and among plant families, and (iii) to investigate the relationship between the community and factors such as phylogeny, size, architectural complexity and leaf traits of the host plants. This chapter is intended for publication in the journal *Austral Ecology*. It is co-authored by Lesley Hughes, who provided suggestions for the experimental design and comments on the manuscript (my contribution to the experimental design: 80%, data collection 100%, data analysis 100% and writing 90%).

Chapter 3

In the third chapter I assessed the amount of herbivore leaf damage on host plants at three sites within their native range. I used a subset of four of the plant species used in Chapter 2 to investigate regional variation in both total leaf damage and in the pattern of damage types (chewing, sucking, mining and galling).

This chapter is intended for publication in the journal *Austral Ecology*. This chapter is co-authored by Lesley Hughes, who provided comments on the manuscript (my contribution to the experimental design: 100%, data collection 100%, data analysis 100% and writing 90%).

Chapter 4

In the fourth chapter I assessed how climate change, in particular increased temperatures, may affect insect communities. I used the same plant species as in Chapter 2 to investigate the insect community in a similar fashion, i.e. focusing on the Coleoptera and Hemiptera community and their herbivore subset. I was interested in determining the relative influence of climate and plant characteristics as drivers of community structure.

Eight plant species were grown from seed. Plants were then transplanted outside their native range into two warmer sites located ca. 600 km north of the host plants' northern most boundary. These plants were thus exposed to a +2.5°C increase in mean annual temperature, which simulates one important aspect of the climate projected ~50 years into the future. A third transplant site was established within the plants' native range and served as a control. All sites had similar soil properties, general vegetation type and average annual precipitation. Insect colonisation was monitored for one year. I then compared the composition and structure of the insect communities between (i) the control site (ii) the warm sites and (iii) on congeneric host plant species native to the warm area. This chapter is intended for submission to the journal *PLoS ONE*. Lesley Hughes and Nigel Andrew are co-authors of this chapter; L. Hughes provided suggestions to the experimental design and comments on the manuscript, N. Andrew provided suggestions on data analyses and comments on the manuscript (my contribution to the experimental design: 80%, data collection 100%, data analysis 90% and writing 90%).

Chapter 5

In the fifth chapter I assessed herbivory on a subset of four plant species used in the transplant experiment, comparing total herbivore damage and pattern of damage types at the warm sites with that of the control site located in the plants' current range. The aim of this work was to make predictions as to how levels of herbivory might be expected to change in a warmer climate.

This chapter is intended for submission to the journal *Austral Ecology*. This chapter is co-authored by Lesley Hughes, who provided comments on the manuscript (my contribution to the experimental design: 80%, data collection 100%, data analysis 100% and writing 90%).

Chapter 6

In the sixth chapter I summarise the main findings from the separate research chapters, discuss the assumptions and limitations of the methods, and suggest future directions of research in this field.

Appendix I contains a paper to which I contributed during my PhD candidature. It investigates the foraging ecology of the Australian desert ant *Melophorus bagoti*.

- Schultheiss, P. & Nooten S. S. (2013). Foraging patterns and strategies in an Australian desert ant. *Austral Ecology* in press. doi:10.1111/aec.12037

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CHAPTER II

Role of plant family and plant architecture in driving insect community structure: a comparison of nine Australian plant species

This chapter is intended for submission to *Austral Ecology*

Role of plant family and plant architecture in driving insect community structure: a comparison of nine Australian plant species

Sabine Nooten[1], Lesley Hughes[1]

[1] Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

Abstract

While there has been longstanding interest in the factors that shape the composition and structure of insect communities, many fundamental questions remain. We compared species composition, and the distribution of feeding guilds within Coleoptera and Hemiptera assemblages collected from nine plant species, selected from three of the largest Australian plant families. We compared the relative role of host plant family and architectural traits in explaining insect community characteristics. Assemblage composition varied significantly among plant species within families. Numbers of Coleoptera and Hemiptera morphospecies collected from each plant species varied greatly, and there was little commonality in morphospecies among plants within each family. When the feeding guild structure of the Coleoptera and Hemiptera assemblages was considered as a whole, there was no consistency within host plant families and among plants with similar architectural traits (leaf size). In contrast, when the guild structure of only the phytophagous members of these two orders was considered, assemblage structure was found to be consistent among plant species with a similar leaf size.

Keywords: Coleoptera – Hemiptera – insects – herbivores – community – composition – structure – feeding guild – relatedness – plant architecture

Introduction

Insects are the most diverse group of organisms on earth, and account for a large proportion of global biodiversity (Wilson 1988; May 1990; Chapman 2009). Phytophagous insects alone account for approximately one quarter of all described species (Strong et al. 1984). Insect faunas vary considerably among different host plant species (e.g. Southwood et al. 1982a; Cornell & Kahn 1989; Peeters et al. 2001; Proches 2008) and there has been longstanding interest in understanding the mechanisms responsible for this variation (e.g. Hochuli 1996; Lewinsohn et al. 2005). Factors that may be associated with the structure and composition of insect communities include plant community composition and structural diversity (Southwood et al. 1979; Woodcock et al. 2007; Schaffers et al. 2008; Woodcock & Pywell 2009) and the host plants' geographic extent and density within local or regional vegetation (Southwood 1961; Southwood et al. 1982b; Kennedy et al. 1984; Novotny et al. 2012). Physical and chemical attributes of the individual plant species have also been investigated in relation to insect community composition (Lawton 1983; Strong et al. 1984). Variation in the amount and composition of secondary metabolites in particular, has attracted much attention (Jones & Lawton 1991; Ricklefs & Marquis 2012). Recognition that closely related species share similar nutritional values and chemistry that determine their smell, taste and palatability for phytophagous insects (Strong et al. 1984; Tallamy 2004), has led to several investigations of the predictive value of plant phylogeny for understanding the structure and composition of herbivore communities (Novotny et al. 2002; Ødegaard et al. 2005; Weiblen et al. 2006; Nipperess et al. 2011).

In addition to describing insect faunas by species composition, communities can also be characterised on the basis of the distribution of feeding types or guilds (Root 1973; Simberloff & Dayan 1991). This approach allows the characterisation of the community structure based on the distribution of members within particular feeding guilds, such as herbivores, scavengers and predators. This trait-based insect guild structure may be idiosyncratic for each host plant species or may show a relationship with traits such as 'plant architecture'. This term was coined by Lawton (1983) to describe the aggregate of a variety of plant traits including size, growth

form and the seasonal development, persistence and variety of above ground parts. Combinations of several plant architectural traits have been found to have significant predictive power in explaining insect community structure based on feeding guilds (Moran & Southwood 1982; Basset 1996; Campos et al. 2006). In particular, leaf traits such as shape, size and age have been found to be strongly associated with phytophagous insect community structure (Moran & Southwood 1982; Basset 1996; Peeters 2002).

The insect fauna of the Australian continent is particularly rich and highly endemic (Cranston 2009). Nearly 60,000 species have been described (Yeates et al. 2003). There are five mega-diverse orders, including the Hemiptera (4,453 described species) and Coleoptera (22,000 described species); the latter is estimated to comprise about 40-50% of the total number of the Australian insect fauna. The diversification of Australia's insect fauna is associated with major plant radiations, especially those of the dominant genera *Eucalyptus* (Myrtaceae, 700 species) and *Acacia* (Fabaceae, Mimosoideae, 950 species) (Austin et al. 2004; Cranston 2009).

Considering the richness of the Australian insect fauna (Yeates et al. 2003), there have been relatively few studies describing insect communities and their associations with plants. In general, the studies that have been done have either focused on the relationship of the communities with host plant traits (Woinarski & Cullen 1984; Peeters 2002; Sinclair & Hughes 2008) or with plant phylogeny (Majer et al. 2000; Harvey et al. 2010) but rarely both (but see Nipperess et al. 2011). In the present study, we collected the Coleoptera and Hemiptera fauna from nine host plant species from three major Australian plant families (Fabaceae, Myrtaceae and Proteaceae). We investigated the structure and composition of these faunas (both in their entirety, and for phytophagous members alone) within and among families, and in relation to several plant architectural traits.

Material and Methods

Host plant species

Plant species within the Myrtaceae (1848 species), Proteaceae (1116 species) and Fabaceae (1402 species) dominate many vegetation types in Australia, especially open woodlands, dry sclerophyll forests and shrublands (Augee & Fox 2000). We selected three host plant species from each of these three families. Within each family the three species were relatively distantly related to each other, as indicated by published phylogenies (George 1998; Wilson et al. 2004; Brown et al. 2006). The following three species from the Fabaceae were selected: subfamily Mimosoideae (1) *Acacia parvipinnula* Tindale, (subgenus Phyllodineae), (2) *Acacia obtusata* Sieber ex DC (subgenus Phyllodineae), subfamily Faboideae (3) *Daviesia corymbosa* Sm. We chose the following three species from the Myrtaceae: (4) *Angophora hispida* Sm. Blaxell, (5) *Callistemon pinifolius* J.C. Wendl., (6) *Leptospermum squarrosum* Gaertn.; and three species from the Proteaceae: (7) *Hakea gibbosa* Sm. Cav., (8) *Isopogon anethifolius* (Salisb.) Knight, and (9) *Telopea speciosissima* Sm. R. Br.

All the selected plant species were sclerophyllous understory shrubs, and locally common (> 25 individuals in an ~250 m^2 area) within the vegetation type 'Sydney Coastal Dry Sclerophyll Forest' (Keith 2004). The canopy cover of this vegetation is open (30-70% cover) and dominated by large myrtaceous tree species such as *Angophora costata, Corymbia gummifera, Eucalyptus capitellata, E. racemosa* and *E. haemastoma*. This vegetation formation grows on extremely low-nutrient soils derived from Hawkesbury sandstone (Groves 1994). Annual mean precipitation varies between 1000-1300 mm (Keith 2004), and annual mean temperatures range from 13.8°C to 21.7°C (Bureau of Meteorology, Melbourne, Australia).

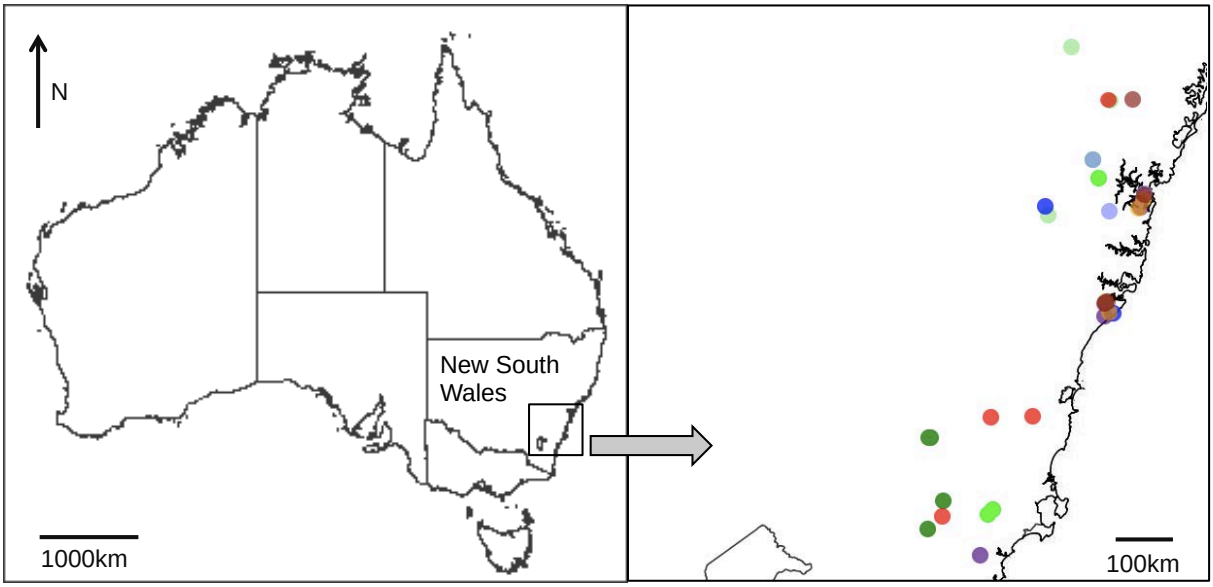

Figure 1: Location of insect collection field sites for nine host plant species. Fabaceae: *A. obtusata* (dark green), *A. parvipinnula* (light green), *D. corymbosa* (green); Myrtaceae: *A. hispida* (light blue), *C. pinifolius* (blue), *L. squarrosum* (purple); Proteaceae: *H. gibbosa* (light brown), *I. anethifolius* (red), *T. speciosissima* (brown). Note: dots may overlap where multiple plant species were sampled at the same location.

Field sites

The nine selected plant species all have relatively narrow geographic ranges in coastal southeast New South Wales, Australia, including the Sydney Basin and extending latitudinally from approximately Newcastle (32° 55' 33.6"S, 151° 46' 51.6" E) to Nowra (34° 52' 22.7"S, 150° 36' 10.8"E). Four field collection sites were selected across the geographic range of each species (Figure 1). The collection sites were different for each species because no location could be found where all nine species grow together; details of the locations are listed in Table A1 in the Appendix.

Survey design

Arthropods were collected on four occasions during autumn and summer 2009 / 2010 following the protocol of Andrew & Hughes (2004). On each sampling occasion, ten individual plants per plant species were haphazardly selected in an area of approximately 100 × 100 m, and sprayed with a 0.6% pyrethrum solution (total of 360 individual samples). Sampling occurred in the morning between 7.00 and 11.00 h on low wind days. Each sample consisted of all arthropods that fell onto four collecting trays (each 50 × 30 cm), previously placed under each plant. Arthropods were subsequently transferred into 70% ethanol. The flowering condition of each individual plant was noted.

On each sampling occasion, the following architectural traits were measured for each sampled plant:

(i) plant height

(ii) plant density (Nipperess et al. 2011): a stick of 1 m in length was pushed through the plant along the horizontal, vertical and oblique axes and the number of times that foliage touched the stick was recorded.

(iii) leaf area: ten leaves (per plant species and site) were haphazardly selected, scanned and then measured with the software programme ImageJ (Rasband 2003).

Insect community characterisation

We focused on insects within the orders Coleoptera and Hemiptera because they were the most abundant in the collected samples and contain a high proportion of phytophagous species. Individuals within these orders can also be reliably identified to family level and feeding guilds can generally be assigned at this level. Insect identification followed the procedure described in Nipperess et al. (2011). All adult insects were sorted to morphospecies using the protocol of Oliver and Beattie (1993); specimens were sorted into recognisable taxonomic units, (i.e. morphospecies) based on morphological differences, and subsequently identified to family level. Adult Coleoptera and Hemiptera were assigned to feeding guilds, based on their mouthpart morphology and targeted plant tissue, in accordance with the dominant feeding type among members of the family by following the descriptions of Lawrence and Britton (1991). The family Cicadellidae (Hemiptera) was an exception to this method because species within this family have very heterogeneous feeding habits. Morphospecies in this family were identified to subfamily level for feeding guild assignments, using the identification key of Fletcher (2009). Morphospecies within the order Coleoptera were assigned to one of four feeding guilds: leaf chewers, fungivores, predators and scavengers. Morphospecies within the order Hemiptera were divided into five feeding guilds: mesophyll feeders, phloem feeders, xylem feeders, predators, and seed predators (Table 1). Nymphs and larvae were excluded from the analyses because of the difficulty relating them to their adult forms (Andrew & Hughes 2007).

We compared the insects collected from each host plant species in two ways. Firstly, numbers of morphospecies within feeding guilds were compared from the entire collection of Coleoptera and Hemiptera (‘full dataset’). For the full dataset, mesophyll, phloem and xylem feeders were pooled into a general guild of ’sap suckers’, because we were interested in the general patterns of herbivore vs. non-herbivore guilds. Secondly, we investigated patterns within the subset of phytophagous species (‘herbivore dataset’).

Table 1: Feeding guild classification, based on insect mouthpart morphology and targeted plant tissue, for (i) Coleoptera and (ii) Hemiptera families.

(i) Coleoptera

Feeding guild	Superfamily	Family
leaf chewer	Chrysomeloidea	Cerambycidae, Chrysomelidae
	Buprestoidea	Buprestidae
	Curculionidea	Attelabidae, Belidae, Brentidae, Curculionidae
fungivore	Elateroidea	Elateridae, Cantharidae
	Cucujoidea	Endomychidae, Lathridiidae, Phalacridae
	Microsporoidea	Microsporidae
	Staphylinoidea	Ptiliidae
	Tenebrionoidea	Colydiidae, Melandryidae
predator	Cleroidea	Cleridae, Melyridae, Trogossitidae
	Cucujoidea	Coccinelidae, Silvanidae
	Staphylinoidea	Staphylinidae
	Tenebrionoidea	Ripiphoridae
scavenger	Bostrichoidea	Anobiidae
	Cucujoidea	Nitidulidae
	Scarabaeoidea	Scarabaeidae, Trogidae
	Tenebrionoidea	Aderidae, Anthicidae, Mordellidae, Oedemeridae, Tenebrionidae

(ii) Hemiptera

Feeding guild	Suborder	Superfamily	Family / subfamily
phloem feeder*	Auchenorrhyncha	Fulgoroidea	Achilidae, Delphacidae, Eurybrachidae, Flatidae, Fulgoridae, Tropiduchidae
	Auchenorrhyncha	Membracoidea	Cicadellidae, subfamilies: Deltocephalinae, Eurymelidae, Lassinae, Tartessinae, Ulopinae, Xestocephalinae
		Membracoidea	Membracidae
	Sternorrhyncha	Aleyrodoidea	Aleyrodidae
		Aphidoidea	Aphididae
		Coccoidea	Coccidae
		Psylloidea	Psyllidae
xylem feeder*	Auchenorrhyncha	Cercopoidea	Cercopidae
mesophyll feeder*	Auchenorrhyncha	Membracoidea	Cicadellidae, subfamily Typhlocybinae
	Heteroptera	Miroidea	Miridae, Tingidae
		Lygaeoidea	Piesmatidae
predator	Heteroptera	Reduvioidea	Reduviidae
seed predator	Heteroptera	Cimicoidea	Anthocoridae
		Lygaeoidea	Rhyparochromidae, Cymidae, Oxycarenidae
		Coreoidea	Alydidae

*mesophyll, phloem and xylem feeders are combined in a category of ‘sap sucker’ for the complete dataset but analysed separately for the herbivore dataset.

Statistical analyses

To increase the statistical power of the analyses, data for each of the four collection events were pooled to produce as complete samples of the insect fauna across the range of each plant species as possible.

Coleoptera and Hemiptera morphospecies richness, diversity and density

To compare Coleoptera and Hemiptera morphospecies richness and diversity (for the 'full dataset') among plant species within each family, and to assess adequacy of sampling for each plant species, the following estimators and indices were computed in the programme EstimateS 8.2 (Colwell 2006): The Chao-1 index is a non-parametric species richness estimator that expresses the minimum of the expected species richness of a plant species; it is calculated by using 1000 randomised occurrences of singletons and doubletons (Chao et al. 2000). Simpson's diversity index (D) was used as a non-parametric measure of diversity giving the probability of any two individuals drawn at random from an infinitely large community belonging to the same species (Simpson 1949). Because a large value of D indicates a low diversity, it is generally expressed as the reciprocal value (1/D). Simpson's D is one of the most meaningful and robust diversity indices available, because it captures the variance of the species abundance distribution (Magurran 2004). We assessed species richness per specified number of rarefied individuals (n = 42) and produced Coleman's species rarefaction curves. The adequacy of sampling was assessed for each plant species by generating species accumulation curves (Gotelli & Colwell 2001). The number of morphospecies collected was then divided by the mean Chao-1 index value and expressed as a percentage value to estimate the proportion of morphospecies collected from the minimum expected insect species pool.

To compare the number of Coleoptera and Hemiptera morphospecies collected from individual plant species among sites, we used the total number of morphospecies collected in each sample (n = 40, each sample equals 4 trays). This is termed morphospecies density and should not be confused with morphospecies richness (Gotelli & Colwell 2001). To compare morphospecies densities on individual plant species within plant families, untransformed count data were used in

generalised linear models (GLM) (in SPSS, v20), based on a negative binomial distribution (Warton et al. 2011). This method produces negligible bias compared to the use of log or square root transformed count data in models based on a normal distribution (O'Hara & Kotze 2010).

Plant traits

To determine whether any of the three architectural plant traits (height, density or leaf size) have predictive power for understanding the distribution of feeding guilds (for the full dataset and the herbivore dataset, respectively) we used DISTLM, a distance-based redundancy analysis (Anderson 2001; McArdle & Anderson 2001), in the programme PRIMER v6 (Clarke & Gorley 2006). The three plant variables were log-transformed and analysed together, using the forward selection process in the non-parametric permutation procedure for multivariate multiple regression, to test for an association between guild structure and plant trait. The analyses were based on Bray-Curtis similarity matrices and square root transformed multivariate feeding guild data. The three architectural plant traits together explained only 4.3% of variation in the Coleoptera and Hemiptera (full dataset) structure. Of the three traits included, leaf size explained the highest proportion of variance (1.8%, $p = 0.002$; height 0.08%, $p = 0.067$; density 1.4%, $p = 0.012$). The three traits explained 5.08% total variation for the herbivore dataset with leaf size again explaining the greatest proportion (3.7%, $p = 0.001$; height 1.3%, $p = 0.059$; density 0.08%, $p = 0.151$). We grouped plant species into three classes according to their leaf size: group 'small leaves' (*C. pinifolius, H. gibbosa* and *L. squarrosum;* leaf size: 0.2-1.1 cm^2), group 'medium leaves' (*A. obtusata, D. corymbosa* and *I. anethifolius;* leaf size: 5.0-13.9 cm^2) and group 'large leaves' (*A. hispida*, *A. parvipinnula* and *T. speciosissima;* leaf size: 26.0-32.3 cm^2). The distribution of feeding guilds (feeding guild structure) was then compared among plants within these leaf size groups (see following section).

Coleoptera and Hemiptera assemblage composition and feeding guild structure

Coleoptera and Hemiptera assemblages were compared in terms of morphospecies composition among plant species within each family, and in terms of the distribution of each feeding guild (assemblage structure) (i) among plant species

within each family and (ii) among plant species with similar leaf size. Comparisons among plant species were performed for both the full dataset and the herbivore subset. Assemblage composition among plant species within families was compared using the SIMPER function in the program PRIMER v6 (Clarke & Gorley 2006). Assemblage structure in terms of feeding guilds was compared among plant species within families, and among plant species with similar leaf size, using the multivariate extension of generalised linear models (mGLM) based on negative binomial regression (Warton et al. 2011). The computation was conducted using the mvabund package (Wang et al. 2012) in the R statistical environment, version 2.14.1 (R Development Core Team 2011).

We also analysed the influence of flowering on the assemblage structure using the PERMANOVA statistical add-on package (Anderson 2001; McArdle & Anderson 2001), for the programme PRIMER v6 (Clarke & Gorley 2006). A Bray-Curtis measure of dissimilarity based on square root transformed multivariate feeding guild data was used, for both the full dataset and the herbivore subset, in a nested permutational MANOVA (PERMANOVA) with the factor ‘flowering condition’ nested in the factor ‘plant species’. Additionally, non-metric multidimensional scaling (nMDS) plots were produced to compare the feeding guild structure on plants in flowering vs. non-flowering plant condition.

Results

A total of 14,125 arthropods were collected from 360 individual plants, of which 2,122 (15%) belonged to the orders Coleoptera (1,685, 12%) and Hemiptera (437, 3%); these individuals were identified to morphospecies. The phytophagous subset consisted of 853 Coleoptera (6%) and 367 Hemiptera (2.5%).

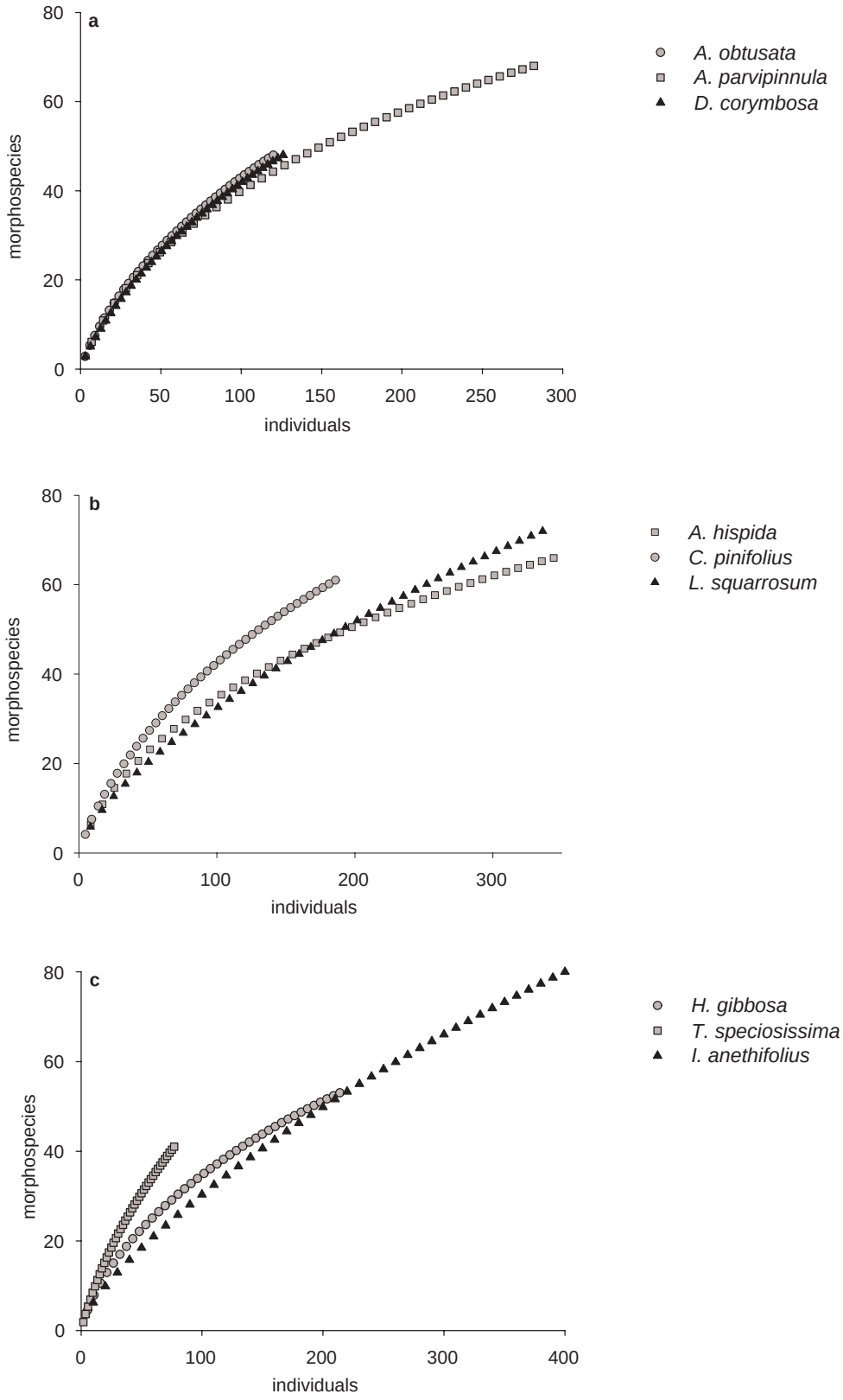

Figure 2: Coleman's rarefaction curves for Coleoptera and Hemiptera morphospecies richness from nine plant species from three families: (a) Fabaceae, (b) Myrtaceae and (c) Proteaceae.

Morphospecies richness, density and Simpson's diversity: within-family comparisons

Morphospecies richness varied little within the Fabaceae, but there was a wide variation within the Myrtaceae and Proteaceae, where values ranged from 16 (*I. anethifolius*) to 27 (*T. speciosissima*) (Fig. 2 and Table 2). The Chao-1 estimation varied within all three families, ranging from 84 (*A. obtusata*) to 170 (*I. anethifolius*). There was variation of morphospecies diversity within each family, with Simpson's diversity indices ranging from 0.03 to 0.12. Adequacy of sampling ranged from 44% for *T. speciosissima* (Proteaceae) to 68% for *A. parvipinnula* (Fabaceae) (Table 2). An asymptote of species accumulation after four collection events was not reached for any of the nine plant species (Fig. 3). The number of morphospecies collected from each plant species (morphospecies density) was not significantly different for plant species within the Myrtaceae (Table 3, Fig. 4). Within the Fabaceae, overall morphospecies density was not significantly different among plant species, but species-pair comparisons showed that *A. parvipinnula* had a significantly higher morphospecies density than the other two Fabaceae species. Within the Proteaceae, overall morphospecies density was significantly different among plant species, and species-pair comparisons showed that *T. speciosissima* had a significantly lower morphospecies density than the remaining two Proteaceae species.

Assemblage composition: within-family comparisons

A total of 267 morphospecies of Coleoptera and 110 morphospecies of Hemiptera were collected. Of this total, 234 (62%) were classified as phytophagous (Coleoptera n = 136, Hemiptera n = 98). The numbers of morphospecies within Coleoptera and Hemiptera families varied greatly among plant species, e.g. values for Chrysomelidae ranged from 2 for *D. corymbosa* to 12 for *A. parvipinnula* (see Table A2, Appendix). Coleoptera were consistently the dominant order collected on all plant species (Table 4), with *D. corymbosa* supporting the least number (n = 35) and *I. anethifolius* supporting the most (n = 67). The number of morphospecies of Hemiptera ranged from 10 (*C. pinifolius)* to 23 (*A. hispida)*. Phytophagous Coleoptera per plant species ranged from 8 (*D. corymbosa)* to 32 (*L. squarrosum*). Phytophagous Hemiptera ranged from 8 (*C. pinifolius*) to 19 (*A. parvipinnula*).

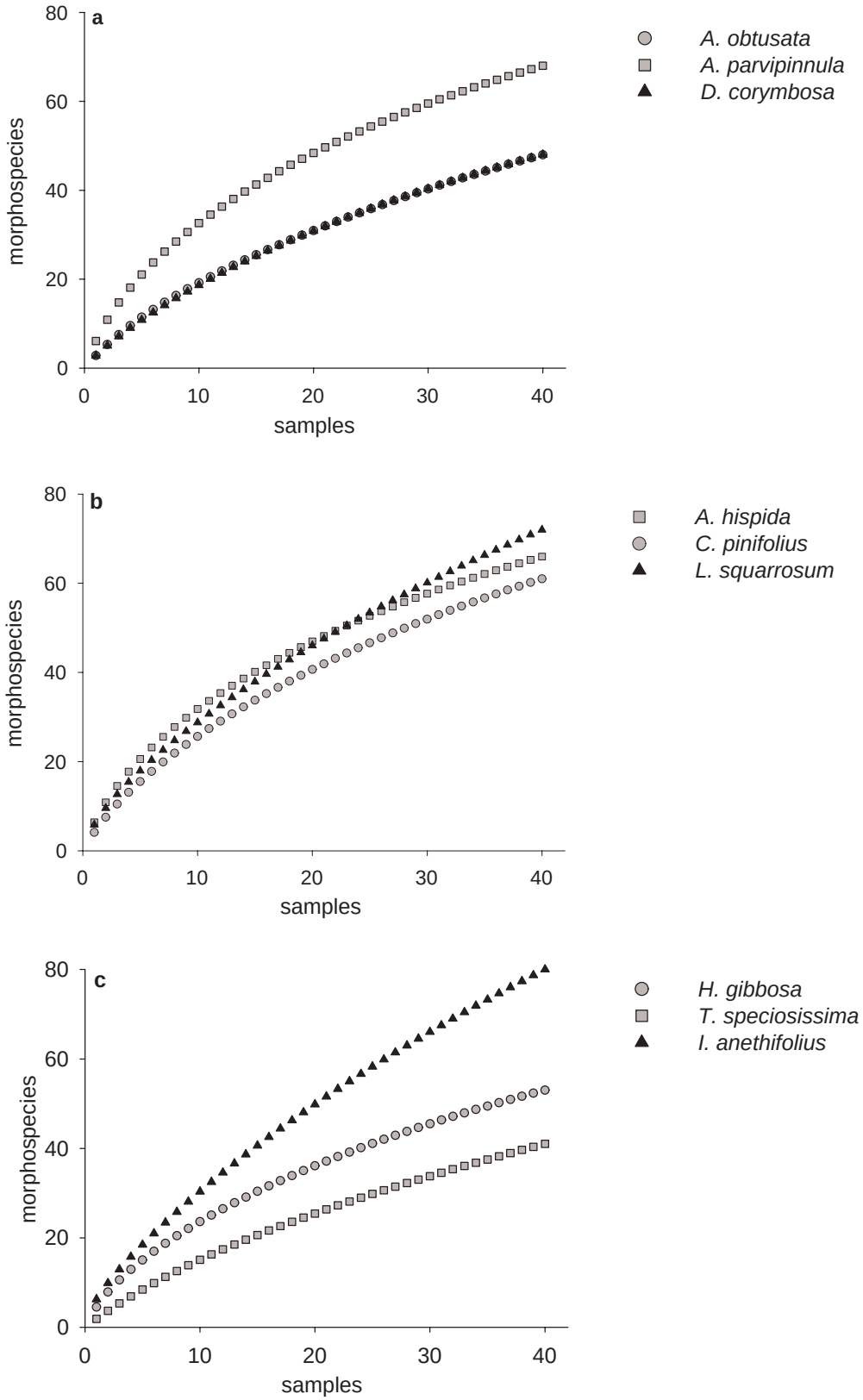

Figure 3: Species accumulation curves for Coleoptera and Hemiptera morphospecies richness from nine plant species from three families: (a) Fabaceae, (b) Myrtaceae and (c) Proteaceae.

Table 2: Morphospecies richness indices for nine plant species from three families. Total number of morphospecies (# Msp), morphospecies richness per rarefied number of 42 individuals (richness); Chao-1 index (Chao-1), adequacy of sampling: number of morphospecies/Chao-1 in percent (#Msp/Chao); Simpson's diversity index, expressed as reciprocal value (1/D).

Plant family / species	# Msp	Richness	Chao-1	# Msp/Chao (%)	1/D
Fabaceae					
A. obtusata	48	24	84	57	0.05
A. parvipinnula	67	23	100	68	0.05
D. corymbosa	44	23	87	55	0.1
Myrtaceae					
A. hispida	64	20	107	62	0.1
C. pinifolius	61	24	111	55	0.06
L. squarrosum	72	18	146	49	0.12
Proteaceae					
H. gibbosa	52	20	86	62	0.07
I. anethifolius	76	16	170	47	0.13
T. speciosissima	40	27	93	44	0.03

Table 3: Summary statistics for generalised linear model (GLM) analyses of Coleoptera and Hemiptera morphospecies densities from nine plant species within three families, degrees of freedom (2,117); Wald-X^2-Statistic (Wald-X^2) and p-values (overall, and for pairwise comparisons between plant species within families) are shown, p-value (p).

Plant family	Wald-X^2	p			
		overall			
			AO-AP*	AO-DC	AP-DC
Fabaceae	5.25	0.072	**< 0.05**	0.769	**< 0.05**
			AH-CP	AH-LS	CP-LS
Myrtaceae	1.618	0.445	0.258	0.867	0.332
			HG-IA	HG-TS	IA-TS
Proteaceae	12.737	**< 0.01**	0.106	**< 0.05**	**< 0.001**

note: significant values are in bold.

*pairwise comparisons between plant species within families:
Fabaceae: *A. obtusata* (AO), *A. parvipinnula* (AP), *D. corymbosa* (DC);
Myrtaceae: *A. hispida* (AH), *C. pinifolius* (CP), *L. squarrosum* (LS);
Proteaceae: *H. gibbosa* (HG), *I. anethifolius* (IA), *T. speciosissima* (TS).

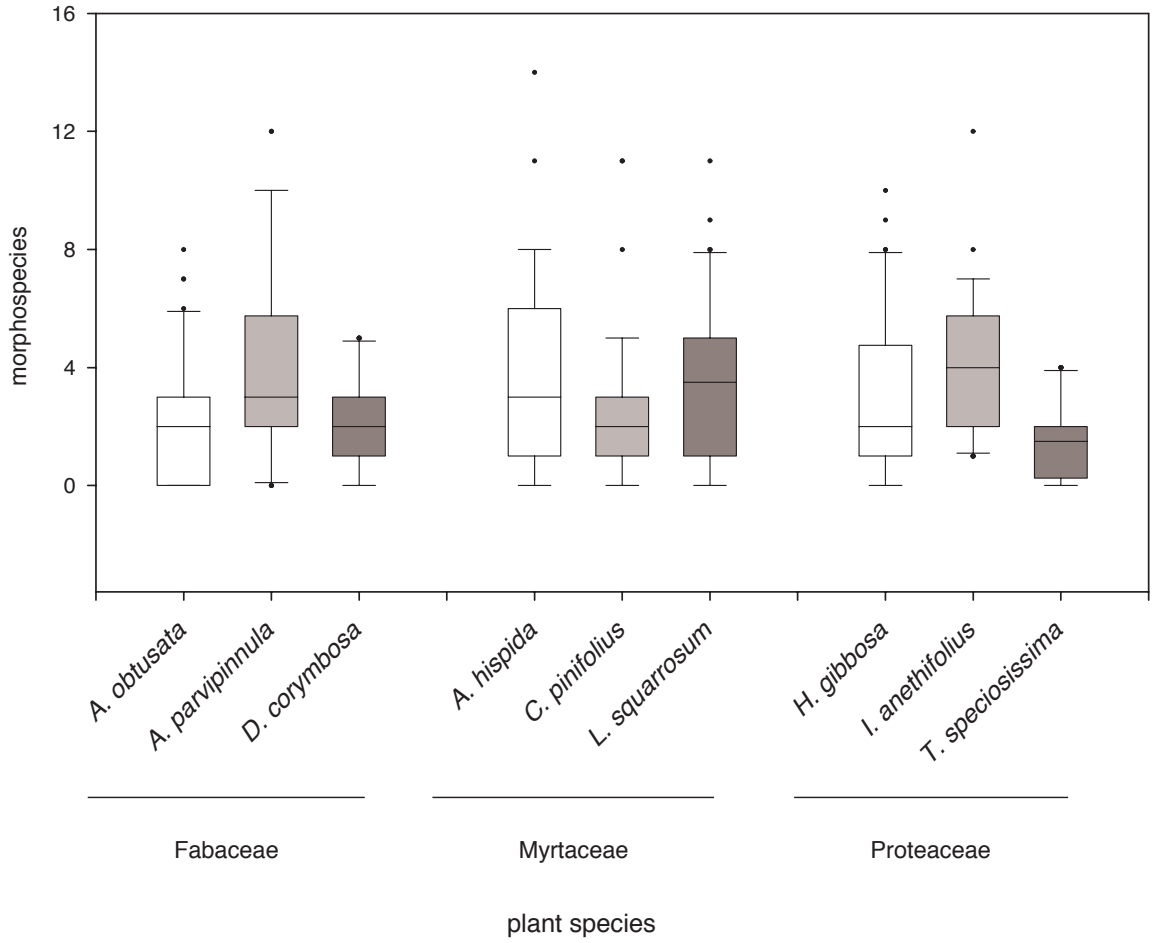

Figure 4: Morphospecies density for Coleoptera and Hemiptera from nine plant species from three families (Fabaceae, Myrtaceae and Proteaceae). Boxes show median and upper and lower quartile. Whiskers show 10th and 90th percentile.

There was a high level of variation in numbers of Coleoptera and Hemiptera morphospecies among plant species within families, e.g. within the Proteaceae, the number of Coleoptera morphospecies ranged from 30 to 67; within the Myrtaceae the number of Hemiptera ranged from 10 to 23 (Table 4). This variation was also found in the phytophagous subset of the data. Morphospecies variation was particularly evident for Coleoptera across all families. For Hemiptera, morphospecies variation was only evident within the Fabaceae and Myrtaceae. Ratios of Coleoptera to Hemiptera morphospecies were largely consistent across all plant species (Table 4).

Overall, there was very little commonality of morphospecies among the host species within the three plant families (Table 5). In the Fabaceae there was an average of 1.5% co-occurring morphospecies for the full dataset, and 0.2% for the herbivore dataset. Within the Myrtaceae for the full dataset there was an average of 1.9% morphospecies overlap and 2.5% for the herbivore dataset. Within the Proteaceae for the full dataset there was an average of 2.5% co-occurring morphospecies and 1.8% for the herbivore dataset.

The relatively few co-occurring morphospecies that were found predominately occurred within the Coleoptera (Table A3, Appendix). Two ubiquitous species of fungivores (family Ptiliidae) occurred within all families. Co-occurring morphospecies within the Myrtaceae included predators (Staphylinidae), fungivores (Lathridiidae), leaf chewers (Brentidae, Chrysomelidae) and a seed predator (Oxycarenidae). Within the Proteaceae, co-occurring morphospecies were leaf chewers (Brentidae) and predators (Staphylinidae).

Table 4: Numbers of Coleoptera (Cole) and Hemiptera (Hemi) morphospecies for the entire community and the herbivore subset, ratios of Coleoptera to Hemiptera morphospecies (ratio C:H), % herbivores from full dataset (herbi %).

Family	Full dataset		ratio	Herbivore dataset		
Plant species	Cole	Hemi	C:H	Cole	Hemi	herbi (%)
Fabaceae						
A. obtusata	38	10	1:0.3	18	11	57
A. parvipinnula	47	20	1:0.4	22	19	61
D. corymbosa	31	13	1:0.4	8	13	45
Myrtaceae						
A. hispida	40	24	1:0.5	23	21	67
C. pinifolius	51	10	1:0.2	24	8	52
L. squarrosum	52	20	1:0.4	32	13	63
Proteaceae						
H. gibbosa	40	12	1:0.3	18	11	56
I. anethifolius	64	12	1:0.2	22	10	40
T. speciosissima	29	11	1:0.4	15	11	62

Table 5: Similarities (%) of Coleoptera and Hemiptera morphospecies for (i) the full dataset and (ii) the herbivore subset, within plant families.

Plant species	Similarities (%) between plant species		
Fabaceae	AO-AP*	AO-DC	AP-DC
(i) full dataset	1.1	2.0	1.4
(ii) herbivore subset	0.4	0.2	0.1
Myrtaceae	AH-CP	AH-LS	CP-LS
(i) full dataset	0.9	1.7	3.2
(ii) herbivore subset	0.8	2.3	4.4
Proteaceae	HG-IA	HG-TS	IA-TS
(i) full dataset	3.8	1.5	2.1
(ii) herbivore subset	3.8	0.6	1.0

*pairwise comparisons between plant species within families:
Fabaceae: *A. obtusata* (AO), *A. parvipinnula* (AP), *D. corymbosa* (DC);
Myrtaceae: *A. hispida* (AH), *C. pinifolius* (CP), *L. squarrosum* (LS);
Proteaceae: *H. gibbosa* (HG), *I. anethifolius* (IA), *T. speciosissima* (TS).

Assemblage structure

Coleoptera and Hemiptera guilds

Within-family comparisons

Overall guild structure and species-pair comparisons for the full dataset were significantly different among species within plant families, indicating that there was little consistency in assemblage structure at this level (Table 6). In the Fabaceae, sap suckers were consistently found on all plant species (Table A4, Appendix), but leaf chewers were the dominant feeding guild on the two *Acacia* species, and predators dominated on *D. corymbosa*. Differences in guild structure among all plant species were also driven by differences in the proportion of fungivores, and by differences in the numbers of sap suckers between the two *Acacia* species. *Daviesia corymbosa* harboured fewer leaf chewers and more predators. Within the Myrtaceae, the dominant feeding guild on all three plant species was leaf chewing (Table A4, Appendix). Differences in guild structure among plant species were mainly driven by a higher number of sap suckers on *A. hispida,* a higher number of scavengers on *C. pinifolius,* and a higher number of seed predators on *L. squarrosum*. Within the Proteaceae, leaf chewing was the dominant guild on all plant species (Table A4, Appendix). Differences in guild structure among the three plant species were mainly driven by variability in the number of fungivores. *Isopogon anethifolius* also harboured more predators while *T. speciosissima* supported more sap suckers.

Comparisons within groups of similar leaf size

Assemblage structure for the full dataset showed little consistency for plant species within groups of similar leaf size; within each leaf size group, overall guild structure was significantly different (Fig. 5, Table 6). Within the ‘small leaves’ group, comparisons between individual plant species were significant for two of the species-pairs (*C. pinifolius* – *L. squarrosum* and *H. gibbosa* – *L. squarrosum*). Differences in guild structure were mainly driven by greater numbers of seed predators and fewer scavengers on *L. squarrosum* (Fig. 5a). Within the ‘medium leaves’ group, one species-pair comparison was significant (*A. obtusata* – *D. corymbosa*). Differences in feeding guilds were mainly driven by fewer leaf chewers and scavengers on *D. corymbosa* (Fig. 5b). Within the ‘large leaves’ group all comparisons between

individual plant species were significant. Differences in guild structure among the three species in this group were mainly driven by variability in numbers of sap suckers and leaf chewers (Fig. 5c).

Table 6: Summary statistics for multivariate generalised linear model analyses (mGLM) of feeding guild data for the full dataset. Pairwise comparisons (i) within plant families and (ii) within similar 'leaf size' groups are shown. Degrees of freedom (2,117), Wald-X^2-Statistic (Wald-X^2) and p-values (overall, and for pairwise comparisons between plant species), p-value (p).

(i) Plant family	Wald-X^2	p			
		overall			
			AO-AP*	AO-DC	AP-DC
Fabaceae	7.613	**< 0.001**	**< 0.01**	**< 0.001**	**< 0.001**
			AH-CP	AH-LS	CP-LS
Myrtaceae	6.903	**< 0.001**	**< 0.01**	**< 0.001**	**< 0.05**
			HG-IA	HG-TS	IA-TS
Proteaceae	7.726	**< 0.001**	**< 0.01**	**< 0.05**	**< 0.05**

(ii) Leaf size	Wald-X^2	p			
		overall			
			CP-HG*	CP-LS	HG-LS
small	5.347	**< 0.01**	0.053	**0.026**	**0.020**
			AO-DC	AO-IA	DC-IA
medium	8.113	**< 0.001**	**< 0.05**	0.055	0.055
			AP-AH	AP-TS	AH-TS
large	7.816	**< 0.001**	**< 0.01**	**< 0.01**	**< 0.001**

note: significant values are in bold.

*pairwise comparisons between plant species within families:

Fabaceae: *A. obtusata* (AO), *A. parvipinnula* (AP), *D. corymbosa* (DC);
Myrtaceae: *A. hispida* (AH), *C. pinifolius* (CP), *L. squarrosum* (LS);
Proteaceae: *H. gibbosa* (HG), *I. anethifolius* (IA), *T. speciosissima* (TS).

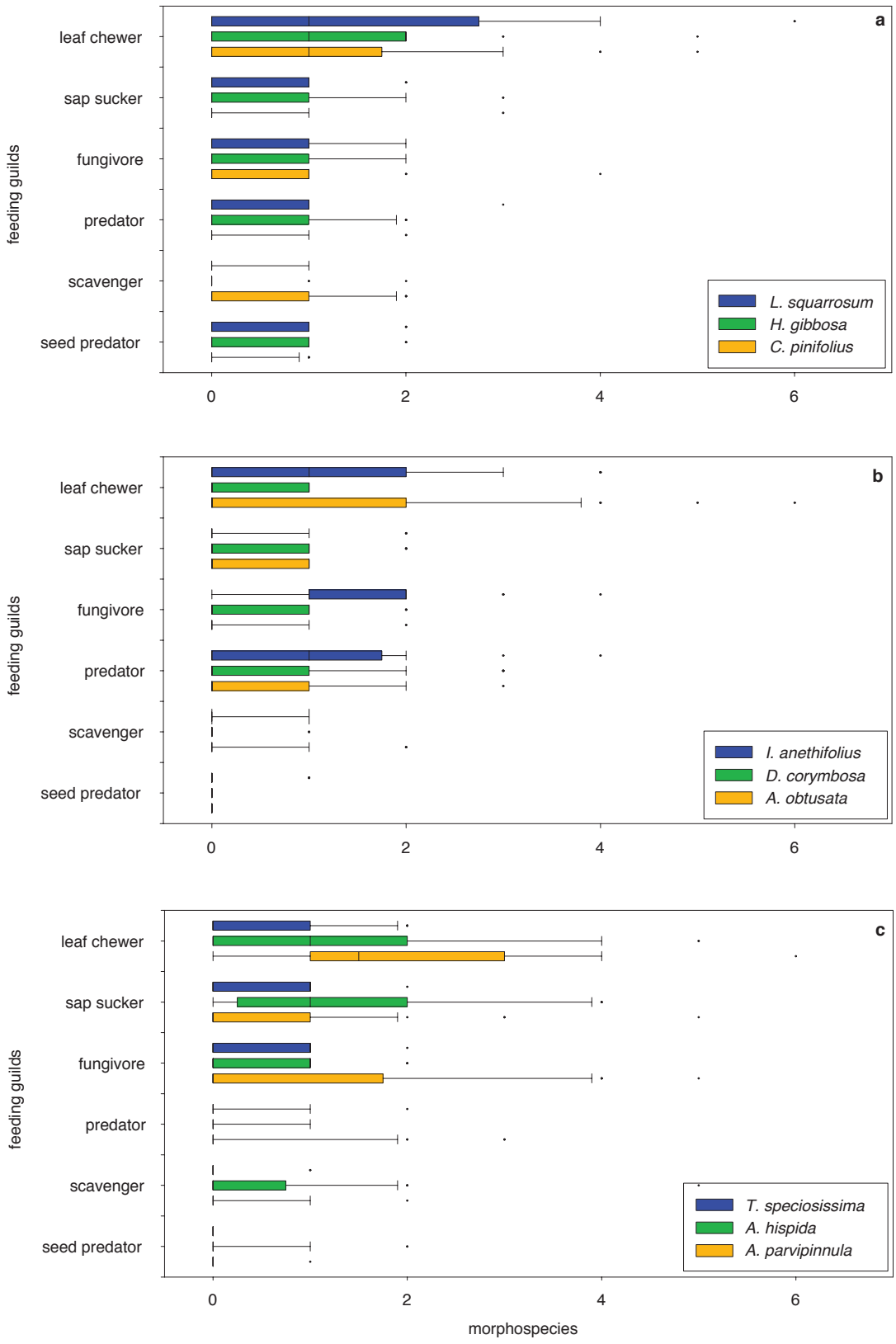

Figure 5: Coleoptera and Hemiptera feeding guild structure for nine host plant species, grouped by 'leaf size': (a) small leaves, (b) medium leaves and (c) large leaves. Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

Phytophagous Coleoptera and Hemiptera assemblage

Within-family comparisons

Assemblage structure for the herbivore dataset showed little consistency among the individual host plant species within families; overall herbivore guild structure was significantly different in all analyses (Table 7). Leaf chewers dominated on all species. Within the Fabaceae, all comparisons between individual plant species were significant (Table 7). The dominant herbivore guild on the two *Acacia* species was leaf chewing, and for *D. corymbosa* it was phloem feeding. Differences in herbivore guild structure among individual plant species were driven by differences in mesophyll feeders and leaf chewers (Table A5, Appendix). Within the Myrtaceae, comparisons between individual plant species were significant for two species-pairs (*A. hispida – C. pinifolius* and *A. hispida – L. squarrosum*) (Table 7). Differences in herbivore guild structure among plant species were mainly caused by greater numbers of phloem feeders on *A. hispida* (Table A5, Appendix). Within the Proteaceae, comparisons between individual plant species were significant for two species-pairs (*H. gibbosa – T. speciosissima* and *I. anethifolius – T. speciosissima*). Differences in herbivore guild structure were mainly due to fewer numbers of leaf chewers on *T. speciosissima* (Table A5, Appendix).

Comparisons within groups of similar leaf size

Assemblage structure for the herbivore dataset was largely consistent for plant species within groups of similar leaf size, as almost all (seven out of nine) species-pair comparisons were not significantly different (Fig. 6, Table 7). For the ‘small leaves’ group, overall herbivore guild structure and all comparisons among individual plant species were not significantly different, which was largely due to similarities in dominance by leaf chewers (Fig. 6a). Within the ‘medium leaves’ group, assemblage structure was consistent among all plant species, mainly due to similarities in the proportion of phloem feeders (Fig. 6b). Within the ‘large leaves’ group, two species-pair comparisons were significantly different (*A. parvipinnula – T. speciosissima* and *A. hispida – T. speciosissima*); differences in herbivore guild structure were mainly due to there being fewer leaf chewers and mesophyll feeders on *T. speciosissima* (Fig. 6c).

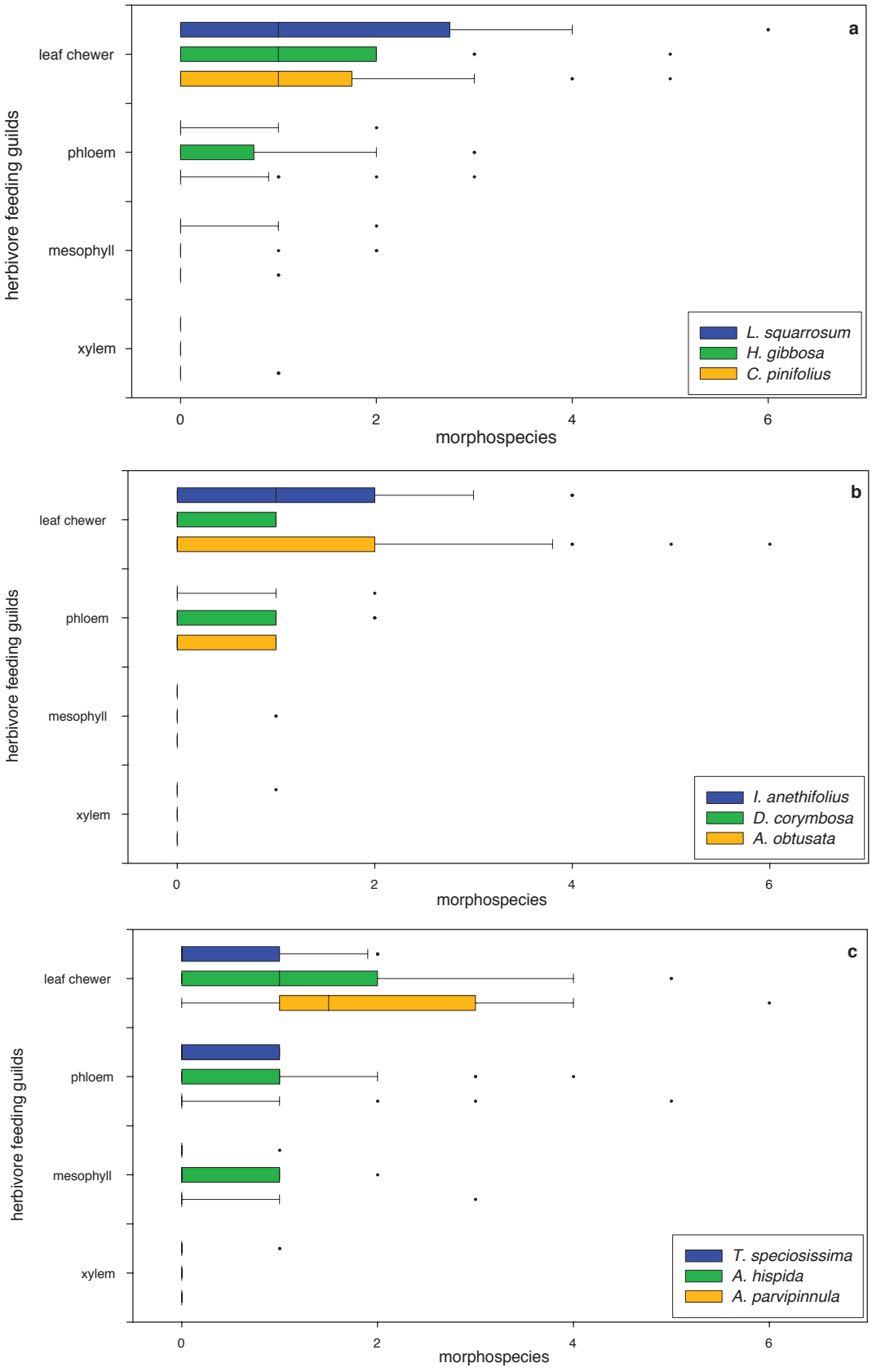

Figure 6: Herbivore Coleoptera and Hemiptera feeding guild structure for nine host plant species, grouped by 'leaf size': (a) small leaves, (b) medium leaves and (c) large leaves. Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

Table 7: Summary statistics for multivariate generalised linear model analyses (mGLM) of feeding guild data for the herbivore subset. Pairwise comparisons (i) within plant families and (ii) within similar 'leaf size' groups are shown. Degrees of freedom (2,117), Wald-X^2-Statistic (Wald-X^2) and p-values (overall, and for pairwise comparisons between plant species), p-value (p).

(i) Plant family	Wald-X^2	p			
		overall			
			AO-AP*	AO-DC	AP-DC
Fabaceae	5.736	**< 0.001**	**< 0.01**	**< 0.01**	**< 0.01**
			AH-CP	AH-LS	CP-LS
Myrtaceae	5.525	**< 0.001**	**< 0.001**	**< 0.001**	0.118
			HG-IA	HG-TS	IA-TS
Proteaceae	4.272	**< 0.001**	0.429	**0.030**	**0.014**

(ii) Leaf size	Wald-X^2	p			
		overall			
			CP-HG*	CP-LS	HG-LS
small	3.022	0.148	0.427	0.162	0.226
			AO-DC	AO-IA	DC-IA
medium	4.636	**< 0.001**	0.146	0.630	0.146
			AP-AH	AP-TS	AH-TS
large	6.050	**< 0.001**	0.063	**< 0.001**	**< 0.001**

note: significant values are in bold.

*pair wise comparisons between plant species within families:
Fabaceae: *A. obtusata* (AO), *A. parvipinnula* (AP), *D. corymbosa* (DC);
Myrtaceae: *A. hispida* (AH), *C. pinifolius* (CP), *L. squarrosum* (LS);
Proteaceae: *H. gibbosa* (HG), *I. anethifolius* (IA), *T. speciosissima* (TS).

Influence of flowering on assemblage structure

Overall flowering condition of individual host plants had a significant influence on feeding guild structure, for both the entire Coleoptera and Hemiptera assemblage (Pseudo-$F_{6,211}$ = 5.121, p-perm < 0.001), and the herbivore subset (Pseudo-$F_{6,211}$ = 4.813, p-perm < 0.001). The nMDS plots showed no clustering of assemblages on flowering plants (Fig. 7a, b).

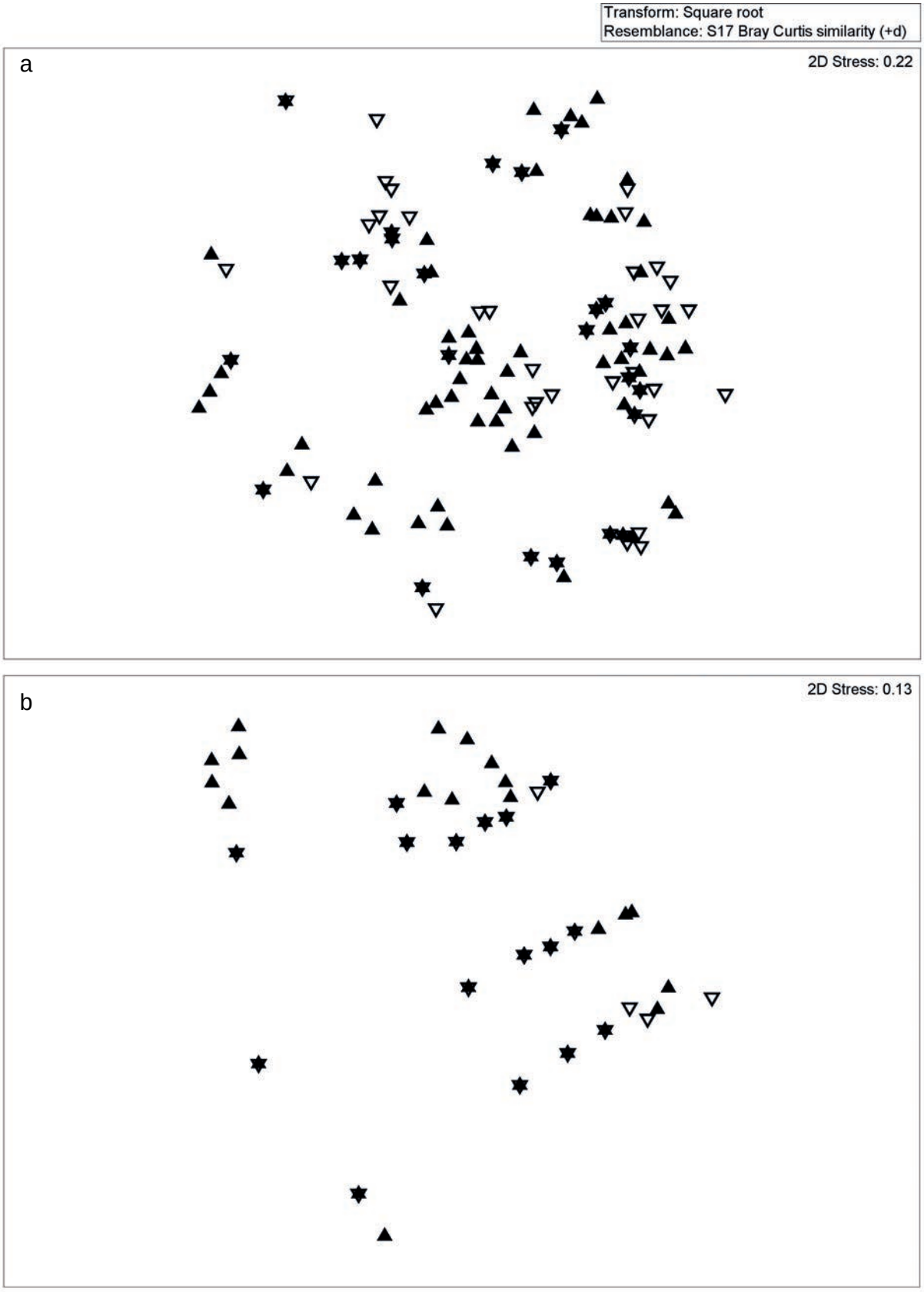

Figure 7: Non-metric multidimensional scaling (nMDS) plot for (a) the entire Coleoptera and Hemiptera feeding guild structure, and (b) the herbivore subset. Individual plants with flowers (open triangles) and without flowers (filled triangles) from six plant species are shown.

Discussion

Our results revealed little commonality in Coleoptera and Hemiptera morphospecies composition or feeding guild structure within each plant family, with each host species supporting a distinctive suite of insects. Estimated species richness and morphospecies densities also showed little similarity among host species within families. This suggests that within these families, chemical and physical characteristics of host plant species may vary enough to affect species interactions across trophic levels. When the subset of phytophagous morphospecies was considered, feeding guild structure still showed little consistency between plant families, although it did indicate more commonality among plant species with similar leaf size.

Assemblage composition

There were striking differences in the suite of Coleoptera and Hemiptera morphospecies supported by the plant species within each of the three families (though it has to be kept in mind that we did not collect the entire Coleoptera and Hemiptera fauna). In the full dataset, the overlap in species composition between plant species was only 2%, on average, with even less overlap (1.5%) for the herbivore subset. Plant species within the Myrtaceae showed the highest number of co-occurring morphospecies, while the Fabaceae showed the lowest. This heterogeneity of composition suggests that the nutritional, chemical and/or physical characteristics, even within a plant family, vary enough to support a distinctive assemblage of specialised insect species. Our results reflect those of Peeters et al. (2001), who assessed herbivore communities on 18 plant species in tall open eucalypt forests in southeast Australia, finding that each plant species was associated with a characteristic herbivore fauna. Other studies, however, have shown that some similarity in the associated insect community may be found within host plant genera (Weiblen et al. 2006; Nipperess et al. 2011).

Estimated species richness

Estimations for Coleoptera and Hemiptera species richness and diversity varied widely within two of the three families (Myrtaceae and Proteaceae). Within the Proteaceae we found that the Coleman's rarefaction curve for *T. speciosissima* was particularly steep, indicating that a high number of singletons were collected from this plant species. Our results reflect those from an earlier study, where numbers of phytophagous insect species varied greatly among eucalypt species (Morrow 1977). Considering the strong diversification of insects associated with Australia's most speciose plant families, the Myrtaceae and Fabaceae (Austin et al. 2004; Cranston 2009), these results are not particularly surprising.

Coleoptera and Hemiptera assemblage structure

The structure of the Coleoptera and Hemiptera assemblages, as described by the proportions of morphospecies classified into different feeding guilds, showed little consistency among species within any of the three host plant families. Host plant-specific variations in guild structure within each family were mainly driven by variability in the number of species of leaf chewers, sap suckers and fungivores. This variation in guild representation is in accord with findings of Woinarski & Cullen (1984), who found a wide range of variation in arthropod community structure on 156 plant species from forests and woodlands in southeast Australia. These authors found that differences in arthropod community structure between plant species were mainly due to wide variations in numbers of predators and sap suckers.

We found, however, that the presence and absence of flowers on individual plants within a plant species had a significant effect on Coleoptera and Hemiptera guild structure. This too is in line with previous results from Woinarski & Cullen (1984), who found that the flowering condition of host plant contributed to the shaping of the arboreal invertebrate community.

Within the Myrtaceae, differences in guild structure were mainly due to variation in sap suckers, especially Psyllidae, and seed predators. *Angophora hispida* in particular, harboured more sap suckers. Previous studies that assessed the insect fauna on *Eucalyptus* species, which are closely related to *Angophora* (Wilson et al. 2004), have also found high numbers of sap sucking Hemiptera, with particularly high

numbers of Psyllidae (Woinarski & Cullen 1984; Fensham 1994). In the present study a relatively high number of Psyllidae were also collected from the two *Acacia* species within the Fabaceae (Mimosoideae), consistent with previous studies which found a high number of Psyllidae associated with *Acacia* species across open forests and woodlands in Australia (Woinarski & Cullen 1984), and on Australian Acacias in South Africa (Proches 2008).

We found that even within a single genus (*Acacia,* Fabaceae) differences in guild structure can be large (Fig. 5, Table 6). The number of fungivores on *A. parvipinnula,* for example, was much higher than on *A. obtusata*. *Acacia parvipinnula* is structurally different, as it is characterised by a high plant architectural density and by finely divided compound leaves, features that provide a suitable surface for the attachment and growth of epiphytic fungi and thus attract higher numbers of fungivores. Similarly, higher numbers of fungivores were found on two other plant species (*H. gibbosa* and *I. anethifolius*) with similar architectural characteristics.

Our finding that Coleoptera and Hemiptera guild structure (including non-herbivores) showed little consistency either within plant families or among plant species of similar leaf size, indicates that factors other than phylogenetic relatedness or leaf architecture are important influences on assemblage structure. Plant height and density were also found to have minor effects (see Methods section). Additional plant architectural factors may include growth form, volume, or plant complexity (Lawton 1983). These traits may influence guild structure by providing variation in resources offered by different host plant species. Plant height, for example, has been shown to be associated with insect feeding guilds on a species of tree (*Anadenanthera macrocarpa*) in Brazil (Campos et al. 2006), and plant structural complexity has been found to have an influence on the guilds associated with *Opuntia* cacti (Moran 1980). Other factors that may explain feeding guild relationships may be the species' chemistry (Jones & Lawton 1991; Ricklefs & Marquis 2012), and/or the composition and vegetation structure of the local plant community (Rand 2003; Schaffers et al. 2008). In addition, the chemical and physical characteristics of individual plant species may influence species interactions across trophic levels; this may operate across all feeding guilds, including herbivores, scavengers, fungivores and predators (Price et al. 1980). Presence or absence of top

predators, such as birds, may also greatly influence the trophic structure of arthropod communities on eucalypts (Recher & Majer 2006).

Phytophagous Coleoptera and Hemiptera assemblage structure

The phytophagous Coleoptera and Hemiptera assemblage, based on herbivore feeding guild structure, showed little consistency within the three host plant families. Variations in herbivore guild structure within each family were mainly driven by variability in numbers of leaf chewers and mesophyll feeders. Our findings concur with those of Peeters et al. (2001), who found that the taxonomic affinities of the host plant species did not strongly relate to the similarities of the herbivore guild structure. Wide variations in the representation of arboreal phytophagous guilds among 28 British tree species have also been found (Cornell & Kahn 1989).

Our results showed that the flowering condition of individual plants also influenced the herbivore assemblage structure, contributing to the observed differences in feeding guild structure among plant species. Similarly, Peeters et al. (2001) showed that the presence or absence of flowers affected the herbivore assemblages on 15 understorey plant species.

The only consistency we found was for the phytophagous Coleoptera and Hemiptera assemblage in relation to leaf size. Our findings reflect those of Peeters (2002), who found a strong correlation between the functional composition of herbivore guilds and leaf structural traits on 18 plant species with leaves of highly variable size, shape and structure. An earlier study by Moran & Southwood (1982), which assessed the guild structure of arboreal arthropods on six tree species on two continents (Africa and Europe), also found that trees with similar leaf shape (broad or narrow) harboured a similar herbivore feeding guild structure.

Analysis of the dominant feeding guilds within the leaf size groups revealed a trend of increasing numbers of phloem feeders with leaf size. One possible reason for this result is that the veins on larger leaves are more accessible to phloem feeders. Our findings are consistent with those of Peeters et al. (2001) who found that densities of phloem feeders were greater on broad leaves than on spine-like leaves.

Conclusion

The individual plant species sampled in this study support an idiosyncratic suite of Coleoptera and Hemiptera, with little commonality of assemblages supported by host species within a plant family. Community structure, as described by the distributions of insects in different feeding guilds, also showed little similarity among plant species when the full complement of species was considered. However, when plant species were grouped by leaf size, some consistencies amongst the distribution of guilds of phytophagous insects emerged.

Acknowledgements

We thank Patrick Schultheiss and Katherine McClellan for help with insect collection in the field. We are grateful to Manuel Nagel for help with insect sorting in the lab. We are most grateful to Kerinne Harvey and Nigel Andrew for comments on earlier versions of this manuscript. This study was supported by a Macquarie University research excellence scholarship (iMQRES) to Sabine Nooten.

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Appendix

Table A1: Locations of four field collection sites for each of nine plant species across their native range.

Plant species	Site #	Site name	Latitude	Longitude
A. obtusata	1	Tallong	34° 43' 18.732"S	150° 3' 43.9914"E
	2	Wingello	34° 43' 12.1434"S	150° 4' 26.688"E
	3	Morton	35° 0' 56.4834"S	150° 8' 54.852"E
	4	Oallen road	35° 8' 39.156"S	150° 3' 25.5594"E
A. parvipinnula	1	Castlereagh	33° 40' 49.8354"S	150° 46' 29.2794"E
	2	Mogo creek	33° 8' 38.2554"S	151° 5' 30.84"E
	3	Yengo	32° 56' 14.856"S	150° 55' 21.3594"E
	4	Yengo	32° 53' 11.2554"S	150° 52' 23.5194"E
D. corymbosa	1	Marramarra	33° 30' 28.548"S	151° 1' 35.796"E
	2	Morton	35° 4' 37.7034"S	150° 23' 57.408"E
	3	Olney	33° 7' 47.6394"S	151° 13' 1.9194"E
	4	Morton	35° 3' 13.608"S	140° 25' 35.4"E
A. hispida	1	Royal	34° 8' 13.5954"S	151° 2' 40.1994"E
	2	Ku-ring-Gai	33° 34' 58.512"S	151° 17' 3.0834"E
	3	Marramarra	33° 25' 19.3794"S	150° 59' 28.752”E
	4	Berowra	33° 39' 48.9954"S	151° 5' 18.6"E
C. pinifolius	1	Londonderry	33° 38' 28.7154"S	150° 43' 28.2"E
	2	Royal	34° 8' 16.9794"S	151° 6' 26.9994"E
	3	Royal	34° 8' 16.188"S	151° 6' 22.32"E
	4	Royal	34° 5' 19.536"S	151° 3' 57.2394"E
L. squarrosum	1	Ku-ring-Gai	33° 37' 30"S	151° 15' 38.8794"E
	2	Ku-ring-Gai	33° 38' 35.556"S	151° 15' 46.8"E
	3	Royal	34° 9' 7.4874"S	151° 3' 34.5594"E
	4	Morton	35° 15' 51.0834"S	35° 15' 51.0834"E
H. gibbosa	1	Royal	34° 5' 8.34"S	151° 4' 0.84"E
	2	Ku-ring-Gai	33° 36' 37.1874"S	151° 16' 36.12"E
	3	Ku-ring-Gai	33° 38' 50.1714"S	151° 15' 11.1594"E
	4	Royal	34° 8' 10.2114"S	151° 5' 18.96"E
I. anethifolius	1	Meryla	34° 37' 35.1474"S	150° 24' 44.9994"E
	2	Morton	35° 5' 10.3914"S	150° 8' 33.7194"E
	3	Budderoo	34° 37' 47.928"S	150° 39' 19.08"E
	4	Royal	33° 8' 6.8994"S	151° 5' 3.12"E
T. speciosissima	1	Budderoo	34° 37' 22.7274"S	150° 39' 18.8994"E
	2	Royal	34° 5' 46.788"S	151° 3' 38.268"E
	3	Ku-ring-Gai	33° 35' 6.108"S	151° 16' 59.2674"E
	4	Olney	33° 7' 51.4806"S	151° 13' 5.5194"E

Table A2: Morphospecies richness of Coleoptera and Hemiptera families collected from nine host plant species, including feeding guilds.

Insect order		Fabaceae		
Family	Feeding guild	*Acacia obtusata*	*Acacia parvipinnula*	*Daviesia corymbosa*
Coleoptera				
Aderidae	scavenger			1
Anobiidae	scavenger	1		
Anthribidae	scavenger		1	
Attelabidae	leaf chewer			1
Belidae	leaf chewer	1		
Brentidae	leaf chewer	2	4	2
Buprestidae	leaf chewer		1	1
Cantharidae	predator	1	1	3
Chrysomelidae	leaf chewer	7	12	2
Cleridae	predator	1	1	
Coccinelidae	predator	2	5	
Curculionidae	leaf chewer	7	5	2
Elateridae	fungivore		1	1
Endomychidae	fungivore		3	1
Lathridiidae	fungivore	3	4	
Melandryidae	fungivore		1	
Mordellidae	scavenger	1	2	1
Nitidulidae	scavenger		1	
Nemonychidae	leaf chewer	1		
Ptiliidae	fungivore	1	2	2
Silvanidae	fungivore			1
Scarabaeidae	scavenger	2		
Staphylinidae	predator	5	3	12
Tenebrionidae	scavenger	3		
sum		*38*	*47*	*31*
Hemiptera				
Achilidae	phloem feeder	1		
Aleyrodidae	phloem feeder			1
Aphididae	phloem feeder	2		
Cicadellidae				
Deltocephalinae	phloem feeder		1	1
Iassinae	phloem feeder		1	
Tartessinae	phloem feeder		1	
Typhlocybinae	mesophyll feeder		1	
Ulopinae	phloem feeder			2

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Table A2: *continued*

Insect order		Fabaceae		
Family	Feeding guild	*Acacia obtusata*	*Acacia parvipinnula*	*Daviesia corymbosa*
Coccidae	phloem feeder		1	1
Membracidae	phloem feeder	2	1	3
Miridae	mesophyll feeder		1	1
Pentatomidae	mesophyll feeder		2	
Piesmatidae	mesophyll feeder		1	1
Psyllidae	phloem feeder	5	8	3
Rhyparochromidae	seed predator		1	
Tingidae	mesophyll feeder		1	
sum		*10*	*20*	*13*

Insect order		Myrtaceae		
Family	Feeding guild	*Angophora hispida*	*Callistemon pinifolius*	*Leptospermum squarrosum*
Coleoptera				
Aderidae	scavenger		5	
Anthicidae	scavenger		1	1
Brentidae	leaf chewer	6	7	5
Buprestidae	leaf chewer			1
Cantharidae	predator		1	1
Cerambycidae	leaf chewer			1
Chrysomelidae	leaf chewer	7	9	11
Coccinelidae	predator	2	1	3
Curculionidae	leaf chewer	10	8	14
Endomychidae	fungivore			2
Lathridiidae	fungivore	4	6	5
Microsporidae	fungivore	1		1
Mordellidae	scavenger	3	3	1
Nitidulidae	scavenger	1	1	
Oedemeridae	scavenger	1		
Ptiliidae	fungivore	1	2	2
Silvanidae	fungivore			1
Scarabaeidae	scavenger	1		
Staphylinidae	predator	1	5	2
Tenebrionidae	scavenger			1
Trogidae	scavenger	1		
Trogossitidae	predator	1		
sum		*42*	*50*	*52*

continued next page

Table A2: *continued*

Insect order		Myrtaceae		
Family	Feeding guild	*Angophora hispida*	*Callistemon pinifolius*	*Leptospermum squarrosum*
Hemiptera				
Alydidae	seed predator	1		
Cercopidae	xylem feeder		1	
Cicadellidae				
Idiocerinae	phloem feeder			1
Deltocephalinae	phloem feeder	3		
Tartessinae	phloem feeder	2	1	2
Typhlocybinae	mesophyll feeder			4
Xestocephalinae	phloem feeder	1		
Coccidae	phloem feeder	1		
Membracidae	phloem feeder		1	1
Miridae	mesophyll feeder	6		
Nogodinidae	phloem feeder		1	
Oxycarenidae	seed predator	2	1	3
Pentatomidae	mesophyll feeder	1		3
Piesmatidae	mesophyll feeder		1	
Psyllidae	phloem feeder	7	3	2
Reduviidae	predator		1	
Rhyparochromidae	seed predator		1	4
sum		*24*	*11*	*20*

Insect order		Proteaceae		
Family	Feeding guild	*Hakea gibbosa*	*Isopogon anethifolius*	*Telopea speciosissima*
Coleoptera				
Aderidae	scavenger	1	1	1
Anthribidae	scavenger	1		
Brentidae	leaf chewer	2	4	2
Cantharidae	predator	5	3	1
Cerambycidae	leaf chewer	1		
Chrysomelidae	leaf chewer	5	9	7
Cleridae	predator		1	1
Coccinelidae	predator	1	3	1
Colydiidae	fungivore		1	
Curculionidae	leaf chewer	10	9	6
Elateridae	fungivore	1		
Endomychidae	fungivore	1	2	1

continued next page

Table A2: *continued*

Insect order		Proteaceae		
Family	Feeding guild	*Hakea gibbosa*	*Isopogon anethifolius*	*Telopea speciosissima*
Lathridiidae	fungivore	4	6	2
Melandryidae	fungivore		1	
Melyridae	predator			1
Microsporidae	fungivore		1	
Mordellidae	scavenger		2	1
Nitidulidae	scavenger		2	
Phalacridae	fungivore	1		
Ptiliidae	fungivore	2	3	2
Ripiphoridae	predator		1	
Scarabaeidae	scavenger	1		
Silvanidae	fungivore	1		1
Staphylinidae	predator	3	14	2
Tenebrionidae	scavenger		1	
sum		*40*	*64*	*29*
Hemiptera				
Aleyrodidae	phloem feeder			2
Achilidae	phloem feeder		1	
Alydidae	seed predator	1		
Aphididae	phloem feeder			1
Cercopidae	xylem feeder		1	1
Cicadellidae				
Idiocerinae	phloem feeder			
Deltocephalinae	phloem feeder			
Tartessinae	phloem feeder			1
Ulopinae	phloem feeder		1	
Xestocephalinae	phloem feeder	1		
Coccidae	phloem feeder		1	1
Flatidae	phloem feeder		1	
Nogodinidae	phloem feeder	1		
Oxycarenidae	seed predator		1	
Piesmatidae	mesophyll feeder			1
Psyllidae	phloem feeder	7	5	4
Tingidae	mesophyll feeder	2		
Rhyparochromidae	seed predator		1	
sum		*12*	*12*	*11*

Table A3: Numbers of co-occurring Coleoptera and Hemiptera morphospecies for nine plant species within three families, including feeding guild and morphospecies name (morph ID).

Plant family					
Feeding guild	Family	Morph ID	Plant species		
Fabaceae			AO*	AP	DC
leaf chewer	Brentidae	Cole 066		1	1
leaf chewer	Chrysomelidae	Cole 126	1	1	
		Cole 045	1	1	
	Curculionidae	Cole 114	1	1	
	Elateridae	Cole 062		1	1
phloem feeder	Psyllidae	Psy 088		1	1
fungivore	Endomychidae	Cole 006		1	1
	Lathridiidae	Cole 005	1	1	
		Cole 046	1	1	
	Ptiliidae	Cole 033	1	1	1
		Cole 061		1	1
predator	Coccinelidae	Cole 632	1	1	
	Staphylinidae	Cole 456	1		1
scavenger	Mordellidae	Cole 115	1	1	
	Tenebrionidae	Cole 065	1	1	
Myrtaceae			AH	CP	LS
leaf chewer	Brentidae	Cole 021	1		1
		Cole 116	1	1	1
		Cole 166	1	1	
	Chrysomelidae	Cole 027	1		1
		Cole 091	1		1
		Cole 196	1		1
		Cole 519		1	1
	Curculionidae	Cole 024	1	1	1
		Cole 192		1	1
		Cole 212	1		1
phloem feeder	Cicadellidae	Ledri 002	1		1
	Psyllidae	Psy 094		1	1
fungivore	Endomychidae	Cole 006	1		1
	Lathridiidae	Cole 003	1	1	1
		Cole 005	1	1	1
		Cole 046		1	1
	Ptiliidae	Cole 033	1	1	1
		Cole 061		1	1
predator	Staphylinidae	Cole 023	1	1	1
		Cole 456		1	1
scavenger	Mordellidae	Cole 002	1	1	1
seed predator	Rhyparochromidae	Lyga 012		1	1
	Oxycarenidae	Lyga 014	1	1	1
		Lyga 014b	1		1

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Table A3: *continued*

Proteaceae			HG	IA	TS
leaf chewer	Brentidae	Cole 066		1	1
		Cole 166	1	1	1
	Chrysomelidae	Cole 299	1	1	
	Curculionidae	Cole 272	1		1
phloem feeder	Psyllidae	Psy 104	1		1
xylem feeder	Cercopidae	Cerco 003		1	1
fungivore	Endomychidae	Cole 006		1	1
	Lathridiidae	Cole 005	1		1
		Cole 046	1	1	
	Ptiliidae	Cole 033	1	1	1
		Cole 061	1	1	1
predator	Cantharidae	Cole 049	1	1	
		Cole 285	1		1
	Staphylinidae	Cole 023	1	1	1
		Cole 047	1	1	

*plant species within families:
Fabaceae: *A. obtusata* (AO), *A. parvipinnula* (AP), *D. corymbosa* (DC);
Myrtaceae: *A. hispida* (AH), *C. pinifolius* (CP), *L. squarrosum* (LS);
Proteaceae: *H. gibbosa* (HG), *I. anethifolius* (IA), *T. speciosissima* (TS).

Table A4: Number of morphospecies within Coleoptera and Hemiptera feeding guilds from nine host plant species.

Plant family	# Morphospecies		
Feeding guild	Plant species		
Fabaceae	*A. obtusata*	*A. parvipinnula*	*D. corymbosa*
fungivore	4	11	6
leaf chewer	18	22	8
predator	9	10	15
sap sucker	10	19	13
scavenger	7	4	2
seed predator	0	1	0
sum	*48*	*67*	*44*
Myrtaceae	*A. hispida*	*C. pinifolius*	*L. squarrosum*
fungivore	6	9	11
leaf chewer	23	24	32
predator	4	8	6
sap sucker	21	8	13
scavenger	7	10	3
seed predator	3	2	7
sum	*64*	*61*	*72*
Proteaceae	*H. gibbosa*	*I. anethifolius*	*T. speciosissima*
fungivore	10	14	6
leaf chewer	18	22	15
predator	9	22	6
sap sucker	11	10	11
scavenger	3	6	2
seed predator	1	2	0
sum	*52*	*76*	*40*

Table A5: Number of morphospecies within the phytophagous Coleoptera and Hemiptera feeding guilds from nine host plant species.

Plant family		# Morphospecies	
Feeding guild		Plant species	
Fabaceae	*A. obtusata*	*A. parvipinnula*	*D. corymbosa*
leaf chewer	18	22	8
mesophyll feeder	0	6	2
phloem feeder	10	13	11
xylem feeder	0	0	0
sum	*28*	*41*	*21*
Myrtaceae	*A. hispida*	*C. pinifolius*	*L. squarrosum*
leaf chewer	23	24	32
mesophyll feeder	7	1	7
phloem feeder	14	6	6
xylem feeder	0	1	0
sum	*44*	*32*	*45*
Proteaceae	*H. gibbosa*	*I. anethifolius*	*T. speciosissima*
leaf chewer	18	22	15
mesophyll feeder	2	9	1
phloem feeder	9	1	9
xylem feeder	0	0	1
sum	*29*	*32*	*26*

CHAPTER III

Patterns of insect herbivory on four Australian plant species

This chapter is intended for submission to *Austral Ecology*

Patterns of insect herbivory on four Australian plant species

Sabine Nooten[1], Lesley Hughes[1]

[1] Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

Abstract

Australia harbours a very diverse phytophagous insect fauna, but there is little information about patterns of insect herbivory in dominant forest systems, especially in dry sclerophyll forests. Here we assess variation in leaf herbivory in four species of narrow-ranged sclerophyllous shrubs across their geographic distribution. We assessed total leaf damage, as well as damage by type. We found that total leaf damage was highly variable across each plant's range. The main leaf damage types were chewing, mining and sucking. The proportion of damage attributed to each damage type showed an idiosyncratic pattern for each plant species. These patterns also varied significantly across the plants' geographic ranges.

Keywords: Leaves – herbivory – damage types – chewing – sap sucking – mining – dry sclerophyll forest – local pattern – Australia

Introduction

Insect herbivory is the consumption of plant material by phytophagous insects. It can encompass many different kinds of interactions, which may differ in duration and harmfulness to the plant. Plants offer a multitude of physical and chemical defences to reduce herbivore pressure. Herbivores, on the other hand, have evolved to cope with these defences and the host plants' nutritional value (e.g. Coley & Barone 1996; Hochuli 1996). Herbivore-host plant relationships affect food webs, nutrient cycling and community diversity (Schowalter 1986). The assessment of herbivory and damage types contributes to a better understanding of the diversity of phytophagous insects in local forest communities.

In Australia, herbivory has been studied on large canopy trees throughout major forest systems, such as open woodlands (Landsberg & Gillieson 1995), tropical eucalypt forests (Fensham 1994), and cool, temperate and warm rainforest systems (Lowman 1984, 1985). Relatively little attention has been paid to herbivory in dry sclerophyll systems, despite their dominance over much of the continent (but see Lowman 1995). The few published studies quantifying herbivory on Australian native plant species have generally focused on *Eucalyptus* (Myrtaceae) (Morrow & Fox 1989; Landsberg & Gillieson 1995; Christie & Hochuli 2005); eucalypts are dominant within most vegetation types, especially open, dry sclerophyll forests (Augee & Fox 2000) and are important for Australian forestry. Very few studies have focused on the herbivore damage suffered by less conspicuous plant species, such as shrubs or herbs (but see Moles & Westoby 2000; Harvey et al. 2012).

In this study we quantified damage by insect herbivores on four shrub species from dry sclerophyll forests in southeast Australia. This vegetation type is dominated by evergreen *Eucalyptus* trees with an open canopy cover of 30-70% (Specht & Specht 2002) and covers about 1.4 million hectares of the continent (Keith 2004). Plant species growing within this vegetation type are characterised by having sclerophyllous leaves that are high in structural compounds, such as cellulose and lignin (Specht & Specht 2002). These hardened leaves are generally associated with soils of low fertility (Keith 2004); they are relatively drought resistant (Beadle 1966) and also relatively long lived (Wright & Cannon 2001).

We selected four common sclerophyllous shrub species, belonging to three major Australian plant families (Fabaceae, Myrtaceae and Proteaceae), and assessed leaf herbivore damage and the pattern of herbivory attributed to different types of herbivores, such as chewing, sucking, mining and galling. Previous studies have investigated either the amount of total leaf herbivory due to one particular damage type, for example for chewing (Lowman 1984), or mining (Sinclair & Hughes 2008) or a combination of these two types (Moles & Westoby 2000). In addition to these conspicuous herbivory types (chewing, mining and galling), we included sap sucking; sucking insects such as phloem feeders, can cause just as much damage to the plant as chewing (Coley & Barone 1996; Leigh 1997).

Material and Methods

Plant selection

The four species sampled were *Acacia obtusata* Sieber ex DC (Fabaceae, Mimosoideae), *Daviesia corymbosa* Sm. (Fabaceae, Faboideae), *Angophora hispida* Sm. Blaxell (Myrtaceae) and *Telopea speciosissima* Sm. R. Br. (Proteaceae). Each species is a locally common sclerophyllous understory shrub with relatively broad leaves. The species are all found within the vegetation formation ‘Sydney Coastal Dry Sclerophyll Forest’ (Keith 2004). This vegetation has an open canopy cover dominated by large sclerophyllous trees (*Angophora costata*, *Corymbia gumifera* and several eucalypt species, including *E. capitellata, E. racemosa* and *E. haemastoma*). This vegetation type occurs on extremely low-nutrient soils derived from Hawkesbury sandstone (Groves 1994). Annual mean precipitation varies between 1000-1300 mm (Keith 2004), and annual mean temperature is approximately 17.75°C (Bureau of Meteorology, Melbourne, Australia).

Field sites

We sampled plants from three sites across each species' range (Fig. 1). Collection sites differed between species (Table 1) but were all located within the region spanning the Sydney basin and extending north to Newcastle (32° 55' 33.6"S, 151° 46' 51.6"E) and south to Nowra (34° 52' 22.8"S, 150° 36' 10.8"E). All sites were located in dry sclerophyll forests, with an open canopy cover dominated by eucalypts. Sites were chosen such that the focal species was locally abundant (more than 25 individuals in an approximately 250 m^2 area).

Table 1: Locations of three field collection sites for the four plant species across the native range.

Species	Site #	Site name	Latitude	Longitude
A. obtusata	1	Tallong	34° 43' 18.732"S	150° 3' 43.991"E
	2	Wingello	34° 43' 12.143"S	150° 4' 26.688"E
	3	Morton	35° 0' 56.4834"S	150° 8' 54.852"E
D. corymbosa	4	Marramarra	33° 30' 28.548"S	151° 1' 35.796"E
	5	Morton	35° 4' 37.7034"S	150° 23' 57.408"E
	6	Olney	33° 7' 47.6394"S	151° 13' 1.9194"E
A. hispida	7	Royal	34° 8' 13.5954"S	151° 2' 40.1994"E
	8	Ku-ring-Gai	33° 34' 58.512"S	151° 17' 3.0834"E
	9	Marramarra	33° 25' 19.379"S	150° 59' 28.752"E
T. speciosissima	10	Budderoo	34° 37' 22.727"S	150° 39' 18.899"E
	11	Royal	34° 5' 46.7880"S	151° 3' 38.268"E
	12	Ku-ring-Gai	33° 35' 6.1080"S	151° 16' 59.267"E

Leaf collection

Sampling occurred on three occasions over the period December 2009 to January 2010. On each sampling occasion, ten individual plants per site per species were haphazardly selected. Twenty mature, fully expanded leaves per plant were haphazardly collected. We note that this sampling method may underestimate total herbivory if whole leaves are consumed (Lowman 1984) but is useful for comparative purposes.

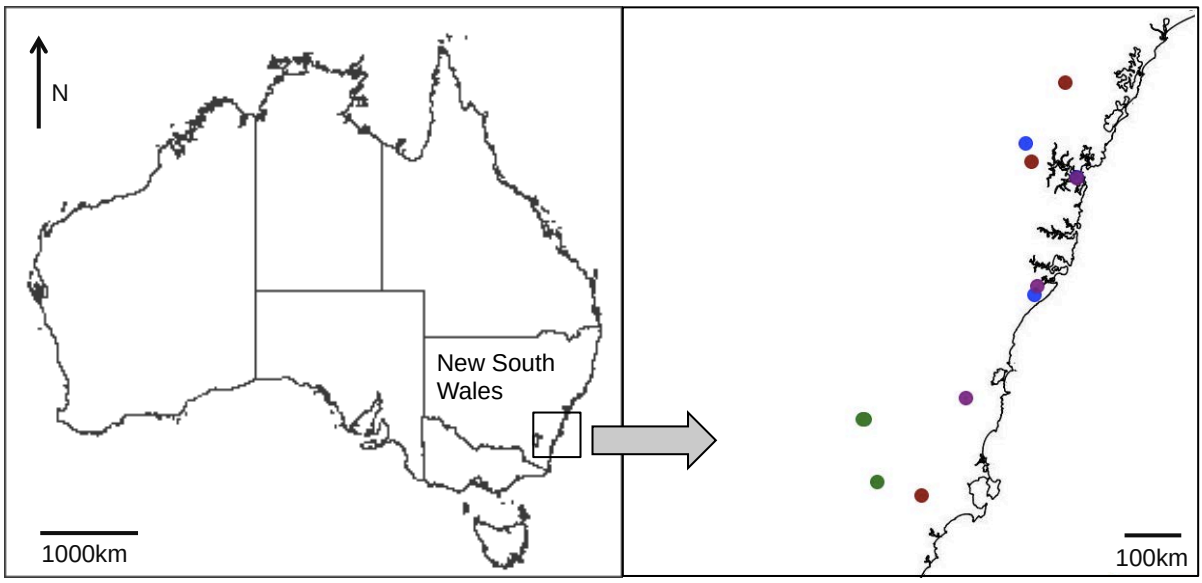

Figure 1: Collection sites: *A. obtusata* (green), *D. corymbosa* (dark red), *A. hispida* (blue) and *T. speciosissima* (purple). N marks north.

Herbivory assessments

We assessed the percentage missing leaf area due to all types of herbivory, and the proportions of separate occurring herbivory types, which were chewing, sap sucking, mining and galling. Herbivory assessments of a total of 2,400 leaves (4 species × 3 sites × 10 plants × 20 leaves) were made.

One of the damage types assessed, chewing, is caused by insects that use mandibles to chew through leaf tissue, including Coleoptera (adults and larvae), Lepidoptera (caterpillar larvae), Hymenoptera, Symphyta (sawfly larvae), Orthoptera (grasshoppers, all instars) and Phasmatodea (stick insects, all instars) (Elliott et al. 1998). Chewing was classified as the loss of all layers of leaf tissue, which leads to holes that either occurred within or from the edge of the leaf. To estimate the missing area from the leaf edge, we drew approximate leaf margins in relation to the leaf symmetry (Morrow & Fox 1989; Carpenter & Cappuccino 2005). Sap sucking damage is generally caused by insects using stylets that pierce the surface of the leaf to suck up liquids, such as phloem sap, xylem sap or cell contents from mesophyll tissue (Elliott et al. 1998). This damage was identified as circular punctures, surrounded by lighter coloured tissue. Species from the Hemiptera (all instars), Thysanoptera (all instars) and the Acari (mites) feed in this manner. We classified mining damage as serpentine or blotched dead areas, where the outer layer was detached from the leaf. This is caused by larval stages of insects within the Coleoptera, Lepidoptera, Diptera and Hymenoptera that chew internal leaf tissue between the upper and lower surface of the leaf (Elliott et al. 1998; Sinclair & Hughes 2010). Galls are a reaction of plants to the effect of insect saliva, resulting in the growth of plant tissue (Fernandes & Price 1992). This damage was identified as leaf tissue that protruded out from the flat leaf surface. We used the following sources for the identification of damage types: Hockings (1980), McMaugh et al. (1985), Jones & Elliot (1986) and Labandeira et al. (2007).

Statistical analyses

We compared total herbivore leaf damage and types of damage firstly among the four plant species, to assess if there are differences among plant species, and secondly among the three collection sites for each species. We standardised data on

percentage herbivory to fit probability values between 0 and 1. To improve normality, a logit transformation was used instead of the commonly used arcsine, following suggestions by Warton & Hui (2011). For the assessment of total leaf herbivory we used a nested ANOVA design in SPSS v20 for both comparisons; among plant species (the factor 'sites' was nested in the 'factor plant species') and for each plant species among sites (the factor 'individual plants' was nested in the factor 'sites'). We compared proportions of leaf damage types using a permutational MANOVA (PERMANOVA) on the basis of Euclidean distance matrices (Anderson 2001), with the same design as described above. This analysis was performed with the PERMANOVA + add-on package for PRIMER *v*6 (Clarke & Gorley 2006).

Results

Total herbivore leaf damage

There was considerable variation in total leaf damage among plant species, values ranging from approximately 7% (*D. corymbosa)* to 22% (*A. hispida*) (Table 2); the average across all plant species was 14.6% ± 14.3%. Overall, herbivore leaf damage was not significantly different among plant species ($F_{3,8}$ = 1.770, p = 0.23). However, all species pair comparisons were significantly different (p < 0.001), except for *A. obtusata – T. speciosissima* (p = 0.938).

Total herbivory was also significantly different among the three collection sites for two plant species, *A. hispida* ($F_{2,27}$ = 14.526, p < 0.001) and *T. speciosissima* ($F_{2,27}$ = 7.009, p < 0.01); but there were no significant differences for *A. obtusata* ($F_{2,27}$ = 2.248, p = 0.125) and *D. corymbosa* ($F_{2,27}$ = 3.071, p = 0.063).

For each plant species, levels of herbivory were also highly variable and significantly different among individual plants within each site (p < 0.001), with values ranging from 0% to 85% (Fig. 2).

Table 2: Mean and standard deviation (M ± SD) for percentage of total herbivore leaf damage and damage types (chewing, sucking, mining and galling) from four plant species averaged over three sites across the plant species' native range.

Species	Total	Chew	Suck	Mine	Gall
A. obtusata	18.7 ± 18.6	7.5 ± 11.3	3.7 ± 6.8	7.2 ± 9.5	0 ± 0
D. corymbosa	7.2 ± 8.0	2.1 ± 4.2	2.9 ± 3.7	2.1 ± 3.4	0.1 ± 0.2
A. hispida	22.6 ± 15.7	12.2 ± 13.6	4.8 ± 4.4	3.6 ± 5.6	2.1 ± 3.2
T. speciosissima	9.9 ± 14.8	3.9 ± 10.0	1.8 ± 2.3	4.3 ± 9.4	0.1 ± 0.8

Herbivore leaf damage types

The dominant damage type averaged across all plant species and sites was chewing (6.4 ± 9.8%), followed by mining (4.3 ± 7.0%) and sucking (3.3 ± 4.3%). Galling contributed the least damage (0.6 ± 1.1%). All four damage types were found on three plant species, with only *A. obtusata* lacking galling damage. The proportions of damage types varied considerably between species (Fig. 3); the major types were chewing and mining on *A. obtusata*, sucking on *D. corymbosa*, chewing on *A. hispida* and mining and chewing on *T. speciosissima* (Table 2). Overall there was no significant difference in the proportions of damage types among the four plant species (Pseudo-$F_{3,12}$ = 1.001, p-perm = 0.51). Species pair comparisons showed that there was no significant difference between species pairs (p values ranging from p = 0.176 to p = 0.702).

Three plant species had significantly different proportions of leaf damage types among sites: *A. obtusata* (Pseudo-$F_{2,27}$ = 3.960, p-perm = 0.012), *D. corymbosa* (Pseudo-$F_{2,27}$ = 11.653, p-perm < 0.001), and *T. speciosissima* (Pseudo-$F_{2,27}$ = 8.945, p-perm < 0.001). Proportions of damage types on *A. hispida* did not differ between sites (Pseudo-$F_{2,27}$ = 2.286, p-perm = 0.163).

For three plant species, proportions of herbivore damage types were again highly variable and significantly different among individual plants within each site (p < 0.001), *A. hispida*, however, showed no significant difference among individual plants (p = 0.456). The highest contribution of individual damage types to total herbivory on individual plants was chewing for three plant species, and sucking for

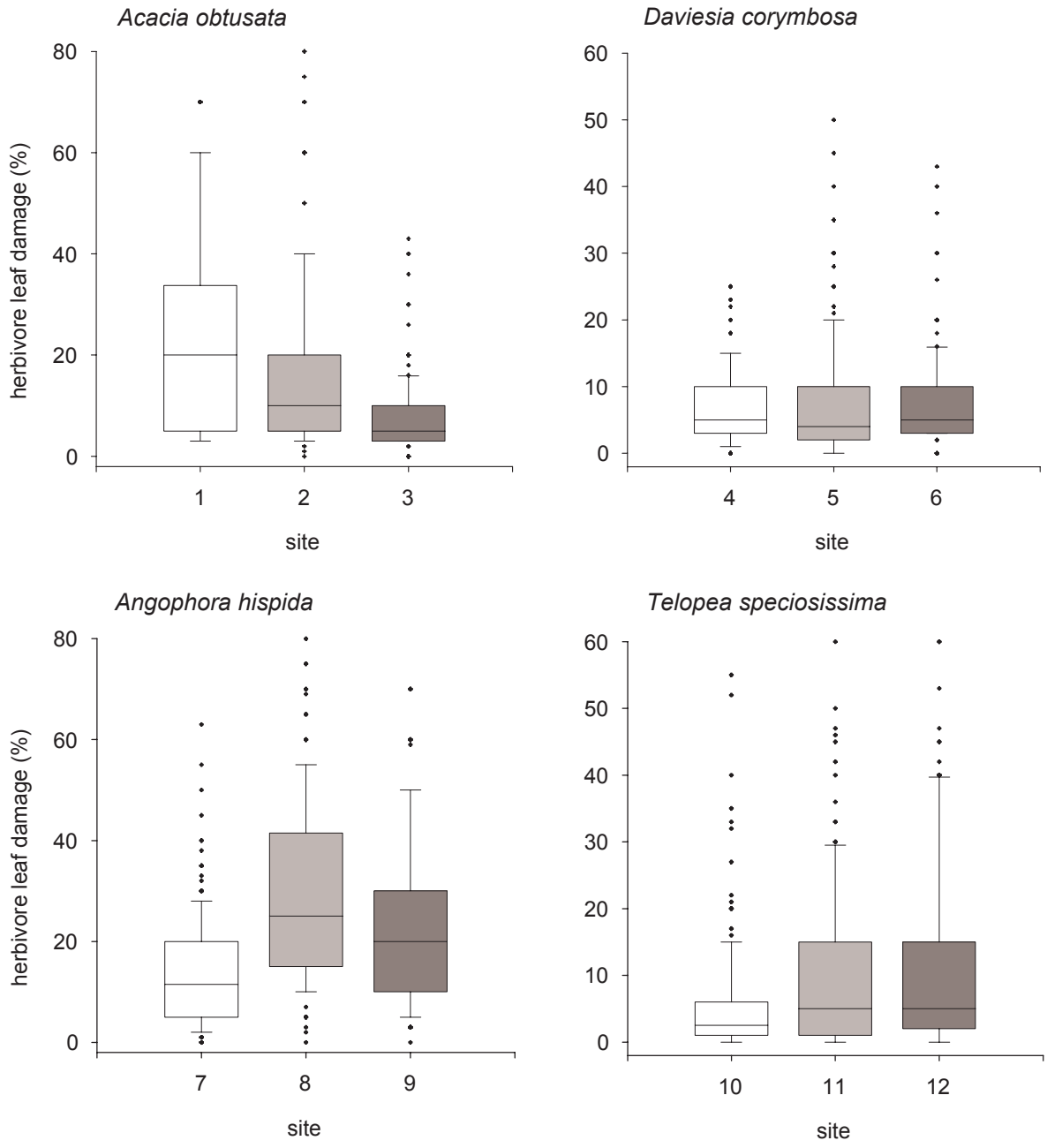

Figure 2: Total herbivore leaf damage on four plant species at three sites across the plants' geographic range. Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

one (*D. corymbosa*). For *A. obtusata* proportions of individual damage types on single plants ranged from 0-68% for chewing, and from 1-50% for sucking and mining damage (Fig. 3). For *D. corymbosa*, values ranged from 0-65% for sucking damage, from 0-33% for chewing and from 1-41% for mining. For *A. hispida*, values ranged up to 82% for chewing, from 0-50% for sucking, from 1-41% for mining and from 0-16% for galling. For *T. speciosissima,* values ranged from 1-83% for chewing, and from 0-60% for sucking and mining damage.

Discussion

We found that the amount of total leaf herbivory on all four shrub species was somewhat higher than found in previous studies in temperate forests, but within the range previously found for dry sclerophyll canopy trees. There was a high level of variation within plant species and sites, demonstrating the patchy distribution of herbivore insects in space and time. Levels of total leaf loss were higher for plant species from the most species rich genus (*Acacia*), consistent with the idea that there has been a strong diversification of insects associated with major plant radiations. Leaf damage was mainly inflicted by chewers, followed by miners and sap suckers, but the relative proportion of damage types varied widely among the plant species. Leaf damage patterns also showed little consistency across the plants' native range, suggesting that herbivory may also be affected by factors such as the composition of the local plant species community and variation in vegetation structure.

Total herbivore leaf damage

We found that the average amount of total herbivory across all four species of shrubs was relatively high (14.6%, range from 7.2 to 22.6%) compared to that found for temperate forests in general (< 10% leaf loss; Coley & Barone 1996). Our results, however, are very consistent with those of Lowman (1985) who found an average of 13% leaf area loss in canopy trees in dry sclerophyll forests in southeast Australia.

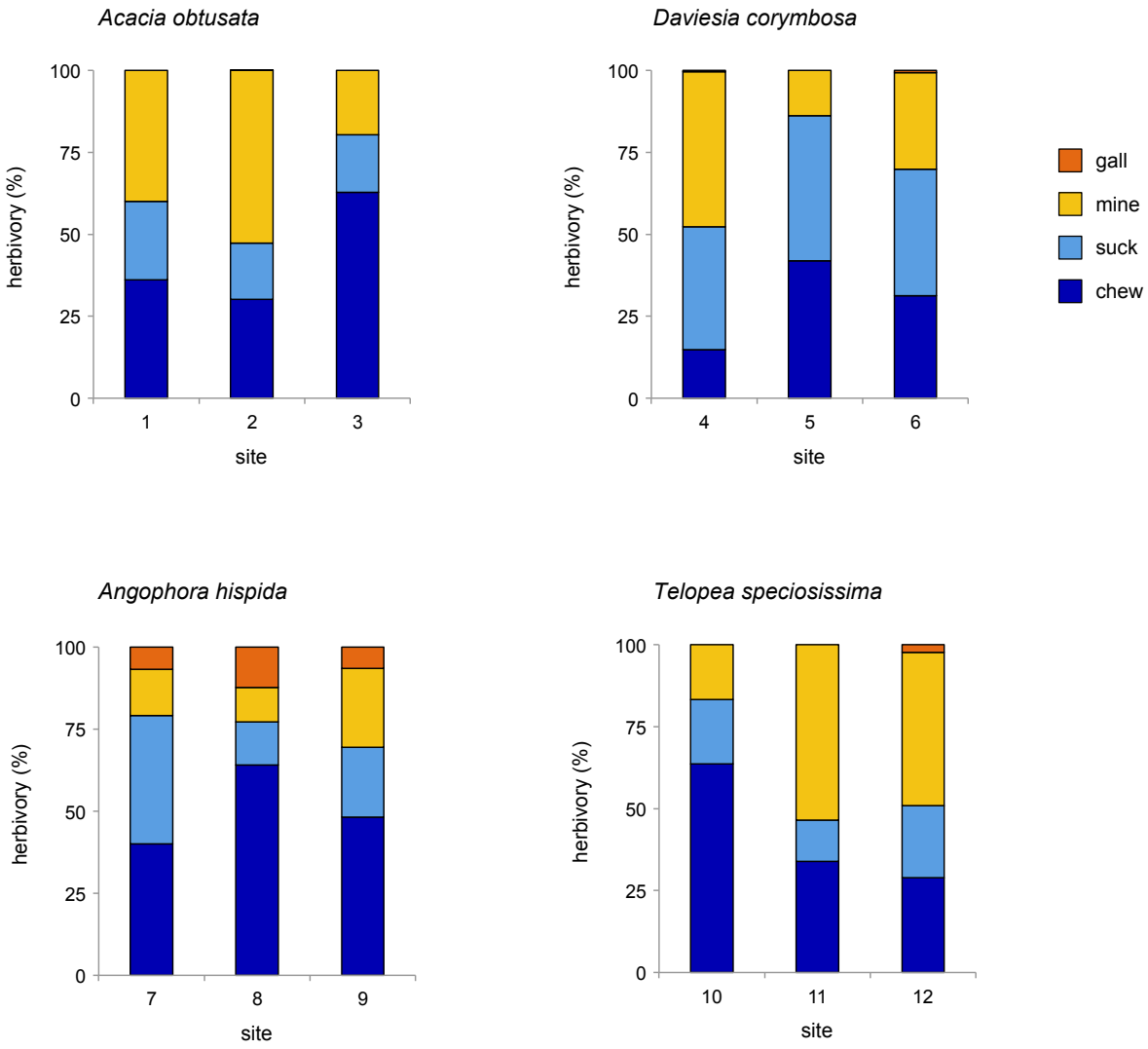

Figure 3: Proportions of herbivore leaf damage types (chewing, sucking, mining and galling) on four plant species at three sites across the plants' geographic range.

Similarly, a study conducted by Springett (1978) showed that dry sclerophyll forests across Australia experienced more intense herbivory (about 15-30%), than comparable temperate forest systems on other continents. Our finding of similarity of herbivore pressure on the different growth forms in this vegetation type contrasts with the four fold differences found between understory and canopy trees in temperate and warm rainforests (Lowman 1995). Consistent with our study, Lowman (1985) found a wide range of variability (5-25%) in herbivore damage among individual eucalypt species. Likewise, there was a similar range of values for total leaf herbivory (4.8-32.5%) on canopy tree species within various Australian rainforest systems (Lowman 1985), but averages for leaf loss were generally higher in these systems, ranging from 14% for subtropical, to 22% for warm and 27% for cool temperate rainforests. Herbivore leaf loss in temperate forests of < 9% has been found in North America (e.g. Adams & Zhang 2009), and < 7% across northern Europe (e.g. Kozlov 2007).

A study conducted within the same national park (Ku-ring-Gai Chase NP) as some of our collection sites, reported a slightly lower average (10%) for total leaf herbivory, obtained from expanding leaves of 51 plant species from 17 families (Moles & Westoby 2000). This slightly lower value may be associated with age differences in the leaves compared to those in the present study (but see Coley & Barone 1996).

We found a high level of variation in the amount of total herbivore leaf damage across the range of all four plant species even though each species had a relatively small range (ca. 2 degrees of latitude) and all sites were located in similar vegetation. Within plant species and sites, variation in leaf herbivory was very high, ranging from 0% to 85% on single leaves. This result is consistent with numerous other studies that report similar magnitudes of variation for leaf herbivory between individual plants, species and stands (Lowman 1985; Landsberg & Ohmart 1989; Lowman 1995; Moles & Westoby 2000; Andrew & Hughes 2005).

The highest levels of herbivory were found on *Angophora hispida* (22.6% ± 15.7%) (Myrtaceae) and *Acacia obtusata* (18.7% ± 18.6%) (Fabaceae). These species belong to, or are closely related to, particularly large Australian genera. The genus *Angophora* is closely related to the genus *Eucalyptus* (Wilson et

al. 2004), which comprises about 700 species and is similarly dominant across the continent in all but the arid zone (Augee & Fox 2000). *Acacia* is the most species rich genus, comprising approximately 950 species, and is dominant throughout most Australian vegetation types, including woodlands and shrublands (Augee & Fox 2000). Furthermore, plant nitrogen content may also contribute to levels of herbivory. Acacias are associated with nitrogen fixing symbionts, which enrich the plant's phyllodes with nitrogen, providing a more valuable food source for insect than plants without these symbionts (e.g. Strauss & Zangerl 2002). Some of the highest levels of herbivory reported anywhere in the world are for eucalypt species. Average values for total herbivory ranged up to 38%, assessed on dominant eucalypt species in eastern Victoria (Landsberg & Gillieson 1995) and up to 17.7%, on herbarium specimens of *Eucalyptus* (Morrow & Fox 1989). Our results are consistent with the idea that host species from more species rich genera and families may harbour a more diverse suite of associated phytophagous insects, in turn associated with greater damage (e.g. Price 2002). Strong diversifications of insects associated with Australia's major plant radiations, such as the Mimosoideae (especially for the genus *Acacia*) and within the Myrtaceae (particularly the genus *Eucalyptus*) have been well documented (Austin et al. 2004; Cranston 2009).

Herbivore damage types

Damage on all four plant species was consistently dominated by chewing, sucking and mining. This finding is consistent with other studies that assessed leaf herbivore damage types along the east coast of Australia, on a range of native and exotic herbaceous plant species (Harvey et al. 2012), and for an *Acacia* species (Andrew & Hughes 2005). Likewise, on a native shrub species in North America, leaf herbivory was mainly caused by chewers and sap suckers (Genton et al. 2005). Across the same continent, four widespread tree species (*Acer, Quercus, Fagus* and *Liquidambar*), were mainly damaged by chewing and skeletonising herbivores, accounting for 70-98% of total folivory (Adams & Zhang 2009). In northern and central Europe, the main damage type on two native tree species (*Betula*) was chewing (Kozlov 2007).

Chewing was generally the dominant damage type. The highest proportion of chewing was found on *A. hispida* where chewing inflicted on average 53% of the total leaf herbivory, suggesting that insects with chewing mouthparts from the orders Coleoptera, Lepidoptera, Orthoptera and Phasmatodea were the main herbivores. Such a dominance of leaf chewers is consistent with the results described in Chapter 2, where the herbivore feeding guild structure of the associated Coleoptera and Hemiptera community was assessed. The proportion of the feeding guild 'leaf chewers', based on morphospecies richness, was higher than the 'sap suckers' (see Chapter 2, Fig. 6c). Our results are also consistent with those from other studies within Australia. For example, an assessment of a wide range of eucalypt species throughout the southeast of the continent revealed that chewing was the dominant form of leaf herbivory (Landsberg & Gillieson 1995). This also concurs with the large numbers of phytophagous Coleoptera found on eucalypt species (Morrow 1977).

We found that sap sucking, although much less conspicuous, was also a major leaf damage type on all four plant species. On *D. corymbosa,* sap sucking was the dominant feeding type, accounting for about 40% of the total damage. Here too, the proportion of insects of the guild 'sap suckers' was highest (see Chapter 2, Fig. 6b). On *A. hispida,* sap sucking was the second most dominant feeding type, inflicting 21% of the total, and on the other two plant species (*A. obtusata* and *T. speciosissima*) sap sucking was still a major component with average values of about 20% of total folivory. Our results concur with a previous study, where herbivore leaf damage types on *Acacia falcata* were assessed over a period of three months, and sap sucking damage was found to be the second most dominant damage type (Andrew & Hughes 2005). Sap sucking has been found to have profound effects on plant performance by reducing leaf mass and changing crown conditions in eucalypts (Cunningham et al. 2009). Consistent with findings in Australia, herbivore leaf damage on a native shrub species in Canada was mainly caused by sap sucking (Genton et al. 2005). A recent meta-analysis by Zvereva et al. (2010) on 32 woody plant species revealed that damage caused by sap feeders significantly reduced growth (-29%), reproduction (-17%) and photosynthesis (-27%). These findings demonstrate that neglecting sap sucking damage in leaf herbivory assessments could lead to a substantial underestimation of the total herbivore leaf damage suffered by host plants (reviewed in Andrew et al. 2012).

Other factors that might also influence proportions of herbivore leaf damage types on host plants include soil properties, because they may influence the nutritional content of foliage, or the local plant species composition and vegetation structure, as this will influence the local phytophagous insect species richness and influences the efficiency of herbivores discovering their host plant (reviewed in Schowalter 1986). The composition of the local plant species community was not assessed in this study, but can have a significant effect on leaf herbivory such as leaf mining (Sinclair & Hughes 2008).

Conclusion

We found that total herbivore leaf damage on four sclerophyllous understory species is relatively high compared to the average for temperate forests, but congruent with that from dry sclerophyll canopy trees. There was a high level of variability among sites and individual plants, most likely reflecting the patchy distribution of phytophagous insects in time and space. Plant species from species rich genera showed higher levels of herbivory than those from smaller genera, potentially reflecting the strong diversification of Australian insects with major plant genera.

Leaf damage was mainly inflicted by chewing, sucking, and mining herbivores. The results demonstrate the importance of including sap sucking damage in herbivory assessments. Patterns of damage types were plant species-specific. There was also considerable variation in damage types at different sites across each plant's range, once again reflecting patchy insect distribution, but also indicating that additional factors such as the local plant species composition may be important.

Acknowledgements

We thank Katherine McClellan for assistance in the field. We are grateful to Katherine McClellan and Nigel Andrew for comments on earlier versions of this manuscript. This study was supported by a Macquarie University research excellence scholarship (iMQRES) to Sabine Nooten.

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CHAPTER IV

Potential impacts of climate change on insect communities: a transplant experiment

This chapter is intended for submission to *PLoS ONE*

Potential impacts of climate change on insect communities: a transplant experiment

Sabine Nooten[1], Nigel Andrew[2], Lesley Hughes[1]

[1] Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

[2] Centre for Behavioural and Physiological Ecology, University of New England, Armidale, NSW 2351, Australia

Abstract

Climate change will have profound impacts on the distribution, abundance and ecology of all species. We used a multi-species transplant experiment to investigate the potential effects of a warmer climate on insect community composition and structure. Eight native Australian plant species were transplanted outside their native range into a climate approximately 2.5°C (mean annual temperature) warmer than their native range. Subsequent insect colonisation was monitored for 12 months. We compared the insect communities on transplanted host plants at the warmer sites with control plants transplanted within the species' native range. Comparisons were also made among transplanted plants at warmer sites and congeneric plant species native to this area. We found that the morphospecies composition of the colonising Coleoptera and Hemiptera communities differed markedly between transplants at the control compared to the warmer sites. Differences in community structure, as described by the distribution of different feeding guilds, were also found. However, the structure of the herbivorous insect community showed a higher level of consistency between plants at control and warm sites. There were marked differences in community composition and feeding guild structure, for both herbivores and non-herbivores, between transplants and congenerics at the warm sites. These results suggest that as the climate warms, considerable turnover in the composition of insect communities may occur, but the structure of insect herbivore communities may retain elements of their present day structure.

Keywords: Climate change – transplant experiment – latitude – insects – herbivores – community – composition – structure – feeding guild – Coleoptera – Hemiptera

Introduction

The distribution, abundance and ecology of all species will be affected by current climate change (Hughes 2000; Root et al. 2003; Parmesan 2006; Rosenzweig et al. 2008; Visser 2008; Hoffmann & Sgro 2011; Parmesan et al. 2011). Species are expected to respond individualistically to climate change, resulting in changes in interactions, such as competition, predation or parasitism, with far-reaching consequences for community structure, composition and function (Tylianakis et al. 2008; Thackeray et al. 2010; Hughes 2012). The decoupling of present-day interactions between plants and insects may be particularly important. Many insects are already responding sensitively to climatic changes over the past few decades, via range shifts and changes in phenology (Parmesan et al. 1999; Forister & Shapiro 2003; Musolin 2007; Wilson et al. 2007; Merrill et al. 2008; Kearney et al. 2010). Mismatches in interactions have occurred, due to temporal (e.g. Visser & Both 2005; Parmesan 2007) and spatial (e.g. Parmesan et al. 1999; Musolin 2007; Merrill et al. 2008) decoupling. Further, significant changes in the structure of species assemblages are already apparent in both temperate and tropical regions (e.g. Emmerson et al. 2005; Walther 2010; Sheldon et al. 2011).

Increasing temperature may have particularly profound impacts on the composition of insect communities because it will affect almost all life history parameters, including emergence, growth rate, and voltinism (Bale et al. 2002; Cornelissen 2011). A field-based warming experiment that manipulated several factors (temperature, CO_2 and water) showed that temperature had the largest effect on insect community composition and structure as a result of individualistic responses of both individual species and of different feeding guilds (Villalpando et al. 2009).

Disruptions of current plant-insect communities may have particularly far reaching consequences for terrestrial ecosystems because plants and their associated phytophagous insects comprise a major proportion of terrestrial biodiversity - approximately 50% of all described species (Strong et al. 1984; Wilson

1988; Chapman 2009). Insects perform many important ecosystem services, such as pollination, but they can also be significant pests (Harrington et al. 2001; Netherer & Schopf 2010).

What shapes plant-insect communities?

Understanding the factors that currently shape plant-insect communities is fundamental to predicting how such assemblages will be affected as the climate continues to change. Several non-mutually exclusive factors have been suggested as important drivers affecting the composition and structure of plant-insect communities. For example, MacArthur (1972) suggested that community assembly may be chiefly driven by climatic factors, and that these may operate via impacts on species interactions. In contrast, Strong et al. (1984) suggested that the major drivers of the phytophagous community are the physical and chemical characteristics of the host plants. In the present study, we tested the role of the host plant and climatic factors as possible drivers of plant-insect community assembly, under current and warmer climate conditions.

How can we predict climate change impacts on communities?

There are significant challenges for predicting future impacts of climate change at the community level and several approaches have been taken. Dynamic vegetation models have been developed to project future changes in plant communities (e.g. Malcolm et al. 2002; Murray et al. 2012), and field surveys have examined turnover of community composition and structure along either altitudinal (Colwell et al. 2008; Chen et al. 2009; Garibaldi et al. 2011) or latitudinal gradients (e.g. Andrew & Hughes 2004; Andrew & Hughes 2005).

Transplant experiments offer powerful, though rarely used, tools for assessing potential impacts of climate change at the community level. Those transplant experiments that have been performed have mostly focused on plant (Bruelheide 2003; Egli et al. 2004; Ibanez et al. 2008; De Frenne et al. 2011; Haggerty & Galloway 2011; Van der Veken et al. 2012), or soil communities (Briones et al. 1997; Sohlenius & Bostroem 1999; Shaw & Harte 2001; Rey et al. 2007; Budge et al.

2011), with only a few focused on plant-insect assemblages (Andrew & Hughes 2007; Marsico & Hellmann 2009; Pelini et al. 2009).

In this study we used a multi-species transplant experiment to investigate potential changes in plant-insect communities under a warmer climate. We compared community composition, in terms of the number and identity of morphospecies, and community structure, in terms of feeding guilds (Root 1973; Simberloff & Dayan 1991) on plants at warmer sites, compared to those within their native range, and to those on species native to the warmer sites.

Material and Methods

The field transplant experiment was conducted in eastern Australia, with the same eight plant species as described in Chapter II. *Isopogon anethifolius,* however, was not included in this study, due to difficulties in germinating. All individual plants were grown from seed then planted into field sites (i) within the species' native range and (ii) outside the native range into a warmer climate. Subsequent insect colonisation was monitored for one year.

Host plant species

Eight host plant species from three major Australian plant families, the Fabaceae, Myrtaceae and Proteaceae, were selected. From the Fabaceae (subfamily Mimosoideae): *Acacia parvipinnula* Tindale, (subgenus Phyllodineae), *Acacia obtusata* Sieber ex DC (subgenus Phyllodineae), and from the subfamily Faboideae, *Daviesia corymbosa* Sm. From the Myrtaceae: *Angophora hispida* Sm. Blaxell, *Callistemon pinifolius* J.C. Wendl., and *Leptospermum squarrosum* Gaertn. From the Proteaceae: *Hakea gibbosa* Sm. Cav. and *Telopea speciosissima* Sm. R. Br. Within each family, the species chosen are relatively distantly related, according to the most recently published phylogenies (George 1998; Wilson et al. 2004; Brown et al. 2006).

Each plant species has a fairly narrow distribution in coastal south-east New South Wales, including the Sydney Basin and extending latitudinally from approximately Newcastle (32° 55' 33.6"S, 151° 46' 51.6"E) in the north, to Nowra (34° 52' 22.8"S, 150° 36' 10.8"E) in the south. All the species are common understory shrubs in the vegetation type 'Sydney Coastal Dry Sclerophyll Forest' (Keith 2004), growing on low-nutrient, freely draining soils derived from Hawkesbury sandstone (Groves 1994). Collectively, the distributions of the species range from 0-700 m in elevation, with average precipitation of 1000-1300 mm p.a. (Keith 2004) and approximately 17.7°C average annual temperature (Bureau of Meteorology, Melbourne, Australia).

All plants were established from seed in the glasshouse facilities at Macquarie University in January 2009. Seeds from species in the Fabaceae were pre-treated with boiling water. Once germinated, seedlings were transferred into 5 cm square tubes filled with a potting – sand mix (4:1 ratio). Slow release fertilizer (Osmocote ® for Australian native plants, Baulkham Hills, NSW, Australia) was applied according to the manufacturer's instructions. Seedlings were subjected to the natural photoperiod and watered twice daily. When roots were established, plants were transferred into 13 cm pots and if necessary after six months, were transferred once more into 25 cm square pots to prevent root circling. After seven months, plants were placed outside the glasshouse to acclimatise to natural weather conditions, and grown for a further six months. One species, *Acacia parvipinnula*, had to be successively cut back to 150 cm because it grew much faster than the other species.

Field sites

We selected three field sites to receive the transplants. One site was located in the approximate centre of all the plant species' native ranges, at Mt. Ku-ring-Gai (33° 39' 39.3798"S, 151° 8' 5.6472"E), 38 km north of Sydney, referred to hereafter as the control site (C). Two warmer sites were located near Grafton in northern New South Wales (NSW), ca. 600 km north of the northern-most boundaries of the species' native ranges. The sites were located 8 km apart, one in Minnie Water (29° 46' 26.76"S, 153° 17' 23.244"E) referred to as warm site 1 (W1) hereafter and the other in Wooli (29° 53' 8.124"S, 153° 15' 58.752"E) known as warm site 2 (W2) (Fig. 1).

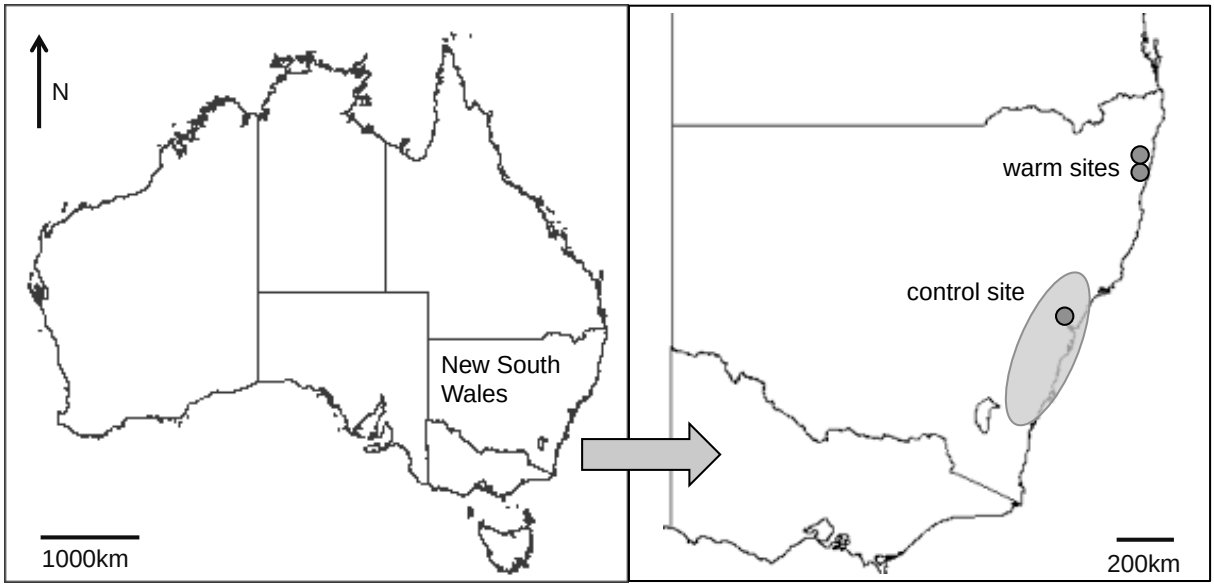

Figure 1: Location of the three transplant sites: one control site within the current range of eight host plant species (grey oval); and two warm sites, located ca. 600 km north of the northern boundary of the plant species' range. N marks north. See Figure A5 for a more detailed visualisation of each plant species' distribution.

Mean annual temperature, calculated over the last 30 years, near the control site was 17.25°C (nearest weather station: Sydney) and 19.75°C near the two warmer sites W1 and W2 (nearest weather station: Grafton) (Bureau of Meteorology, Melbourne, Australia). The mean annual precipitation at the warmer sites (1340 mm) was slightly higher than at the control site over the same period (1164 mm). The difference in mean annual temperature of approximately 2.5°C between the control and the two warmer sites reflects the current projections for warming in NSW by the year 2050 (NSW Department of Environment, Climate Change and Water, 2010; CSIRO 2012). Annual precipitation for the three sites is within the projected patterns for mid- and north-coastal areas of NSW. The control site and W1 were situated in dry sclerophyll forest with 10-30% canopy cover of tall eucalypt trees, mainly *Angophora costata*. The W2 site was coastal heath with 1-15% canopy cover dominated by *Banksia* spp.

Six soil samples (10 cm diameter × 10 cm depth) were taken at each transplant site and at two sites within Ku-ring-Gai Chase national park (where most of the eight plant species naturally co-occur), with soils derived from the Hawkesbury sandstone. Soil samples were tested for total Nitrogen, Phosphorus and Potassium content by a soil testing facility (SESL, Thornleigh, NSW, Australia). Total N, P and K values for the control site (N: 0.113% w/w, P: 0.005% w/w and K: 0.001%) were slightly higher than W1 (N: 0.053% w/w, P: 0.002% w/w and K: 0.012%) and W2 (N: 0.03% w/w, P: 0.007% w/w and K: 0.021%) but comparable to the two sites in Ku-ring-Gai Chase National Park (N: 0.078% w/w, P: 0.002% w/w and K: 0.046%).

All transplant sites were fenced to exclude vertebrate herbivores. Shortly before being transported to the transplant sites, all plants were sprayed with insecticide (0.6% pyrethrum/water solution) to remove all external insects that may have colonised the plants during their establishment at Macquarie University. In March/April 2010, 640 plants were transplanted into the three sites: 160 individual plants at the control site (20 plants per species) and 240 plants each at W1 and W2 (30 individual plants per plant species per site). The eight species were planted in random positions within each site, 1.5 m apart in a 36 m × 12 m grid. Plants were watered in for three days after transplantation.

Insect collection

Arthropods were collected on three occasions, in September and December 2010, and in March 2011, with pyrethrum knockdown following the protocol of Andrew & Hughes (2004). Sampling occurred in the morning between 7.00 and 11.00 h on low wind days. At each site, at each collection event, ten individual plants per host plant species were haphazardly selected and sprayed with a 0.6% pyrethrum water solution. All arthropods that fell onto four collecting trays (each 50 × 30 cm) previously placed beneath the plant were transferred into 70% ethanol. For each sampling event, different individual plants were chosen for insect collection. Using the same protocol, collections were also made from four plant species native to the warm transplant area, belonging to the same genera as five of the transplanted species: *Acacia longifolia* Andrews, subsp. *sophorae* Labill. (Fabaceae, subgenus Phyllodineae), *Callistemon pachyphyllus* Cheel (Myrtaceae), *Hakea actites* W.R. Barker (Proteaceae) and *Leptospermum trinervum* Sm. Joy Thomps. (Myrtaceae). Ideally, insects would have been collected from congeneric plant species for all eight transplant species, but only four could be located in the warm transplant area.

The height of all transplanted individuals was measured at the time of transplantation and again after 12 months. We also assessed total leaf herbivory after 12 months on 10 randomly selected individual plants per species at each site. For each plant, the percentage missing leaf area was visually assessed *in situ*, and an average value for leaf loss was estimated for individual plant species. Additionally, a more thorough analysis of total leaf herbivory within specific damage types was conducted for a subset of plant species (see Chapter 5). In March 2011, all transplanted shrubs were removed prior to flowering to comply with the conditions of the scientific license.

Table 1: Feeding guild classification, based on mouthpart morphology and targeted plant tissue, for (i) Coleoptera and (ii) Hemiptera families.

(i) Coleoptera

Feeding guild	Superfamily	Family
leaf chewer	Chrysomeloidea	Cerambycidae, Chrysomelidae
	Buprestoidea	Buprestidae
	Curculionoidea	Attelabidae, Belidae, Brentidae, Curculionidae
fungivore	Tenebrionoidea	Colydiidae, Zopheridae
	Cucujoidea	Endomychidae, Lathridiidae
	Microsporoidea	Microsporidae
	Staphylinoidea	Ptiliidae
predator	Cucujoidea	Coccinellidae, Cucujidae
	Staphylinoidea	Pselaphidae, Staphylinidae
scavenger	Tenebrionoidea	Aderidae, Anthicidae, Mordellidae, Tenebrionidae
	Bostrichoidea	Anobiidae
	Cucujoidea	Nitidulidae
	Scarabaeoidea	Scarabaeidae

continued next page

(ii) Hemiptera

Feeding guild	Suborder	Superfamily	Family/subfamily
phloem feeder*	Auchenorrhyncha	Fulgoroidea	Achilidae, Delphacidae, Eurybrachidae, Flatidae, Fulgoridae, Tropiduchidae
	Auchenorrhyncha	Membracoidea	Cicadellidae, subfamilies: Deltocephalinae, Eurymelinae, Iassinae, Tartessinae, Ulopinae, Xestocephalinae
		Membracoidea	Membracidae
	Sternorrhyncha	Aleyrodoidea	Aleyrodidae
		Aphidoidea	Aphididae
		Coccoidea	Coccidae
		Psylloidea	Psyllidae
mesophyll feeder*	Auchenorrhyncha	Membracoidea	Cicadellidae, subfamily Typhlocybinae
	Heteroptera	Miroidea	Miridae, Tingidae
		Pentatomoidea	Pentatomidae, Scutelleridae
xylem feeder*	Auchenorrhyncha	Cercopoidae	Cercopidea, Clastopteridae
predator	Heteroptera	Dipsocoroidea	Schizopteridae
		Naboidea	Nabidae
		Reduvioidea	Reduviidae
seed predator	Heteroptera	Cimicoidea	Anthocoridae
		Lygaeoidea	Rhyparochromidae, Cymidae
		Coreoidea	Alydidae

*mesophyll, phloem and xylem feeders are combined in a category of ‘sapsucker’ for the complete dataset but analysed separately for the herbivore dataset.

Insect community characterisation

We focused on the orders Coleoptera and Hemiptera because they were dominant within the samples. Insect identification followed the routine described in Nipperess et al. (2011). All adult insects from the Coleoptera and Hemiptera were sorted to morphospecies using the protocol from Oliver & Beattie (1993), and subsequently identified to family level. We excluded larvae (Coleoptera) and nymphs (Hemiptera) from the analyses because of the difficulty in relating them to the corresponding adults (Andrew & Hughes 2007). Adult Coleoptera and Hemiptera were assigned to functional feeding guilds, based on the morphology of their mouthparts, feeding method and targeted plant tissues. Feeding guilds were assigned to whole families by choosing the feeding type expressed by the largest number of members of the family following the descriptions by Lawrence & Britton (1991). An exception to this method was the family Cicadellidae (Hemiptera), in which morphospecies were identified to subfamily level for feeding guild assignments, using the identification key provided by Fletcher (2009); this was necessitated by the highly heterogeneous nature of feeding habits within this taxon.

Morphospecies within the order Coleoptera were divided into four feeding guilds: leaf chewers, fungivores, predators and scavengers. Morphospecies within the order Hemiptera were assigned to one of five feeding guilds: mesophyll feeders, phloem feeders, xylem feeders, predators and seed predators (Table 1).

Two types of comparisons were made for the insects collected from each host plant species. Firstly, we compared numbers of morphospecies within feeding guilds from the entire collection of Coleoptera and Hemiptera (hereafter known as the ‘full dataset’). For the full dataset, we pooled the mesophyll, phloem and xylem feeders into a general guild of ’sapsuckers’, as we were interested in general patterns within both herbivore and non-herbivore guilds. Secondly, we compared only phytophagous species within these orders, referred to hereafter as the ‘herbivore dataset’, using a more finely divided herbivore feeding guild structure.

Statistical analyses

Host plant performance

We investigated possible site effects on plant height and leaf herbivory after 12 months using separate one-way ANOVAs (SPSS) for (i) all plant species pooled and (ii) for each host plant species separately. A single two way-ANOVA was not used because for individual plant species the assumption of homogeneity of variance (assessed by Levene's test), even after transformation, could not always be met. In these instances a Welch's ANOVA (resulting in fractional degrees of freedom) was used (Welch 1951), which is more robust to violation of this assumption. Tukey's post hoc tests were performed to test between means. Growth data were square root transformed to improve normality where appropriate. Herbivory data were logit transformed instead of the commonly used arcsine, following suggestions by Warton & Hui (2011).

Coleoptera and Hemiptera morphospecies richness, diversity and density

The following estimators of Coleoptera and Hemiptera morphospecies richness and species accumulation curves were computed using the programme EstimateS 8.2 (Colwell 2006) for each site: (i) with all eight host plant species pooled, to investigate a possible overall site effect, and (ii) for individual host plant species. Coleman's species rarefaction curves were generated and morphospecies richness among sites was compared per specified number of individuals (pooled plant species n = 979; individual plant species n = 17). We used the Chao-1 index as the estimator for the total number of species at each site and for each plant species (Chao et al. 2000). The Chao-1 index is a non-parametric species richness estimation index that expresses the lower bound of the expected species richness; the calculation is made via 1000 randomised occurrences of singletons and doubletons (Chao et al. 2000). Simpson's diversity index (D) was used as a non-parametric measure for morphospecies diversity. It gives the probability of any two individuals drawn at random from an infinitely large community belonging to the same species (Simpson 1949). As a large value of D indicates low species diversity, Simpson's D is usually reported as the reciprocal value (1/D). This index is one of the most meaningful and robust diversity indices available because it captures the variance of the species

abundance distribution (Magurran 2004). To assess the adequacy of sampling at each site, species accumulation curves were generated (Gotelli & Colwell 2001) and then the number of morphospecies collected was divided by the mean Chao-1 index value, resulting in an estimate of the proportional number of morphospecies collected from the expected plant species pool.

To compare the number of Coleoptera and Hemiptera morphospecies collected from individual plant species among sites, we used the total number of morphospecies collected in each sample (n = 30, each sample equals 4 trays); this is termed morphospecies density (Gotelli & Colwell 2001). To compare morphospecies density among sites, untransformed count data were used in generalised linear models (GLM) (using SPSS v20), based on negative binomial distributions (Warton et al. 2011). As pointed out by O'Hara & Kotze (2010), this method produces negligible bias compared to the use of log or square root transformed count data in models based on a normal distribution.

Coleoptera and Hemiptera community composition and structure

Data for each of the three collection events were pooled to produce as complete samples of the insect fauna on each host plant species as possible. We compared the insect community in terms of (1) morphospecies composition and (2) the distribution of each feeding guild among sites, for each plant. Comparisons were performed using both the full dataset (all Coleoptera and Hemiptera morphospecies), and for the subset of phytophagous morphospecies in both orders.

Community composition was compared (i) for pooled plant species among sites and congenerics and (ii) in terms of morphospecies overlap among sites within and between plant species. In the programme PRIMER *v*6 (Clarke & Gorley 2006), we firstly compared community composition, using Bray-Curtis dissimilarity matrices, based on morphospecies presence / absence data, for both the full dataset and the herbivore subset, to produce non-metric multidimensional scaling (nMDS) plots. Secondly, morphospecies overlap was compared using the SIMPER function in the programme PRIMER *v*6 (Clarke & Gorley 2006).

Community structure, in terms of feeding guilds, was compared using the multivariate extension of generalised linear models (mGLM), based on negative binomial regression (Warton et al. 2011). The computation was conducted using the mvabund package (Wang et al. 2010) in the R statistical environment version 2.14.1 (R Development Core Team 2011).

We investigated whether there was consistency in community structure among plant species within plant families at the control site. Then two hypotheses about possible drivers of community structure were tested: firstly, that community structure is chiefly associated with host plant identity (Strong et al. 1984), and secondly, that community structure is chiefly associated with climatic factors (MacArthur 1972). To examine the role of host plant identity as a driver, we compared community structure (i) between the control site and each warmer site W1 and W2, and (ii) between W1 and W2. To examine the role of climatic factors, we compared community structure on five of the transplanted plant species (iii) between each warmer site W1 and W2 and the congeneric host plant species in the warmer transplant area.

Results

Host plant performance

Of the 640 transplanted individual plants 204 (32%) died during the 12 month tenure of the experiment. Mortality rates varied slightly among sites: control site (40%), W1 (31%) and W2 (27%), but varied markedly among species: *A. hispida* (59%), *T. speciossima* (57%), *D. corymbosa* (56%), *A. obtusata* (46%), *H. gibbosa* (20%), *A. parvipinnula* (10%), *L. squarrosum* (10%) and *C. pinifolius* (0%).

Overall growth after 12 months (as measured by differences in plant height) for pooled plant species was not significantly different among sites ($F_{2,407}$ = 2.169, p = 0.116). For the individual plant species, growth was significantly different among sites for three of the eight plant species (Table 2). For *A. obtusata*, growth was significantly higher at the site W2, for *C. pinifolius* growth was significantly lower at W1 and for *T. speciosissima* it was significantly higher at the control site. Mean

growth varied among plant species; values ranged from a minimum of 3 cm (*T. speciosissima*) to a maximum of approximately 200 cm (*A. parvipinnula*), but most height increases were between 20 and 50 cm (Fig. A1, Appendix 2).

Values for mean leaf herbivory after 12 months varied among plant species but was not significantly different among sites (Welch-$F_{2,153.5}$ = 0.773, p = 0.463). Overall herbivory was greatest for *A. hispida*, with an average of 23% leaf loss across all sites, followed by *A. obtusata* (17%), *L. squarrosum* (14%), *T. speciosissima* and *A. parvipinnula* (11%), *D. corymbosa* (10%) *C. pinifolius* (9%) and *H. gibbosa* (8%), Herbivory on individual host species was significantly different between sites for only *A. parvipinnula,* which suffered significantly more herbivory at W1 (Table 3, Fig. A2, Appendix 2).

Table 2: Summary of ANOVA results and pairwise comparisons for net growth rate of eight plant species after 12 months at three transplant sites: control (C), warm 1 (W1) and warm 2 (W2); degrees of freedom (df), F-Statistic (F) and p-value (p) overall and for pairwise comparisons between sites.

Plant species	df	F	p			
			overall	C-W1	C-W2	W1-W2
Fabaceae						
A. obtusata	2,35	5.026	**0.012**	0.177	**< 0.01**	0.438
A. parvipinnula	2,67	0.370	0.692			
D. corymbosa	2,23	0.395	0.678			
Myrtaceae						
A. hispida	2,31	2.961	0.067			
C. pinifolius	2,76	10.241	**< 0.001**	**0.01**	0.264	**< 0.001**
L. squarrosum	2,65	2.068	0.135			
Proteaceae						
H. gibbosa	2,67	0.585	0.429			
T. speciosissima	2,28	30.068	**< 0.01**	**< 0.01**	**< 0.01**	0.985

note: significant values are in bold.

Table 3: Summary of ANOVA results for leaf herbivory from eight plant species after 12 months at three transplant sites: control (C), warm 1 (W1) and warm 2 (W2); degrees of freedom (df), F-Statistic (F) and p-value (p) overall and for pairwise comparisons between sites.

Plant species	df	F	p			
			overall	C-W1	C-W2	W1-W2
Fabaceae						
A. obtusata	2,26	0.738	0.488			
A. parvipinnula	2,15.99	5.715	**0.013**	0.052	0.346	0.562
D. corymbosa	2,25	0.638	0.537			
Myrtaceae						
A. hispida	2,25	0.108	0.898			
C. pinifolius	2,17.47	2.824	0.087			
L. squarrosum	2,15.49	2.664	0.101			
Proteaceae						
H. gibbosa	2,27	1.106	0.345			
T. speciosissima	2,27	1.053	0.363			

note: significant values are in bold.

Coleoptera and Hemiptera morphospecies richness, diversity and density

A total of 33,387 arthropods were collected from transplants and congeneric plant species. Of these 5,973 (18%) from the two orders Coleoptera (n = 1,847 or 6%) and Hemiptera (n = 4,126, or 12%) were identified to morphospecies. The phytophagous subset comprised 582 Coleoptera (2%) and 4,031 Hemiptera (12%).

Pooled host plant species

Estimators of Coleoptera and Hemiptera morphospecies richness for the pooled plant species showed that there was a slight site effect, with W1 being richer in morphospecies but less diverse (as indicated by Simpson's D) (Table 4). Morphospecies richness varied among sites as shown by Coleman's rarefaction curve (Fig. 2a); richness was highest at W1 (196 morphospecies per rarefied number of individuals; n = 979) and lowest at the control site (125 morphospecies) (Table 4). The expected number of morphospecies, as estimated by the Chao-1 index, was highest at W1, suggesting that 473 species would be associated with all eight plant

species at this site, followed by W2 and lastly the control site. Simpson's diversity index was similarly high at the control and warm site W2; W1 showed the lowest value.

Adequacy of sampling at the control site was 56%. A slightly smaller proportion of the species pool was collected at the two warmer sites, 46% at W1 and 49% at W2. Species accumulation varied among sites (Fig. 2b). The rate was highest at W1, and lower at the control site and W2. An asymptote of species accumulation after three collection events was not reached at any of the sites.

Individual host plant species

For the individual plant species, there was little variation among sites in morphospecies richness, but Chao-1 estimation and adequacy of sampling varied markedly (Table 4). Morphospecies richness per rarefied number of individuals (n = 17) varied little among plant species and sites, with values ranging from 5 (*D. corymbosa*) to 13 (*A. hispida*) (Table 4). The expected number of morphospecies, as estimated by the Chao-1 index, varied greatly among plant species and sites, values ranged from 40 (*A. hispida*) to 257 (*A. parvipinnula*). The Simpson's diversity index for individual plant species varied among sites and species, from 0.04 (*T. speciosissima*) to 0.59 (*A. parvipinnula*). The total number of collected Coleoptera and Hemiptera morphospecies at individual sites ranged from 13 (*T. speciosissima*) to 109 morphospecies (*A. parvipinnula*) (Fig. A3, Appendix 2).

Adequacy of sampling was generally higher at the control site than at the warmer sites: values for individual plant species and sites ranged from 11% (*T. speciosissima*) to 63% (*C. pinifolius*). An asymptote of species accumulation after three collection events was not reached for any of the eight plant species (Fig. A4, Appendix 2).

Coleoptera and Hemiptera morphospecies densities on transplants varied little among sites, with six plant species showing no significant differences (Table 5, Fig. 3). Only two plant species (*L. squarrosum* and *T. speciosissima*) had a significantly higher morphospecies density at the control site.

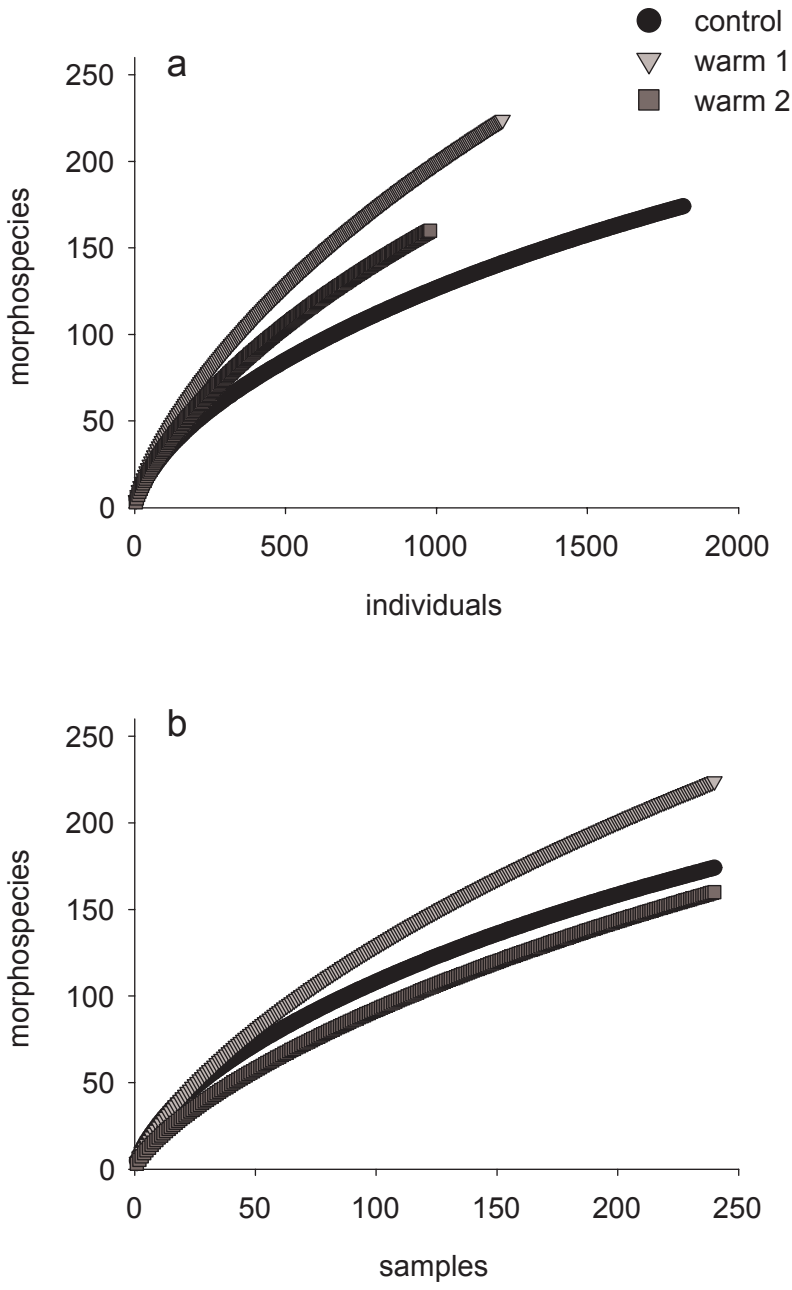

Figure 2: (a) Coleman's rarefaction and (b) species accumulation curves for pooled plant species at three transplant sites: control, warm 1 and warm 2.

Table 4: Morphospecies richness indices for the three transplant sites (i) pooled plant species (ii) eight individual transplanted species and (iii) four congeneric plant species in the warm area: control (C), warm 1 (W1) and warm 2 (W2), total number of morphospecies (# Msp), species richness per rarefied number of individuals (richness), Chao-1 index, adequacy off sampling: number of morphospecies/Chao-1 in percent (# Msp/Chao), Simpson's diversity index (reciprocal) (Simpson 1/D).

Plant species	Site	# Msp	Richness	Chao-1	# Msp/Chao (%)	Simpson 1/D
(i) pooled plant species						
	C	174	125	312	56	0.19
	W1	221	196	473	46	0.01
	W2	160	160	321	49	0.17
(ii) individual plant species						
A. obtusata	C	44	10	100	44	0.10
	W1	32	8	164	20	0.18
	W2	33	9	229	14	0.22
A. parvipinnula	C	69	5	167	41	0.59
	W1	109	9	245	45	0.16
	W2	73	9	257	28	0.14
D. corymbosa	C	29	12	96	30	0.05
	W1	39	11	95	41	0.10
	W2	14	5	34	41	0.54
A. hispida	C	22	9	40	55	0.19
	W1	25	13	125	20	0.05
	W2	23	9	66	35	0.18
C. pinifolius	C	42	12	66	63	0.06
	W1	31	11	68	46	0.11
	W2	25	7	49	51	0.35
L. squarrosum	C	60	10	110	55	0.14
	W1	43	12	139	31	0.05
	W2	30	7	70	43	0.28
H. gibbosa	C	36	8	65	56	0.25
	W1	41	12	114	36	0.07
	W2	20	6	84	24	0.32
T. speciosissima	C	27	12	108	25	0.05
	W1	24	13	224	11	0.05
	W2	13	13	68	19	0.04

continued next page

Plant species	Site	# Msp	Richness	Chao-1	# Msp/Chao (%)	Simpson 1/D
(iii) congeneric plant species						
A. longifolia		124	7	27	0.45	0.14
H. actites		61	12	114	0.54	0.07
C. pachyphyllus		41	12	94	0.44	0.07
L. trinervum		103	12	215	0.48	0.07

Table 5: Summary statistics for generalised linear model (GLM) analyses of Coleoptera and Hemiptera morphospecies densities from eight plant species at three transplant sites: control (C), warm 1 (W1) and warm 2 (W2); degrees of freedom (2,117), Wald-X^2-Statistic (Wald-X^2) and p-value (p) overall and for pairwise comparisons between sites.

Plant species	Wald-X^2	p			
		overall	C-W1	C-W2	W1-W2
Fabaceae					
A. obtusata	2.584	0.275			
A. parvipinnula	2.265	0.232			
D. corymbosa	5.220	0.074			
Myrtaceae					
A. hispida	0.247	0.884			
C. pinifolius	3.655	0.161			
L. squarrosum	6.090	**0.048**	0.140	**0.024**	0.363
Proteaceae					
H. gibbosa	4.942	0.084			
T. speciosissima	7.421	**0.024**	0.281	**0.011**	0.099

note: significant values are in bold.

Community composition

Comparisons among sites and congeneric plant species

Non-metric multidimensional scaling (nMDS) plots revealed that there was some similarity in community composition within each of the three transplant sites and within the four congeneric plant species (Fig. 4). Community composition for morphospecies of the full dataset (Fig. 4a) showed less clustering than those from the herbivore subset only (Fig. 4b).

Comparison of transplanted plant species at control and warm sites

A total of 354 morphospecies of Coleoptera (n = 97) and Hemiptera (n = 257) were collected from the transplanted shrubs at the three sites. Of these 273 (77%) were classified as phytophagous (Coleoptera n = 30, Hemiptera n = 243). Numbers of Coleoptera and Hemiptera morphospecies varied markedly among sites and plant species (Table A1, Appendix 1; Table A6, Appendix 3). For Coleoptera, values for individual sites ranged from 5 (*A. hispida,* at control site) to 51 (*A. parvipinnula,* at W1). For Hemiptera, values ranged from 6 (*T. speciosissima,* at W2) to 56 (*A. parvipinnula,* at W1). Phytophagous Coleoptera occurred in lower numbers than phytophagous Hemiptera; numbers for phytophagous Coleoptera ranged from 0 (*A. hispida,* at W1) to 18 (*A. parvipinnula,* at W1), and for phytophagous Hemiptera from 6 (*T. speciosissima,* at W2) to 55 (*A. parvipinnula,* at W1). The percentage of herbivore morphospecies from the full dataset was on average higher at the control site (81%) than at the warm sites W1 (72%) and W2 (65%). This trend was largely consistent for the individual plant species (Table A1, Appendix 1).

Overall, there was little commonality in morphospecies identity among the three sites; among the transplants at the control site 29 morphospecies (17%) were co-occurring. Of these, three belonged to the order Coleoptera (two Lathridiidae and one Ptiliidae), and 26 to the order Hemiptera, of which were one each from the families Delphacidae and Lygaeidae, five each from Coccidae and Psyllidae, six Aphididae and eight Cicadellidae.

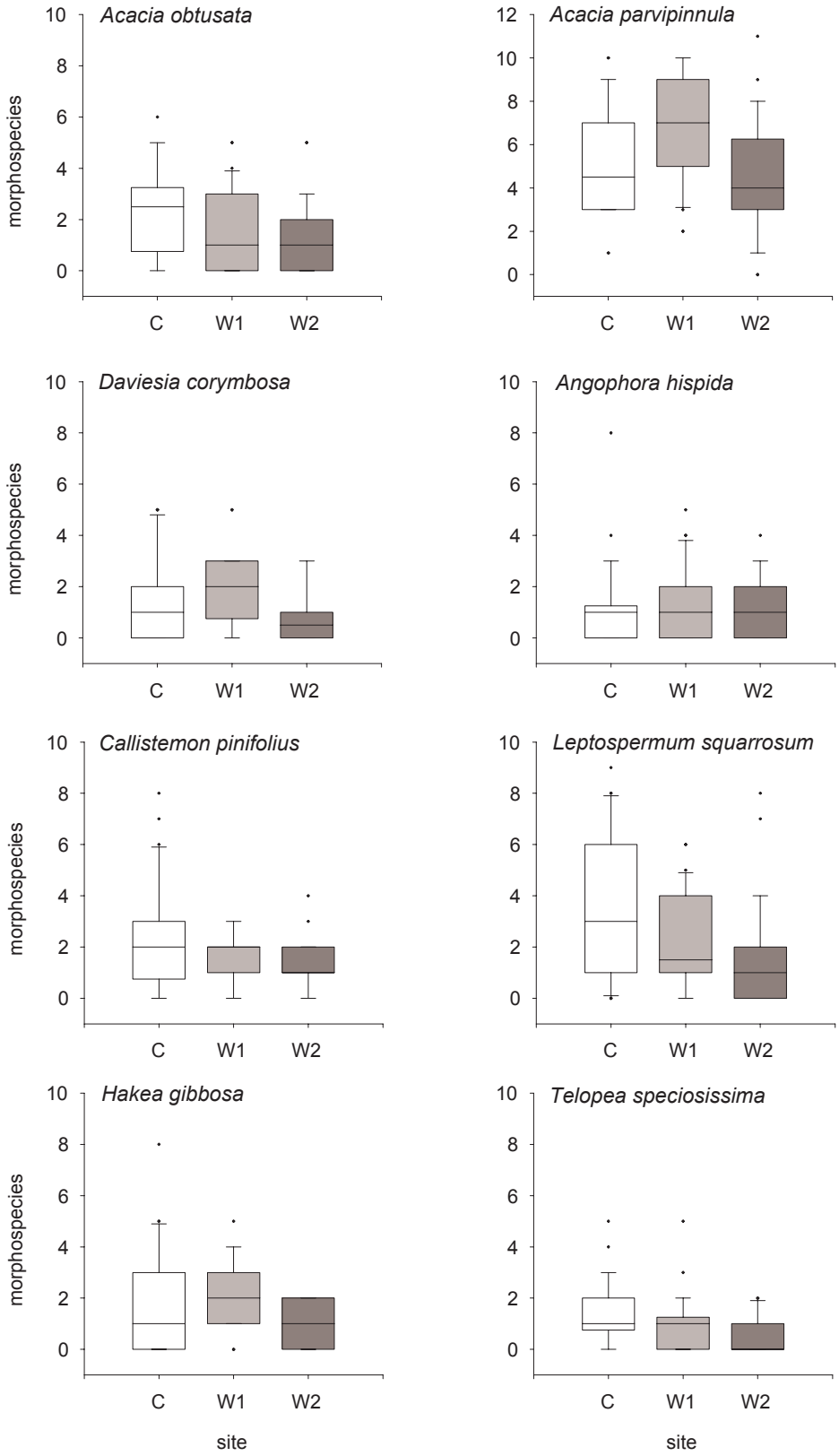

Figure 3: Morphospecies density for Coleoptera and Hemiptera from eight plant species at three transplant sites: control (C), warm 1 (W1) and warm 2 (W2). Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

At W1, 26 morphospecies (12%) were co-occurring, of which 10 belonged to Coleoptera (one each from the families Cantharidae, Chrysomelidae, Curculionidae, Lathridiidae, Ptiliidae, Staphylinidae, and two each from Coccinelidae and Scarabaeidae) and 16 Hemiptera, one each from the families Fulgoridae and Membracidae, two Coccidae, three Psyllidae and Cicadellidae, and six Aphididae. At W2 16 morphospecies (10%) were co-occurring, of these were 7 from the order Coleoptera (three Chrysomelidae, and one each from Anobiidae, Brentidae, Endomychidae and Ptiliidae), and 9 Hemiptera, belonging to the families Aphididae (five), Delphacidae and Membracidae (one each) and Lygaeidae (two).

There was also little similarity of morphospecies among the host plant species within the three plant families (Table 6). In the Fabaceae similarity of morphospecies at the three transplant sites was only 3.2% (full dataset, averaged across plant species) and even less for the herbivore dataset (1.2%). In the Myrtaceae there was an average of 2.3% similarity in morphospecies among all three sites (full dataset), and only 0.6% for the herbivore dataset. In the Proteaceae there was an average of 3.1% similarity for the full dataset and 0.3% for the herbivore dataset (Table 6).

Similarity in morphospecies among sites was similarly low for individual host plant species (Table 6). For the full dataset, values ranged from 0.1% (*C. pinifolius*) to 10.6% (*D. corymbosa*), for the herbivore dataset from 0% for four plant species to 3.6% (*A. parvipinnula*). As for the plant families, individual plant species supported more co-occurring morphospecies within the full dataset than for the herbivore dataset. For the full dataset, similarities were higher between the two warm sites W1 and W2 than between these sites and the control.

When morphospecies co-occurred at individual plant species among transplant sites, they tended to be fungivores from the families Ptiliidae and Lathridiidae (Coleoptera), phloem feeders from the families Aphididae and Coccidae (Hemiptera) and mesophyll feeders from the family Cicadellidae, subfamily Typhlocybinae (Table A2, Appendix 1). Numbers of co-occurring morphospecies between the control and any warm site ranged from 1 (*D. corymbosa*) to 8 (*A. parvipinnula*), and between W1 and W2 they ranged from 2 (*T. speciosissima*) to 26 (*A. parvipinnula*).

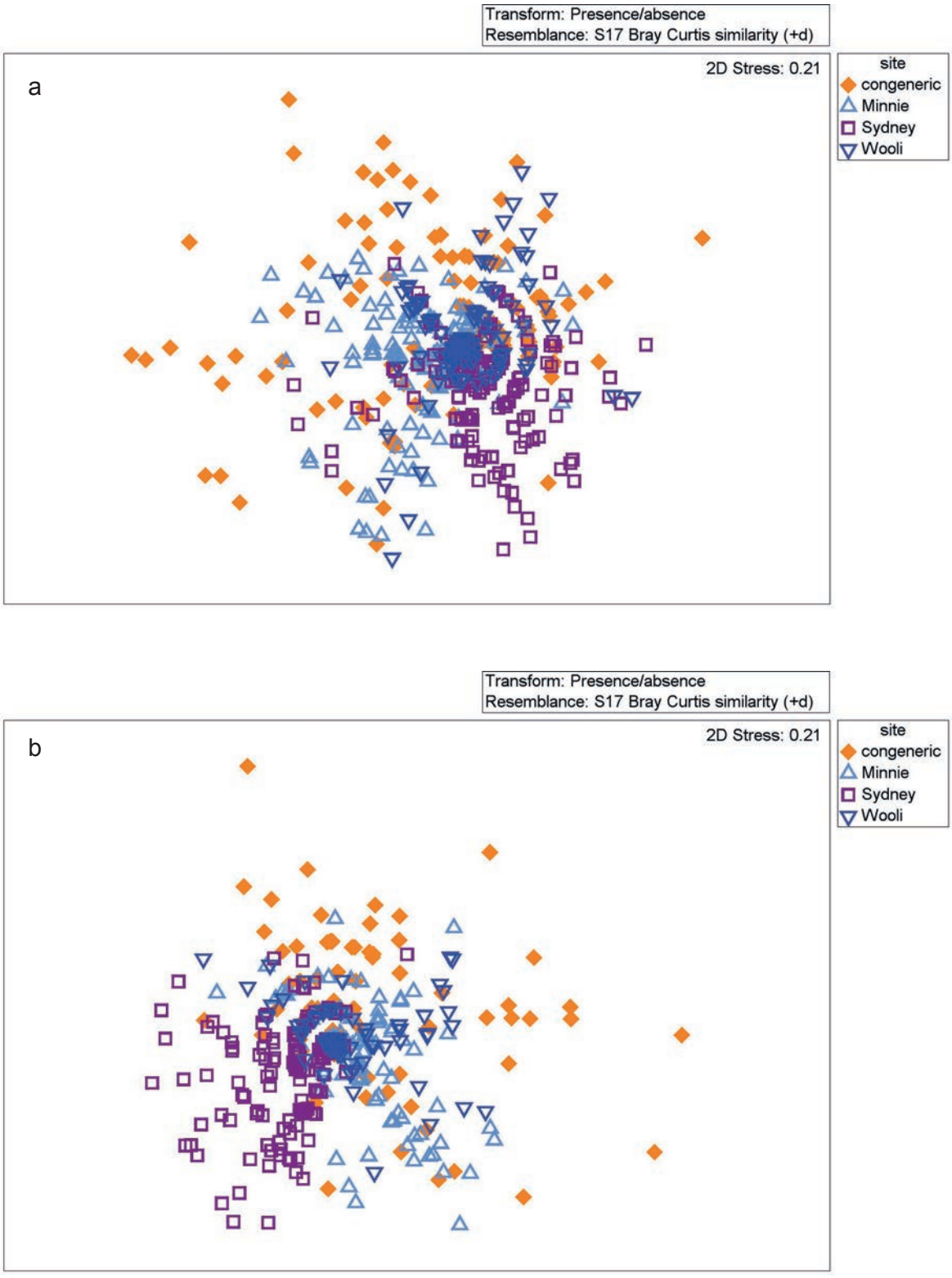

Figure 4: Non-metric multidimensional scaling plot of community composition at three transplant sites and congeneric plant species for morphospecies from (a) the full dataset and (b) the herbivore dataset.

Comparison of congeneric and transplanted plant species at the warm sites

A total of 271 morphospecies of Coleoptera (n = 136) and Hemiptera (n = 135) were collected from 120 individual plants of the four congeneric plant species native to the warm transplant area. Of these, 66% were classified as herbivores (Coleoptera n = 152, Hemiptera n = 197) (Table 7). There were 40 (15%) morphospecies co-occurring among the congeneric plant species, of which 27 belonged to the order Coleoptera and 13 to the Hemiptera. Within the Coleoptera there were one each from the families Aderidae, Brentidae, Cerambycidae, Chrysomelidae, Pselaphidae, Scarabaeidae, Staphylinidae, Trogossitidae, two each from the families Cantharidae and Mordellidae, three each from the families Lathridiidae and Ptiliidae, four Coccinellidae and five Curculionidae. Within the Hemiptera, there was one each from the families Aphididae, Membracidae, Reduviidae, Schizopteridae and Tropiduchidae, and eight Psyllidae.

There were few morphospecies in common between the transplants at W1 and W2 and the native congeneric plant species. For the full dataset, values ranged from 0.2% (*H. gibbosa* and congeneric *Hakea*) to 5.2% (*A. parvipinnula* and congeneric *Acacia*). For the herbivore dataset, values ranged from 0% (*C. pinifolius* and congeneric *Callistemon*) to 5.7% (*A. parvipinnula* and congeneric *Acacia*) (Table 7). On average, there was slightly more overlap in morphospecies for the full dataset (1.7%) than for the herbivore dataset (1.2%).

Co-occurring morphospecies tended to be fungivores from the families Ptiliidae and Lathridiidae (Coleoptera), phloem feeders from the family Aphididae (Hemiptera), predators from the families Cantharidae and Staphylinidae (Coleoptera) and scavengers from the family Scarabaeidae (Coleoptera) (Table A3, Appendix 1). Numbers of co-occurring morphospecies between the congeneric plant species and any warm site ranged from 6 (*H. actites* and *H. gibbosa*) to 42 (*A. longifolia* and *A. parvipinnula*).

Table 6: Similarities (%) of Coleoptera and Hemiptera morphospecies from eight host plant species, for (i) the full dataset and (ii) the herbivore subset, among sites: control (C), warm 1 (W1) and warm 2 (W2).

Plant species	Similarities (%) between sites		
	C-W1	C-W2	W1-W2
(i)			
Fabaceae average	1.6	0.8	7.3
A. obtusata	1.2	1.3	6.4
A. parvipinnula	3.2	1.0	4.9
D. corymbosa	0.5	0.1	10.6
Myrtaceae average	0.6	1.0	5.4
A. hispida	1.1	2.1	4.2
C. pinifolius	0.3	0.1	4.7
L. squarrosum	0.5	0.8	7.4
Proteaceae average	1.9	3.6	3.8
H. gibbosa	2.8	5.8	3.9
T. speciosissima	1.1	1.3	3.7
(ii)			
Fabaceae average	1.5	0.2	2.0
A. obtusata	0.7	0.1	2.3
A. parvipinnula	3.0	0.6	3.6
D. corymbosa	0.8	0.0	0.0
Myrtaceae average	0.6	0.4	0.7
A. hispida	1.2	0.1	0.0
C. pinifolius	0.5	0.0	1.7
L. squarrosum	0.0	0.3	0.4
Proteaceae average	0.3	0.4	0.4
H. gibbosa	0.5	0.8	0.0
T. speciosissima	0.0	0.0	0.7

Table 7: Similarities (%) of Coleoptera and Hemiptera morphospecies for (i) the full dataset and (ii) the herbivore subset, from five transplanted plant species at the two warm sites and four congeneric plant species native to the warm area: congeneric (conge), warm 1 (W1) and warm 2 (W2).

Plant species:	Similarities (%)	
congeneric – transplanted	conge-W1	conge-W2
(i)		
A. longifolia – A. obtusata	1.6	1.2
A. longifolia – A. parvipinnula	5.2	2.8
C. pachyphyllus – C. pinifolius	0.5	1.1
L. trinervum – L. squarrosum	2.0	1.5
H. actites – H. gibbosa	0.2	0.5
(ii)		
A. longifolia – A. obtusata	0.7	0.5
A. longifolia – A. parvipinnula	5.7	3.0
C. pachyphyllus – C. pinifolius	0.1	0.0
L. trinervum – L. squarrosum	2.0	0.1
H. actites – H. gibbosa	0.2	0.1

Community structure

Within-family comparisons of guild structure at the control site

Community structure for both the full dataset and the herbivore dataset at the control site was consistent among the individual host plant species within two of the three families, Myrtaceae and Proteaceae (Table 8), but differed significantly among the host species within the Fabaceae. Within the Fabaceae, differences in guild structure were mainly driven by variation in the dominant feeding guild, the sapsuckers, and to a lesser extent by variability among the leaf chewers and predators (in the two *Acacia* species) and by fungivores (lacking in *Daviesia corymbosa*).

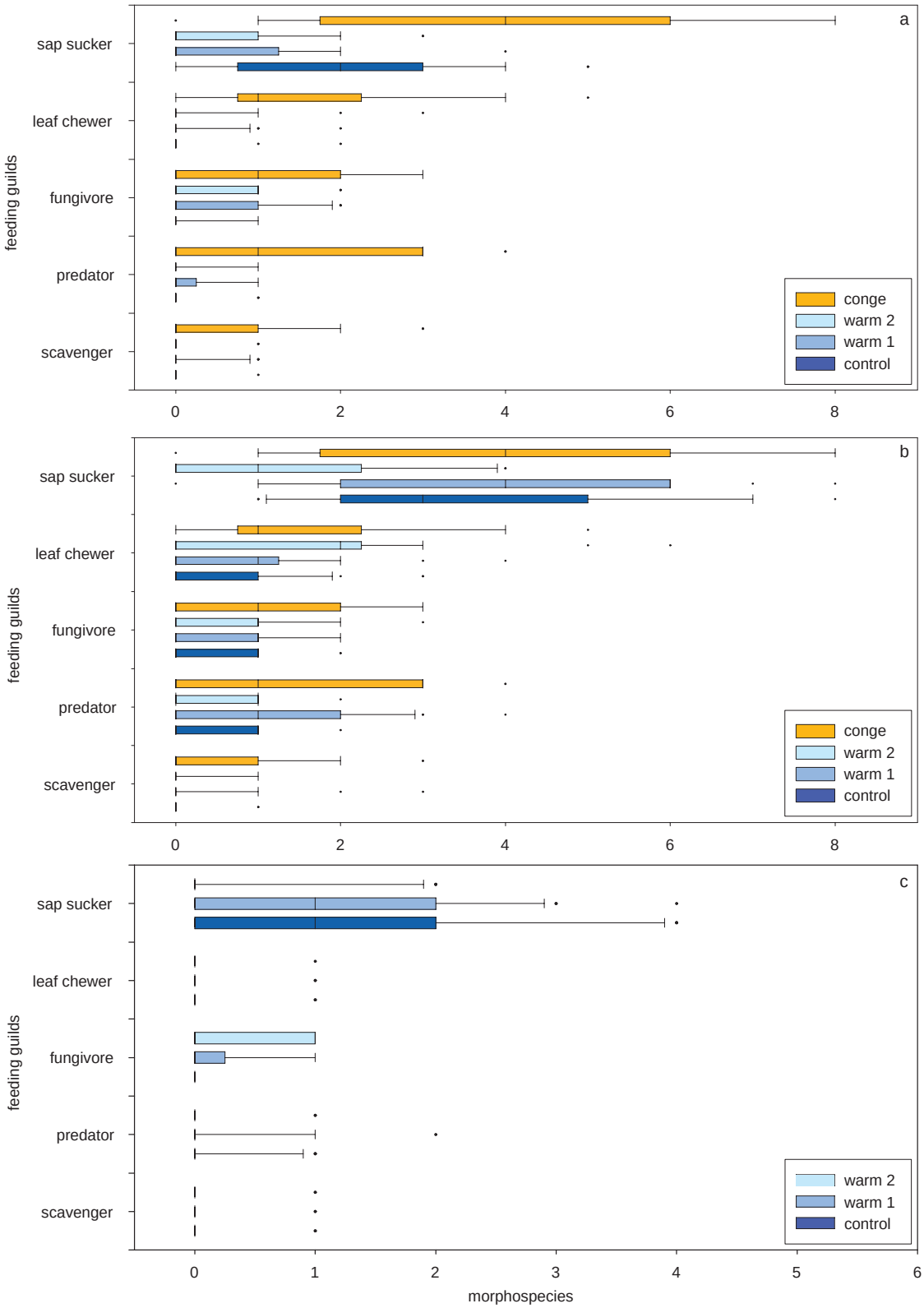

Figure 5: Coleoptera and Hemiptera feeding guild structure, from three Fabaceae species: *A. obtusata* (a), *A. parvipinnula* (b) and *D. corymbosa (*c), at three transplant sites: control, warm 1 and warm 2, and from a congeneric species, *A. longifolia,* (conge) at the warm sites. Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

Table 8: Summary statistics for multivariate generalised linear model analyses (mGLM) of feeding guild species richness data from eight transplanted species within three families at the control site within the native range (i) for the entire Coleoptera and Hemiptera community and (ii) for the herbivore subset; degrees of freedom (df), Wald-X^2-Statistic (Wald-X^2) and p-value (p) overall and for pairwise comparisons between sites.

Plant family	df	Wald-X^2	p			
			overall			
(i)				AO-AP*	AO-DC	AP-DC
Fabaceae	2,87	7.735	**< 0.001**	**< 0.001**	**0.018**	**< 0.001**
				AH-CP	AH-LS	CP-LS
Myrtaceae	2,87	4.34	**< 0.01**	0.475	0.109	0.464
				HG-TS		
Proteaceae	2,58	1.632	0.381	0.684		
(ii)				AO-AP	AO-DC	AP-DC
Fabaceae	2,87	7.7097	**< 0.001**	**< 0.001**	0.067	**< 0.001**
				AH-CP	AH-LS	CP-LS
Myrtaceae	2,87	4.756	**< 0.01**	0.401	0.368	0.368
				HG-TS		
Proteaceae	2,58	1.519	0.364	0.579		

note: significant values are in bold.

*pairwise comparisons between plant species within families:

Fabaceae: *A. obtusata* (AO), *A. parvipinnula* (AP), *D. corymbosa* (DC);

Myrtaceae: *A. hispida* (AH), *C. pinifolius* (CP), *L. squarrosum* (LS);

Proteaceae: *H. gibbosa* (HG), *I. anethifolius* (IA), *T. speciosissima* (TS).

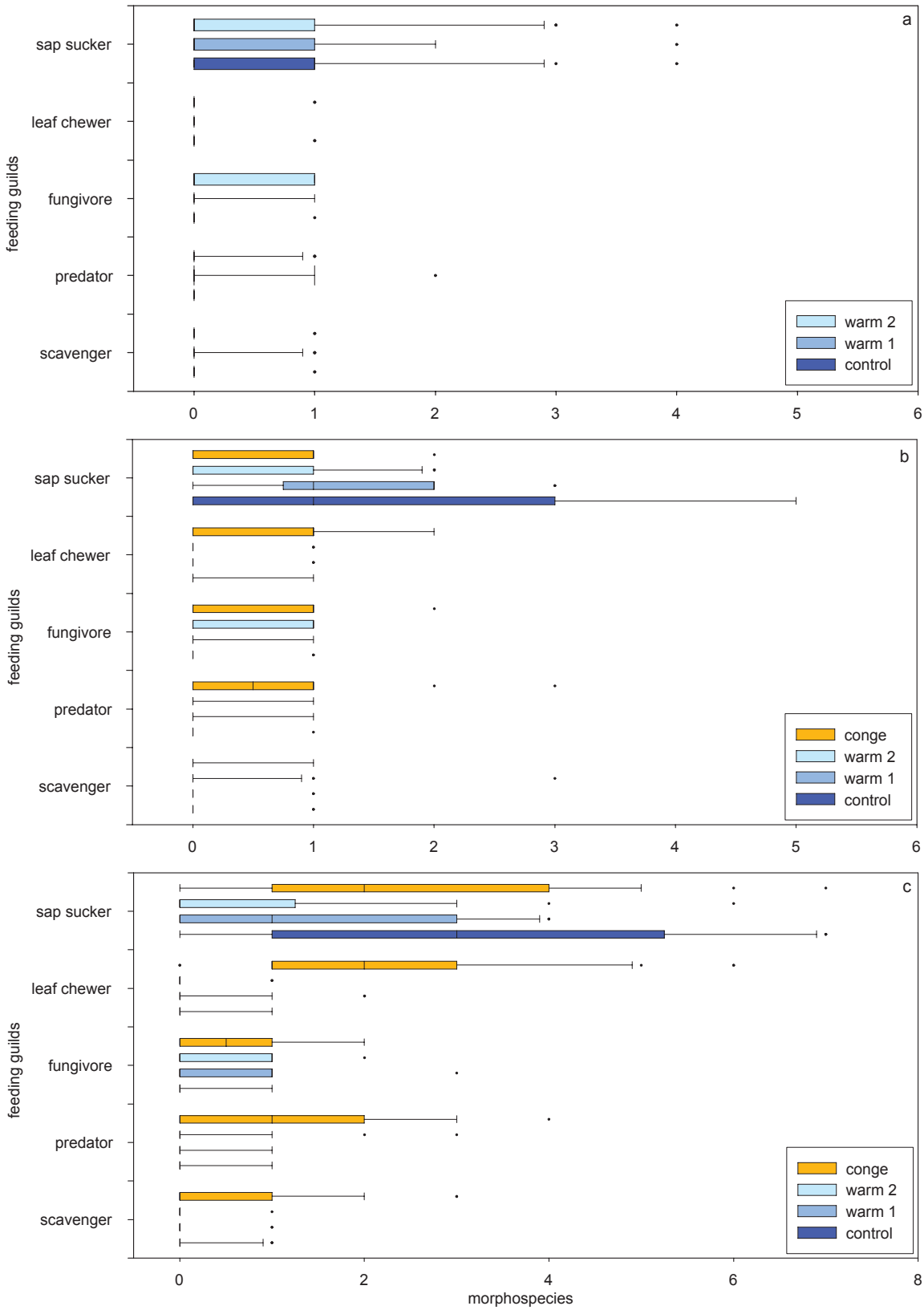

Figure 6: Coleoptera and Hemiptera feeding guild structure, from three Myrtaceae species: *A. hispida* (a), *C. pinifolius* (b) and *L. squarrosum* (c), at three transplant sites: control, warm 1 and warm 2, and from congeneric species (conge): *C. pachyphyllus* (b), *L. trinervum* (c) at the warm sites. Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

Comparison of guild structure between transplanted plant species at control and warm sites

For the full dataset, the guild structure on five of the plant species (two within the Myrtaceae, two within the Proteaceae and one within the Fabaceae) was not significantly different between the control and warm site W1 (Table 9). There was less consistency in guild structure between the control site and warm site W2 with only two plant species (one each from Fabaceae and Proteaceae) showing no significant differences (Fig. 5, 6, 7; Table A4, Appendix 1). Guild structure between the two warm sites was largely consistent; there were no significant differences for seven out of eight plant species (Table 9). For all eight plant species at all sites, the dominant guild was sapsuckers (Fig. 5, 6, 7). Differences in guild structure between the control site and the warm sites W1 and W2 were mainly driven by a reduction in sapsuckers and an increase in the guilds predators and scavengers at the warm sites.

Within the herbivore dataset, community structure was largely consistent among sites (Fig. 8, 9, 10; Table A5, Appendix 1). There were no significant differences in guild structure between the control and warm site W1 for any of the eight species (Table 10). The herbivore guild structure on three plant species was not significantly different between the control and warm site W2. Of these, two species were within the Myrtaceae and one within the Fabaceae. Guild structure between the two warm sites showed some consistency for four plant species, one from the Fabaceae and three from the Myrtaceae, with no significant differences between W1 and W2. For all eight plant species at all sites, the phloem feeders were the dominant herbivore guild (Fig. 8, 9, 10). Differences in herbivore guild structure between the control site and W2 were mainly driven by either a reduction in phloem feeders at W2 (for two plant species, one each from Fabaceae and Myrtaceae), or an increase in phloem feeders at W2 for three plant species (one Fabaceae and two Proteaceae). Differences in herbivore guild structure between the two warm sites were mainly due to an increase of mesophyll feeders at W1 for all four plant species (two each from Fabaceae and Myrtaceae).

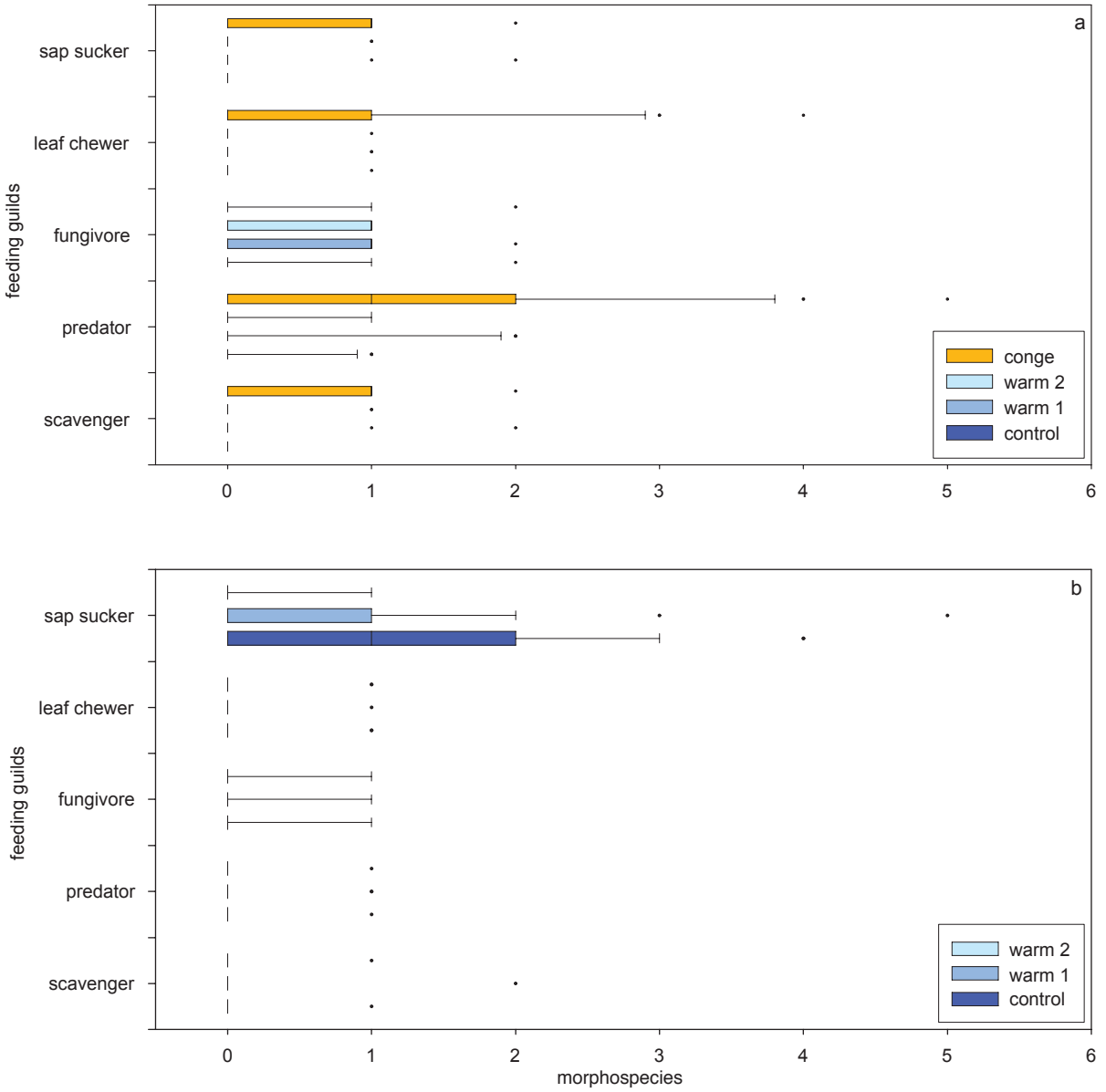

Figure 7: Coleoptera and Hemiptera feeding guild structure, from two Proteaceae species: *H. gibbosa* (a) and *T. speciosissima* (b), at three transplant sites: control, warm 1 and warm 2, and from a congeneric species, *H. actites,* (conge) at the warm sites. Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

Table 9: Summary statistics for multivariate generalised linear model analyses (mGLM) of feeding guild species richness data, for the entire Coleoptera and Hemiptera community structure (i) Pairwise comparisons between sites are shown: control (C), warm 1 (W1) and warm 2 (W2). (ii) Pairwise comparisons between the two warm sites and a congeneric host plant species in this area are shown: congeneric (conge), warm 1 (W1) and warm 2 (W2); degrees of freedom (df), Wald-X^2-Statistic (Wald-X^2) and p-value (p) overall and for pairwise comparisons between sites.

Plant species	df	Wald-X^2	p			
			overall	C-W1	C-W2	W1-W2
(i)						
Fabaceae						
A. obtusata	2,85	5.615	**< 0.001**	**< 0.01**	**< 0.001**	0.912
A. parvipinnula	2,87	8.014	**< 0.001**	0.143	0.145	0.142
D. corymbosa	2,87	4.419	**< 0.01**	**0.042**	**< 0.001**	**< 0.01**
Myrtaceae						
A. hispida	2,86	2.852	0.249	**0.023**	**0.028**	0.445
C. pinifolius	2,87	5.382	**< 0.001**	0.212	**< 0.01**	0.185
L. squarrosum	2,87	4.92	**< 0.001**	0.086	**< 0.01**	0.337
Proteaceae						
H. gibbosa	2,87	4.148	**0.015**	0.364	**0.029**	0.140
T. speciosissima	2,87	3.964	**< 0.01**	0.732	0.052	0.262

Plant species	df	Wald-X^2	p		
			overall	W1-conge	W2-conge
(ii)					
Fabaceae					
A. obtusata	2,85	12.44	**< 0.001**	**< 0.01**	**< 0.01**
A. parvipinnula	2,87	7.457	**< 0.001**	**< 0.01**	**< 0.01**
Myrtaceae					
C. pinifolius	2,87	7.127	**< 0.001**	**< 0.001**	0.365
L. squarrosum	2,87	9.794	**< 0.001**	**< 0.001**	**< 0.001**
Proteaceae					
H. gibbosa	2,87	7.039	**< 0.001**	**< 0.01**	**< 0.001**

note: significant values are in bold.

Table 10: Summary statistics for multivariate generalised linear model analyses (mGLM) of feeding guild species richness data, for only the herbivore Coleoptera and Hemiptera community structure. (i) Pairwise comparisons between sites are shown: control (C), warm 1 (W1) and warm 2 (W2). (ii) Pairwise comparisons between the two warm sites and a congeneric host plant species in this area are shown: congeneric (conge), warm 1 (W1) and warm 2 (W2); degrees of freedom (df), Wald-X^2-Statistic (Wald-X^2) and p-value (p) overall and for pairwise comparisons between sites.

Plant species	df	Wald-X^2	p			
			overall	C-W1	C-W2	W1-W2
(i)						
Fabaceae						
A. obtusata	2,85	5.54	**< 0.001**	0.354	0.364	0.594
A. parvipinnula	2,87	6.824	**< 0.001**	0.252	**< 0.001**	**< 0.001**
D. corymbosa	2,87	4.177	**< 0.001**	0.550	**0.012**	**< 0.01**
Myrtaceae						
A. hispida	2,86	2.937	0.08	0.415	0.398	0.407
C. pinifolius	2,87	4.749	**< 0.01**	0.126	**< 0.001**	0.069
L. squarrosum	2,87	5.715	**< 0.001**	0.379	0.379	0.480
Proteaceae						
H. gibbosa	2,87	3.617	**0.024**	0 .778	**0.017**	**0.016**
T. speciosissima	2,87	3.502	**0.012**	0.118	**0.022**	**< 0.001**

Plant species	df	Wald-X^2	p		
			overall	W1-conge	W2-conge
(ii)					
Fabaceae					
A. obtusata	2,85	10.78	**< 0.001**	**< 0.001**	**< 0.001**
A. parvipinnula	2,87	7.179	**< 0.001**	**< 0.001**	**< 0.001**
Myrtaceae					
C. pinifolius	2,87	6.021	**< 0.001**	**< 0.001**	**< 0.001**
L. squarrosum	2,87	7.83	**< 0.001**	**< 0.001**	**< 0.001**
Proteaceae					
H. gibbosa	2,87	5.07	**< 0.01**	**< 0.01**	**< 0.001**

note: significant values are in bold.

Comparison of guild structure between transplants and congenerics at warm sites

For the full dataset, there was no consistency in community structure among the transplants at the two warm sites and congeneric plant species native to the warm area (Table 9; Fig. 5, 6, 7) for all except one of the five species-pair comparisons. Differences in guild structure between transplants at the warm sites and their congeneric partner plants were mainly driven by an increase of leaf chewers and predators at the congeneric species native to the warm area.

Within the herbivore dataset, there was no consistency in community structure between the transplants at the two warm sites and their congeneric partners (Fig. 8, 9, 10); the herbivore guild structure was significantly different for all five species-pair comparisons (Table 10). Differences in herbivore guild structure between transplants at the two warm sites W1 and W2 and their congeneric partner plants were mainly due to a greater numbers of leaf chewers on the congeneric plant species (Fig. 8, 9, 10).

General distribution of feeding guilds

For all transplanted plant species within the families Fabaceae, Myrtaceae and Proteaceae, the dominant feeding guild found at all sites within the entire Coleoptera and Hemiptera community was the sap suckers (Fig. 5, 6, 7; Table A4, Appendix 1). Sap suckers were also dominant on the congeneric plant species within the Fabaceae. Within the Myrtaceae, leaf chewers were also a major feeding guild. For one congeneric plant species within the Proteaceae (*H. actites*), predators and leaf chewers were dominant (Fig. 7). Within the herbivore subset, the dominant herbivores were phloem feeders for all transplanted plant species at all sites (Fig. 8, 9, 10; Table A5, Appendix 1), whereas for the congeneric species both leaf chewers and phloem feeders dominated.

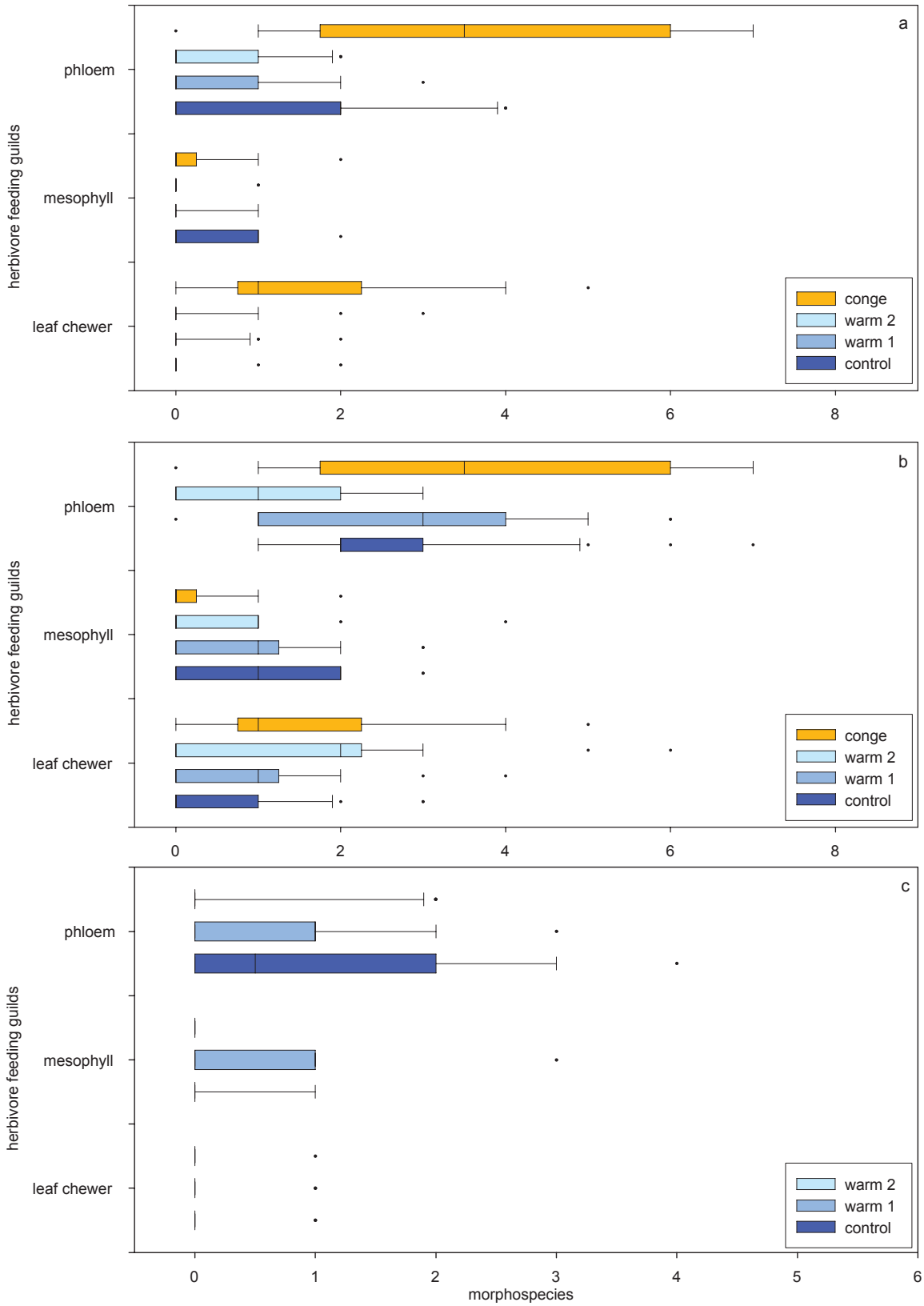

Figure 8: Herbivore Coleoptera and Hemiptera feeding guild structure, from three Fabaceae species: *A. obtusata* (a), *A. parvipinnula* (b) and *D. corymbosa* (c), at three transplant sites: control, warm 1 and warm 2, and from a congeneric species, *A. longifolia* (conge), at the warm sites. Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

Discussion

The Coleoptera and Hemiptera fauna that colonised plants transplanted to warmer sites displayed an almost complete turnover of morphospecies composition compared to the control site within the native range. This turnover could not be attributed to differences in plant growth between sites. The guild structure of the Coleoptera and Hemiptera communities was also markedly different between the warm and control sites for five of the eight host plant species. By contrast, when only the herbivores were considered, guild structure proved far more consistent among sites, and this was reflected in a relatively consistent level of herbivore damage. These results suggest that as the climate warms, significant differences in the composition of insect communities could occur, but that at least within the herbivore component, species may tend to be progressively replaced by others within the same guild.

Community composition

There were marked differences in Coleoptera and Hemiptera morphospecies composition among all sites (see Table 6). Whilst a substantial component of this apparent turnover is likely to have been due, in part, to the under-sampling of the complete fauna (as indicated by the lack of asymptotes in the rarefaction curves for virtually all species at all sites), the results may also reflect a fundamental characteristic of the macroecology of Australian insects. Australian insects are generally considered to display a high level of endemism with narrow geographic ranges (Austin et al. 2004; Cranston 2009). A previous transplant experiment conducted in the same general region also found a high level of species turnover along the latitudinal extent of the host plant's range, as well as between the native and warmer transplant sites (Andrew & Hughes 2007). A transplant experiment, assessing impacts of climate warming on a montane meadow in Europe, also revealed that plant community composition was distinctly altered (Bruehlheide et al. 2003). Similarly, a transplant experiment performed on soil nematode communities showed that community composition at the warmer sites was markedly altered

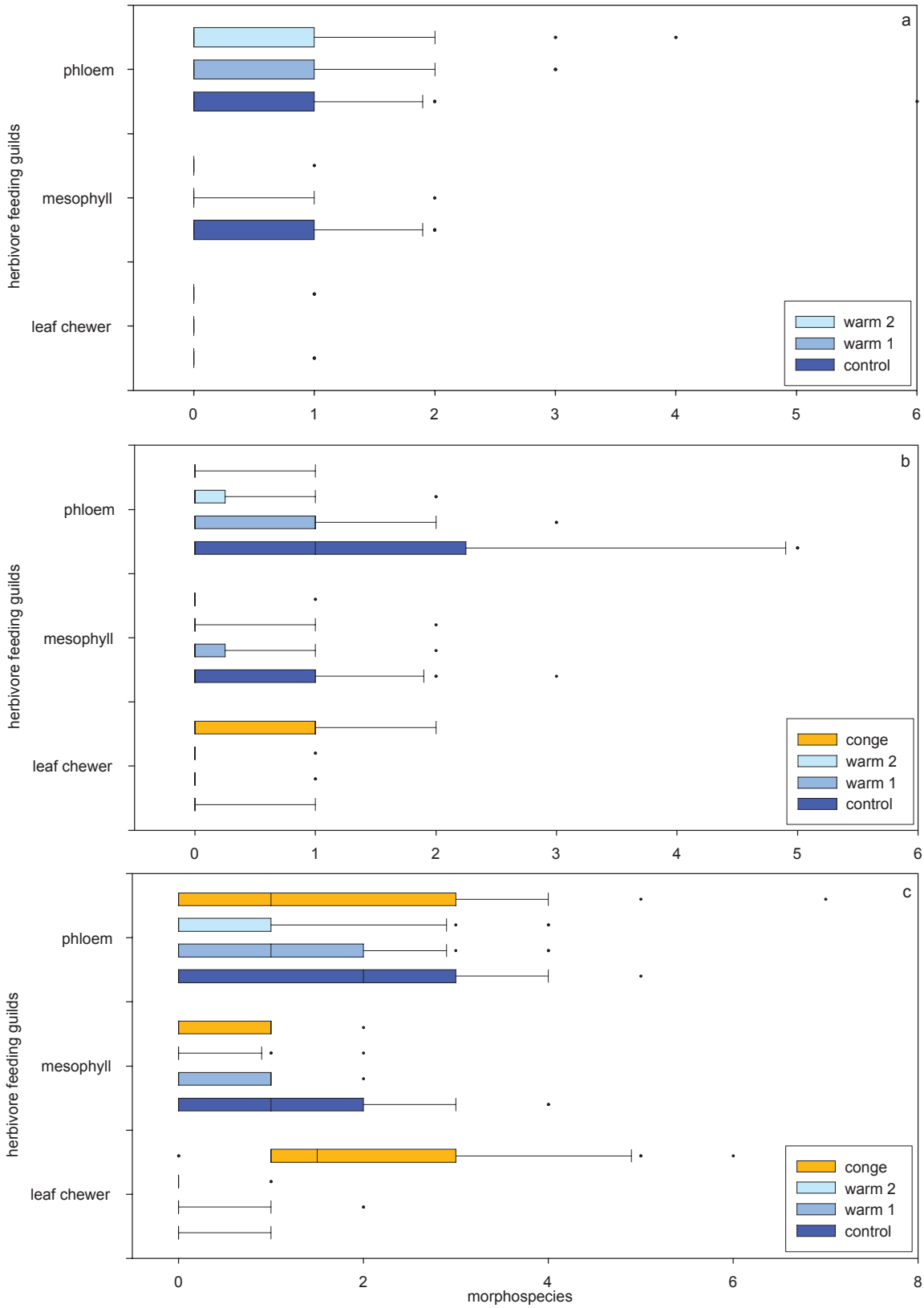

Figure 9: Herbivore Coleoptera and Hemiptera feeding guild structure, from three Myrtaceae species: *A. hispida* (a), *C. pinifolius* (b) and *L. squarrosum* (c), at three transplant sites: control, warm 1 and warm 2, and from congeneric species (conge): *C. pachyphyllus* (b), *L. trinervum* (c), at the warm sites. Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

(Budge et al. 2011). A microarthropod community, subjected to experimentally increased temperature, also showed substantial changes in community composition (Kardol et al. 2011). Experimental temperature increase in an old-field experiment has also been found to alter insect community composition, particularly within the herbivore guilds (Villalpando et al. 2009). Several observational studies conducted along environmental temperature gradients, either latitudinal or altitudinal, have also found considerable turnover in insect community composition (Novotny et al. 2005; Colwell et al. 2008; Gonzalez-Megias et al. 2008; Lessard et al. 2011).

We found that the morphospecies turnover between the two warm sites was very high, even though the two sites were only 8 km apart. For individual species, we collected, on average, between 11% and 51% of the minimum expected species pool associated with the plant species. This low overlap is likely to be at least partly due to insufficient sampling, a problem common to studies of insect diversity in which collection of a complete insect fauna is often prohibitive in terms of time and labour. Sampling is always a tradeoff between depth (e.g. taking many samples on one species, as in Andrew & Hughes 2007) and breadth (taking samples from many sites or many species). In this study we chose to focus on breadth so as to search for general patterns across multiple plant species.

Over the 12 month survey period, we found that there were generally more Coleoptera and Hemiptera morphospecies that colonised the transplants at the control site and W1 than at W2 (see Table 4). This result may have been due to differences in habitat between the sites: the control site and W1 were both located in a dry sclerophyll forest with a tall eucalypt canopy that provided approximately 30-50% cover. W2, however, was located in coastal heath with sparse (~20%) *Banksia* cover and had lower plant species diversity. This reduction in the local plant species richness and sparser structure may have led to a lower number of morphospecies at W2. Our findings are in accord with results from previous studies showing a positive relationship between Coleoptera and Hemiptera species richness and vegetation structural complexity (Southwood et al. 1979; Woodcock et al. 2007), or local plant species diversity (Rand 2003; Schaffers et al. 2008).

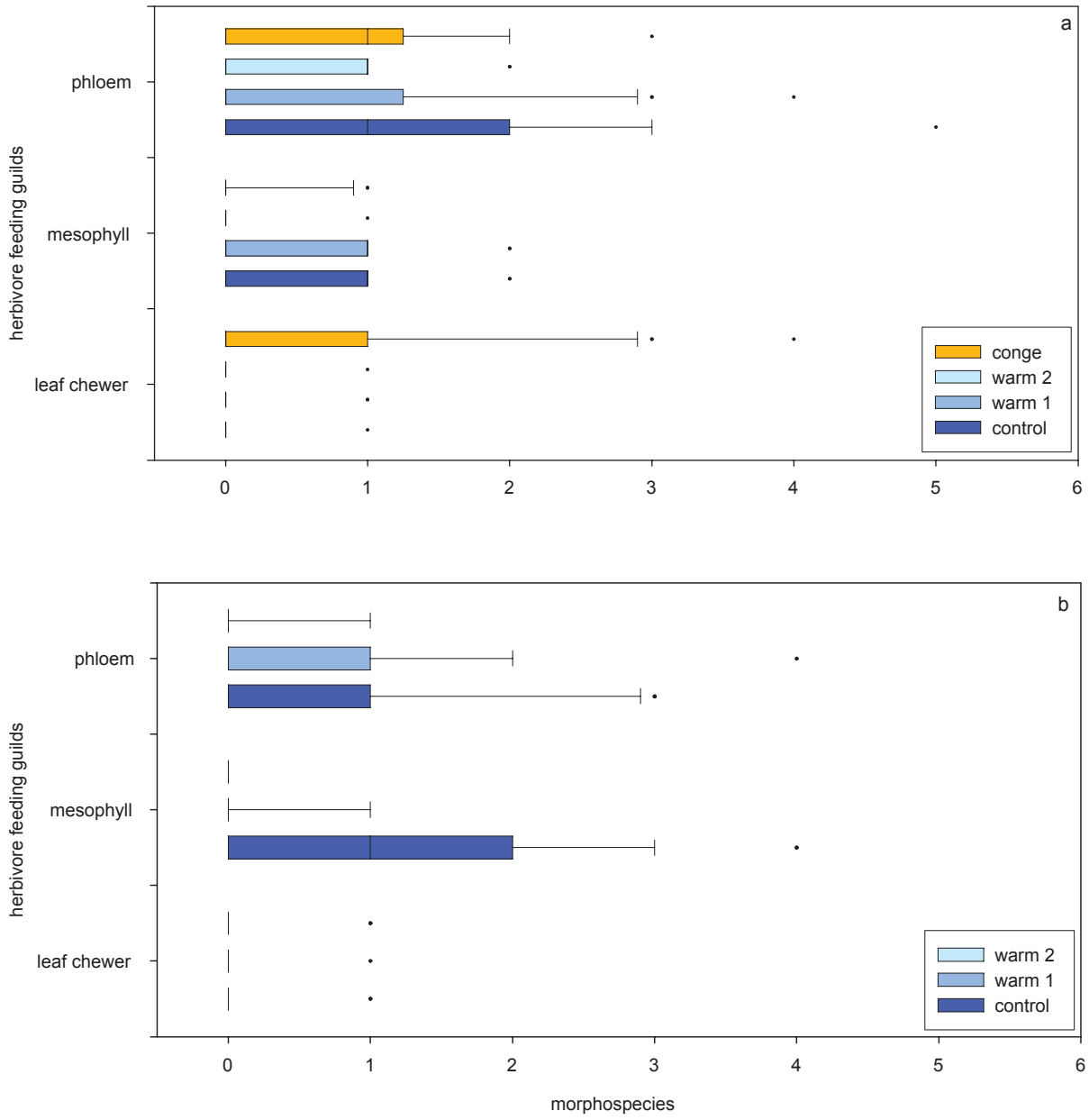

Figure 10: Herbivore Coleoptera and Hemiptera feeding guild structure, from two Proteaceae species: *H. gibbosa* (a) and *T. speciosissima* (b), at three transplant sites: control, warm 1 and warm 2, and from a congeneric species, *H. actites* (conge), at the warm sites. Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

Further, the number of insect species may also depend on the size of the host plant, with larger plants harbouring more insect species (Lawton 1983; Strong et al. 1984). In our case this may explain the observed pattern on three plant species: one at the control site and two at the warm sites. In contrast, two plant species grew less at the control site, but showed the highest number of insects there (see Figure A1, Appendix 2 and Table 4). It is possible that colonisation rate is higher in places where plant species occur naturally (Strong et al. 1984).

We found marked differences in the numbers of morphospecies within different feeding guilds (see Table A4 in Appendix 1). The dominant guild comprised the sapsuckers, mainly phloem feeders from the Cicadellidae and Psyllidae (Hemiptera); this pattern was consistent for all eight host plant species. This result reflects general patterns in Australia's fauna. The Psyllidae are particularly rich in species and the group has radiated in step with the genera *Eucalyptus* (Myrtaceae) and *Acacia* (Fabaceae, Mimosoideae) (Majer et al. 1997; Austin et al. 2004). We found a particularly high number of Psyllidae (25 morphospecies) associated with one of the *Acacia* species we sampled (*A. parvipinnula*) (see Table A6 in Appendix 3). Similarly, high numbers of Psyllidae on other *Acacia* species have been found across various vegetation types in southeast Australia (Woinarski & Cullen 1984; Andrew & Hughes 2005), and on *Acacia* species of Australian origin in South Africa (Proches 2008).

Community structure – control vs. warm sites

The feeding guild structure of the Coleoptera and Hemiptera as a whole was relatively consistent between the control site and warm site W1; no significant differences were found in structure for five of the eight host plant species (one Fabaceae and two each from the Myrtaceae and Proteaceae) between these two sites (see Table 9). These consistencies were driven by similar distributions of particular feeding guilds, which were different within each family: Within the Proteaceae, numbers of members within all guilds were similar; within the Myrtaceae minor feeding guilds (leaf chewer, scavenger and fungivore) were consistent, and within the Fabaceae, major feeding guilds (sapsuckers and leaf chewers) were

similar (see Fig. 5, 6, 7). This suggests that individual host plant identity is an important driver of feeding guild structure.

We found that, when differences in guild structure occurred, they were mainly driven by a reduction of sapsuckers and an increase of predators and scavengers at the warm sites (see Fig. 5, 6, 7). This suggests that predators and scavengers may benefit from a warmer temperature. Similarly, increased temperature in an old-field experiment led to a distinct shift in guild structure, where numbers of predators significantly increased (Villalpando et al. 2009).

Coleoptera and Hemiptera feeding guild structure showed little consistency between the control site and W2, with six of the eight plant species supporting significantly different proportions of feeding guilds. These differences were mainly driven by either higher numbers of fungivores (*D. corymbosa, A. hispida* and *C. pinifolius*) or fewer sapsuckers (*A. obtusata, L. squarrosum* and *H. gibbosa*) at W2. The most likely factors that may have contributed to these differences include the differences in structural complexity and plant species composition at W2. It has been shown previously that variations in structural complexity of sward, located at field margins in Great Britain, had a significant effect on the arthropod community structure (Woodcock et al. 2007), with phytophagous groups responding differently to an increase of structural complexity than predatory groups.

Herbivore community structure – control vs. warm sites

The feeding guild structure of the herbivorous component of the Coleoptera and Hemiptera communities was very consistent between the control site and warm site W1, with no significant difference between these two sites for any of the eight host plant species (see Table 10). These two sites had very similar vegetation and this result indicates that with a warming of 2-3ºC little change in the broad structure of the phytophagous community might be expected (see also Andrew & Hughes 2007).

When comparisons were made between the control site and W2 however, little consistency in structure was found, with five of the eight plant species supporting significantly different proportions of guilds. As noted above, differences in the structure and species composition of the surrounding vegetation between these two

sites is the most likely explanation for the differences, emphasising the potential importance of the ecological community context in determining assemblages on individual plant species.

Congenerics vs. transplants at warm sites

There was a striking difference in the feeding guild structure between the transplants at the warm sites and their congeneric partner plant native to the warm sites (see Tables 9, 10). This pattern was evident for both the entire Coleoptera and Hemiptera community and the phytophagous subset only. These differences were mainly driven by the higher numbers of leaf chewers and predators on the congeneric partner plants, compared to the transplants. It is possible that differences in plant age contributed to these differences – the transplanted plants were all less than 2 years old whereas the congenerics were of mixed ages. However this result also indicates that the chemical and physical characteristics of individual plants species are important in driving the distribution of feeding niches on plants, and that there is significant variability in these traits, even within genera.

Other approaches for studying climate change impacts

The results of this multi species field transplant experiment corroborate findings from some earlier studies, employing different approaches to investigate the effects of increasing temperatures on plant-insect communities. These approaches include field-based warming experiments, glasshouse experiments and species distribution models. While such approaches are very useful when single species are considered, their usefulness for studying entire communities is limited. For example, field-based warming experiments are limited to the experimental plot; glasshouse experiments are isolated from the outside environment; and species distribution models, which are usually performed on single species only, cannot yet incorporate biotic interactions. Field transplant experiments, on the other hand, can offer realistic simulations of the effects of climate change on entire communities.

Caveats

A potential limitation to this study might be that transplanting these eight plant species outside their native range, into the field sites W1 and W2, may have been associated with a confounding factor, that insect species, particularly phytophagous insects, may have smaller ranges than their associated host plants (Strong et al. 1984). This geographical distance might have led to an unavoidable change in community composition. Nonetheless, this study offers a very realistic assessment of how mobile insects may colonise new host plants as they migrate to track climate change.

Conclusion

We found an almost complete turnover in community composition between transplanted plants between their native range and warmer sites, indicating that with the current rate of warming a new suite of Coleoptera and Hemiptera species might colonise these eight host plant species within their native range during the next decades. Differences in feeding guild structure were also found, although at least some of these differences were likely to have been associated with differences in habitat types of the sites. We found more consistency in community structure of the herbivores, compared to the assemblage as a whole, suggesting that as phytophagous species migrate to track climate change they may colonise new host plants by replacing species within the same functional guild. While field transplant experiments such as this are time- and labour-intensive, they offer a valuable complement to laboratory and glasshouse experiments for understanding climate-change impacts.

Acknowledgements

We thank Marty Swain, from the Clarence River Valley Council, for providing space for the two warm sites and Margaret Morgan for the control site. We are most grateful to Neville O'Loughlin, who was a great help for fencing and transplanting. We thank Nola Hancock and Claudia Schlegel for help with transplanting, Patrick Schultheiss for help with transplanting, insect collection and comments on earlier drafts of the manuscript, Muhammad Masood for his help in the glasshouse, Matt Binns for help with the R code and NSW National Parks and Wildlife Service for permission to collect specimens. This study was supported by a Macquarie University research excellence scholarship (iMQRES) to Sabine Nooten.

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Appendix 1

Table A1: Numbers of Coleoptera and Hemiptera morphospecies for the entire community (full data set) and their herbivore subset (herbivore dataset), at three sites: control (C), warm 1 (W1) and warm 2 (W2); % herbivore morphospecies (% herbi); for (i) pooled plant species, (ii) for individual plant species and (iii) for congeneric plant species at the warm sites.

Plant species	Site	full dataset		herbivore dataset		% herbi
		Cole	Hemi	Cole	Hemi	
(i) pooled plant species						
	C	47	127	21	120	81
	W1	85	136	27	131	72
	W2	64	96	21	85	65
(ii) individual plant species						
A. obtusata	C	9	35	3	34	84
	W1	16	16	4	13	53
	W2	16	17	7	16	67
A. parvipinnula	C	21	46	11	43	81
	W1	51	56	18	55	68
	W2	34	37	13	33	65
D. corymbosa	C	4	24	2	22	86
	W1	9	30	2	27	75
	W2	6	7	1	6	53
A. hispida	C	5	17	2	17	86
	W1	11	14	0	14	56
	W2	6	16	2	14	72
C. pinifolius	C	7	34	4	32	87
	W1	9	22	2	22	77
	W2	10	13	2	10	52
L. squarrosum	C	13	45	4	45	84
	W1	17	25	6	24	71
	W2	7	22	2	17	66
H. gibbosa	C	6	29	1	27	80
	W1	16	25	2	25	66
	W2	9	10	1	9	53
T. speciosissima	C	7	20	2	20	81
	W1	7	17	1	17	75
	W2	7	6	1	6	62

continued next page

Table A1: *continued*

Plant species	Site	full dataset		herbivore dataset		% herbi
		Cole	Hemi	Cole	Hemi	
(iii) Congeneric plant species						
A. longifolia		67	59	24	54	62
H. actites		37	24	13	19	52
C. pachyphyllus		28	13	10	9	46
L. trinervum		56	25	21	23	54

Table A2: Numbers of co-occurring Coleoptera and Hemiptera morphospecies for eight plant species at three sites: control (C), warm 1 (W1) and warm 2 (W2), including feeding guild and morphospecies name (morph ID).

Plant species				Site		
	Feeding guild	Family / Subfamily	morph ID	C	W1	W2
Fabaceae						
A. obtusata						
	leaf chewer	Chrysomelidae	Cole 126		1	1
			Cole 590		1	1
	mesophyll feeder	Typhlocybinae	Cidel 002		1	1
	phloem feeder	Aphididae	Aphi 039	1		1
			Aphi 038		1	1
		Coccidae	Cocco 001	1	1	
	fungivore	Lathridiidae	Cole 005	1	1	
			Cole 474	1	1	
		Ptiliidae	Cole 033		1	1
			Cole 061	1	1	1
	predator	Coccinellidae	Cole 461		1	1
		Nabidae	Nabi 007		1	1
		Reduviidae	Redu 001	1	1	
	scavenger	Scarabaeidae	Cole 480		1	1
A. parvipinnula						
	leaf chewer	Brentidae	Cole 516		1	1
		Chrysomelidae	Cole 126	1	1	1
			Cole 590	1	1	1
			Cole 554		1	1
			Cole 612		1	1

continued next page

Table A2: *continued*

Plant species / Feeding guild	Family / Subfamily	morph ID	Site C	Site W1	Site W2
	Curculionidae	Cole 024	1	1	
		Cole 533	1		1
		Cole 589		1	1
mesophyll feeder	Typhlocybinae	Cidel 002		1	1
		Cidel 003	1	1	
phloem feeder	Aphididae	Aphi 039		1	1
	Coccidae	Cocco 001	1	1	1
		Cocco 019		1	1
	Delphacidae	Del 006		1	1
	Membracidae	Mem 001		1	1
		Mem 002		1	1
		Mem 004		1	1
	Psyllidae	Psy 006	1	1	
		Psy 012	1	1	
fungivore	Lathridiidae	Cole 005	1	1	1
		Cole 042		1	1
		Cole 474		1	1
	Ptiliidae	Cole 061		1	1
predator	Cantharidae	Cole 459	1	1	1
	Coccinellidae	Cole 593		1	1
		Cole 594		1	1
		Cole 616		1	1
D. corymbosa					
phloem feeder	Coccidae	Cocco 001	1	1	
fungivore	Ptiliidae	Cole 061		1	1
scavenger	Scarabaeidae	Cole 480		1	1
Myrtaceae					
A. hispida					
mesophyll feeder	Typhlocybinae	Cidel 003		1	1
phloem feeder	Coccidae	Cocco 01	1		1
fungivore	Ptiliidae	Cole 061	1	1	1
predator	Coccinellidae	Cole 464		1	1
C. pinifolius					
mesophyll feeder	Typhlocybinae	Cidel 003	1	1	
phloem feeder	Aphididae	Aphi 027		1	1
		Aphi 028		1	1
fungivore	Ptiliidae	Cole 061		1	1

continued next page

Table A2: *continued*

Plant species			Site		
Feeding guild	Family / Subfamily	morph ID	C	W1	W2
L. squarrosum					
phloem feeder	Aphididae	Aphi 009	1	1	1
		Aphi 013		1	1
	Coccidae	Cocco 003		1	1
fungivore	Lathridiidae	Cole 005	1	1	1
		Cole 042		1	1
	Ptiliidae	Cole 061	1	1	1
predator	Staphylinidae	Cole 588		1	1
Proteaceae					
H. gibbosa					
mesophyll feeder	Typhlocybinae	Cidel 003	1	1	
		Cidel 038		1	1
phloem feeder	Aphididae	Aphi 022		1	1
		Aphi 030		1	1
	Coccidae	Cocco 006	1	1	
	Psyllidae	Psy 006	1	1	
		Psy 014	1	1	
		Psy 024	1	1	
fungivore	Ptiliidae	Cole 033	1		1
		Cole 061	1	1	1
	Endomychidae	Cole 467		1	1
T. speciosissima					
phloem feeder	Aphididae	Aphi 013		1	1
fungivore	Ptiliidae	Cole 033	1	1	
		Cole 061	1	1	1

Table A3: Numbers of co-occurring Coleoptera and Hemiptera morphospecies for five plant species at the warm sites and four congeneric species native to the warm area (conge), warm 1 (W1) and warm 2 (W2), including feeding guild and morphospecies name (morph ID).

Plant species Feeding guild	Family / Subfamily	morph ID	conge	W1	W2
A. obtusata – A. longifolia					
leaf chewer	Buprestidae	Cole 477	1		1
	Chrysomelidae	Cole 554	1		1
		Cole 596	1	1	
	Curculionidae	Cole 467	1		1
mesophyll feeder	Typhlocybinae	Cidel 002	1	1	1
phloem feeder	Coccidae	Cocco 001	1	1	
	Membracidae	Mem 001	1		1
	Psyllidae	Psy 042	1	1	
	Xestocephalinae	Cidel 011	1		1
fungivore	Lathridiidae	Cole 005	1	1	
	Ptiliidae	Cole 033	1	1	1
		Cole 061	1	1	1
predator	Coccinellidae	Cole 461	1	1	1
	Staphylinidae	Cole 600	1	1	
scavenger	Scarabaeidae	Cole 463	1	1	1
predator	Coccinellidae	Cole 461		1	1
	Nabidae	Nabi 007		1	1
	Reduviidae	Redu 001	1	1	
scavenger	Scarabaeidae	Cole 480		1	1
A. parvipinnula – A. longifolia					
leaf chewer	Brentidae	Cole 538	1	1	
	Buprestidae	Cole 500	1		1
	Cerambycidae	Cole 491	1	1	
	Chrysomelidae	Cole 554	1	1	1
	Curculionidae	Cole 024	1	1	
		Cole 517	1	1	
mesophyll feeder	Typhlocybinae	Cidel 002	1	1	1
		Typhlo 001	1	1	
	Miridae	Mir 001	1	1	
phloem feeder	Aphididae	Aphi 012	1	1	
		Aphi 041	1	1	1
	Coccidae	Cocco 001	1	1	1
		Cocco 019	1	1	1

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Table A3: *continued*

Plant species Feeding guild	Family / Subfamily	morph ID	conge	W1	W2
	Delphacidae	Del 011	1	1	
		Del 032	1	1	
	Fulgoridae	Ful 001	1	1	
	Membracidae	Mem 001	1	1	1
		Mem 004	1	1	1
		Mem 005	1	1	
	Psyllidae	Psy 012	1	1	1
		Psy 020	1	1	
		Psy 042	1	1	
		Psy 061	1	1	
	Tropiduchidae	Tro 007	1	1	
fungivore	Endomychidae	Cole 647	1		1
	Colydidae	Cole 488	1	1	
	Lathridiidae	Cole 005	1	1	1
		Cole 042		1	1
		Cole 474		1	1
	Ptiliidae	Cole 033	1	1	
		Cole 061	1	1	1
predator	Cantharidae	Cole 491	1	1	1
	Coccinellidae	Cole 461	1	1	
		Cole 464	1	1	
		Cole 552	1		1
		Cole 555	1	1	
		Cole 593	1	1	1
		Cole 632	1	1	
		Cole 061		1	1
	Staphylinidae	Cole 600	1	1	1
scavenger	Aderidae	Cole 416	1	1	
		Cole 618	1	1	
	Mordellidae	Cole 579	1		1
	Salpingidae	Cole 492	1	1	
seed predator	Rhyparochromidae	Lyga 008	1		1
C. pinifolius – C. pachyphyllus					
phloem feeder	Aphididae	Aphi 013	1	1	
fungivore	Lathridiidae	Cole 005	1	1	1
	Ptiliidae	Cole 061	1	1	1
predator	Coccinellidae	Cole 623	1		1
	Staphylinidae	Cole 600	1	1	
scavenger	Scarabaeidae	Cole 463	1		1

continued next page

Table A3: *continued*

Plant species Feeding guild	Family / Subfamily	morph ID	conge	W1	W2
L. squarrosum – L. trinervum					
leaf chewer	Brentidae	Cole 507	1	1	
	Chrysomelidae	Cole 518	1	1	
	Curculionidae	Cole 024	1	1	
phloem feeder	Deltocephalinae	Cidel 028	1		1
	Eurybrachidae	Eury 001	1	1	
	Psyllidae	Psy 020	1	1	
fungivore	Lathridiidae	Cole 005	1	1	1
	Ptiliidae	Cole 061	1	1	1
predator	Cantharidae	Cole 459	1	1	
	Staphylinidae	Cole 600	1	1	
scavenger	Scarabaeidae	Cole 463	1	1	
H. gibbosa – H. actites					
leaf chewer	Buprestidae	Cole 477	1		1
phloem feeder	Aphididae	Aphi 030	1	1	1
fungivore	Ptiliidae	Cole 033	1		1
		Cole 061	1	1	1
predator	Cantharidae	Cole 459	1	1	
	Staphylinidae	Cole 587	1		1

Table A4: Morphospecies richness within feeding guilds from the entire Coleoptera and Hemiptera community; from eight host plant species at three sites: control (C), warm 1 (W1) and warm 2 (W2) and congeneric plant species (conge) in the warm area.

Plant species	Site			conge
Feeding guild	C	W1	W2	
Fabaceae				
A. obtusata				
fungivore	4	5	4	8
leaf chewer	3	4	7	24
predator	2	7	4	21
sap sucker	34	13	16	54
scavenger	1	3	2	13
seed predator	0	0	0	5
sum	*44*	*32*	*33*	*125*
A. parvipinnula				
fungivore	3	9	8	8
leaf chewer	11	18	13	24
predator	7	19	9	21
sap sucker	43	55	33	54
scavenger	2	6	6	13
seed predator	0	0	2	5
sum	*68*	*107*	*71*	*125*
D. corymbosa				
fungivore	0	1	2	NA
leaf chewer	2	2	1	
predator	2	7	2	
sap sucker	22	27	6	
scavenger	2	2	2	
sum	*28*	*39*	*13*	
Myrtaceae				
A. hispida				
fungivore	1	3	1	NA
leaf chewer	2	0	2	
predator	0	5	3	
sap sucker	17	14	14	
scavenger	2	3	2	
sum	*22*	*25*	*22*	

continued next page

Table A4: *continued*

Plant species	Site			conge
Feeding guild	C	W1	W2	
C. pinifolius				
fungivore	1	1	2	6
leaf chewer	4	2	2	10
predator	1	5	4	11
sap sucker	32	22	10	9
scavenger	2	1	4	4
seed predator	1	0	1	0
sum	*41*	*31*	*23*	*40*
L. squarrosum				
fungivore	4	6	2	8
leaf chewer	4	6	2	21
predator	3	4	7	20
sap sucker	45	24	17	46
scavenger	2	2	1	6
seed predator	0	0	0	0
sum	*58*	*42*	*29*	*101*
Proteaceae				
H. gibbosa				
fungivore	4	4	3	5
leaf chewer	1	2	1	13
predator	3	7	4	18
sap sucker	27	25	9	19
scavenger	0	3	2	7
sum	*35*	*41*	*19*	*62*
T. speciosissima				
fungivore	3	2	3	NA
leaf chewer	2	1	2	
predator	1	2	1	
sap sucker	20	17	6	
scavenger	1	2	1	
sum	*27*	*24*	*13*	

Table A5: Morphospecies richness within feeding guilds from only the herbivore Coleoptera and Hemiptera community; collected from eight host plant species at three sites: control (C), warm 1 (W1) and warm 2 (W2); and congeneric plant species (conge) in the warm area.

Plant species	Site			conge
Feeding guild	C	W1	W2	
Fabaceae				
A. obtusata				
leaf chewer	3	4	7	24
mesophyll feeder	5	1	2	7
phloem feeder	29	12	13	47
xylem feeder	0	0	1	0
sum	*37*	*17*	*23*	*78*
A. parvipinnula				
leaf chewer	11	18	13	24
mesophyll feeder	9	14	11	7
phloem feeder	34	41	22	47
sum	*54*	*73*	*46*	*78*
D. corymbosa				
leaf chewer	2	2	1	NA
mesophyll feeder	5	6	0	
phloem feeder	17	21	6	
sum	*24*	*29*	*7*	
Myrtaceae				
A. hispida				
leaf chewer	2	0	2	NA
mesophyll feeder	4	3	1	
phloem feeder	13	10	13	
xylem feeder	0	1	0	
sum	*19*	*14*	*16*	
C. pinifolius				
leaf chewer	4	2	2	10
mesophyll feeder	4	4	4	2
phloem feeder	28	18	6	6
xylem feeder	0	0	0	1
sum	*36*	*24*	*12*	*19*

continued next page

Table A5: *continued*

Plant species	Site			conge
Feeding guild	C	W1	W2	
L. squarrosum				
leaf chewer	4	6	2	21
mesophyll feeder	9	4	3	12
phloem feeder	35	20	14	33
xylem feeder	1	0	0	1
sum	*49*	*30*	*19*	*67*
Proteaceae				
H. gibbosa				
leaf chewer	1	2	1	13
mesophyll feeder	3	3	1	3
phloem feeder	24	22	8	15
xylem feeder	0	0	0	1
sum	*28*	*27*	*10*	*32*
T. speciosissima				
leaf chewer	2	1	1	NA
mesophyll feeder	5	3	0	
phloem feeder	15	14	6	
sum	*22*	*18*	*7*	

Appendix 2

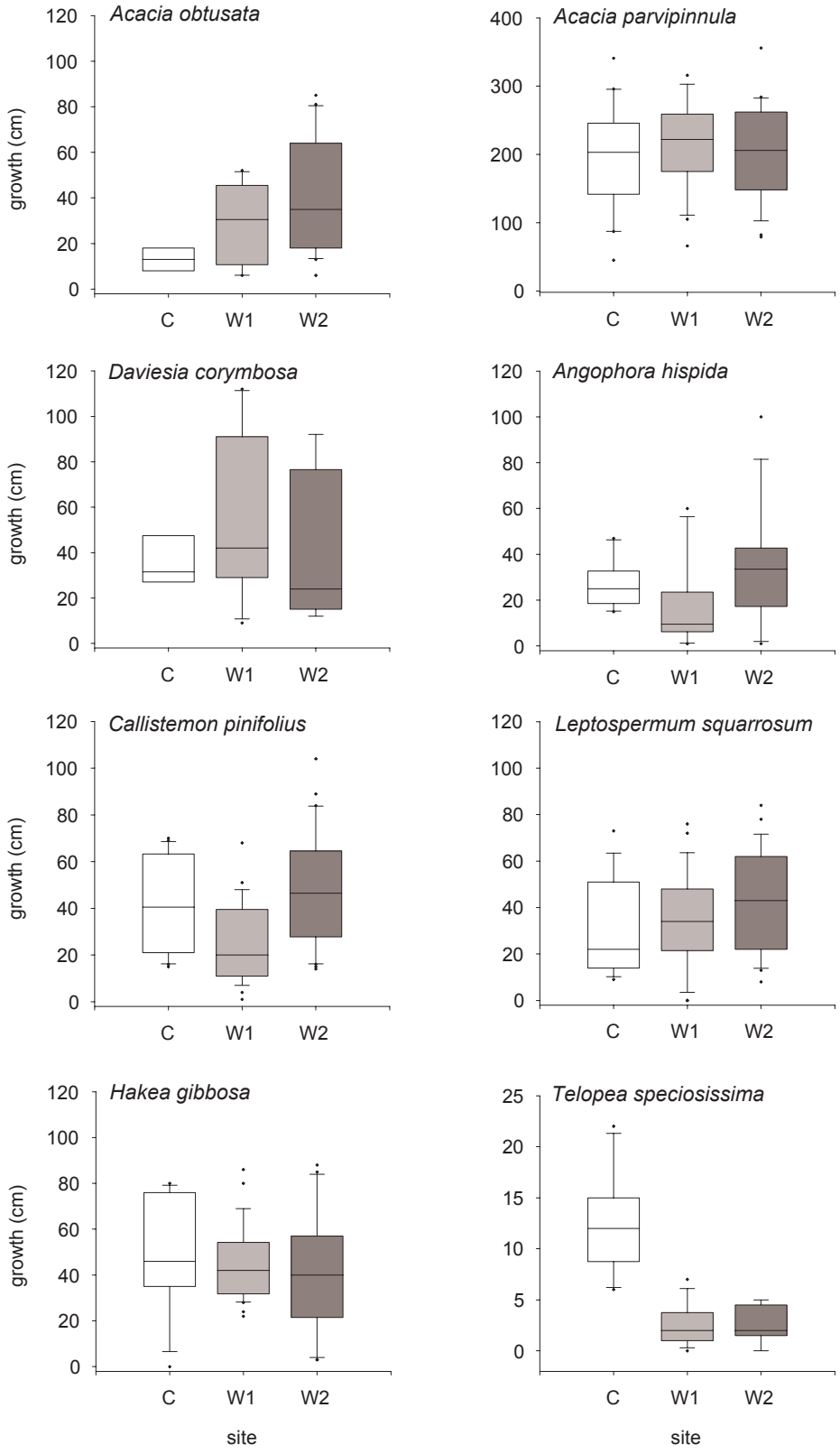

Figure A1: Net growth of eight plant species after 12 months at three transplant sites: control (C), warm 1 (W1) and warm 2 (W2). Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

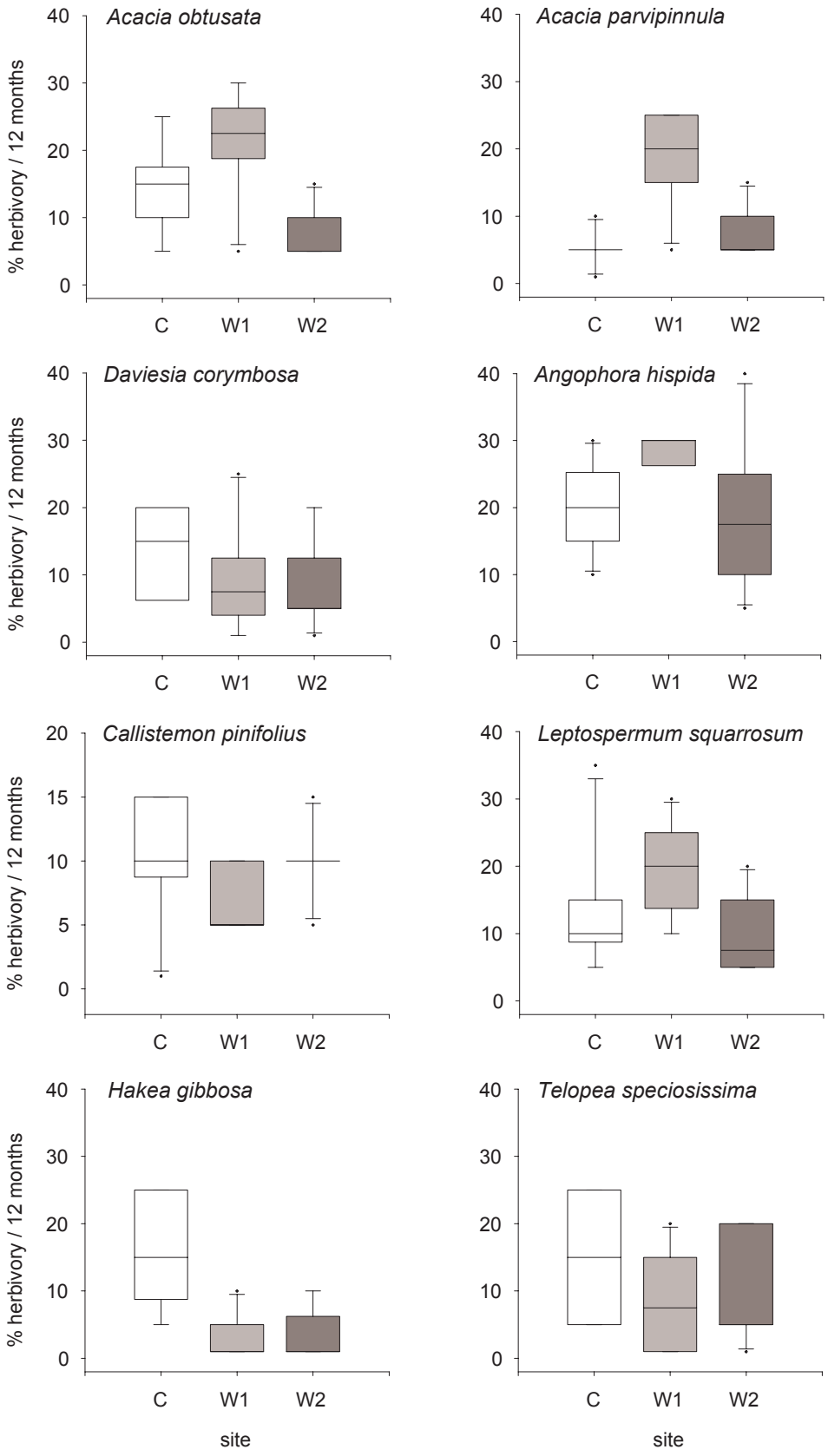

Figure A2: Herbivore leaf damage from eight plant species after 12 months at three transplant sites: control (C), warm 1 (W1) and warm 2 (W2). Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

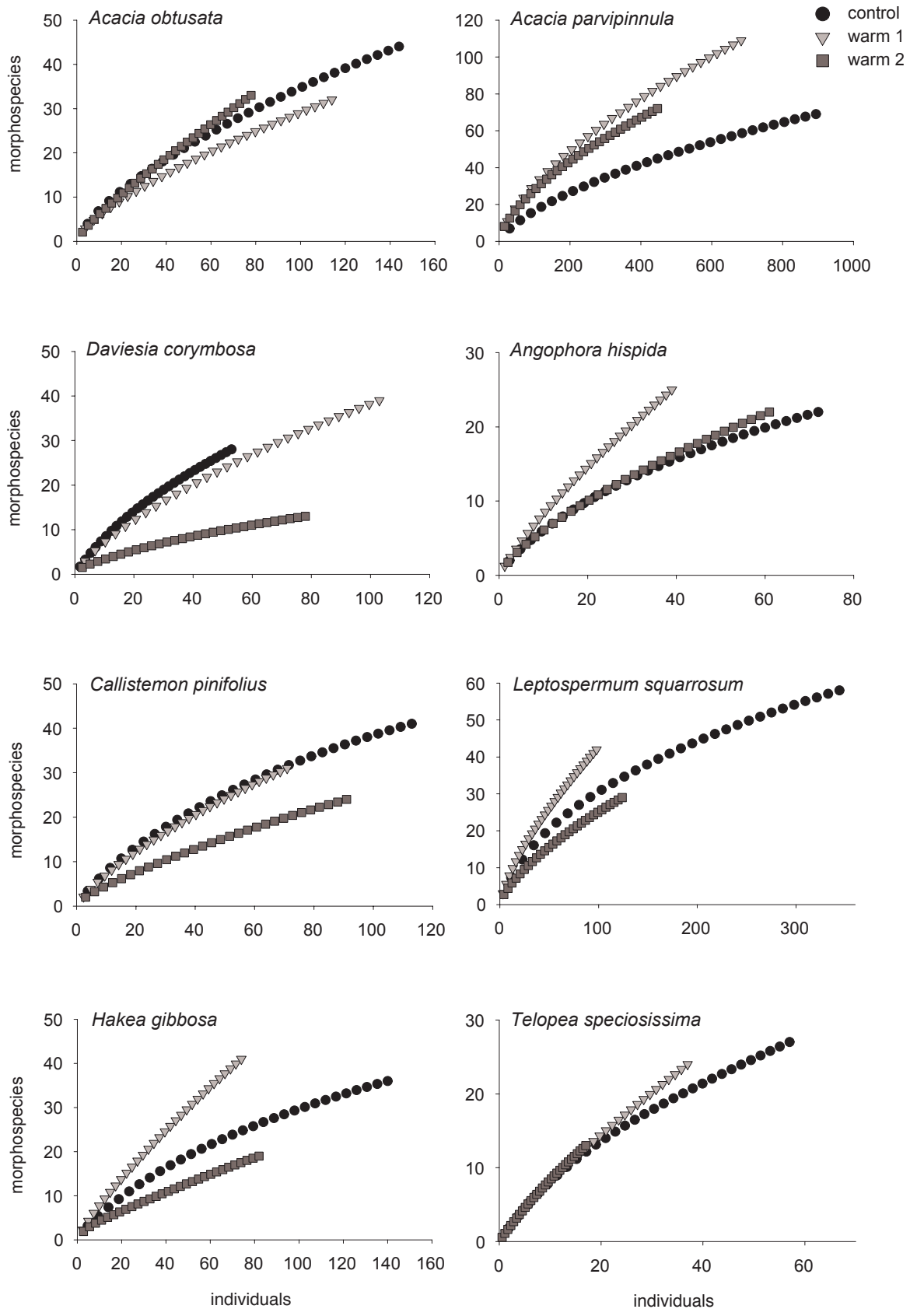

Figure A3: Coleman's rarefaction curves from eight plant species at the three transplant sites: control, warm 1 and warm 2.

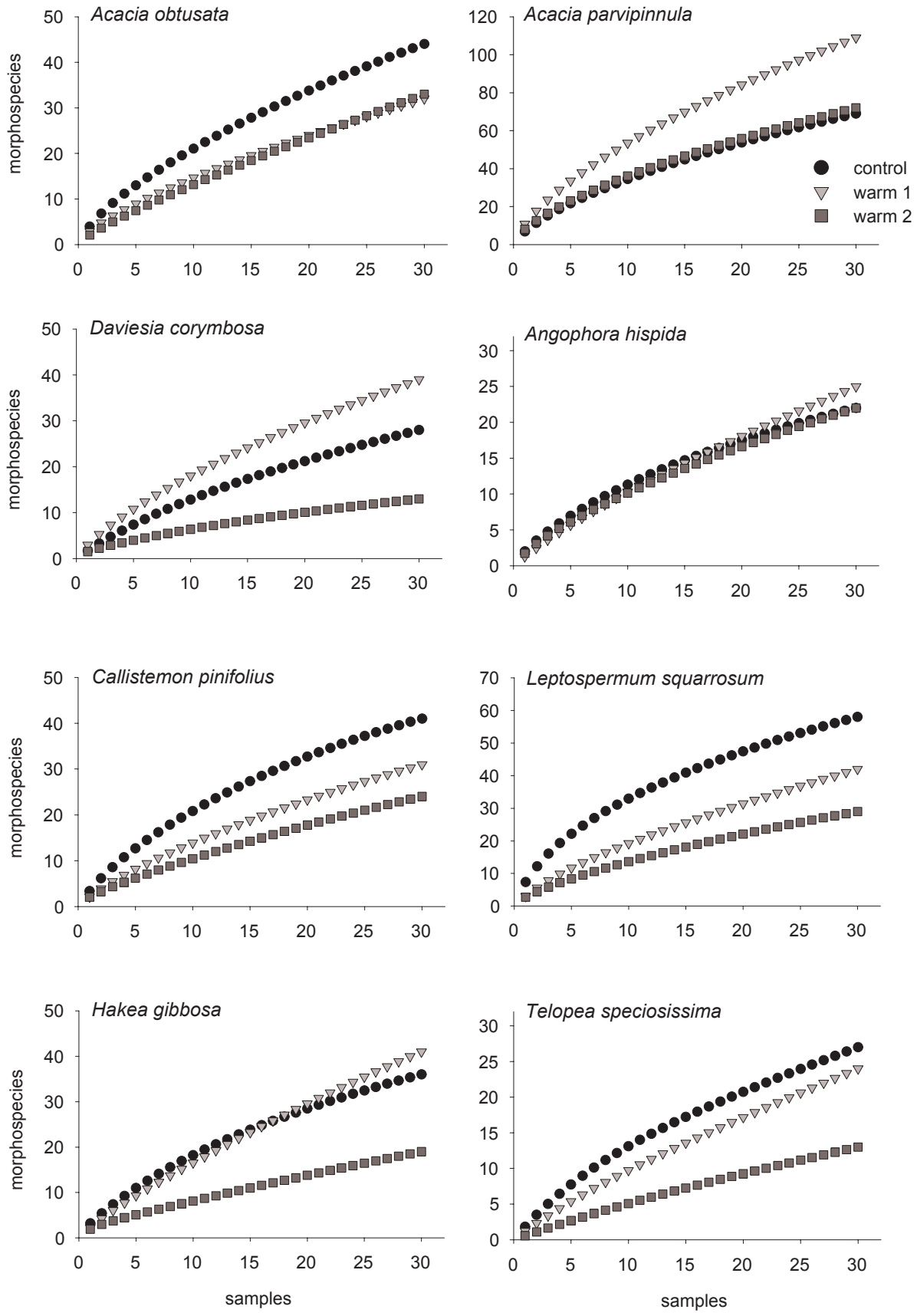

Figure A4: Species accumulation curves from eight plant species at three transplant sites: control, warm 1 and warm 2.

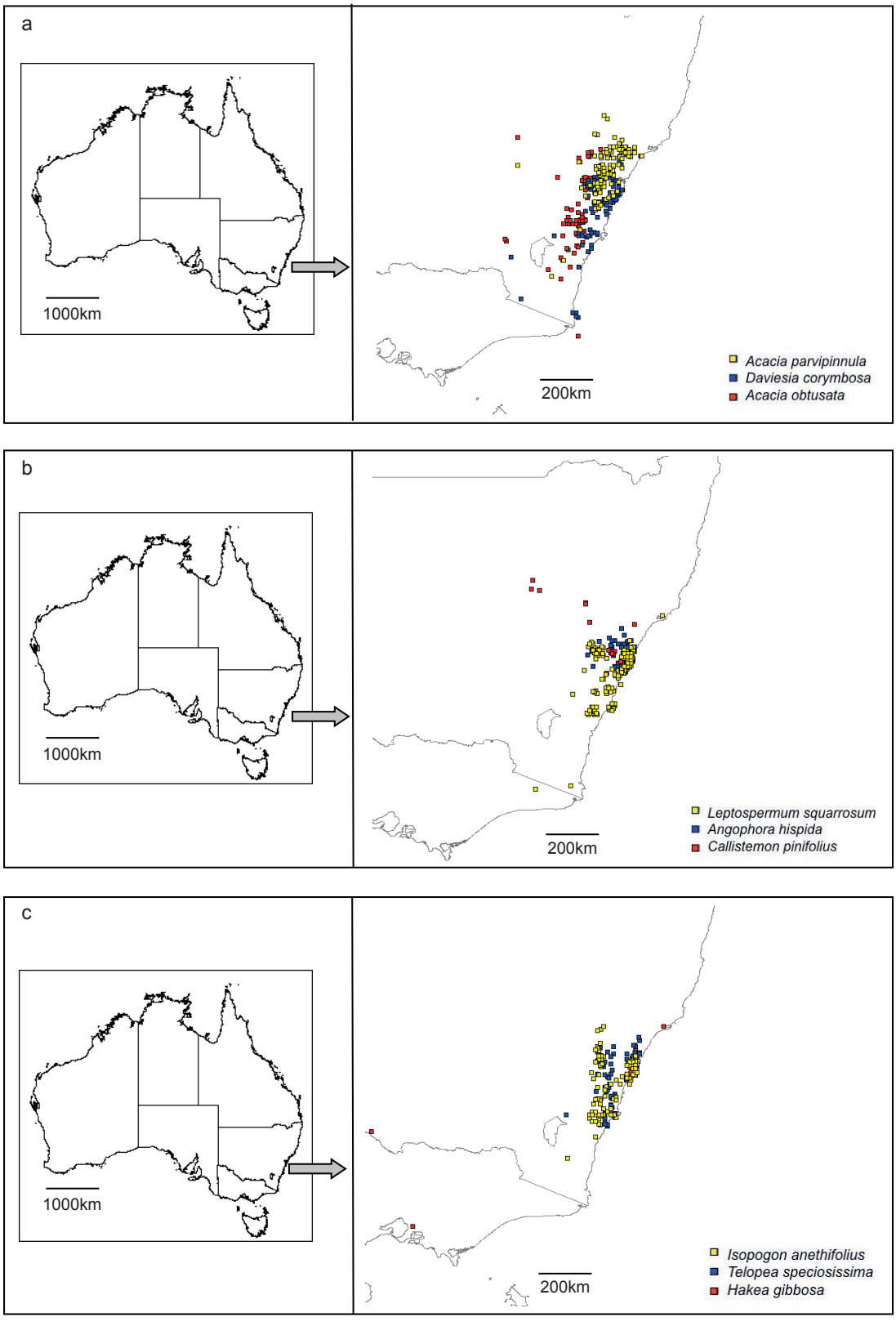

Figure A5: Species distribution maps for nine plant species from three families; (a) Fabaceae, (b) Myrtaceae and (c) Proteaceae.

Appendix 3

Table A6: Numbers of Morphospecies (# Msp) within Coleoptera and Hemiptera families collected from eight host plant species at three sites: control site (C), warm 1 (W1) and warm 2 (W2), including feeding guilds.

Acacia obtusata

Family	Site			# Msp	Feeding guild
	C	W1	W2		
Coleoptera					
Anobiidae		1		1	
Buprestidae			1	1	leaf chewer
Chrysomelidae	1	4	5	8	leaf chewer
Coccinellidae	1	2	1	2	predator
Curculionidae	2		1	3	leaf chewer
Elateridae		1		1	fungivore
Endomychidae	1		2	3	fungivore
Lathridiidae	1	2		2	fungivore
Pselaphidae			1	1	predator
Ptiliidae	2	2	2	2	fungivore
Scarabaeidae		2	2	3	scavenger
Staphylinidae		2	1	3	predator
Tenebrionidae	1			1	scavenger
sum	*9*	*16*	*16*	*31*	
Hemiptera					
Achilidae		1		1	phloem feeder
Aleyrodidae	1	1		2	phloem feeder
Aphididae	6	2	5	11	phloem feeder
Cercopoidae			1	1	xylem feeder
Coccidae	6	2	2	9	phloem feeder
Delphacidae		1	2	3	phloem feeder
Cicadellidae					
Deltocephalinae	2			2	phloem feeder
Iassinae		2		2	phloem feeder
Tartessinae			1	1	phloem feeder
Typhlocybinae	5	1	1	6	mesophyll feeder
Xestocephalinae	4		1	5	phloem feeder
Fulgoridae		1		1	phloem feeder
Membracidae			1	1	phloem feeder
Miridae			1	1	mesophyll feeder
Nabidae		2	1	2	predator
Psyllidae	10	2	1	13	phloem feeder
Reduviidae	1	1		2	predator
sum	*35*	*16*	*17*	*63*	

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Table A6: *continued*
Acacia parvipinnula

Family	Site			# Msp	Feeding guild
	C	W1	W2		
Coleoptera					
Aderidae		2	1	3	scavenger
Anthribidae	1		1	2	scavenger
Brentidae		3	1	4	leaf chewer
Buprestidae	1		1	2	leaf chewer
Cantharidae	1	2	1	2	predator
Cerambycidae		1		1	leaf chewer
Chrysomelidae	8	8	8	18	leaf chewer
Coccinellidae	2	11	6	16	predator
Colydiidae		1		1	fungivore
Cucujidae	1			1	predator
Curculionidae	2	6	3	8	leaf chewer
Endomychidae			3	3	fungivore
Lathridiidae	3	5	3	7	fungivore
Lycidae		1		1	scavenger
Microsporidae			1	1	fungivore
Mordellidae		1	1	2	scavenger
Ptiliidae		3	1	3	fungivore
Salpingidae		1		1	scavenger
Scarabaeidae	1	1	3	5	scavenger
Staphylinidae	1	5		6	predator
sum	*21*	*51*	*34*	*87*	
Hemiptera					
Aleyrodidae	2	1		3	phloem feeder
Anthocoridae			1	1	predator
Aphididae	5	4	4	12	phloem feeder
Blissidae		1		1	mesophyll feeder
Coccidae	4	2	4	7	phloem feeder
Cymidae			1	1	seed predator
Delphacidae	3	7	4	13	phloem feeder
Cicadellidae					
Deltocephalinae	2	1	2	5	phloem feeder
Iassinae		3		3	phloem feeder
Tartessinae	1	1	2	4	phloem feeder
Typhlocybinae	8	10	6	22	mesophyll feeder
Xestocephalinae	2	4		6	phloem feeder
Eurybrachidae		1	1	1	phloem feeder
Fulgoridae		1		1	phloem feeder
Membracidae		4	4	5	phloem feeder
Miridae	1	1	3	5	mesophyll feeder
Nabidae	1	1	1	3	predator
Pentatomidae		1	2	3	mesophyll feeder
Psyllidae	15	11	1	25	phloem feeder
Reduviidae	2			2	predator
Rhyparochromidae			1	1	seed predator
Scutelleridae		1		1	mesophyll feeder
Tropiduchidae		1		1	phloem feeder
sum	*46*	*56*	*37*	*126*	

continued next page

Table A6: *continued*

Daviesia corymbosa

Family	Site			# Msp	Feeding guild
	C	W1	W2		
Coleoptera					
Hydrophilidae		1		1	predator
Anobiidae			1	1	scavenger
Chrysomelidae		1		1	leaf chewer
Coccinellidae		2	1	3	predator
Curculionidae	2	1	1	4	leaf chewer
Endomychidae			1	1	fungivore
Mordellidae	1			1	scavenger
Nitidulidae		1		1	scavenger
Ptiliidae		1	1	1	fungivore
Scarabaeidae		1	1	1	scavenger
Staphylinidae		1		1	predator
Tenebrionidae	1			1	scavenger
sum	*4*	*9*	*6*	*17*	
Hemiptera					
Aphididae	5	5	4	16	phloem feeder
Coccidae	3	2		4	phloem feeder
Cicadellidae					
Deltocephalinae		2		2	phloem feeder
Tartessinae	1			1	phloem feeder
Typhlocybinae	5	6		11	mesophyll feeder
Xestocephalinae	1	2		3	phloem feeder
Delphacidae	2	4	2	8	phloem feeder
Fulgoridae		1		1	phloem feeder
Nabidae	1	2	1	4	predator
Psyllidae	5	5		12	phloem feeder
Reduviidae	1	1		2	predator
sum	*24*	*30*	*7*	*64*	

continued next page

Table A6: *continued*

Angophora hispida

Family	Site			# Msp	Feeding guild
	C	W1	W2		
Coleoptera					
Anobiidae		1		1	scavenger
Anthicidae		1	1	2	scavenger
Buprestidae	1			1	leaf chewer
Cantharidae		1		1	predator
Chrysomelidae	1		1	2	leaf chewer
Coccinellidae		2	1	2	predator
Curculionidae			1	1	leaf chewer
Mordellidae	1			1	scavenger
Pselaphidae		1		1	predator
Ptiliidae	1	3	1	3	fungivore
Scarabaeidae		1		1	scavenger
Staphylinidae		1		1	predator
Tenebrionidae	1		1	2	scavenger
sum	*5*	*11*	*6*	*19*	
Hemiptera					
Aleyrodidae	1		2	3	phloem feeder
Aphididae	3	2	5	10	phloem feeder
Cercopidae		1		1	xylem feeder
Coccidae	1	1	2	3	predator
Delphacidae	2	4	1	7	phloem feeder
Cicadellidae					
Deltocephalinae		2	1	3	phloem feeder
Typhlocybinae	4	2	1	6	mesophyll feeder
Xestocephalinae	1			1	phloem feeder
Flatidae			1	1	phloem feeder
Nabidae			1	1	predator
Pentatomidae		1		1	mesophyll feeder
Psyllidae	5	1		6	phloem feeder
Schizopteridae			1	1	predator
Tropiduchidae			1	1	phloem feeder
sum	*17*	*14*	*16*	*45*	

continued next page

Table A6: *continued*

Callistemon pinifolius

Family	Site			# Msp	Feeding guild
	C	W1	W2		
Coleoptera					
Anobiidae			1	1	scavenger
Anthribidae	1			1	scavenger
Brentidae	1			1	leaf chewer
Cantharidae		1		1	predator
Chrysomelidae	1	2	2	5	leaf chewer
Coccinellidae		2	1	3	predator
Curculionidae	2			2	leaf chewer
Lathridiidae	1			1	fungivore
Mordellidae	1		1	2	scavenger
Pselaphidae			1	1	predator
Ptiliidae		1	2	2	fungivore
Scarabaeidae		1	2	3	scavenger
Staphylinidae		2		2	predator
sum	*7*	*9*	*10*	*25*	
Hemiptera					
Aleyrodidae	1	1		2	phloem feeder
Aphididae	8	5	3	14	phloem feeder
Coccidae	3	2	1	6	phloem feeder
Delphacidae	1	1	2	4	phloem feeder
Cicadellidae					
Deltocephalinae		1		1	phloem feeder
Iassinae		2		2	phloem feeder
Typhlocybinae	4	4	3	10	mesophyll feeder
Xestocephalinae	3	1		4	phloem feeder
Fulgoridae		1		1	phloem feeder
Nabidae	1		2	3	predator
Pentatomidae			1	1	mesophyll feeder
Psyllidae	12	4		16	phloem feeder
Rhyparochromidae	1		1	2	seed predator
sum	*34*	*22*	*13*	*66*	

continued next page

Table A6: *continued*

Leptospermum squarrosum

Family	Site			# Msp	Feeding guild
	C	W1	W2		
Coleoptera					
Anobiidae			1	1	scavenger
Brentidae		2		2	leaf chewer
Cantharidae	1	1		2	predator
Chrysomelidae	2	2	2	6	leaf chewer
Coccinellidae	1		1	2	predator
Colydiidae	1			1	fungivore
Curculionidae	2	2		4	leaf chewer
Endomychidae		1		1	fungivore
Lathridiidae	2	2	1	3	fungivore
Microsporidae		1		1	fungivore
Ptiliidae	1	1	1	1	fungivore
Salpingidae		1		1	scavenger
Scarabaeidae	2	1		3	scavenger
Staphylinidae	1	2	1	3	predator
Zopheridae		1		1	fungivore
sum	13	17	7	32	
Hemiptera					
Aleyrodidae	1			1	phloem feeder
Aphididae	10	5	6	17	phloem feeder
Coccidae	6	2		7	phloem feeder
Delphacidae	1	5	4	10	phloem feeder
Cicadellidae					
Deltocephalinae	5	1	3	9	phloem feeder
Typhlocybinae	9	3	3	15	mesophyll feeder
Xestocephalinae	2		1	3	phloem feeder
Eurybrachidae		1		1	phloem feeder
Flatidae		1		1	phloem feeder
Miridae		1		1	mesophyll feeder
Machaerotinae	1			1	xylem feeder
Nabidae		1	3	4	predator
Psyllidae	10	5		15	phloem feeder
Reduviidae			2	2	predator
sum	45	25	22	87	

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Table A6: *continued*

Hakea gibbosa

Family	Site			# Msp	Feeding guild
	C	W1	W2		
Coleoptera					
Anobiidae			1	1	scavenger
Buprestidae			1	1	leaf chewer
Cantharidae		3		3	predator
Chrysomelidae		2		2	leaf chewer
Coccinellidae	1	2	1	4	predator
Curculionidae	1			1	leaf chewer
Endomychidae		1	1	1	fungivore
Lathridiidae	2	2		4	fungivore
Mordellidae		1		1	scavenger
Ptiliidae	2	1	2	2	fungivore
Scarabaeidae		2		2	scavenger
Staphylinidae		2	2	4	predator
Tenebrionidae			1	1	scavenger
sum	*6*	*16*	*9*	*28*	
Hemiptera					
Aleyrodidae			2	2	phloem feeder
Aphididae	7	4	3	12	phloem feeder
Coccidae	4	1		4	phloem feeder
Cicadellidae					
Deltocephalinae		1		1	phloem feeder
Typhlocybinae	3	2	1	4	mesophyll feeder
Xestocephalinae	4	1		5	phloem feeder
Tartessinae		1		1	phloem feeder
Delphacidae	3	6	1	10	phloem feeder
Membracidae			1	1	phloem feeder
Miridae		1		1	mesophyll feeder
Nabidae	1		1	2	predator
Psyllidae	6	8		11	phloem feeder
Reduviidae	1			1	predator
Tropiduchidae			1	1	phloem feeder
sum	*29*	*25*	*10*	*56*	

continued next page

Table A6: *continued*

Telopea speciosissima

Family	Site			# Msp	Feeding guild
	C	W1	W2		
Coleoptera					
Anobiidae		1		1	scavenger
Anthribidae			1	1	scavenger
Cantharidae	1	1		2	predator
Chrysomelidae	2		1	3	leaf chewer
Curculionidae		1		1	leaf chewer
Endomychidae			1	1	fungivore
Lathridiidae	1		1	2	fungivore
Mordellidae	1			1	scavenger
Nemonychidae			1	1	leaf chewer
Ptiliidae	2	2	1	2	fungivore
Scarabaeidae		1		1	scavenger
Staphylinidae		1	1	2	predator
sum	*7*	*7*	*7*	*18*	
Hemiptera					
Aphididae	4	4	4	11	phloem feeder
Coccidae	4	1		5	phloem feeder
Delphacidae	1	2		3	phloem feeder
Cicadellidae					
Deltocephalinae	1			1	phloem feeder
Iassinae		1		1	phloem feeder
Tartessinae		1		1	phloem feeder
Typhlocybinae	4	2		6	mesophyll feeder
Xestocephalinae		1		1	phloem feeder
Fulgoridae		1		1	phloem feeder
Membracidae		1		1	phloem feeder
Miridae	1			1	mesophyll feeder
Psyllidae	4	3	2	9	phloem feeder
Tropiduchidae	1			1	phloem feeder
sum	*20*	*17*	*6*	*42*	

CHAPTER V

Potential impacts of climate change on patterns of insect herbivory on four Australian plant species

This chapter is intended for submission to *Austral Ecology*

Potential impacts of climate change on patterns of insect herbivory on four Australian plant species

Sabine Nooten[1], Lesley Hughes[1]

[1] Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

Abstract

We present a multispecies transplant experiment aimed at assessing potential climatic impacts on patterns of leaf herbivory. Four native Australian plant species were transplanted outside their native range into a climate 2.5°C warmer in annual mean temperature. After 12 months, we assessed the types and amount of herbivore leaf damage, compared to plants transplanted to a control site within the native range. The overall amount of foliage loss to herbivores ranged from approximately 3% to 10% across species and sites, a range consistent with most estimates of leaf loss in other studies. The most common types of leaf damage were sucking and chewing and this pattern was consistent for all four plant species at all sites.

Keywords: Climate change – insect herbivory – damage types – transplant experiment – Australia – sclerophyll

Introduction

Climate change will have profound impacts on the ecology of virtually all species (Hughes 2000; Parmesan & Yohe 2003; Root et al. 2003; Rosenzweig et al. 2008). Individualistic responses of species to environmental changes, for example by alterations in their phenology, distribution or abundance, may result in the decoupling of current trophic interactions (Tylianakis et al. 2008; Thackeray et al. 2010; Hughes 2012). Interactions between plants and their insect herbivores in particular, may alter if herbivores (and insects in general) respond more rapidly to climatic change, because of their greater mobility and faster life cycles (Bale et al. 2002). Such disruptions to present-day plant-herbivore associations are expected to lead to changes in the magnitude and/or pattern of herbivore pressure on host plants (Coley 1998; Cornelissen 2011). Considering that plants and their associated phytophagous insects comprise approximately 50% of all described species (Strong et al. 1984), and that their interactions are key elements affecting community structure and food webs worldwide (Coley 1998), understanding how climate change will affect these interactions is critical.

Several lines of evidence indicate that in a changing climate, plants may suffer more herbivore pressure (Wilf & Labandeira 1999; Wilf et al. 2001; Currano et al. 2008). Firstly, in earlier periods of warming, such as during the late Palaeocene-early Eocene, fossil leaf records show an increased frequency of herbivore attack and a greater diversity of insect damage (Wilf & Labandeira 1999; Wilf et al. 2001; Currano et al. 2008). Secondly, some studies have indicated that plants in the tropics are subject to more intense herbivore pressure than those at higher latitudes (Coley & Barone 1996). Thirdly, rising temperatures have already decreased development times and increased the number of generations per year in some insect species, with devastating results for their host plants (Logan et al. 2003; Battisti et al. 2006; Netherer & Schopf 2010). Added to these impacts, there is a great deal of experimental evidence that the lower nitrogen content of plant tissues under increasing levels of atmospheric CO_2 may increase herbivore consumption rates (reviewed in Zvereva & Kozlov 2006; Stiling & Cornelissen 2007; Cornelissen 2011).

A number of methods have been used to investigate potential changes in plant-herbivore interactions in relation to climate change. Experimental manipulations of temperature, CO_2 and other factors have been carried out at a small scale in glasshouse or growth chamber experiments (e.g. Johns et al. 2003), or in the field (e.g. Barton et al. 2009; Pelini et al. 2011). These types of experiments are often limited by the number of factors that can be tested, and by the spatial scale over which they can be carried out. An alternative approach is a field transplant experiment, in which plants are moved into a site with a different climate, to simulate future climate conditions within the current geographic range. This approach enables a test of future impacts at a community level. To date few studies have investigated potential patterns of herbivory using transplant experiments. Those that have been performed have used a single host plant species transplanted along an altitudinal (Garibaldi et al. 2011), or latitudinal gradient (Andrew & Hughes 2007).

In this study we investigated the potential future impacts of climate change on patterns of leaf herbivory for four Australian native plant species, by transplanting the plants into a warmer climate. We focused on two questions: do plants in a warmer climate (1) suffer increases in the total amount of herbivore damage and (2) become subject to changes in the types of damage?

Material and Methods

The data presented here were collected as part of a larger study investigating climate impacts on plant-associated insect communities (Chapter 4). More detailed information on the setup of the transplant experiment can be found in the methods section of Chapter 4. In the present study, total arthropod leaf damage and damage types were assessed.

Plant selection & field sites

A subset of four plant species was selected (of the eight species transplanted, as described in Chapter 4), based on their leaves being of a suitable size and shape to enable leaf damage to be visually assessed: *Acacia obtusata* Sieber ex DC (Fabaceae: Mimosoideae); *Daviesia corymbosa* Sm. (Fabaceae: Faboideae); *Angophora hispida* Sm. Blaxell (Myrtaceae); and *Telopea speciosissima* Sm. R. Br. (Proteaceae).

Plants were established from seed in the glasshouse facilities at Macquarie University in January 2009. In March 2010 they were transplanted into three sites, one control site (C) within the plants' native range, and two warmer sites (W1 and W2), located 600 km north of the northern most boundary of the plants' current distribution. The warmer sites were approximately 2.5°C warmer, in terms of mean annual temperature, but had similar average annual precipitation and soil properties (Fig. 1). All sites were fenced to exclude vertebrate herbivores. The tenure of the experiment was twelve months (March 2010 – March 2011), after which all transplanted shrubs were removed prior to flowering to comply with the conditions of the scientific license.

Leaf collection

Sampling was conducted in March 2011. Ten individual plants of each species were haphazardly selected at each site. Twenty mature, fully expanded leaves were haphazardly collected per plant. It should be noted that this sampling method underestimates total herbivory because leaves and other plant parts that are eaten entirely are not taken into account (Lowman 1984), but is nonetheless suitable for comparative purposes.

Herbivory measurements

The percentage missing leaf area due to all types of herbivory, and the proportions of separate damage types, which were chewing, grazing, skeletonizing, sap sucking and mining, were assessed. Herbivory assessments of a total of 2,400 leaves (4 species × 3 sites × 10 plants × 20 leaves) were made.

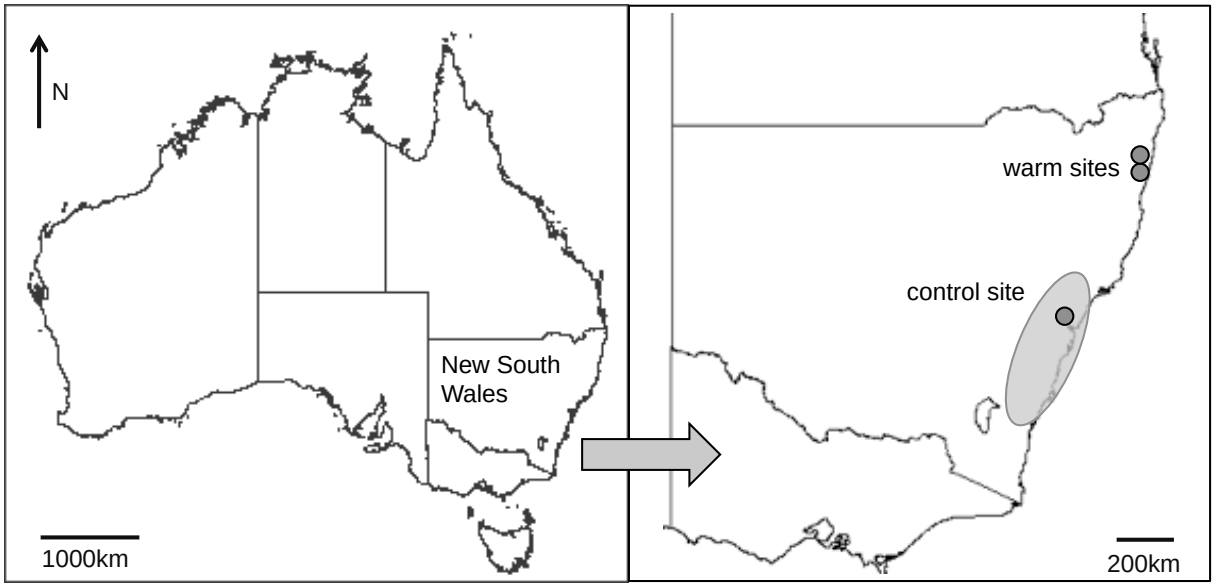

Figure 1: Location of three transplant sites: one control site within the current range of four host plant species (grey oval); and two warm sites, located ca. 600 km north of the northern boundary of the plant species range. N marks north.

Three damage types, chewing, grazing and skeletonizing, are caused by insects using mandibles to chew through leaf tissue and are principally performed by species from the Coleoptera (adults and larvae), Lepidoptera (caterpillar, larvae), Symphyta (sawfly, larvae), Orthoptera (grasshoppers, all instars) and Phasmatodea (stick insects, all instars) (Elliott et al. 1998). Chewing was classified as the complete loss of all layers of leaf tissue, leading to holes either on the edge or within the leaf. For leaves with damage along the edge, approximate leaf margins were drawn in relation to the symmetry of the leaf, to estimate the missing area (Carpenter & Cappuccino 2005). Grazing was identified as the removal or abrasion of surface tissue without the complete loss of all layers of the leaf. Skeletonizing was identified as the removal of inter-veinal tissue, leaving only the leaf vein skeleton. Sap sucking damage was identified as circular punctures, surrounded by lighter coloured tissue, which is caused by arthropods using stylets (sucking mouthparts) to pierce the surface and suck up fluids, such as phloem sap, xylem sap or cell contents from mesophyll tissue (Elliot et al. 1998). Most sucking damage can be attributed to species from the Hemiptera (all instars), Thysanoptera (all instars) and Acari (mites). Although sucking damage may be less conspicuous and more difficult to quantify, phloem feeders can remove as much plant biomass as chewers (Leigh 1997). Mining damage was classified as serpentine or blotched dead areas, where the outer layer is detached from the leaf, caused by larval stages of insects using mandibles to chew internal leaf tissue. Most leaf miners are species within the orders Coleoptera, Lepidoptera, Diptera and Hymenoptera (Elliott et al. 1998; Sinclair & Hughes 2010). The following sources were used to identify damage types: Hockings (1980), McMaugh et al. (1985), Jones & Elliot (1986) and Labandeira et al. (2007).

Statistical analyses

For each plant species, we compared firstly total leaf herbivory and secondly the proportions of types of damage among the three transplant sites. Data for percentage leaf loss was standardised to fit probabilities between 0 and 1. To improve normality, a logit transformation was used instead of the commonly used arcsine, following suggestions by Warton & Hui (2011). To compare total herbivory, a nested ANOVA design was used in SPSS v20; the factor ‘individual plant’ was nested in the factor ‘site’. To compare the proportions of leaf damage types, we used

a multivariate analysis by permutation, based on Euclidean distance (Anderson 2001), performed with the PERMANOVA + add-on package for PRIMER *v*6 (Clarke & Gorley 2006). Again, a nested design was used, as described above.

Results

Total herbivore leaf damage

Total herbivore leaf damage on the four transplanted plant species, after 12 months, was generally low at all three sites, ranging from 3.6% ± 5.5% for *D. corymbosa* to 10.6% ± 13.8% for *A. hispida* (Table 1). All plant species showed a high level of variation in total leaf herbivory within each site, with values ranging from 0% to 62% (Fig. 2). Overall herbivore leaf damage was significantly different among sites for one species, *A. hispida* (Table 2). However, pairwise comparisons between sites were significant for all four plant species, but there was little consistency as to which site showed greatest damage. Two species, *D. corymbosa* and *T. speciosissima,* showed significantly lower levels of damage at the warm sites. *Acacia obtusata* had a slightly higher amount of herbivory at W1 (10.5% ± 9.7%) than at the control site (8.9% ± 11.2%), but the average across the two warm sites was 8.5%. *Angophora hispida* showed similar amounts of leaf loss at W1 (10.6%) and the control site (Table 1).

Table 1: Mean and standard deviation (M ± SD) for percentage of total herbivore leaf damage (total) and damage types (chew, suck, mine, skeletonize and graze) from four plant species at three sites after 12 months: control (C), warm 1 (W1) and warm 2 (W2).

Plant species	Site	Total	Chew	Suck	Mine	Skelet.	Graze
A. obtusata	C	8.9 ± 11.2	4.3 ± 11.4	4.2 ± 3.2	0 ± 0		0.5 ± 1.6
	W1	10.5 ± 9.7	2.1 ± 5.3	7.7 ± 6.9	0 ± 0.4		0.6 ± 1.9
	W2	6.6 ± 7.1	1.3 ± 5.0	5.2 ± 5.4	0.1 ± 0.6		0.1 ± 0.6
D. corymbosa	C	6.8 ± 6.8	2.9 ± 6.0	3.7 ± 3.2	0.1 ± 1.0		0.6 ± 2.4
	W1	3.6 ± 5.5	1.0 ± 4.9	2.3 ± 2.8	0.1 ± 0.7		0.2 ± 0.9
	W2	4.9 ± 8.8	2.6 ± 8.7	2.1 ± 2.7	0.1 ± 1.0		0.1 ± 0.9
A. hispida	C	10.6 ± 8.7	2.0 ± 6.6	6.6 ± 5.5	0.7 ± 2.7	0.1 ± 0.9	
	W1	12.5 ± 14.2	2.5 ± 6.5	5.6 ± 7.3	0 ± 0.4	2.5 ± 5.6	
	W2	8.0 ± 9.1	3.4 ± 8.0	3.7 ± 4.6	0.6 ± 2.3	0.4 ± 2.7	
T. speciosissima	C	9.3 ± 9.9	3.6 ± 8.8	5.1 ± 5.4	0 ± 0.6	0.6 ± 0.4	
	W1	4.8 ± 7.0	3.0 ± 7.1	1.8 ± 1.8	0 ± 0	0.1 ± 0.5	
	W2	7.2 ± 8.0	3.2 ± 6.8	3.2 ± 4.0	0.1 ± 0.8	0.6 ± 2.2	

Table 2: Summary of ANOVA results for total herbivore leaf damage from four plant species at three transplant sites after 12 months: control (C), warm 1 (W1) and warm 2 (W2); degrees of freedom (df), F-Statistic (F) and resulting p-value (p) for overall test and pairwise comparisons between sites.

Plant species	df	F	p			
			overall	C-W1	C-W2	W1-W2
A. obtusata	2,26	1.398	0.265	**0.044**	0.468	**< 0.001**
D. corymbosa	2,25	2.025	0.153	**< 0.001**	**< 0.001**	0.579
A. hispida	2,25	7.007	**< 0.01**	**< 0.001**	0.446	**< 0.001**
T. speciosissima	2,27	5.243	0.244	**< 0.01**	0.205	0.181

note: significant values are in bold.

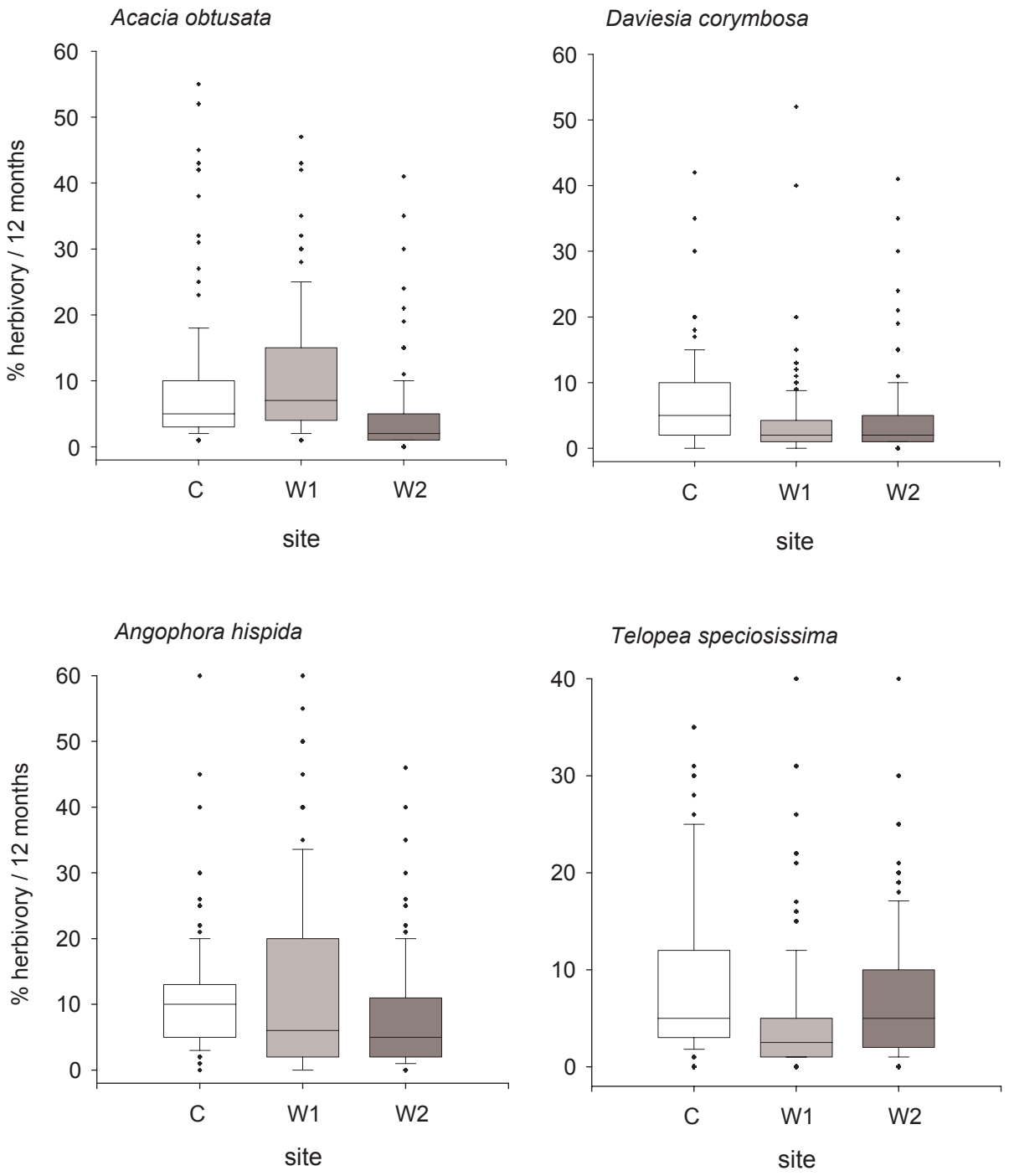

Figure 2: Total herbivore leaf damage on four plant species at three transplant sites after 12 months: control (C), warm 1 (W1) and warm 2 (W2). Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile.

Herbivore leaf damage types

The main damage types were sucking and chewing, with an average leaf loss from sucking of 4.3% across all sites and species, and 2.7% for chewing. Damage from mining, averaged across all plant species and sites was 0.2%. Damage from grazing (0.3%) occurred on the two plant species from the Fabaceae, while a small amount of skeletonizing (0.7%) was recorded on the remaining two plant species.

The overall proportions of herbivore leaf damage types were significantly different among the three sites for one plant species (*A. hispida*) (Table 3, Fig. 3). *Angophora hispida* showed significantly more chewing damage at W2 (average 3.4%), and significantly more skeletonizing (average 2.5%) at W1. There was no significant difference in the proportion of damage types among sites for *A. obtusata,* which showed slightly more chewing damage at the control site (average 4.3%), while both warm sites showed greater amounts of sucking damage (average 6.4%). In *D. corymbosa,* the main damage types, chewing and sucking, occurred in similar proportions at all three sites (Table 3, Fig. 3). *Telopea speciosissima* showed similar proportions of chewing and sucking at the control site and W2.

Table 3: Summary of PERMANOVA results for herbivore leaf damage types from four plant species at three transplant sites after 12 months: control (C), warm 1 (W1) and warm 2 (W2); degrees of freedom (df), Pseudo-F per 9999 permutations (Pseudo-F) and resulting p-value (p-perm), for overall test and pairwise comparisons between sites.

Plant species	df	Pseudo-F	p-perm			
			overall	C-W1	C-W2	W1-W2
A. obtusata	2,26	1.483	0.375	0.341	0.221	0.641
D. corymbosa	2,25	0.828	0.432	0.418	0.719	0.333
A. hispida	2,25	3.386	**0.013**	**0.030**	0.079	**0.013**
T. speciosissima	2,27	0.391	0.756	0.847	0.455	0.717

note: significant values are in bold.

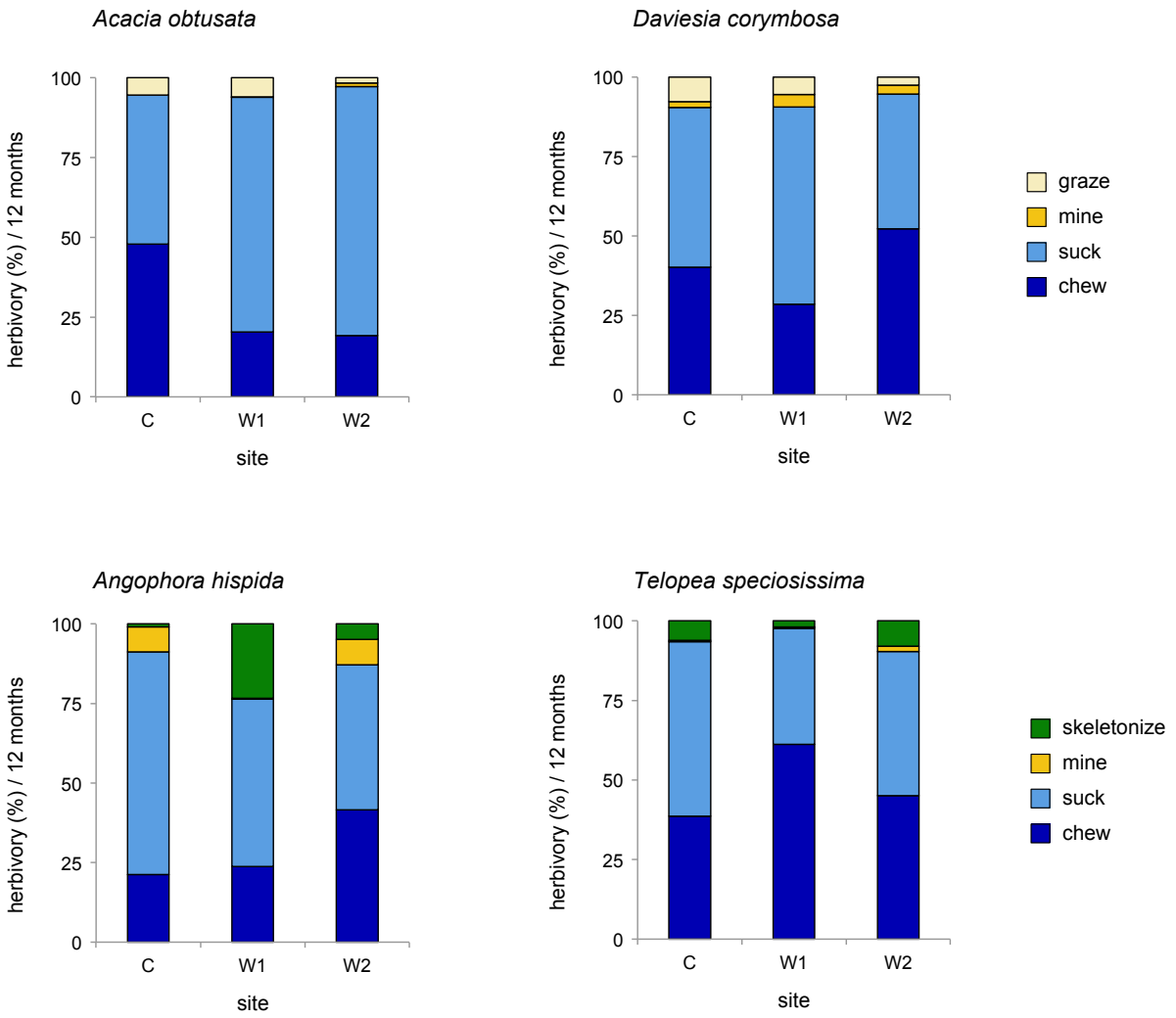

Figure 3: Proportions of herbivore leaf damage types (chew, suck, mine, skeletonize and graze) on four plant species at three transplant sites after 12 months: control (C), warm 1 (W1) and warm 2 (W2).

Discussion

We found that total leaf herbivory ranged from approximately 3% to 10% across all plant species. There was no consistent pattern between control and warmer sites, as some species showed more damage at the cooler site, and others at the warmer sites. The proportions of damage types, however, were relatively consistent among sites, with sucking and chewing damage being dominant across all plant species. Overall, our results do not provide evidence for the hypothesis that herbivore pressure will consistently increase in a warmer climate, but do indicate that individualistic responses of species are to be expected.

Total leaf herbivory

In the present study, levels of total leaf herbivory after 12 months ranged from 3.6% to 10.6% across all plant species at all sites. These values are well within the range of those from a previous study on sclerophyllous plant species native to the Sydney region, which found an average of 10% for 51 plant species from 17 families (Moles & Westoby 2000). These herbivory levels also reflect those from a review across 42 studies that reported 7.1% annual leaf loss in temperate forest systems (Coley & Barone 1996). We found a high level of variation in herbivore leaf damage within sites and individual plants, with values ranging from 0% and 62% on single leaves. Similarly, high levels of variation in leaf herbivory between individual plants, species and stands have been reported previously (Lowman 1985; Landsberg & Ohmart 1989; Lowman 1995; Moles & Westoby 2000; Andrew & Hughes 2005).

The finding that there was no consistent increase in total herbivory at the warmer sites compared to the control sites is in accord with results from a previous transplant experiment in Australia, in which the host plant *Acacia falcata* was transplanted to a site approximate 3°C warmer than the mid-point of its native range (Andrew & Hughes 2007). In contrast, two other transplant experiments have found a consistent increase of herbivory at warmer sites: A reciprocal transplant experiment using a latitudinal gradient in North America, conducted with three plant species from coastal salt marshes (*Spartina alternifolia* (grass), *Solidago sempervirens* (forb) and *Iva frutescens* (shrub)) showed that herbivore damage was two orders of magnitude

greater for plants transplanted to low- than to high-latitudes (Pennings et al. 2009); the authors linked this strong latitudinal difference with the higher abundance of chewing herbivores at lower latitudes. Similarly, a reciprocal transplant experiment of *Nothofagus pumilio* along an altitudinal gradient in Argentina, found that total leaf damage and frequency was higher on plants at the low elevation (warmer) site (Garibaldi et al. 2011), which was related to changes in foliar traits and also an increased insect abundance at this site. Both studies (Pennings et al. 2009 and Garibaldi et al. 2011) linked the increase of total herbivory at the warmer sites to a higher abundance of herbivores, whereas in the present study no such trend occurred.

Other studies investigating herbivory along environmental gradients have also found differences between species. For example, Kozlov (2007) assessed herbivore leaf damage along latitudinal and longitudinal gradients across northern and central Europe on two *Betula* species; one species showed an increase of leaf herbivory in relation to higher summer temperatures at the northern (cooler) end of the gradient, whereas the other species showed no such trend (Kozlov 2007).

In the present transplant experiment, two plant species (*D. corymbosa* and *T. speciosissima*) experienced more herbivore pressure at the control site, than at each of the warm sites. The control site was located within the native range of the plant species with its naturally co-occurring herbivore community present. The warm sites however were located outside of the plants' native distribution, and therefore potentially exposed to a different suite of herbivores. Indeed, the results shown in Chapter 4 indicated an almost complete turnover in the phytophagous Coleoptera and Hemiptera community between the control and warm sites (see Chapter 4, Table 6). For two plant species (*D. corymbosa* and *T. speciosissima*) total herbivore leaf damage was particularly low at the warm sites (approximately 5%), which might be due to the lack of congeneric plant species, and therefore specialised herbivores adapted to these genera, in the warmer area. It has been shown that for exotic plant species, total herbivore leaf damage is reduced when no taxonomically closely related native species are present (Harvey et al. 2012).

Herbivore leaf damage types

Leaf damage was chiefly inflicted by chewing and sucking herbivores, and to a much lesser degree by miners, grazers and skeletonizers; this pattern was consistent for all four plant species, across all sites. Likewise, chewing and sucking damage comprised the major types of folivory on a species of shrub (*Acacia falcata*) along a latitudinal gradient in Australia (Andrew & Hughes 2005). Chewing was also the most common damage type on four forest tree species in northern America, where it contributed to up to 98% of the total herbivore leaf damage (Adams & Zhang 2009). A similar trend was found on native populations of a species of shrub in North America where herbivory due to chewing and perforation (sucking) was by far the most common form of damage (Genton et al. 2005). Likewise, on two tree species across northern and central Europe, damage caused by chewing was the most common herbivory type (Kozlov 2007).

Patterns of damage types, compared between the control site and the warmer sites, were host species-specific. For two of the species, *T. speciosissima* and *D. corymbosa*, the proportions of herbivore leaf damage types was very similar among sites. For the other two species, *A. obtusata* and *A. hispida*, damage types were distributed differently among the three sites. These differences were mainly caused by variations in the patterns of chewing and sucking. For *A. obtusata,* the proportion of sucking herbivory was significantly higher at the warm sites compared to the control site, suggesting a greater abundance of phytophagous arthropods with stylet mouthparts (probably from the orders Hemiptera, Thysanoptera or Acari). For *A. hispida* there was significantly greater chewing damage at W2 and skeletonizing at W1, indicating a greater abundance of insects using mandibles to consume plant material, possibly from the orders Coleoptera, Orthoptera, Lepidoptera and Phasmatodea. Similar to the trend of more chewing herbivory at the warm site W1 shown by *A. hispida*, a previous transplant experiment also found an increase of chewing damage on the transplants at warmer sites compared to plants within the native range (Andrew & Hughes 2007).

Conclusion

We found variable patterns of leaf damage both among species, and among sites in different climates, suggesting that general predictions about how herbivory may be affected in future climates will be difficult to make. Nonetheless, certain consistent patterns did emerge, principally that most herbivory will continue to be dominated by chewers and suckers, regardless of the rate and magnitude of climatic change, and that the overall magnitude of foliage loss will be similar to that experienced currently. We also conclude that transplant experiments provide a useful complement to laboratory experiments and gradient studies in the search for understanding of future impacts on species interactions.

Acknowledgements

We would like to thank Patrick Schultheiss for help with fieldwork and comments on earlier manuscripts, Kerinne Harvey for interesting discussions about herbivory and damage types and David Nipperess for advice on statistical analyses. This study was supported by a Macquarie University research excellence scholarship (iMQRES) to Sabine Nooten.

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CHAPTER VI

CONCLUSION

Current and future climate change will have profound impacts on species and communities (Hughes 2000; Parmesan & Yohe 2003; Root et al. 2003; Rosenzweig et al. 2008). Differential responses of single species to climate change, such as changes in phenology, shifts in geographical ranges or alterations in abundances, may lead to the decoupling of current trophic interactions (Tylianakis et al. 2008; Thackeray et al. 2010; Hughes 2012). Such alterations in trophic interactions may result in novel species combinations, leading in turn to profound changes in community composition and structure. A better understanding of how these communities are structured in current climates becomes increasingly important if we want to understand and provide a basis for predicting how new communities may be assembled in a warmer climate. Current plant-insect communities may be particularly susceptible to decoupling, as insects may be capable of responding more rapidly to climate change because of their greater mobility and faster life cycles (Bale et al. 2002). In regard to possible range shifts, current plant-insect communities may respond to a rapidly warming climate in three ways: (i) plants and insects may migrate simultaneously to a new range and their community may persist largely unchanged; (ii) either insects or the associated plant species may fail to migrate or adapt *in situ,* leading to local extinction and community disassembly; (iii) insects may move at a faster pace than their associated plant and colonise new host plant species, forming novel communities.

The overall aim of this thesis was to investigate the potential for current plant-insect communities to undergo decoupling as a response to a warming climate. The approach I have taken was to perform a multispecies transplant experiment - a direct assessment of impacts of a warmer climate on current plant-insect communities. To create a basis for understanding plant-insect assemblages, I also aimed to identify possible factors driving community structure on multiple host plant species from different families within their current climate.

Assumptions, limitations and benefits of this study

Using multiple plant species to investigate plant-insect communities has both advantages and disadvantages: By collecting the insect fauna from nine host plant species within three families, trends and patterns of the insect communities may emerge that may be generalisable across a wider range of plant species and families. On the other hand, investigating multiple plant species meant a necessary trade-off such that the number of possible sites and collection events for each individual plant species was limited. Limiting collections in this way may have resulted in a less complete collection of the insect fauna than might have been the case if I had used fewer host species. This shortcoming may have reduced the power of the statistical analyses and caution needs to be applied when generalising from the results. Furthermore, the number of field transplant sites used in this study is rather small, with only three sites, thus the patterns observed could also reflect site related idiosyncrasies.

The main incentive for the use of a multispecies transplant experiment to assess potential impacts of climate change on plant-insect communities is that this approach offers a direct test of hypotheses under realistic environmental conditions that these communities may experience over the coming decades. Consequently, such transplant experiments provide a rewarding complement to more commonly used approaches, such as glasshouse experiments or gradient studies. However, the study makes several specific assumptions regarding the collection of the insect fauna from multiple plant species in both current and warmer climates, discussed below:

(i) Increasing temperature will be the most important factor in determining species ranges and in influencing species interactions and communities.

This assumption is justified for two main reasons. Firstly, there is abundant evidence that temperature is one of the most important factors limiting the distribution of species in general, and insects in particular (Bale et al. 2002; Thomas 2010). Secondly, confidence in projections of future temperature in specific regions is far stronger than in projections for rainfall and extreme events. In Australia, mean annual temperatures are expected to increase by 1-5ºC by 2070 (CSIRO 2012) and in the eastern region of New South Wales (NSW) by 1ºC to 3ºC (NSW Climate Profile 2010). Projections for precipitation patterns are less certain and vary depending on the region; for mid- and north-coastal areas of NSW increases during summer (~+10-20%) and decreases during winter (~-5-10%) are expected (NSW Climate Profile 2010).

(ii) The entire insect fauna of a host plant was collected.

As the collection of the entire insect fauna is generally an almost impossible task, I generated species accumulation curves to assess adequacy of sampling. This allows for an interpretation of the results in relation to the achieved sampling adequacy (Chapters 2 and 4).

(iii) Any phytophagous insects collected from individual plant species were assumed to actually feed on the plant.

To test this assumption, herbivores would have needed to be collected alive (by beating, branch clipping or hand collection) and subjected to feeding trials. Such an approach would probably have resulted in an even lower adequacy of sampling as the required sampling techniques generally yield lower numbers of insects than the chemical knockdown used here (Moir et al. 2005). Further, the high proportion of rare species in the collection would not have allowed for proper replication of feeding trials. To minimise the collection of non-feeding species (tourists), insect sampling was restricted to early morning hours.

Plant-insect communities within their native range

In this study, community composition, based on the identity of morphospecies, showed little commonality among host plant species, and even within plant families (Chapter 2). A high turnover of community composition has also been found in previous studies among plant species and within families (Morrow 1977; Peeters et al. 2001). These results suggest that physical and chemical characteristics of an individual host species may vary widely enough to support a unique insect community. Feeding guild structure was also found to show a host plant species-specific pattern when the entire Coleoptera and Hemiptera community was considered. No strong associations of a particular structure were found with either family-level pattern or plant architectural traits (Chapter 2). However, when only the phytophagous component was considered, some consistency of structure was found among host plants of similar leaf size, regardless of their phylogenetic relatedness (Chapter 2). These results indicate that the characteristics of the individual host plant species are fundamental for shaping insect communities, and that it may be difficult to infer from individual plant species to genera or family level.

Projections for composition of insect communities

In this study, there was an almost complete turnover in community composition between host plants in their current range compared to the warmer sites (Chapter 4). Profound alterations in community composition have also been found in previous studies as a response to experimentally increased temperature (Villalpando et al. 2009) and among plants within their native range and transplanted to warmer sites (Andrew & Hughes 2007). These results are consistent with observations that many Australian insect species are (i) specialised to one or just a few host plants and/or (ii) have narrow geographic ranges (Austin et al. 2004; Cranston 2009). Narrow ranges may be associated with narrow thermal tolerances (Bale et al. 2002; Ohlemuller et al. 2008). The individualistic community assemblages supported by the host plants used in this study strongly suggest that rapid and dynamic changes in plant-insect relationships may be expected under a changing climate.

A caveat to bear in mind is that transplanting plant species outside their native range, to achieve a temperature gradient, may have been associated with a confounding factor, because plant-associated insect species, particularly herbivores, may have even smaller ranges than their host plants (Strong et al. 1984). This might have led to an inevitable alteration of the insect community, particularly in terms of species composition. Nevertheless, this provides a very realistic test for assessing how mobile insects may colonise new host plants as they migrate to track climate change.

Projections for structure of insect communities

Throughout this study, insect community structure, based on the representation of morphospecies within feeding guilds, showed a host species-specific pattern when the entire Coleoptera and Hemiptera community was considered. When host plants were transplanted into a warmer climate, community structure was maintained on some, but not all species (Chapter 4). In contrast, when the phytophagous component of the communities was considered alone, far more consistency between structure on the warmer transplants compared to the control site within the native range was found. These consistencies in herbivore community structure corroborate results from a previous transplant experiment in southeast Australia in which a single host plant species was used (Andrew & Hughes 2007) and suggest that at least some elements of present-day community structure will be maintained in the future.

Herbivory

We found that the amount of leaf herbivory was highly variable among sites and plant species. Levels of herbivore leaf damage on the four shrubs that were intensively sampled (*A. obtusata, D. corymbosa, A. hispida* and *T. speciosissima*) were higher than some previous estimates for temperate forests (Coley & Barone 1996), but congruent with those of dry sclerophyll forest canopy trees in Australia measured by Lowman (1995) (Chapter 3). High variability among species and sites

was also found on transplanted plants, both within the control and warmer sites (Chapter 5). Patterns of damage types also showed an idiosyncratic pattern for each plant species across its current range (Chapter 3). However, proportions of dominant feeding types on transplants stayed relatively consistent between control and warm sites (Chapter 5). Our results do not confirm the expectation that higher levels of herbivory will occur under a warmer climate (see reviews by Zvereva & Kozlov 2006; Cornelissen 2011).

Future directions

Understanding the factors that shape present-day species relationships and community patterns is crucial for providing a basis for better predicting how a rapidly changing climate will affect ecosystems and biodiversity. To build on the findings of this study, we suggest five priorities for research:

1. The focus of this study was on the orders Coleoptera and Hemiptera, on the grounds that species within these orders generally comprise the largest portion of the herbivorous insect fauna. Describing patterns of composition and structure of other important insect taxa, including butterflies and moths (Lepidoptera), grasshoppers and crickets (Orthoptera), stick insects (Phasmatodea), thrips (Thysanoptera), Hymenoptera and spiders (Araneae), on the same plant species and on species within other genera of the same plant families used in this study would complement our results and show how generalisable these results are over the entire community that is associated with a host plant. All mentioned taxa have been sampled and are being kept in storage to allow future analyses.

2. A better understanding of the extent of host specificity of the phytophagous insects associated with Australian plant species would improve our insights into the probability that insects adapting to climate change by shifting range will switch host plants. Host plant specificity can be assessed by exposing herbivores to foliage from different plant species (Novotny et al. 2002; Novotny & Basset 2005).

3. Throughout this study, the host plant emerged as a fundamental driver of the insect community. A further investigation of underlying mechanisms would greatly

improve predictions as to how these communities will respond to future climate change. For example, community structure could be investigated in relation to plant functional traits, by including morphological measurements and species life history traits, with the aim of building a frequency distribution of traits for each individual host plant species (McGill et al. 2006). As some traits can be associated with microhabitat use or diet (Barton et al. 2011), trait distributions can be used as a baseline for projections of future climate change impacts on plant-insect communities.

4. Using long-term experimental field manipulations, in which assemblages of plant species are subjected to warmer temperatures and/or other variables (CO_2, precipitation) in open-top chambers, to assess impacts on insect communities would be a useful complement to the type of transplant experiment described in the present study. While these types of experiments have been performed on plant communities (e.g. McMurtrie et al. 2008; Barton et al. 2010; Norby et al. 2010), they have rarely been used for plant-insect communities (but see Pelini et al. 2011).

5. Using multiple translocation sites would be useful to determine if observed patterns in plant-insect communities were site related idiosyncrasies or if they are generalisable across multiple species and sites.

These approaches could contribute to improving our knowledge about the processes that shape plant-insect communities, and may ultimately inform us how current and future climate change may affect these assemblages.

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APPENDIX I

Appendix I contains a paper to which I contributed during my PhD candidature. It investigates the foraging ecology of the Australian desert ant *Melophorus bagoti*.

- Schultheiss, P. & Nooten S. S. 2013. Foraging patterns and strategies in an Australian desert ant. *Austral Ecology.* doi:10.1111/aec.12037

Pages 219-228 of this thesis have been removed as they contain published material. Please refer to the following citation for details of the article contained in these pages:

Schultheiss, P., & Nooten, S. S. (2013). Foraging patterns and strategies in an Australian desert ant. *Austral Ecology*, 38(8), 942–951. https://doi.org/10.1111/aec.12037