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# Diversity and assemblage structure of phytophagous Hemiptera along a latitudinal gradient: predicting the potential impacts of climate change

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## ABSTRACT

**Aims** The aims were (1) to assess the species richness and structure of phytophagous Hemiptera communities along a latitudinal gradient, (2) to identify the importance of rare species in structuring these patterns, and (3) to hypothesize about how phytophagous Hemiptera communities may respond to future climate change.

**Location** East coast of Australia.

**Methods** Four latitudes within the 1150 km coastal distribution of *Acacia falcata* were selected. The insect assemblage on the host plant *Acacia falcata* was sampled seasonally over two years. Congeneric plant species were also sampled at the sites.

**Results** Ninety-eight species of phytophagous Hemiptera were collected from *A. falcata*. Total species richness was significantly lower at the most temperate latitude compared to the three more tropical latitudes. We classified species into four *climate change response* groups depending on their latitudinal range and apparent host specificity. Pairwise comparisons between groups showed that the *cosmopolitan*, *generalist feeders* and *specialists* had a similar community structure to each other, but the *climate generalists* had a significantly different structure. Fifty-seven species were identified as rare. Most of these rare species were phloem hoppers and their removal from the dataset led to changes in the proportional representation of all guilds in two groups: the *specialist* and *generalist feeders*.

**Main conclusions** We found no directional increase in phytophagous Hemiptera species richness. This indicates that, at least in the short term, species richness patterns of these communities may be similar to that found today. As the climate continues to change, however, we might expect some increases in species richness at the more temperate latitudes as species migrate in response to shifting climate zones. In the longer term, more substantial changes in community composition will be expected because the rare species, which comprise a large fraction of these communities, will be vulnerable to both direct climatic changes, and indirect effects via changes to their host's distribution.

## Keywords

*Acacia*, community structure, environmental gradient, global warming, guild structure, Heteroptera, Homoptera, insect herbivores, rare species, temperature.

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## INTRODUCTION

Climate change is expected to have significant impacts on the distribution, phenology and abundance of many species over the next few decades (Root *et al.*, 2003). Changes in community structure, and extinctions of some species are also expected (Bale *et al.*, 2002; Thomas *et al.*, 2004). In Australia, there is little

knowledge about factors that currently determine the abundance and distribution of most species (Hughes, 2003), especially invertebrates. This restricts our ability to predict how these species, and the communities they live in, will respond to a rapidly changing climate.

Understanding how herbivorous insect communities will respond to climate change is important for several reasons.

Firstly, insect herbivores comprise a major portion of global biodiversity, representing approximately 57% of the 1.75 million described species (e.g. Price, 2002). Secondly, herbivores have significant impacts on productivity, decomposition, nutrient cycling and other important ecosystem-level processes (e.g. Kremen *et al.*, 1993). Thirdly, many insect herbivores are highly mobile, and may therefore be expected to migrate rapidly in response to shifting climate zones.

In this study we focused on the phytophagous Hemiptera, an important and conspicuous component of many herbivore communities (Kennedy & Southwood, 1984; Majer *et al.*, 1997; Hill *et al.*, 1998). The few published studies on potential impacts of climate change on phytophagous Hemiptera in field-based studies have been primarily concerned with either investigating life-history characteristics and abundances of single species along climatic gradients (Hill & Hodkinson, 1992; Whittaker & Tribe, 1998), or with investigating the impacts of higher temperatures using field manipulations (Bale *et al.*, 1994; Richardson *et al.*, 2000). The potential impacts of a changing climate on Hemiptera assemblages, and indeed, on most other terrestrial insect assemblages, have not been studied. Our approach is to investigate how present-day assemblages are structured along an environmental gradient and on different host species, and to use this information to develop hypotheses as to how community structure and composition may change in the future.

We examined the assemblages of phytophagous Hemiptera on *Acacia* species along an extensive latitudinal gradient in eastern Australia, with our primary focus on the herbivores that feed on *A. falcata*. We have previously described the abundance and biomass of arthropod feeding guilds, the species richness and assemblage structure of the phytophagous Coleoptera, and leaf herbivory along the same gradient, on the same host species (Andrew & Hughes, 2004a,b; 2005).

In this study we compared species richness of phytophagous Hemiptera among latitudes to determine if there is a latitudinal gradient in species richness similar to that found for many other taxa (Rosenzweig, 1995). The similarity of Hemiptera assemblages between adjacent latitudes was compared using two similarity indices: a presence/absence index (Sørensen Incidence) and an index that includes a measure of abundance (Morisita–Horn). We expected that because more species are endemic to latitudes closer to the tropics, species turnover here would be higher (Stevens, 1989; Rosenzweig & Sandlin, 1997; Koleff *et al.*, 2003).

We also examined the role of rare species in determining patterns along the latitudinal gradient because these species may be the most vulnerable to climate change (Saetersdal & Birks, 1997). We defined rare species as those sampled at only one site and in one season from a single host individual. Rare species contribute a significant proportion of species to community structure (Novotny & Basset, 2000; Lucky *et al.*, 2002), but their importance in determining diversity patterns is unclear. We performed analyses of community structure with and without the rare species to investigate their relative influence.

Classifying species into functional groups or feeding guilds (Root, 1973) allows comparisons and generalizations to be made that are not possible using taxonomic groupings alone.

Landsberg & Stafford Smith (1992) developed a scheme to predict how a changing climate and various host plant traits might influence the outbreak of agricultural and forestry pests. We have developed a complementary classification scheme to assess the potential impacts of climate change on herbivore communities. Both feeding guild classifications and classical taxonomic classifications have been used in this study.

We classified the Hemiptera collected into four *climate change response* groups, *cosmopolitan*, *generalist feeders*, *climate generalists* and *specialist feeders*, according to their distribution among latitudes and host species (Andrew & Hughes, 2004). These groups might be expected to respond differently to a rapidly changing climate. Species found at more than one latitude, and on more than one *Acacia* species were classified as *cosmopolitan*. Species found on *A. falcata* and on other congeneric plant species, but at only one latitude, were classified as *generalist feeders*. Species found only on *A. falcata* but at more than one latitude were classified as *climate generalists*. Finally species found at only one latitude and only on *A. falcata* were classified as *specialists*.

In summary, the questions we address in this paper are:

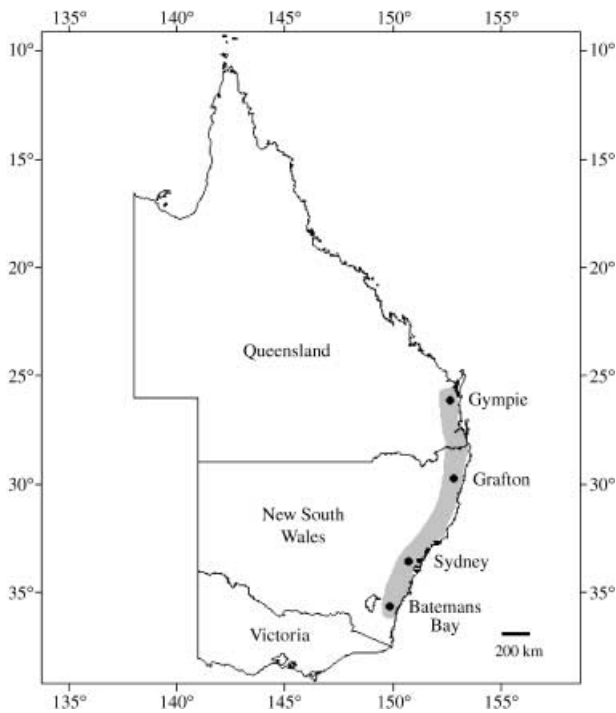
- 1 How does the species richness, similarity, and functional group structure of phytophagous Hemiptera communities change along the coastal latitudinal distribution of a single host plant species?
- 2 Does the exclusion of rare species from the dataset change the trends identified in the full dataset?
- 3 Based on the community patterns described, how might phytophagous Hemiptera communities respond to future climate change?

## METHODS

### Sampling

The focal host plant species, *Acacia falcata*, was chosen because of its extensive coastal latitudinal distribution, spanning 1150 km along the east coast of Australia (Fig. 1). We sampled insects from four latitudes spanning this range: Gympie, Queensland (26°7' S, 153°11' E the most tropical latitude); Grafton, New South Wales (NSW) 29°44' S, 152°58' E; Sydney, NSW (33°36' S, 150°52' E); and Batemans Bay, NSW (35°40' S, 150°20' E the most temperate latitude). At each latitude, we selected three sites where *A. falcata* was abundant (> 100 individual plants per 300 m<sup>2</sup>) and the majority of mature plants were taller than 1.5 m. All sites were located in open eucalypt forests and were at a similar altitude (< 150 m). The distances between sites within latitudes ranged from 2 to 80 km. There was a reduction in mean annual temperature of 4.3 °C from north to south: Gympie (20.2 °C), Grafton (18.3 °C), Sydney (16.9 °C) and Batemans Bay (15.9 °C). There was no latitudinal trend in precipitation: Sydney (second-most southerly latitude) had a lower mean annual precipitation (838 mm) compared to the three other latitudes: Gympie (1104 mm), Grafton (1118 mm) and Batemans Bay (1145 mm).

Arthropods were sampled every three months, from November 1999 (spring) to August 2001 (winter), a total of eight collections over two years. At each site, at each collection time, 10 *A. falcata*



**Figure 1** Map of the coastal distribution of *Acacia falcata* along the east coast of Australia and the latitudes sampled in this study.

plants were haphazardly selected and sprayed with 0.6% pyrethrum/water solution in the morning on low-wind days. All arthropods falling onto four collecting trays (50 × 30 cm) placed beneath the plants were transferred into vials containing 70% ethanol for storage. At sites with co-occurring phyllodinous *Acacia* species (Table 1), five individuals of each *Acacia* species were also sampled using the same protocol. No samples were taken from the three sites at Grafton in February 2001 (summer sample) due to regional flooding. This method of sampling was not used in an attempt to produce a complete inventory of all species that might feed on the *Acacia* species sampled, but as a standardized sampling regime to allow direct comparisons among latitudes and host plant species.

All adult Hemiptera (Heteroptera and Homoptera) were identified to family (subfamily and genus where possible) and

morphospecies (CSIRO, 1991; Fletcher & Larivière, 2001 and updates). Morphospecies were formally identified as separate species by expert taxonomists and will be hereafter referred to as species. Nymphs were excluded from the analyses as it is extremely difficult to associate nymphs with adults of the same species in preserved collections. Only species that were phytophagous as adults were used in this study. If species were known feeders on other host plant genera and not on *Acacia* (as verified by taxonomists) they were excluded from the dataset.

We classified species into five guilds: phloem hoppers, phloem bugs, mesophyll hoppers, mesophyll bugs and xylem hoppers, based on the feeding habit and taxonomic relationship of species within family groupings as reported in CSIRO (1991), Peeters *et al.* (2001) and expert taxonomist advice (G. Cassis, M. Fletcher and G. Taylor, pers. comm.). Phloem hoppers feed on phloem sap and were identified as species from the suborder Auchenorrhyncha, including leafhoppers (most Cicadellidae subfamilies) and planthoppers (Fulgoroidea). Phloem bugs also feed on phloem sap and were identified as species from the suborder Sternorrhyncha, including psyllids (Psylloidea), aphids (Aphididae) and white flies (Aleyrodidae). Mesophyll hoppers feed on mesophyll fluid and were identified as species from the suborder Auchenorrhyncha, family Cicadellidae, subfamily Typhlocybinae. Mesophyll bugs also feed on mesophyll fluid and were identified as species from the Heteroptera (true bugs). Xylem hoppers feed on xylem fluid and were identified as species from the suborder Auchenorrhyncha, including froghoppers (Cercopidae) and leafhoppers from the family Cicadellidae, subfamily Cicadellinae.

### Statistical analysis

Both the density of phytophagous Hemiptera species (the number of species per specified number of samples) and species richness (the number of species present per specified number of individuals) (Gotelli & Colwell, 2001) were assessed for collections from *A. falcata*. Total species richness (sites pooled within latitudes) was analysed using a *G*-test, with Williams' correction for small samples ( $n < 5$ ) applied. Average species density (compared at 70 samples per site), and average species richness (compared at 23 individuals per site, based on Hemiptera abundance recorded at the site with the lowest abundance value) were compared

**Table 1** Host plants sampled in each of four latitudes during this study

Latitude	Longitude	Name	Focal host plant	Co-occurring, phyllodinous <i>Acacia</i> species
26°7' S	153°11' E	Gympie (most tropical)	<i>A. falcata</i> Willd. 1806	<i>A. complanata</i> A. Cunn. ex Benth 1842 <i>A. concurrens</i> Pedley 1974 <i>A. flavescens</i> A. Cunn. ex Benth 1842 <i>A. leptostachya</i> Benth 1864
29°44' S	152°58' E	Grafton	<i>A. falcata</i>	<i>A. leptostachya</i>
33°36' S	150°52' E	Sydney	<i>A. falcata</i>	<i>A. longifolia</i> (Andrews) Willd. 1806 <i>A. leiocalyx</i> (Domin) Pedley 1974
35°40' S	150°20' E	Batemans Bay (most temperate)	<i>A. falcata</i>	<i>A. binervata</i> DC. 1825 <i>A. longifolia</i> <i>A. stricta</i> (Andrews) Willd. 1806

among latitudes by one-way ANOVAS using Datadesk® 6.1 (Velleman, 1997). Data collected from individual plants and from different seasons within sites were pooled. Differences among latitudes were then assessed using sites as replicates. Accumulation curves were generated to assess species richness and species density values for each of 12 sites using *EstimateS* 5.0 (Colwell, 1997).

Assemblage structure, based on relative species richness within four of the feeding guilds, was also compared among latitudes using a *G*-test. Differences between *climate change response* groups in terms of feeding guild structure were analysed using a *G*-test. Feeding guild structure was measured by the percentage of species in each feeding guild from each *climate change response* group. All three statistical procedures were performed on data pooled from individual plants, and from different seasons within sites within latitudes.

Similarity of phytophagous Hemiptera assemblages between adjacent latitudes (sites pooled within latitudes) were compared using two similarity measures: one a presence/absence-based index (Sørensen Incidence) and the other an index that includes an assessment of abundance (Morisita–Horn index). Both measures were calculated using *EstimateS* 5.0 (Colwell, 1997).

Accumulation curves were generated to assess sampling adequacy for each latitude using *EstimateS* 5.0 (Colwell, 1997). Estimates of the total number of species (based on the number of singleton and doubleton species) within the phytophagous Hemiptera assemblage, within latitudes, were made using the Chao-1 index calculated using *EstimateS* 5.0 (Colwell & Coddington, 1994; Chao *et al.*, 2000).

We also conducted the above statistical comparisons on a dataset that excluded rare species (hereafter called the *common species* dataset). Rare species were defined as species collected from only one *A. falcata* individual at one site during one sampling season. The same statistical analyses as described above were carried out on the *common species* dataset.

## RESULTS

### Assemblage composition

Ninety-eight species of phytophagous Hemiptera (identified from 6004 individuals) were collected from *A. falcata*. Forty-eight species were from the family Cicadellidae, six from the family Aleyrodidae, five each from the families Delphacidae, Psyllidae and Tingidae, four each from the families Cixiidae, Coccidae and Miridae, two each from the families Lygaeidae, Meenoplidae, Membracidae and Pentatomidae, and one each from the families Aphididae, Aphrophoridae, Eurybrachyidae, Fulgoridae, Issidae, Piesmatidae, Pseudococcidae, Thaumastocoridae and Tropiduchidae.

Ten species were sampled at all four latitudes (Table 2 — Group 1), with one species, *Acizzia* sp. 8 (Psyllidae) being dominant in abundance at all latitudes. Six species were sampled at the most tropical plus both mid-latitudes (Group 2). Two species were sampled only at the two more temperate latitudes, six species were sampled only from both mid-latitudes and six species were sampled only from the two more tropical latitudes (Group 4). Fifty-seven species (58% of total species) were found only at one of the four latitudes (Group 6).

A further 32 species were collected from eight co-occurring *Acacia* species (Table 1), but not from *A. falcata*, making a total of 130 species collected from all nine *Acacia* species sampled (Table 1). Gympie had the highest number of species collected from all congeneric *Acacia* species (71 species), followed by Grafton and Sydney (57 species each) and then Batemans Bay (40 species).

### Species richness along the latitudinal gradient

The total number of species collected was significantly lower at the most temperate latitude (Batemans Bay) compared to the other, more tropical, latitudes (Fig. 2a: Overall). Average species density and species richness were not significantly different among latitudes (Fig. 3a,b). The species accumulation curves indicated that the most southerly latitude was relatively better sampled than the other three latitudes, but no accumulation curve from any of the four latitudes had reached an asymptote after two years of sampling (Fig. 4a).

We used the Chao-1 index to estimate the expected number of species of the Hemiptera community. This index estimates the number of species expected in a sample based on the number of singleton and doubleton species collected and randomised over 50 iterations. The Chao-1 index estimated that a total of  $149 \pm 27$  phytophagous Hemiptera species should be found on *A. falcata* from all latitudes combined. This estimate is approximately 1.5 times the number of actual species sampled (98 species). The Chao-1 estimation curves for both mid-latitudes, Sydney ( $83 \pm 23$ ) and Grafton ( $78 \pm 18$ ), were continuing to rise and exhibited a high level of variation around the mean (Fig. 5b,c). In contrast, the most temperate latitude (Batemans Bay  $34 \pm 7$ ) and the most tropical latitude estimation curves (Gympie  $61 \pm 9$ ) were relatively closer to asymptoting (Fig. 5a,d).

### Assemblage structure

The number of Hemiptera species on *A. falcata* within the five feeding guilds (phloem hoppers, phloem bugs, mesophyll hoppers, mesophyll bugs and xylem hoppers) was compared among latitudes. Species from all guilds except xylem hoppers were found at all four latitudes: the single species of xylem hopper was collected from Batemans Bay. The total number of species within each guild did not significantly differ among latitudes (Fig. 2a — Guild).

We compared the similarity in guild structure between adjacent latitudes using two species diversity indices. For all guilds, the presence/absence measure (Sørensen Incidence similarity index) showed a directional increase in similarity between adjacent latitudes towards the tropics, but no such trend was found using Morisita–Horn similarity index (Fig. 6a). Phloem bugs were the only guild to exhibit a directional increase in similarity towards the tropics and only for the Sørensen Incidence index (Fig. 7a,b).

### Role of rare species

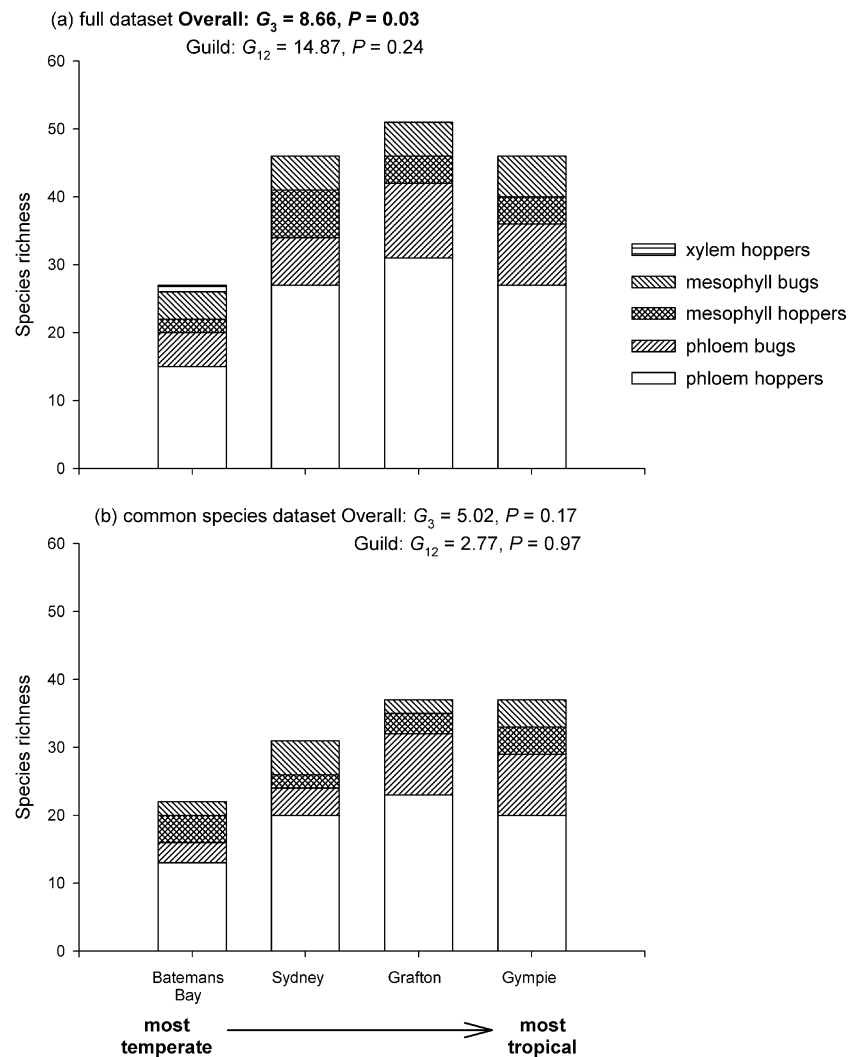
Rare species (those sampled on only one individual of *A. falcata* at one site at one sampling time) were excluded from the dataset

**Table 2** Abundance of phytophagous Hemiptera species collected from *Acacia falcata* at four different latitudes (Batemans Bay, Sydney, Grafton and Gympie). Component feeding guild and family associations are also included. Species are allocated into different *climate change response* groups according to their distributions between latitudes and host plant species — see Results: Assemblage Composition for details

Feeding Guilds	Climate Change Response Group	Family	Species name	Authority	Latitudes			
					Batemans Bay	Sydney	Grafton	Gympie
<b>Group 1</b>								
Phloem bug	Cosmopolitan	Psyllidae	<i>Acizzia</i> sp. 8		161	75	4277	190
Phloem bug	Cosmopolitan	Psyllidae	<i>Acizzia</i> sp. 1		38	5	15	51
Mesophyll hoppers	Cosmopolitan	Cicadellidae	<i>Zygina ipoloea</i>	(Kirkaldy)	2	50	32	7
Phloem hoppers	Cosmopolitan	Cicadellidae	<i>Recilia</i> sp. 1		6	36	4	8
Phloem hoppers	Cosmopolitan	Cicadellidae	<i>Diemoides</i> sp. 13		7	8	13	18
Phloem hoppers	Cosmopolitan	Cicadellidae	Cicad-001		1	20	1	13
Phloem hoppers	Cosmopolitan	Cicadellidae	<i>Balclutha chloe</i>	(Kirkaldy)	3	10	3	11
Phloem hoppers	Cosmopolitan	Cicadellidae	<i>Rubria</i> sp. 1		1	1	2	21
Mesophyll hoppers	Cosmopolitan	Cicadellidae	<i>Zygina sativae</i>	(Evans)	2	15	2	1
Phloem hoppers	Cosmopolitan	Cixiidae	Cixiid A. 10		9	2	4	5
<b>Group 2</b>								
Phloem hoppers	Cosmopolitan	Cicadellidae	<i>Recilia</i> sp. 4			30	12	15
Phloem hoppers	Cosmopolitan	Membracidae	<i>Sextius virescens</i>	(Farimaire)		5	28	26
Phloem bug	Cosmopolitan	Psyllidae	<i>Acizzia</i> sp. 6			3	17	5
Phloem bug	Cosmopolitan	Aphididae	Aphid-004			3	19	32
Phloem hoppers	Climate generalist	Cicadellidae	<i>Balclutha rubrostriata</i>	(Melichar)		2	2	2
Phloem hoppers	Climate generalist	Delphacidae	Delph-002			2	7	2
<b>Group 3</b>								
Phloem hoppers	Climate generalist	Delphacidae	Delph-001		3	2		1
Phloem bug	Cosmopolitan	Psyllidae	<i>Acizzia</i> sp. 2		19		198	68
Phloem hoppers	Cosmopolitan	Cixiidae	Derbidae sp. 1		4		4	9
Mesophyll bug	Climate generalist	Miridae	Phylinae sp. 1		1		6	1
Phloem hoppers	Cosmopolitan	Cicadellidae	Delto-010		1		8	6
<b>Group 4</b>								
Phloem hoppers	Cosmopolitan	Cicadellidae	<i>Linacephalus</i> sp. 1		5	5		
Mesophyll bug	Cosmopolitan	Thaumastocoridae	Thaum-001		2	1		
Phloem hoppers	Cosmopolitan	Delphacidae	Delph-005			9	1	
Phloem hoppers	Cosmopolitan	Cicadellidae	Delto-020			3	1	
Mesophyll bug	Climate generalist	Tingidae	Tingid-005			3	1	
Phloem hoppers	Climate generalist	Cicadellidae	Ledrini sp. 1			2	2	
Phloem hoppers	Climate generalist	Tropiduchidae	<i>Trypetimorpha wilsoni</i>	Huang & Bourgoin		1	1	
Phloem hoppers	Cosmopolitan	Meenoplidae	Meeno-001			1	2	
Phloem bug	Climate generalist	Aleyrodidae	Spondy-005				10	10
Phloem bug	Cosmopolitan	Psyllidae	<i>Acizzia</i> sp. 3				4	4
Phloem hoppers	Cosmopolitan	Cicadellidae	<i>Stirellus fatigandus</i>	Kirkaldy			1	3
Phloem hoppers	Cosmopolitan	Cicadellidae	Delto-016				1	2
Phloem hoppers	Cosmopolitan	Cicadellidae	<i>Hecalus australis</i>	(Evans)			1	2
Phloem hoppers	Cosmopolitan	Cixiidae	Cixiid-003				1	2
<b>Group 5</b>								
Phloem hoppers	Cosmopolitan	Eurybrachyidae	<i>Dardus abbreviatus</i>	(Guerin-Meneville)	3		1	
Phloem hoppers	Cosmopolitan	Cicadellidae	<i>Austrolopa brunensis</i>	Evans	3		2	
Mesophyll bug	Cosmopolitan	Tingidae	Tingid-001		11			1
Mesophyll hoppers	Cosmopolitan	Cicadellidae	Typhlo-005			25		1
Mesophyll hoppers	Climate generalist	Cicadellidae	Typhlo-002			1		1
Mesophyll bug	Cosmopolitan	Miridae	<i>Monalonimi</i> sp. 1			1		5
<b>Group 6</b>								
Phloem bug	Specialist	Coccidae	Coccoid-004		7			
Phloem hoppers	Specialist	Cicadellidae	Delto-022		3			
Mesophyll bug	Specialist	Miridae	Phylinae sp. 2		2			
Phloem bug	Specialist	Aleyrodidae	Alyrod-002		1			

Table 2 Continued

Feeding Guilds	Climate Change Response Group	Family	Species name	Authority	Latitudes			
					Batemans Bay	Sydney	Grafton	Gympie
Phloem hoppers	Specialist	Cicadellidae	Athy sp. 1		1			
Xylem hoppers	Specialist	Cicadellidae	<i>Ishidaella angustata</i>	(Evans)	1			
Phloem hoppers	Specialist	Meenoplidae	Meeno-002		1			
Phloem hoppers	Generalist feeder	Cicadellidae	<i>Horouta perparvus</i>	(Kirkaldy)		9		
Mesophyll hoppers	Generalist feeder	Cicadellidae	<i>Zygina melanogaster</i>	(Kirkaldy)		9		
Phloem bug	Generalist feeder	Coccidae	Coccoid-001			8		
Phloem hoppers	Generalist feeder	Delphacidae	Delph-003			5		
Phloem hoppers	Specialist	Cicadellidae	Delto-021			3		
Mesophyll bug	Specialist	Pentatomidae	Penta-001			2		
Phloem bug	Specialist	Aleyrodidae	Alyrod-005			1		
Phloem hoppers	Specialist	Cicadellidae	<i>Austrocercus</i> sp. 1			1		
Phloem hoppers	Specialist	Cicadellidae	Cicad-010			1		
Phloem hoppers	Generalist feeder	Cicadellidae	Cicad-049			1		
Phloem hoppers	Specialist	Cicadellidae	<i>Exitianus plebeius</i>			1		
Phloem hoppers	Specialist	Membracidae	Membr-002			1		
Mesophyll bug	Specialist	Lygaedidae	<i>Nysius vinitor</i>	Bergroth		1		
Phloem bug	Specialist	Pseudococcidae	Pseudo-001			1		
Phloem hoppers	Specialist	Cicadellidae	<i>Siphanta hebes</i>	(Walker)		1		
Phloem hoppers	Specialist	Cicadellidae	<i>Taslopa montana</i>	Evans		1		
Mesophyll bug	Specialist	Tingidae	Tingid-003			1		
Mesophyll hoppers	Specialist	Cicadellidae	Typhlo-010			1		
Mesophyll hoppers	Generalist feeder	Cicadellidae	<i>Zygina evansi</i>	(Ross)		1		
Mesophyll bug	Generalist feeder	Piesmatidae	Pies-001				6	
Phloem bug	Generalist feeder	Coccidae	Coccoid-002				12	
Phloem bug	Generalist feeder	Aleyrodidae	Alyrod-2				6	
Phloem hoppers	Specialist	Aphidae	Aphro-004				3	
Phloem bug	Specialist	Coccidae	Coccoid-003				3	
Mesophyll bug	Generalist feeder	Tingidae	Tingid-002				3	
Phloem hoppers	Specialist	Cicadellidae	Delto-018				2	
Phloem hoppers	Generalist feeder	Cicadellidae	<i>Batracomorpha</i> sp. 1				1	
Phloem hoppers	Specialist	Cicadellidae	<i>Rosopaella lopada</i>	Webb			1	
Phloem hoppers	Specialist	Cicadellidae	Delto-017				1	
Phloem hoppers	Specialist	Cicadellidae	Delto-019				1	
Phloem hoppers	Specialist	Cicadellidae	<i>Euacanthella palustris</i>	Evans			1	
Phloem hoppers	Specialist	Issidae	Issid-007				1	
Mesophyll bug	Specialist	Miridae	Mirid-003				1	
Phloem hoppers	Specialist	Cicadellidae	<i>Stirellus mitis</i>				1	
Mesophyll hoppers	Specialist	Cicadellidae	Typhlo-008				1	
Mesophyll hoppers	Specialist	Cicadellidae	Typhlo-009				1	
Phloem bug	Generalist feeder	Aleyrodidae	Alyrod-5					4
Phloem hoppers	Generalist feeder	Delphacidae	Delph-004					4
Phloem hoppers	Generalist feeder	Cicadellidae	Delto-023					4
Phloem hoppers	Specialist	Cixiidae	<i>Candicarina pulchra</i>	Loecker				2
Phloem bug	Generalist feeder	Alyrodidae	Spondy-003					2
Mesophyll bug	Generalist feeder	Tingidae	Tingid-004					2
Phloem hoppers	Generalist feeder	Cicadellidae	Delto-014					1
Phloem hoppers	Specialist	Cicadellidae	Delto-015					1
Phloem hoppers	Generalist feeder	Cicadellidae	<i>Diemoides</i> sp. 4					1
Phloem hoppers	Specialist	Fulgoridae	Fulgorid-002					1
Phloem hoppers	Specialist	Cicadellidae	Ledrid-001					1
Phloem hoppers	Specialist	Cicadellidae	Nirvan-001					1
Mesophyll bug	Specialist	Lygaedidae	Penta-005					1
Phloem hoppers	Generalist feeder	Cicadellidae	Ulopin-009					1
		<b>Number of species</b>			<b>27</b>	<b>47</b>	<b>51</b>	<b>45</b>
		<b>Number of unique species</b>			<b>7</b>	<b>19</b>	<b>17</b>	<b>14</b>
		<b>Number of singleton species</b>			<b>5</b>	<b>15</b>	<b>14</b>	<b>8</b>



**Figure 2** Species richness of phytophagous Hemiptera at four latitudes collected from *Acacia falcata*, (a) full dataset, (b) *common species* dataset. Component guild richness also included: phloem hopper, phloem bug, mesophyll bug and mesophyll hopper.  $G$ -test statistics also included (significant values in bold). See Methods for details.

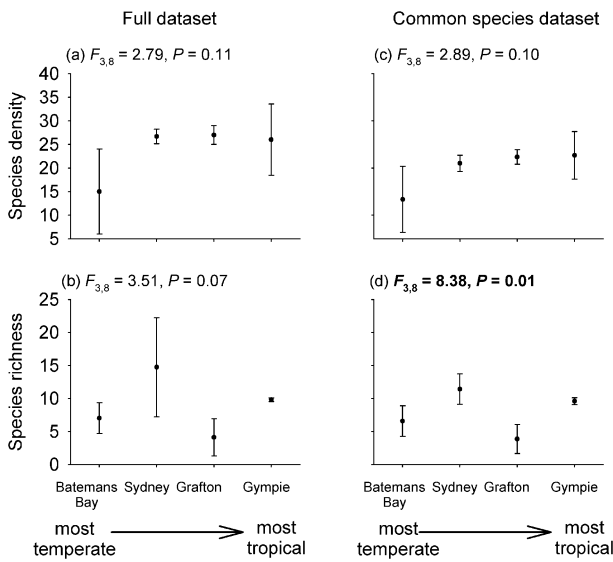
and the above analyses repeated. This *common species* dataset included 57 of the original 98 species sampled from *A. falcata*. The total number of species collected (sites pooled within latitudes) and species within guilds showed no significant differences in assemblage structure among latitudes on *A. falcata* (Fig. 2b). Average species density showed no significant differences among latitudes (Fig. 3c); however, average species richness was significantly lower at Grafton compared to Sydney and Gympie (Fig. 3d). Species accumulation curves and species estimation curves (Chao-1 index) were relatively lower and closer to asymptoting in the *common species* dataset (compared to the full dataset) for all latitudes (Figs 4 and 5). Similarity of communities among adjacent latitudes showed no decrease in similarity towards the tropics, both for the communities as a whole (Fig. 6) and when feeding guilds were assessed separately (Fig. 7); this was a similar result to that for communities in the full dataset.

### Potential responses to climate change

We classified the phytophagous Hemiptera collected from *A. falcata* into groups, depending on their distribution among latitudes

and whether or not they were found on other *Acacia* species (Table 2: *Climate Change Response Group*). These groups might be expected to respond differently to shifts in climatic zones. Species found at more than one latitude and on more than one *Acacia* species were classified as *cosmopolitan* ( $n = 32$ ). Species found only on *A. falcata* but at more than one latitude were classified as *climate generalists* ( $n = 9$ ). Species found on *A. falcata* and at least one other host plant species, but at only one latitude, were classified as *generalist feeders* ( $n = 19$ ). Species found at only one latitude and only on *A. falcata* were classified as *specialists* ( $n = 38$ ).

The relationship between the classification into groups based on potential climate change responses, and the classification into feeding guilds was also assessed. Phloem hoppers were the dominant guild in terms of the relative contribution of species to each of the four *climate change response* groups (Fig. 8). Pairwise comparisons of relative species contribution between the *cosmopolitan* and *climate generalists*, *generalist feeders* and *climatic generalists*, and *climatic generalists* and *specialists* were significantly different (Table 3a). *Climate generalists* had a higher proportion of mesophyll bugs and a lower proportion of phloem bugs compared to the other three response groups (Fig. 8a–d).



**Figure 3** Changes in phytophagous Hemiptera at four different latitudes collected from *Acacia falcata* from the full dataset, (a) species density (based on 70 samples per site), (b) species richness (based on 23 individuals per site); and from the *common species* dataset, (c) species density (based on 70 samples per site), and (d) species richness (based on 23 individuals per site). Mean ( $\pm$  SD) ( $n = 3$ ) per latitude shown.

When rare species were excluded, all pairwise comparisons of relative species contribution between *climate change response* groups were significantly different, except for that between the *generalist feeders* and *climate generalists* (Table 3b, Fig. 8e–h). Most of the rare species were phloem hoppers and their removal from the dataset led to changes in the proportional representation of all guilds in two *climate change response* groups: the *specialist* and *generalist feeders*.

**DISCUSSION**

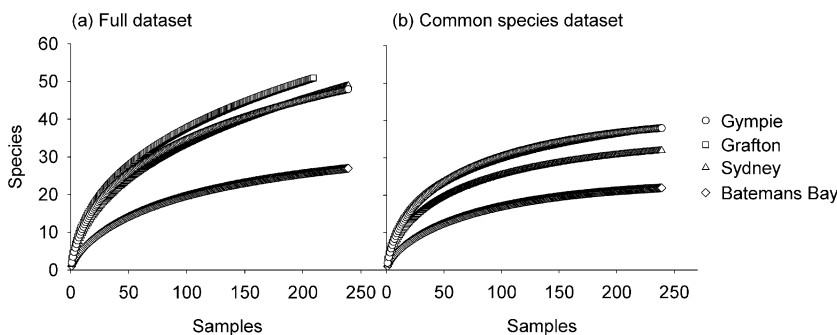
Anomalous warming over the past few decades has already affected the distribution and abundance of many species. Most notably, poleward shifts in geographical ranges of up to several hundred kilometres have been documented in a variety of taxa (e.g. Parmesan *et al.*, 1999; Walther *et al.*, 2002; Root *et al.*, 2003). Individualistic responses of species to current and future changes, especially

**Table 3** G-test pair-wise comparisons between *climate change response* group based on the relative species contribution of different feeding guilds (mesophyll bugs, mesophyll hoppers, phloem bugs, phloem hoppers and xylem hoppers). Significant comparisons are shown in bold

Pair-wise comparison	d.f.	G	P
(a) Full dataset			
Cosmopolitan vs. generalist feeders	4	5.29	0.26
<b>Cosmopolitan vs. climate generalists</b>	4	<b>14.99</b>	<b>&lt; 0.01</b>
Cosmopolitan vs. specialists	4	2.35	0.67
<b>Generalist feeders vs. climate generalists</b>	4	<b>11.17</b>	<b>0.02</b>
Generalist feeders vs. specialists	4	6.47	0.17
<b>Climate generalists vs. specialists</b>	4	<b>11.25</b>	<b>0.02</b>
(b) Common species dataset			
<b>Cosmopolitan vs. generalist feeders</b>	3	<b>15.55</b>	<b>&lt; 0.01</b>
<b>Cosmopolitan vs. climate generalists</b>	3	<b>14.99</b>	<b>&lt; 0.01</b>
<b>Cosmopolitan vs. specialists</b>	3	<b>23.00</b>	<b>&lt; 0.01</b>
Generalist feeders vs. climate generalists	3	4.66	0.20
<b>Generalist feeders vs. specialists</b>	3	<b>41.41</b>	<b>&lt; 0.01</b>
<b>Climate generalists vs. specialists</b>	3	<b>26.24</b>	<b>&lt; 0.01</b>

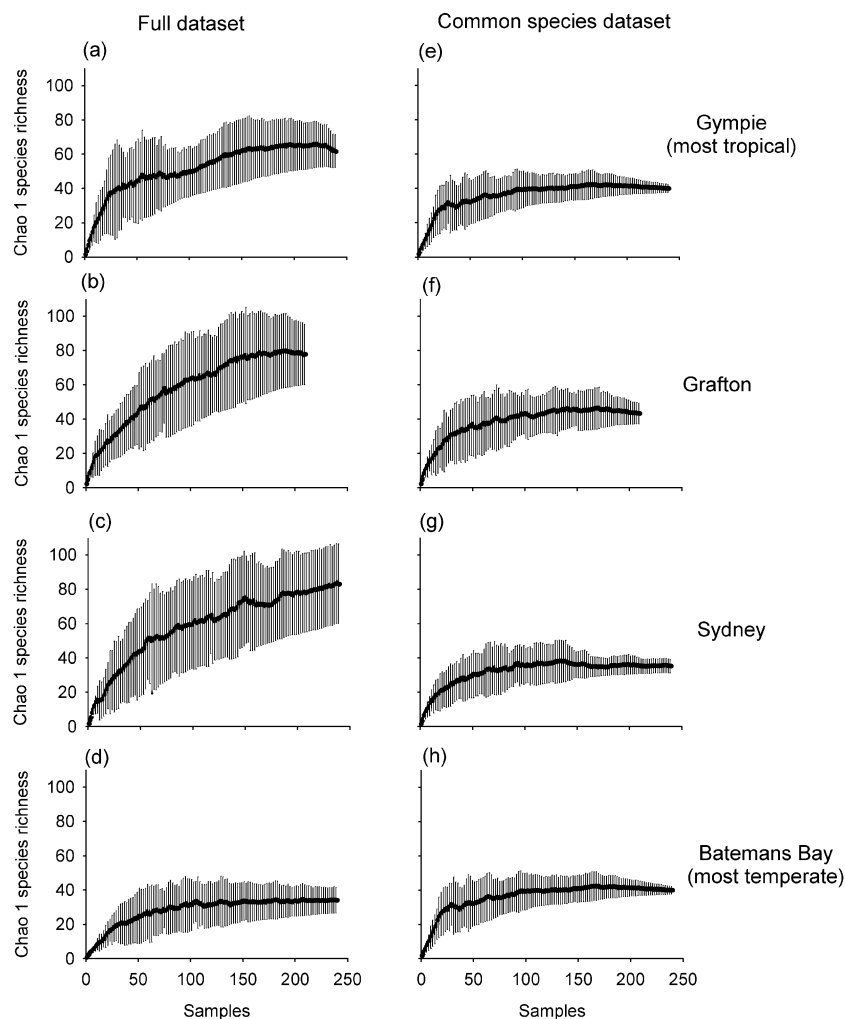
differential migration rates, will result in the progressive decoupling of present day ecological interactions, together with the formation of new relationships, and potentially lead to profound changes in the structure and composition of present-day communities (Hughes, 2000; Harrington *et al.*, 2001; Voigt *et al.*, 2003).

Various methods have been used to predict how species and communities might be affected by climate change, including bi-climatic modelling (Hughes *et al.*, 1996; Beaumont & Hughes, 2002), small-scale experiments in which factors such as temperature or CO<sub>2</sub> are manipulated (e.g. Davis *et al.*, 1998; Buse *et al.*, 1999; Johns & Hughes, 2002) and by examining current patterns of species distribution and community structure along existing climatic gradients (e.g. Hill & Hodkinson, 1992; Hodkinson *et al.*, 1999; Fleishman *et al.*, 2000). Voigt *et al.* (2003) assessed different trophic levels (producers, herbivores and carnivores) within grassland communities at two sites in Germany over two decades, and concluded that sensitivity to climate increases with higher trophic levels, leading to community destabilization. However the mechanisms behind these differences are still unclear and have not been tested in other communities, habitats and climate zones. In this study we used a latitudinal gradient as a surrogate for a changing climate, particularly a shift in temperature.



**Figure 4** Species accumulation curves for phytophagous Hemiptera at four latitudes (most temperate Batemans Bay, Sydney, Grafton, and most tropical Gympie) collected from *Acacia falcata*, (a) per sample collected for full dataset, (b) per sample collected for *common species* dataset.





**Figure 5** Chao-1 species estimation ( $\pm$  SD; 50 randomizations) at four latitudes (Batemans Bay, Sydney, Grafton, Gympie) for phytophagous Hemiptera collected from *Acacia falcata*. Figures a–d include all species; figures e–h include *common species*. See Methods for details.

By identifying patterns in community structure along this gradient, in which habitat type and altitude were consistent, and by classifying species into *climate change response* groups in terms of their distribution among hosts and latitudes, we can hypothesize about their possible responses to future climate change.

### Trends among latitudes

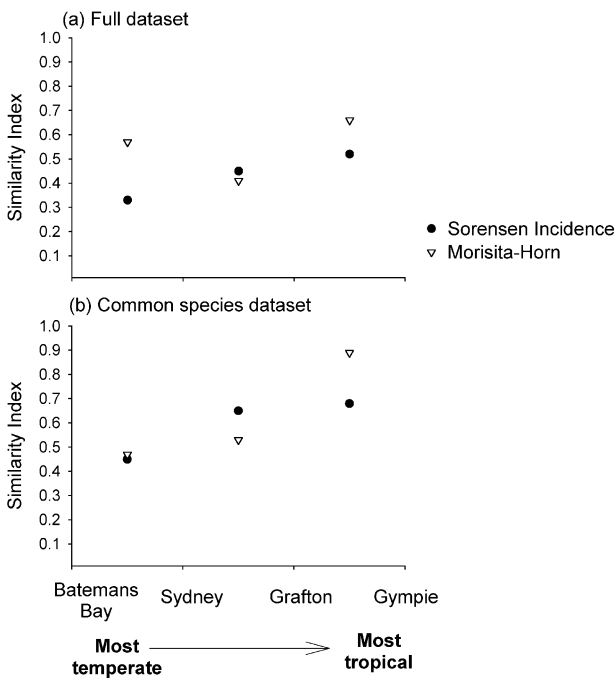
We found no evidence for a progressive increase in total species richness of phytophagous Hemiptera along the latitudinal gradient, although the most temperate latitude, Batemans Bay, had a significantly lower number of species collected than the three more tropical latitudes. If we assume that phytophagous Hemiptera will be able to migrate polewards with a changing climate, this result indicates that the number of species at most latitudes over the coming decades may be similar to that found today, except at the more temperate latitudes where species richness may increase.

Since we did not sample the entire community of phytophagous Hemiptera (as indicated by the non-asymptoting species sample curve and high variance surrounding the Chao-1 species estimator curve), different trends may have emerged with a more

extensive sampling period and a variety of sampling techniques, especially from the three more tropical latitudes.

### Assemblage similarity between adjacent latitudes

We expected that the similarity of phytophagous Hemiptera assemblages between adjacent latitudes would decrease towards the tropics (Gaston & Williams, 1996; Rosenzweig & Sandlin, 1997; Koleff *et al.*, 2003). This expectation was not realized. When species composition within feeding guilds was compared between adjacent latitudes, the trends seen depended on the particular guild assessed. Assemblages of phloem bugs had a high level of similarity between adjacent latitudes. Assemblages of mesophyll hoppers had a higher similarity between adjacent tropical latitudes compared to the more temperate latitudes. Assemblages of phloem hoppers also became more similar among adjacent latitudes towards the tropics, but this trend was more pronounced when the Morisita–Horn index was used. Assemblages of mesophyll bugs generally had low similarity among adjacent latitudes. Only one adult species of xylem hopper (*Ishidaella angusta*: Cicadellinae) was found on *Acacia falcata* and only at Batemans Bay. Therefore changes in Hemiptera species



**Figure 6** Pair-wise comparison of similarity of phytophagous Hemiptera communities between adjacent latitudes (Batemans Bay and Sydney, Sydney and Grafton, Grafton and Gympie) collected from *Acacia falcata* using two different similarity indices: Sørensen incidence, and Morisita–Horn, (a) all species, (b) *common species* dataset. Higher numbers indicate relatively higher similarity in composition among latitudes.

composition on *A. falcata* caused by a warming climate will be difficult to predict.

**Role of rare species**

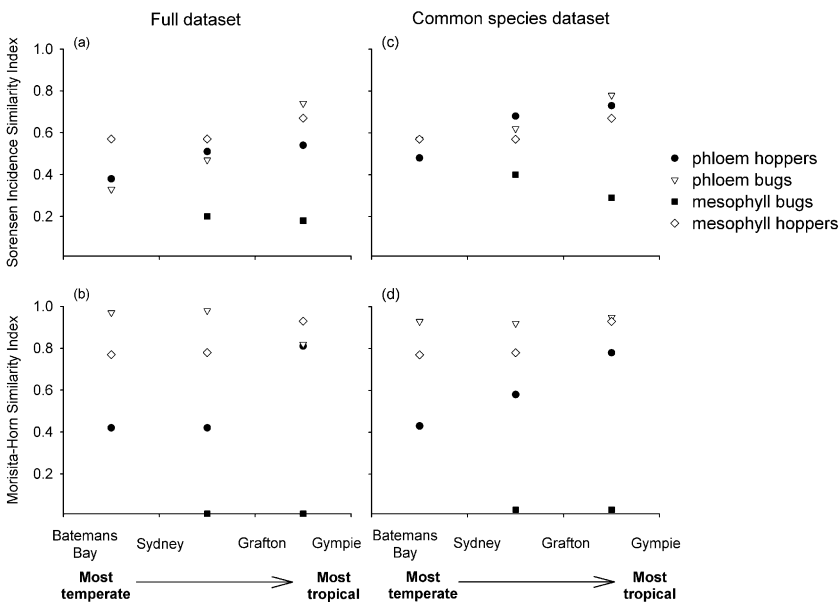
Rare species contributed 42% (41 out of 98 species) of the total community collected from *A. falcata*. Such a large proportion of

species being rare is not uncommon: 45% ( $n = 1050$  species) of insect herbivores were identified as rare on 30 species of trees and shrubs in New Guinea (Novotny & Basset, 2000), and 61% ( $n = 80$ ) of a fish community in the Bristol Channel, UK, were also classified as rare (Magurran & Henderson, 2003). Wagner (2000) found 42% of canopy-dwelling beetle species ( $n = 1433$  morphospecies) were singletons collected from four tree species in Uganda, and Lucky *et al.* (2002) found that up to 62% of arboreal carabid beetles in a Western Amazonian rainforest were also singletons ( $n = 318$  species). The proportion of rare species in the herbivorous beetle communities collected at the same sites as the Hemiptera was also high (55%) (Andrew & Hughes, 2004).

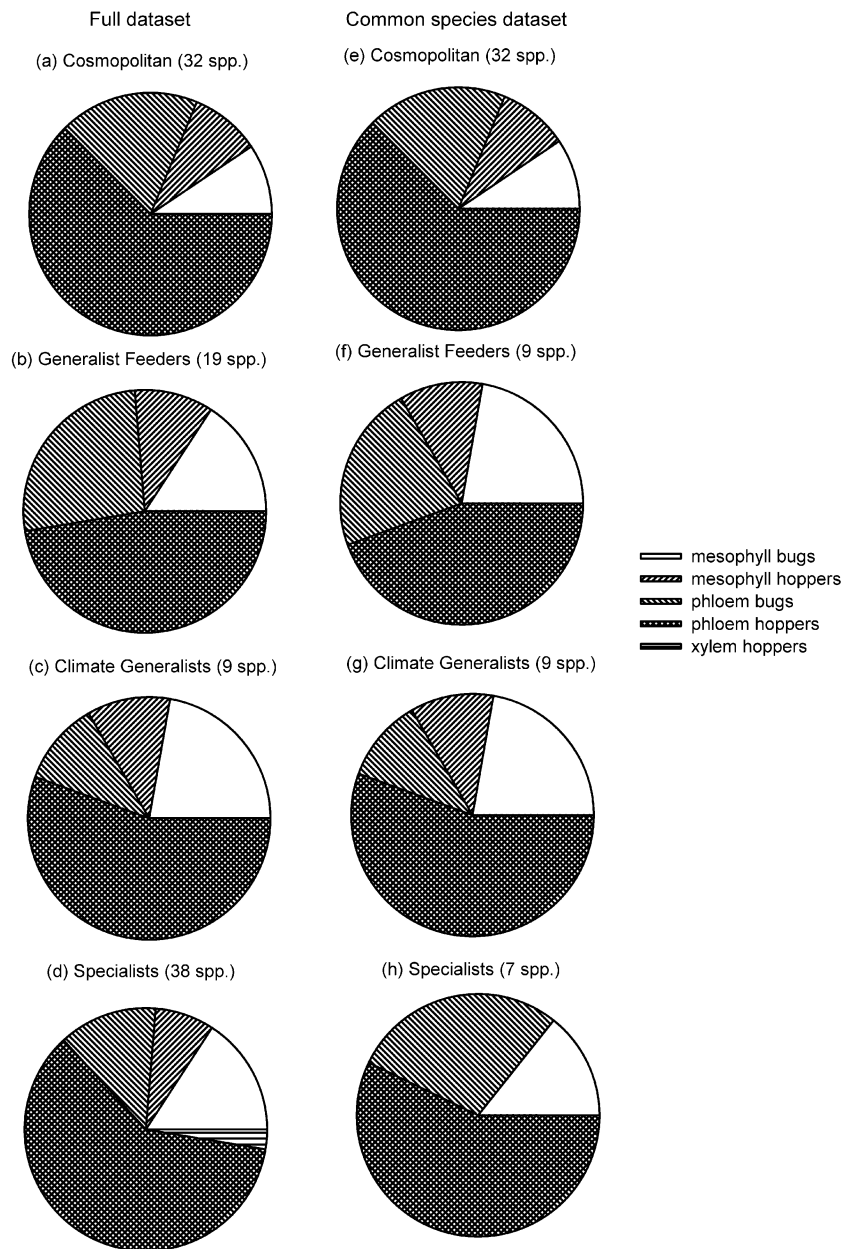
The exclusion of rare species from the dataset essentially strengthened the patterns discerned in the full dataset. There was a significantly lower average species richness at Grafton compared to the adjacent latitudes north (Gympie) and south (Sydney). This can be primarily attributed to the relative high abundance of one species at the Grafton sites, a psyllid (*Acizzia* sp. 8) which reduced the number of species collected per 23 individuals (the measure of species richness per site) at these sites. Rare species contributed a large component of the species richness at all latitudes, but their contribution was not greater at the tropical latitudes. This result is in contrast to that for spider assemblages found by Coddington *et al.* (1996) and for the herbivorous beetle assemblages we sampled at the same sites (Andrew & Hughes, 2004).

**Potential impacts of climate change**

Many species have already responded to the anomalous warming of the past few decades by shifting their distributions to higher latitudes or elevations (Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Root *et al.*, 2003). As the climate continues to warm, species with a wide latitudinal distribution that already encompass a range of temperatures, such as the focal host plant in this study (*A. falcata*), may be better able to cope with changing climate than species with more restricted ranges (Bale *et al.*, 2002). These host species



**Figure 7** Pair-wise comparison of similarity of phytophagous Hemiptera guilds between adjacent latitudes (Batemans Bay and Sydney, Sydney and Grafton, Grafton and Gympie) collected from *Acacia falcata*. Guilds include phloem hoppers, phloem bugs, mesophyll bugs and mesophyll hoppers, (a) full data set compared using Sørensen Incidence similarity index, (b) full data set compared using the Morisita–Horn similarity index, (c) *common species* dataset compared using Sørensen Incidence similarity index, and (d) *common species* dataset compared using Morisita–Horn similarity index. Higher numbers indicate relatively higher similarity in composition among adjacent latitudes.



**Figure 8** Relative contribution of phytophagous Hemiptera to five feeding guilds (mesophyll bugs, mesophyll hoppers, phloem bugs, phloem hoppers, xylem hoppers) in each of four *climate change response* groups (*cosmopolitan*, *climate generalists*, *generalist feeders*, *specialists*). Figure shown for the full dataset (a–d) and the *common species* dataset (e–h). The number of species per classification is shown in parentheses.

in turn will support a diverse herbivore fauna consisting of feeding guilds that may display various responses to a changing climate.

We hypothesize that the future responses of phytophagous insects, such as the Hemiptera described in this study, can potentially be predicted by understanding their current distribution, both geographically and across potential hosts. It should be noted that these are preliminary guild designations in relation to climate change and have been developed based on the assumption that: (i) increasing temperature will be the most important climatic impact on species distributions; (ii) all phytophagous species feeding on the host species were sampled; and (iii) if an insect was collected on a host species, it was also feeding on that plant. This study did not exhaustively sample all Hemiptera species on the host plants nor did we perform feeding trials to determine host plant specificity. With more information available,

many species may be placed into different climate change classifications (e.g. specialists may be found at more than one latitude or on more than one host species). However at this stage, we believe that it is useful to begin developing such classifications, even if our information about these assemblages is incomplete.

In this study, species that were found only on *A. falcata* at one latitude, the *specialists*, comprised 38% of the total sampled. These species may potentially be the most vulnerable to local extinction because they not only have to migrate, but have to do so in conjunction with their host species. Thirty-three percent of species were found at more than one latitude and on more than one host plant, the *cosmopolitan* species. These species may be more resistant to a changing climate and host plant range, either being able to survive *in-situ* or be able to shift to alternative hosts as they migrate to higher latitudes. Species found at only one latitude,

but on *A. falcata* and at least one other host plant species (the *generalist feeders*), comprised 20% of the community. These species will have the flexibility to move between hosts, but may nonetheless be forced to shift geographical range. Nine percent of species were found only on *A. falcata* but at more than one latitude (the *climate generalists*). These species may be constrained by their host plants' responses to a changing climate, and will only colonize new areas once the host plant has successfully established.

We have previously described a similar classification for the herbivorous Coleoptera collected at the same sites (Andrew & Hughes, 2004a). Both the *generalist feeders* and *climate generalists* are in similar proportions for the Hemiptera and the Coleoptera (*generalist feeders*: 20% vs. 21% and *climate generalists*: 9% vs. 7%, respectively). However the Hemiptera have a higher proportion of species in the *cosmopolitan* category compared to Coleoptera (33% vs. 20%, respectively) and a lower proportion of species in the *specialist* group (38% vs. 50%, respectively). This suggests that phytophagous Hemiptera, on the whole, may be better able to adapt to a changing climate than the phytophagous Coleoptera.

In terms of feeding guilds and climate change responses, a consistent community structure was found between the *cosmopolitan*, *generalist feeders* and *specialist* response groups. The *climate generalists* (those species found only on *A. falcata* but at one or more latitudes) exhibited a significantly different community structure to the other three groups. Only nine species were classified as *climate generalists*, compared with between 19 and 38 species for the three other response groups, suggesting that the different structure of this group may be due to small sample size. For all four climate response groups, the phloem hopper guild was the dominant group and had the highest number of species.

Rare species are especially vulnerable to being displaced by a rapidly changing climate. When rare species were excluded from the analysis, most pair-wise comparisons of feeding guild structure between *climate change response* groups were significantly different. This was primarily driven by the reduction of phloem hopper species in the *generalist feeders* and *specialists* response groups. This indicates that if rare species are not able to adapt to a changing climate and one particular guild, such as the phloem hoppers, contains the bulk of rare species, community structure will be significantly modified.

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## BIOSKETCHES

**Nigel Andrew** was recently appointed lecturer in entomology at the University of New England, Armidale, NSW. His research focuses on insect herbivory and insect community structure along environmental gradients, on *Acacia* host plant species and climate change.

**Lesley Hughes** is interested in the impacts of future climate change on species and communities, and particularly the impacts on plant–insect interactions. She is currently working on the impacts of elevated CO<sub>2</sub> and temperature on insect herbivory and spatial patterns of insect diversity.