

Arthropod community structure along a latitudinal gradient: Implications for future impacts of climate change

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Abstract The structure of free-living arthropod communities on the foliage of *Acacia falcata* was assessed along an extensive latitudinal gradient in eastern Australia. We hypothesized that abundance and biomass of arthropods within feeding groups would increase from temperate latitudes towards the tropics. We also hypothesized that the ratio of carnivores to herbivores would be consistent along the latitudinal gradient. Three sites at each of four latitudes, spanning 9° and 1150 km (Batemans Bay, Sydney, Grafton, Gympie in Australia), were sampled every season for 2 years, using pyrethrum knockdown. Abundance and biomass (based on dry weight) of arthropods within eight feeding groups were measured. The relative size of the feeding groups, and the ratio of carnivores to herbivores were then compared among latitudes and seasons. We found no consistent north to south (tropical to temperate) change in feeding group structure in terms of abundance. A weak latitudinal trend was evident for predator biomass, consisting of a reduction from north to south, but no significant trends in biomass for other feeding groups were found. Relative abundance and relative biomass of both carnivores and herbivores, as well as the ratio of carnivores to herbivores were consistent among latitudes. Finally, we compared a subset of these data to arthropod communities found on congeneric host species at individual sites along the latitudinal gradient. Overall, 68% of comparisons showed no significant differences in abundance or biomass within different feeding groups between host plants and among latitudes. We conclude that arthropod communities show consistencies among latitudes and between congeneric host species, in terms of feeding group and trophic structure. These results have implications for predicting the impacts of future climate change on arthropod communities.

Key words: *Acacia*, arthropod, Australia, body size, carnivore, community structure, guild, herbivore, temperature, trophic level.

INTRODUCTION

Decreasing species diversity from tropical to temperate latitudes is a well known phenomenon in a diverse range of organisms (for recent reviews see Rosenzweig 1995; Gaston 2000; Krebs 2001; Hillebrand 2004). Little is known, however, as to whether communities are organized in fundamentally different ways at different latitudes. The few available contrasts of community structure at different latitudes have either compared only one temperate with one tropical community (e.g. macro-invertebrate communities in coastal marine turtle grass meadows; Heck 1979), or have made broad, global comparisons using a range of techniques, sample numbers and seasons (e.g. arthropod-depauperate bracken communities (Compton *et al.* 1989; Shuter & Westoby 1992; Lawton *et al.* 1993), or have compared arthropods on different host

plant species on different continents (e.g. Moran & Southwood 1982; Stork 1987).

Understanding whether and how community structure changes with latitude will become an increasingly important issue as climate zones shift in the future. Global temperatures have increased approximately $0.6 \pm 0.2^\circ\text{C}$ over the past century and global climate models project increases of $1.4\text{--}5.8^\circ\text{C}$ by 2100 (IPCC 2001). There is already evidence that many species have undergone poleward latitudinal shifts in response to recent warming (Johnson 1994; Parmesan 1996; Parmesan *et al.* 1999; Thomas & Lennon 1999; Root *et al.* 2003) and profound changes in community composition and structure are expected in the future (Hughes 2000). The impact of changing precipitation regimes is also an important determinant of insect distributions, although predictions for precipitation changes over the coming century are highly variable. In Australia, for example, they could potentially decrease by up to 40% or increase by up to 60% depending on the region (CSIRO 2001). Understanding how the structure of current communities varies along latitudinal and other environmental gradients will be an important predictive tool for assessing how

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these communities will respond to climatic changes in the future.

Our study focused on arthropod communities occurring on the foliage of a single host plant species, *Acacia falcata*, along an extensive latitudinal gradient in eastern Australia. By comparing arthropods on a single host species we were able to control for habitat differences, other than climate, as much as possible. As ectotherms, arthropods are highly sensitive to temperature (Dobson 1996; Speight *et al.* 1999) and future climatic change is expected to modify their behaviour, population dynamics, interactions with other species, and geographical range (Harrington *et al.* 1999; Ayres & Lombardero 2000; Harrington *et al.* 2001; Bale *et al.* 2002; Beaumont & Hughes 2002). Plants and their associated arthropod faunas comprise more than 79% of all described species (Strong *et al.* 1984; Price 2002), and interactions between these taxa comprise a significant proportion of total, global, species interactions (Price 2002). Altitudinal and latitudinal gradients have been used to predict future impacts of climate change in a few insect communities, with the variation in temperature along the gradient used as a surrogate for changing climate (Whittaker & Tribe 1996, 1998; Bird & Hodkinson 1999; Fielding *et al.* 1999; Hodkinson *et al.* 1999; Progar & Schowalter 2002). With the exception of the study by Progar and Schowalter (2002), however, these studies have examined the response of either a single arthropod species, or of a few species within a single genus.

Predicting how feeding group structure may change along a latitudinal gradient is difficult, as previous studies have only assessed changes in species richness, rather than changes in biomass or species abundance within functional groups. In plant communities, total biomass increases as species number increases (Tilman & Lehman 2001; Tilman *et al.* 2001). As there is a general increase in species diversity towards the tropics in many taxa (Dobzhansky 1950; Fischer 1960; Wolda 1988; Rohde 1992) we firstly hypothesize that total biomass of individual feeding groups will also increase from temperate zones towards the tropics. Second, it is generally accepted that rates of herbivory increase towards the tropics (Coley & Barone 1996). Our second hypothesis therefore is that absolute abundance and biomass within groups of herbivores may also increase in this direction. Our third hypothesis concerns the trophic structure of communities along the gradient. Natural enemies contribute up to 50% of herbivore mortality (Cornell *et al.* 1998), making them an important determinant of herbivore population size. The role of predators and parasitoids at different latitudes can vary according to herbivore life stage, but overall they are important for reducing herbivore populations at all latitudes (Hawkins *et al.* 1997; Cornell *et al.* 1998). Price (1991) has hypothesized that the probability of estab-

lishing biotic interactions between carnivore and herbivore trophic levels is similar between temperate and tropical latitudes. We extend this hypothesis to predict that the ratio of carnivores to herbivores (in terms of abundance and biomass) will be consistent along the latitudinal gradient.

We also compared arthropod feeding group structure between pairs of *Acacia* species at seven sites within latitudes, and among latitudes on *A. falcata* using a subset of the main data set. In plant-associated arthropod communities, host plant characteristics, such as architecture, density, geographical range, leaf form, seasonal development, taxonomic isolation and the levels of anti-herbivore defences, are key determinants of insect species richness and abundance, especially for phytophagous insects (Lawton & Schröder 1977, 1978; Strong 1979; Kennedy & Southwood 1984; Strong *et al.* 1984; Leather 1986; McMillin & Wagner 1998). Studies at both tropical and temperate sites have shown that arthropod community structure varies both within individual host plant species and between congeneric hosts. Variability in arthropod community structure has been shown, for example, by surveys of the arthropod fauna on bracken (*Pteridium aquilinum*) worldwide (Lawton *et al.* 1993), host genera within the family *Cynareae* in Europe (Lawton & Schröder 1978), *Shorea* spp. in Borneo, Malaysia (Stork 1987), eucalypts in the Australian alpine zone (Morrow 1977), and on trees within the genera *Betula*, *Buddleia*, *Quercus*, *Robinia* and *Salix* in Britain and South Africa (Moran & Southwood 1982).

The focus of this article is on the abundance and biomass of arthropods within eight feeding groups collected from foliage. In addition to measuring abundance and biomass (both absolute and relative) of the individual groups, we examined the ratio of carnivores to herbivores. Herbivorous insects may have serious impacts on climatically stressed plants in the future, and carnivores play an essential role in controlling populations of herbivores (Landsberg & Stafford Smith 1992; Gomez & Zamora 1994; Cornell *et al.* 1998; Price 2003).

METHODS

Sampling

Acacia falcata was selected as the focal host plant species because it has an extensive latitudinal range along the east-coast of Australia. The coastal distribution of *A. falcata* extends from south of Moruya, NSW (35°53'S) to Tairo, Qld (25°45'S) a distance of 1150 km (Fig. 1). While *A. falcata* also occurs inland to Bundara, NSW (30°17'S), NSW and Atherton, North Queensland (17°22'S), only the coastal populations of *A. falcata* were surveyed so that altitude (<150 m) was kept approximately constant among sites.

Four latitudes were selected, spanning almost the entire coastal range of *A. falcata* (Fig. 1). From south to north these were Batemans Bay (35°40'S), Sydney (33°36'S), Grafton (29°44'S) and Gympie (26°7'S) in Australia. At each latitude, three replicate sites were selected where *A. falcata* was abundant (>100 individual plants/100 m²), with plants up to 4 m in height. *Acacia falcata* was a conspicuous species at all sites, co-occurring with other understorey *Acacia*, *Bursaria*, *Dillwynia* and *Macrozamia* species. *Eucalyptus* and *Corymbia* species dominated the canopy at all sites. The distances between sites within a latitude ranged from 2 to 80 km. Average annual temperature differed by 4.3°C from the northernmost to southernmost sites (Table 1, ANOVA, $P < 0.001$). We used this natural temperature gradient between latitudes as a surrogate for a changing climate. The coefficient of variation (CV) of mean annual temperature (calculated from

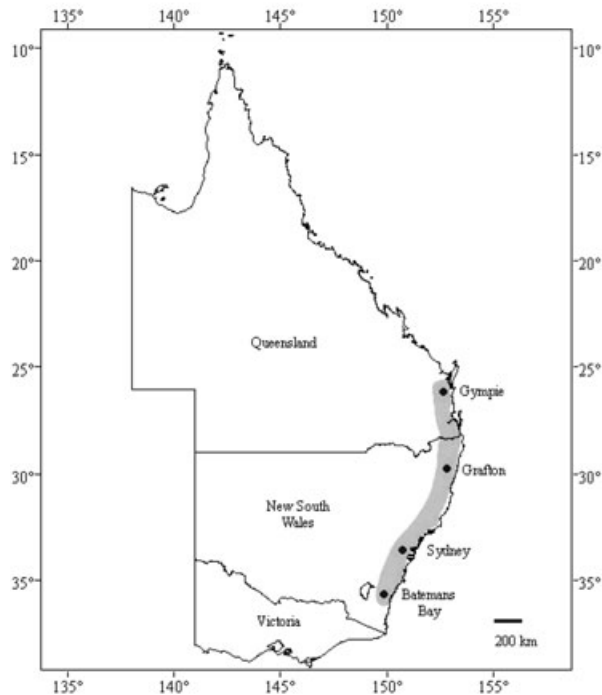


Fig. 1. Map of the coastal distribution of *Acacia falcata* and the latitudes sampled in this study.

daily temperatures over a whole year), a measurement of seasonality, varied significantly among latitudes (ANOVA, $P = 0.0008$), but there was no distinct trend along the latitudinal gradient. Annual precipitation was significantly lower at Sydney compared with the three other latitudes (ANOVA, $P = 0.0129$) but also showed no distinct seasonal trend among latitudes. Coefficient of variation of precipitation was significantly higher at Gympie (ANOVA, $P < 0.0001$) compared with the other three latitudes. All climatic variables were generated using BIOCLIM 5.0 (CRES, Canberra, Australia; Busby 1991).

Arthropod collections were made seasonally from November 1999 (spring) to August 2001 (winter), a total of eight collections. At each site, 10 *A. falcata* plants were haphazardly selected for sampling at each time. A total of 930 plants were sampled. No samples were taken from the three sites at Grafton in February 2001 (summer samples) because of the regional flooding. Plants sampled in previous collections were not resampled for at least 6 months. Four 50 cm × 30 cm collecting trays were placed beneath each shrub before it was sprayed with a 0.6% pyrethrum/water solution using a hand-pumped backpack mister. Plants were sprayed until all leaves were wet and were then left for 30 min before arthropods were collected from the trays. This sampling method targeted free-living, foliage-inhabiting arthropods. The consistent sampling area under each plant standardized the samples among plants, sites, latitudes and seasons. All arthropods falling on the trays were transferred to 70% ethanol for storage. All samples were collected between 7.00 and 11.00 AM, to take advantage of the calmer weather that generally occurs in the morning, and to minimize the collection of mobile arthropods flying through the site (also known as tourists) (Stork & Hammond 1997). We did not attempt to sample the entire arthropod fauna on the host plant species, but used the technique as a standardized method to compare communities. A complete inventory of all species occupying all available habitats, using a variety of collection techniques, was outside the scope of this project. We assumed that the pyrethrum sampling technique had a similar ability to collect free-living arthropods among latitudes and host plant species.

Table 1. Average ($n = 3$ sites) annual temperature, average temperature coefficient of variation (CV – a measure of seasonality), average annual precipitation and average precipitation CV among the four latitudes (Batemans Bay, Sydney, Grafton, Gympie) where arthropods were sampled

Latitude	Annual temperature (°C)	Temp CV	Annual precipitation (mm)	Precipitation CV
Gympie	20.20 (0.35)	1.32 (0.02)	1104.33 (123.87)	49.67 (1.15)
Grafton	18.33 (0.06)	1.38 (0.08)	1117.67 (137.14)	35.67 (2.89)
Sydney	16.87 (0.06)	1.50 (0.04)	837.67 (14.52)	30.67 (1.53)
Batemans Bay	15.87 (0.75)	1.23 (0.01)	1144.67 (33.56)	31.67 (0.58)

Standard deviations are in parentheses.

Arthropod sorting and groupings

Arthropods collected from *A. falcata* were placed into eight groups based on feeding method (Root 1973; Moran & Southwood 1982; Simberloff & Dayan 1991) and taxonomic resolution. The groups were predators, parasites, leaf chewers, sapsuckers, fungivores, scavengers, ants and 'various' (Table 2). If a feeding group could be assigned at the order level, the group was not further subdivided. This was the case for spiders (Araneae), caterpillars (Lepidoptera), grasshoppers (Orthoptera), thrips (Thysanoptera), springtails (Collembola), psocids (Psocoptera) and cockroaches (Blattodea). For orders containing a range of feeding groups, further subdivision and identification were carried out. Individuals in the order Hemiptera were divided into three suborders: Auchenorrhyncha (hoppers), Sternorrhyncha (soft-bodied suckers) and Heteroptera (true bugs). The order Coleoptera (beetles) was identified to family. Feeding habits assigned to the different beetle families were based on Lawrence and Britton (1991) and Lawrence *et al.* (2000). The Hymenoptera were separated into parasitic wasps (Apocrita) and ants (Formicinae). Ants were considered a separate group because they include a variety of functional roles (Andersen 1995) and have a high abundance and biomass at the level of taxonomic resolution used (Davidson *et al.* 2003). The scavenger group included dead wood feeders. Flies (Diptera), mites (Acari), and true bugs (Heteroptera), were placed in an artificial 'various' group as they included a variety of feeding habits at the level of taxonomic resolution used but were generally low in abundance and biomass. No wood-borers, root-feeders or seed-predators were collected with the collection technique used, and no rearing of parasitoids from hosts was attempted.

Biomass measurements were made for each feeding group. Individuals in each group were sorted into seven size classes: < 1 mm, 1 mm < 2 mm, 2 mm < 5 mm, 5 mm < 10 mm, 10 mm < 20 mm, 20 mm < 50 mm and ≥ 50 mm. Ten randomly chosen individuals from each size class in each group were dried at 80°C for 24 h and weighed. An average biomass for each size class within each group was then calculated by multiplying the average biomass by the number of individuals.

Data analysis

Abundance and biomass of the arthropod community were compared among latitudes, among sites within latitudes, and among seasons, using a three-way nested Multivariate Analysis of Variance (MANOVA). These values were $\log_2(x + 1)$ transformed to satisfy the assumption of normality. Pillai's Trace was the test

Table 2. Arthropod taxonomic and feeding groups used in analyses

Feeding group	Name (taxonomic level)
Predator	Spiders (Araneae)
	Ladybirds (Coleoptera: Coccinellidae)
	Rove Beetles (Coleoptera: Staphylinidae)
	Carabids (Coleoptera: Carabidae)
	Scydmaenidae (Coleoptera)
Parasites	Corylophidae (Coleoptera)
	Parasitic Wasps (Hymenoptera: Parasitica)
Leaf Chewer	Leaf Beetles (Coleoptera: Chrysomeloidea)
	Weevils (Coleoptera: Curculionoidea)
	Grasshoppers (Orthoptera)
	Cantharids (Coleoptera: Cantharidae)
	Oedemeridae (Coleoptera)
	Cerambycidae (Coleoptera)
	Buprestidae (Coleoptera)
	Larvae (Coleoptera; Lepidoptera)
	Scirtidae (Coleoptera)
	Sapsucker
Psyllids, etc. (Hemiptera: Sternorrhyncha)	
Thrips (Thysanoptera)	
Fungivore	Leioididae (Coleoptera)
	Phloeotrichidae (Coleoptera)
	Click beetles (Coleoptera: Elateridae)
	Melandryidae (Coleoptera)
	Endomychidae (Coleoptera)
	Erotylidae (Coleoptera)
	Latrididae (Coleoptera)
	Ciidae (Coleoptera)
	Laemophloeidae (Coleoptera)
	Mycetophagidae (Coleoptera)
Scavenger	Anthribidae (Coleoptera)
	Tenebrionids (Coleoptera: Tenebrionidae)
	Clambids (Coleoptera: Clambidae)
	Nitidulidae (Coleoptera)
	Melyridae (Coleoptera)
	Mordellidae (Coleoptera)
	Salpingidae (Coleoptera)
	Springtails (Collembola)
	Bark Lice (Psocoptera)
	Cockroaches (Blattodea)
	Ptiliids (Coleoptera: Ptiliidae)
	Slater (Isopoda)
	Aderids (Coleoptera: Aderidae)
	Anobiids (Coleoptera: Anobiidae)
	Phalacrids (Coleoptera: Phalacridae)
Anthicids (Coleoptera: Anthicidae)	
Scarabs (Coleoptera: Scarabidae)	
Ants	Ants (Hymenoptera: Formicinae)
Various	True Bugs (Hemiptera: Heteroptera)
	Mites (Acari)
	Flies (Diptera)

statistic used to assess overall community differences (Tabachnick & Fidell 2001; Quinn & Keough 2002). In addition, each feeding group was compared among latitudes, sites within latitudes and seasons using

three-way nested Analysis of Variance (ANOVA) (Huberty & Morris 1989; McDonald *et al.* 2002; Quinn & Keough 2002). If the effect of a factor was significant in the ANOVA ($P < 0.05$), a *post hoc* Scheffe's test was used to test for differences among groups. All statistical analyses were performed using Datadesk® 6.1 (Data Description Inc., Ithaca, NY, USA, Velleman 1997).

Changes in both absolute and relative abundance and biomass of carnivores (predators and parasitoids combined) and herbivores (leaf chewers and sapsuckers combined) along the latitudinal gradient were compared using the same statistical methods. The ratio of carnivores to herbivores was also compared among latitudes.

Comparisons between host plants

We also sampled co-occurring phyllodinous acacia species at seven of the *A. falcata* sites, resulting in seven pairwise host species comparisons (Table 3). All *Acacia* species sampled were in the subgenus *Phyllodineae* nested within two sections: section *Phyllodinae* (*A. falcata* Willd., *Acacia binervata* DC., and *Acacia stricta* (Andrews) Willd.) and section *Fuliflorae* (*Acacia concurrens* Pedley, *Acacia longifolia* (Andrews) Willd. ssp. *longifolia* and *Acacia leiocalyx* (Domin) (Pedley).

Four arthropod collections were used, consisting of two summer (1999 and 2000) and two winter (1999 and 2000) samples. At each site, five plants of each host plant species were haphazardly selected. The data for *A. falcata* were randomly chosen from the larger data set such that comparisons between species had the same sample size.

We compared community structure between congeneric host species within sites (seven host plant comparisons). Data from the two summer and two winter collections were pooled because we were interested in overall community structure among latitudes and between host species, rather than in seasonal variation. Differences in arthropod community composition within sites were analysed using one-way MANOVAs on abundance and biomass. Abundance and biomass values were $\log_2(x + 1)$ transformed to satisfy the assumptions of normality. Comparisons were site-specific because not all *Acacia* species occurred at each site (Table 3). We used Pillai's Trace to assess overall community differences (based on feeding groups) between factors (Tabachnick & Fidell 2001; Quinn & Keough 2002). \log_2 abundance and \log_2 biomass within individual feeding groups were compared between plant species using one-way ANOVAs (Huberty & Morris 1989; McDonald *et al.* 2002; Quinn & Keough 2002). Comparisons of \log_2 abundance and \log_2 biomass (absolute and relative) of carnivores (predators and parasitoids combined) and

Table 3. *Acacia* species sampled at different latitudes and sites

Latitude	Focal host plant	Congeneric host species
Gympie – 26°7'S		
Site 1	<i>A. falcata</i>	<i>A. concurrens</i>
Site 2	<i>A. falcata</i>	<i>A. concurrens</i>
Site 3	<i>A. falcata</i>	
Grafton – 29°44'S		
Site 1	<i>A. falcata</i>	
Site 2	<i>A. falcata</i>	
Site 3	<i>A. falcata</i>	
Sydney – 33°36'S		
Site 1	<i>A. falcata</i>	<i>A. longifolia</i>
Site 2	<i>A. falcata</i>	<i>A. leiocalyx</i>
Site 3	<i>A. falcata</i>	
Batemans Bay – 35°40'S		
Site 1	<i>A. falcata</i>	<i>A. binervata</i>
Site 2	<i>A. falcata</i>	<i>A. longifolia</i>
Site 3	<i>A. falcata</i>	<i>A. stricta</i>

herbivores (leaf-chewers and sapsuckers combined) between different host plants within sites, were made using the same statistical methods. All data analyses were performed using Datadesk® 6.1 (Velleman 1997).

RESULTS

A total of 37 918 individual arthropods was collected from *A. falcata* from all sites over the eight sampling periods, comprising 12 827 sapsuckers, 10 927 scavengers, 4184 ants, 3458 parasites, 3344 predators, 2120 leaf chewers, 797 'various' feeders and 281 fungivores.

Overall, there was no north to south trend in total abundance of arthropods associated with *A. falcata*, and no significant differences in arthropod abundance among latitudes (Table 4a: Latitude – MANOVA). The abundance of individuals within three of the eight groups changed significantly among latitudes: predators (Fig. 2a), sapsuckers (Fig. 2d) and scavengers (Fig. 2g), although again there was no consistent north to south trend (Table 4a: Latitude). The remaining five groups showed no significant difference among latitudes in terms of abundance.

The estimated biomass of invertebrates collected was 24 898 mg, comprising 9848 mg of leaf chewers, 5052 mg of predators, 4261 mg of sapsuckers, 2570 mg of ants, 1454 mg of scavengers, 777 mg of fungivores, 585 mg of parasites and 351 mg of 'various' feeders.

As for total abundance, total biomass did not change consistently from north to south along the gradient (Table 4b: Latitude – MANOVA). Of the eight feeding groups, only predators showed a significant latitudinal

Table 4. Summary table of three-way MANOVA for (a) log₂ abundance and (b) log₂ biomass of overall arthropod community, and three-way ANOVAs for the component feeding groups (predator, parasite, chewer, sapsucker, fungivore, ant, scavenger, and 'various') associated with *Acacia falcata* at four latitudes (Batemans Bay, Sydney, Grafton, Gympie) and four seasons (Spring, Summer, Autumn, Winter; replicate years pooled)

Factor	d.f.	(a) Abundance		(b) Biomass	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Latitude					
MANOVA	24, 9	2.32	0.0950	1.64	0.2200
Predator	3, 8	6.75	0.0139	6.86	0.0133
Parasite	3, 8	3.02	0.0939	2.47	0.1364
Chewer	3, 8	0.97	0.4510	1.76	0.2331
Sapsucker	3, 8	6.59	0.0149	1.99	0.1942
Fungivore	3, 8	0.18	0.9056	0.64	0.6079
Ant	3, 8	0.56	0.6533	0.58	0.6438
Scavenger	3, 8	11.25	<0.0001	17.16	<0.0001
Various	3, 8	1.29	0.3427	1.20	0.3709
Season					
MANOVA	24, 57	9.89	<0.0001	8.15	<0.0001
Predator	3, 24	7.30	<0.0001	7.50	<0.0001
Parasite	3, 24	21.52	<0.0001	11.50	<0.0001
Chewer	3, 24	5.10	0.0071	7.13	<0.0001
Sapsucker	3, 24	6.95	<0.0001	1.56	0.2258
Fungivore	3, 24	14.44	<0.0001	5.69	<0.0001
Ant	3, 24	18.20	<0.0001	16.46	<0.0001
Scavenger	3, 24	22.93	<0.0001	22.34	<0.0001
Various	3, 24	6.87	<0.0001	3.85	0.0221
Season × Latitude					
MANOVA	72, 192	1.43	0.0287	1.47	0.0196
Predator	9, 24	2.20	0.0593	2.24	0.0552
Parasite	9, 24	1.01	0.4610	0.65	0.7438
Chewer	9, 24	4.19	0.0024	5.36	0.0005
Sapsucker	9, 24	5.45	<0.0001	2.87	0.0188
Fungivore	9, 24	1.57	0.1808	0.95	0.5019
Ant	9, 24	1.03	0.4487	1.24	0.3177
Scavenger	9, 24	1.29	0.2905	1.27	0.3027
Various	9, 24	1.00	0.4672	1.18	0.3508
Site (Latitude)					
MANOVA	64, 7056	5.65	<0.0001	3.76	<0.0001
Predator	8, 882	2.92	<0.0001	2.42	0.0136
Parasite	8, 882	4.26	<0.0001	4.90	<0.0001
Chewer	8, 882	6.79	<0.0001	3.13	<0.0001
Sapsucker	8, 882	13.40	<0.0001	8.05	<0.0001
Fungivore	8, 882	4.57	<0.0001	2.65	0.0071
Ant	8, 882	13.12	<0.0001	9.08	<0.0001
Scavenger	8, 882	5.30	<0.0001	1.86	0.0632
Various	8, 882	2.97	<0.0001	0.91	0.5095
Season × Site(Latitude)					
MANOVA	192, 7056	3.39	<0.0001	2.82	<0.0001
Predator	24, 882	2.14	<0.0001	2.00	<0.0001
Parasite	24, 882	2.52	<0.0001	3.87	<0.0001
Chewer	24, 882	3.25	<0.0001	1.53	0.0510
Sapsucker	24, 882	6.89	<0.0001	3.99	<0.0001
Fungivore	24, 882	2.67	<0.0001	2.04	<0.0001
Ant	24, 882	4.55	<0.0001	3.37	<0.0001
Scavenger	24, 882	5.74	<0.0001	4.41	<0.0001
Various	24, 882	2.66	<0.0001	1.94	<0.0001

Significant sources of variation are in bold.

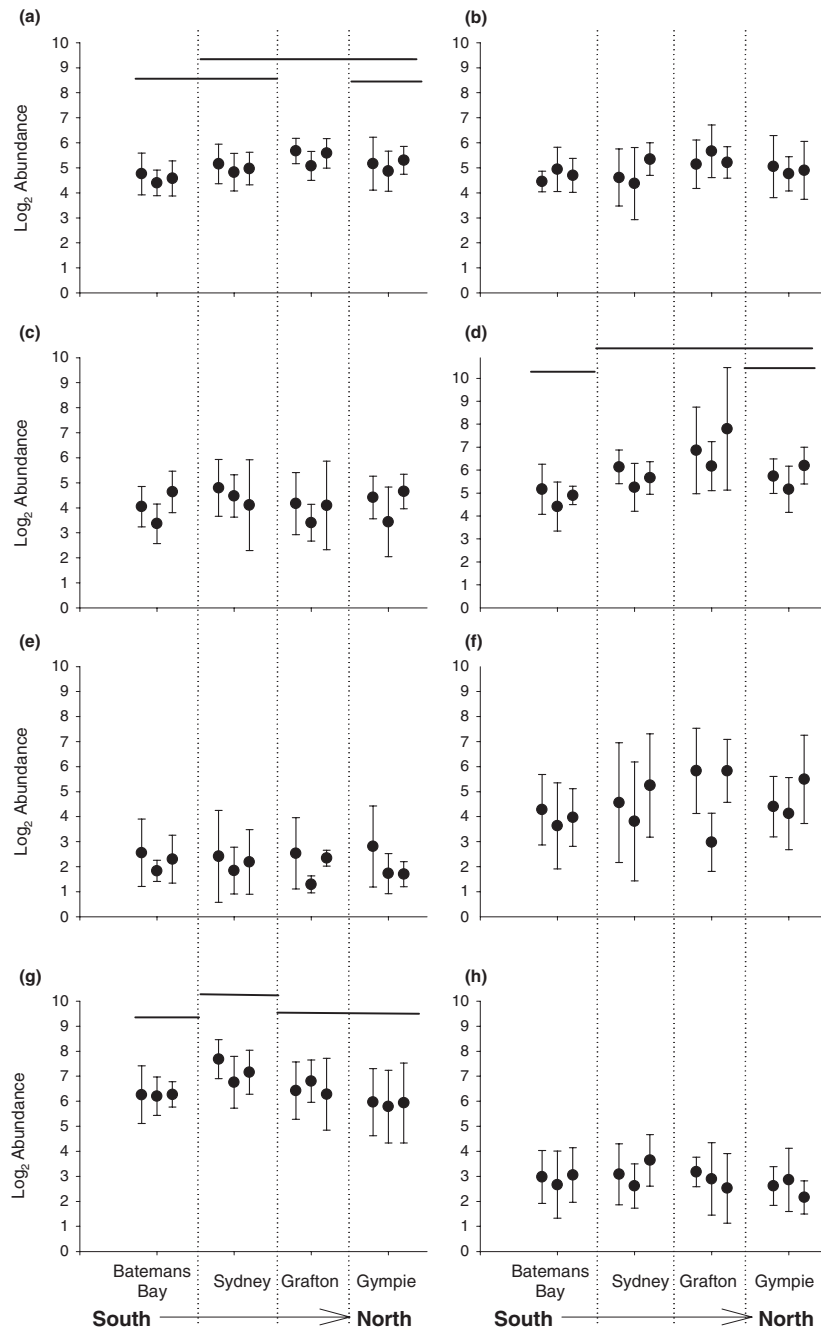


Fig. 2. Abundance of arthropod feeding groups (a) predator, (b) parasite, (c) chewer, (d) sapsucker, (e) fungivore, (f) ants, (g) scavenger and (h) various associated with *Acacia falcata* at each of three sites within four latitudes (Batemans Bay, Sydney, Grafton, Gympie). Mean \log_2 abundance + 1 (\pm SD) within each of eight seasons shown. Results of Scheffe's *post hoc* test are included where appropriate.

trend, which consisted of a reduction from north to south (Table 4b: Latitude – Predator, Fig. 3a). Scavenger biomass also varied significantly among different latitudes (Table 4b: Latitude – Scavenger, Fig. 3g) but not in a directional way. No significant differences in biomass along the gradient were found for the six remaining feeding groups (Table 4b).

Ratio of carnivores to herbivores along the latitudinal gradient

There were significant differences in carnivore abundance (predators and parasitoids) among latitudes, with Grafton (the second most northerly latitude), having more carnivores than Sydney and Batemans

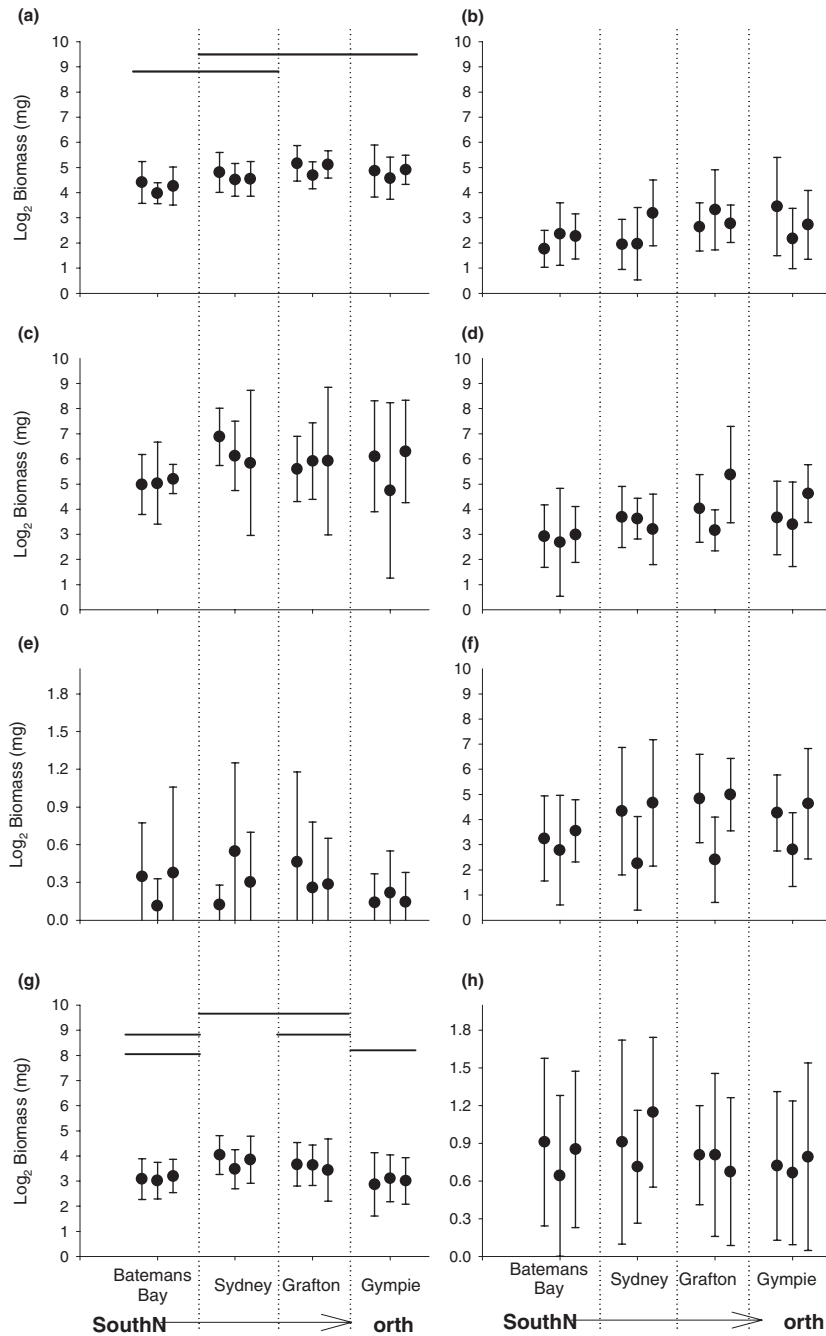


Fig. 3. Biomass of arthropod feeding groups (a) predator, (b) parasite, (c) chewer, (d) sapsucker, (e) fungivore, (f) ants, (g) scavenger and (h) various associated with *Acacia falcata* at each of three sites within four latitudes (Batemans Bay, Sydney, Grafton, Gympie). Mean log_2 biomass + 1 (\pm SD) within each of eight seasons shown. Results of Scheffe's *post hoc* test are included where appropriate.

Bay (Table 5a). Herbivores (chewers and sapsuckers) were also more abundant at Grafton compared with Batemans Bay (Table 5b), but neither carnivores nor herbivores showed a north to south trend in abundance.

Carnivore biomass displayed a latitudinal trend, being significantly higher in Gympie (northern-most site) and Grafton compared with Batemans Bay

(southern-most site) (Table 5c). Herbivore biomass showed no differences among latitudes (Table 5d).

Overall, carnivores comprised 28.2% of the total abundance of the arthropod community sampled, and 34.5% to the total biomass. Herbivores contributed 28.5% of the total arthropod community abundance, and 32.1% of total biomass. Among latitudes, the

Table 5. Summary table of three-way ANOVA for (a) log₂ carnivore abundance (b) log₂ herbivore abundance (c) log₂ carnivore biomass (d) log₂ herbivore biomass (e) carnivore relative abundance (f) herbivore relative abundance (g) carnivore relative biomass (h) herbivore relative biomass (i) ratio carnivore/herbivore abundance, and (j) ratio carnivore/herbivore biomass, associated with *Acacia falcata* at four latitudes along its latitudinal range (Batemans Bay, Sydney, Grafton, Gympie) and during four seasons (Spring, Summer, Autumn, Winter; replicate years pooled)

Factor	d.f.	(a) Carnivore abundance		(b) Herbivore abundance	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Latitude	3, 8	12.029	0.0025	4.5661	0.0381
Season	3, 24	15.701	<0.0001	5.9012	0.0036
Latitude × Season	9, 24	1.2371	0.3195	5.8424	0.0003
Site(Latitude)	8, 882	2.2717	0.0209	13.397	<0.0001
Site(Latitude) × Season	24, 882	2.6998	<0.0001	6.8343	<0.0001
		(c) Carnivore biomass		(d) Herbivore biomass	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Latitude	3, 8	11.124	0.0032	1.511	0.2843
Season	3, 24	9.2346	0.0003	2.3787	0.0948
Latitude × Season	9, 24	1.619	0.1660	3.9264	0.0035
Site(Latitude)	8, 882	1.9362	0.0517	5.3382	<0.0001
Site(Latitude) × Season	24, 882	2.1871	0.0009	2.8794	<0.0001
		(e) Carnivore relative abundance		(f) Herbivore relative abundance	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Latitude	3, 8	3.2845	0.0793	2.6408	0.1210
Season	3, 24	20.663	<0.0001	22.693	<0.0001
Latitude × Season	9, 24	1.7549	0.1307	4.1667	0.0025
Site(Latitude)	8, 882	3.3592	0.0008	4.8498	<0.0001
Site(Latitude) × Season	24, 882	0.78492	0.7588	2.5139	<0.0001
		(g) Carnivore relative biomass		(h) Herbivore relative biomass	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Latitude	3, 8	1.3872	0.3153	0.38559	0.7665
Season	3, 24	2.5538	0.0792	4.4259	0.0130
Latitude × Season	9, 24	2.1021	0.0708	2.5109	0.0347
Site(Latitude)	8, 882	3.285	0.0011	4.7864	<0.0001
Site(Latitude) × Season	24, 882	1.5734	0.0396	2.5075	<0.0001
		(i) Ratio carnivore/herbivore abundance		(j) Ratio carnivore/herbivore biomass	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Latitude	3, 8	0.86469	0.4979	1.2011	0.3697
Season	3, 24	12.325	<0.0001	2.6214	0.0739
Latitude × Season	9, 24	1.8216	0.1161	1.1620	0.3614
Site(Latitude)	8, 882	3.0113	0.0024	0.6434	0.7415
Site(Latitude) × Season	24, 882	1.6479	0.0262	1.1188	0.3148

Significant sources of variation are in bold.

relative abundance and relative biomass of both carnivores and herbivores was consistent (Table 5e–h). The ratio of carnivores to herbivores in terms of absolute abundance and biomass was also consistent among latitudes (approximately 1 : 1, Table 5i,j; Fig. 4).

Seasonal variation of arthropod community structure along the latitudinal gradient

Batemans Bay, the most southerly (temperate) latitude, had the most seasonally consistent feeding group

structure in terms of abundance. Grafton, the second most northerly latitude, was the most variable because of a spike in abundance of sapsuckers in winter at two of the three sites sampled (Fig. 2d). Gympie, the most northerly (tropical) latitude, had the highest abundance and biomass of total arthropods in autumn, but the lowest in winter. It should be noted that the seasonal variability in abundance and biomass (as indicated by the large standard deviation around the means for many sites), reduced the power to determine differences between means among latitudes, for some groups.

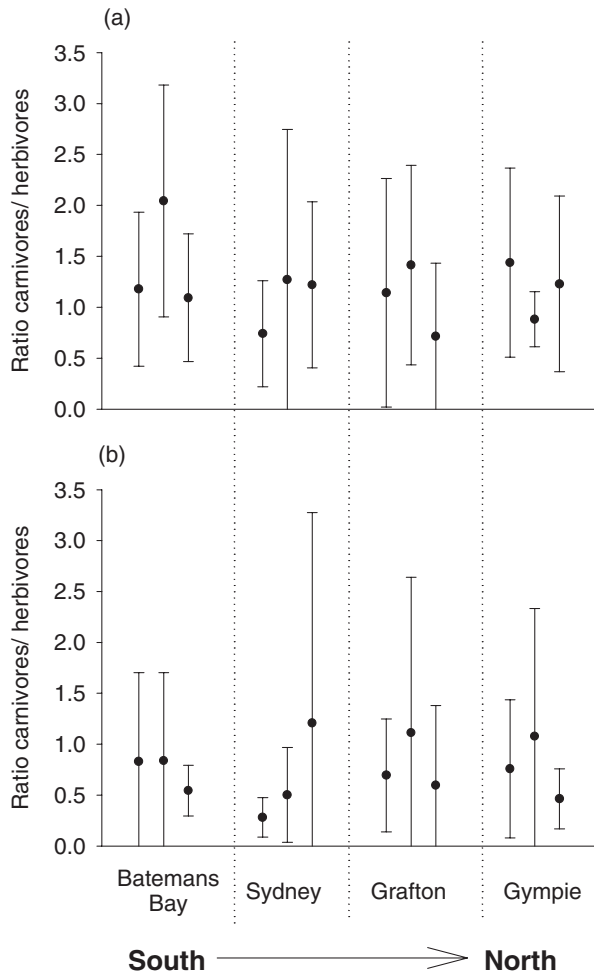


Fig. 4. Ratio of carnivores to herbivores associated with *Acacia falcata* at each of three sites within four latitudes (Batemans Bay, Sydney, Grafton, Gympie). (a) mean abundance (\pm SD) and (b) mean biomass (\pm SD) within each of eight seasons shown.

Comparisons between host species

Overall community structure, in terms of arthropod abundance within groups, was significantly different between host plant species for six of the seven host species comparisons (MANOVA $P < 0.05$; Table 6a). No particular group, however, was consistently different across all comparisons (Table 6a). Host species phylogeny appeared to play little role in explaining differences in feeding group structure. When host species within the same *Acacia* subsection were compared, 50% of comparisons showed significant differences, compared with 47% for comparisons between host plants in different subsections.

Community structure, in terms of biomass, was generally more consistent than that for abundance, with only two of the seven host species comparisons showing significant differences (Table 6b: MANOVA).

As for abundance, no particular group was consistently different across all seven host-species comparisons (Table 6b). Host plant phylogeny had no influence on the significant differences between host species: 12.5% of feeding group differences, in terms of biomass, were between host species within the same section, compared with 20% of comparisons for host species in different sections.

The absolute abundance and biomass of carnivores varied significantly for most host species comparisons (five of the seven comparisons for abundance and six of the seven comparisons for biomass) (Table 7a,b: carnivores). The absolute abundance and biomass of herbivores also varied significantly between host species (five of the seven comparisons for abundance and four of the seven comparisons for biomass).

The relative abundance and biomass of carnivores was consistent between all host species comparisons, except for relative biomass at Gympie Site 1 (Table 7c,d). For herbivores, significant differences occurred between host species for three (out of seven) comparisons for both abundance and biomass.

The ratios of carnivores to herbivores were generally consistent between host species comparisons within sites, although ratios between sites ranged from an average abundance of 0.9 : 1–2.7 : 1 and an average biomass of 0.8 : 1–16 : 1 (Table 7e). The only exception was Site 1 within the most tropical latitude (Gympie) where carnivore: herbivore biomass ratios were significantly higher on *A. concurrens* (average ratio 3 : 1) compared with *A. falcata* (average ratio 0.8 : 1) (Table 7e).

DISCUSSION

This study provides an assessment of arthropod community structure, in terms of abundance and biomass within feeding groups, along an extensive latitudinal distribution of a single host plant species within comparable habitat types, and from temperate to subtropical climatic zones and among congeneric host species within sites. This information can be used to assess some of the potential impacts of climate change on arthropod communities at a regional level. Species richness patterns of herbivore species, including Coleoptera (Andrew & Hughes 2004), Hemiptera (Andrew & Hughes in press) and other taxa, as well as herbivory (Andrew & Hughes 2005) along the latitudinal gradient, will be examined in other articles.

Arthropod community structure along the latitudinal gradient

We expected that abundance and biomass of arthropods within feeding groups would be greater towards the tropical end of the latitudinal gradient. Contrary to this expectation, we found no distinct north to

Table 6. Summary table of one-way MANOVA for (a) log₂ absolute abundance and (b) log₂ absolute biomass of the overall community (MANOVA), and component feeding groups (predator, parasite, leaf-chewer, sapsucker, fungivore, ant, scavenger, and ‘ various’) for seven *Acacia* host species comparisons at individual sites

Factor	d.f.	Batemans Bay			Sydney			Gympie							
		Site 1 <i>A. falcata</i> vs. <i>A. stricta</i>	Site 2 <i>A. falcata</i> vs. <i>A. bimerzata</i>	Site 3 <i>A. falcata</i> vs. <i>A. longifolia</i>	Site 1 <i>A. falcata</i> vs. <i>A. longifolia</i>	Site 2 <i>A. falcata</i> vs. <i>A. tetocalyx</i>	Site 1 <i>A. falcata</i> vs. <i>A. concurrens</i>	Site 2 <i>A. falcata</i> vs. <i>A. concurrens</i>							
		F-ratio	P	F-ratio	P	F-ratio	P	F-ratio	P						
(a) Absolute abundance															
MANOVA	8, 25	2.28	0.0599	6.39	0.0002	2.93	0.0187	18.70	<0.0001	37.80	<0.0001	5.19	0.0007	2.40	0.0447
Predators	1, 32	3.86	0.0581	28.04	<0.0001	14.13	0.0007	13.37	0.0009	3.92	0.0572	10.58	0.0027	0.68	0.4166
Parasites	1, 32	7.86	0.0085	0.38	0.5420	1.80	0.1886	26.42	<0.0001	17.42	0.0002	1.04	0.3147	2.03	0.1636
Leaf-chewers	1, 32	1.13	0.2966	19.22	0.0001	1.61	0.2137	28.38	<0.0001	4.67	0.039	27.21	<0.0001	1.28	0.2668
Sapsuckers	1, 32	14.14	0.0007	0.03	0.8705	2.95	0.0957	7.44	0.0103	8.86	0.0058	2.57	0.1190	0.09	0.7608
Fungivores	1, 32	0.33	0.5877	7.35	0.0107	0.73	0.4001	1.00	0.3248	284.55	<0.0001	0.35	0.5586	2.57	0.1188
Ants	1, 32	0.96	0.3345	24.73	<0.0001	8.48	0.0065	21.76	<0.0001	0.00	0.9785	0.73	0.3983	12.44	0.0013
Scavengers	1, 32	2.88	0.0995	16.92	0.0003	0.01	0.9229	0.70	0.4105	6.01	0.0204	4.50	0.0417	1.57	0.2192
Various	1, 32	0.64	0.4292	6.74	0.0141	1.54	0.2237	21.30	<0.0001	0.15	0.7039	8.21	0.0073	9.45	0.0043
(b) Absolute biomass															
MANOVA	8, 25	0.41	0.4095	0.98	0.4718	2.29	0.0539	1.54	0.1941	41.00	<0.0001	5.25	0.0006	1.49	0.2115
Predators	1, 32	0.03	0.8628	1.04	0.3149	4.27	0.047	1.64	0.2092	2.86	0.1013	0.00	0.9860	3.41	0.0739
Parasites	1, 32	0.28	0.6012	2.49	0.1246	0.09	0.7678	1.23	0.2755	2.36	0.1352	5.67	0.0234	0.31	0.5840
Leaf-chewers	1, 32	2.10	0.1568	0.02	0.8827	6.34	0.017	1.11	0.2993	0.34	0.5638	3.21	0.0828	1.38	0.2490
Sapsuckers	1, 32	2.65	0.1136	3.46	0.0722	1.18	0.2847	0.23	0.6332	2.09	0.1594	0.73	0.4008	1.57	0.2186
Fungivores	1, 32	0.07	0.7958	4.74	0.037	1.82	0.1872	2.09	0.1578	44.12	<0.0001	12.20	0.0014	0.99	0.3264
Ants	1, 32	9.74	0.0038	0.06	0.8010	1.60	0.2155	1.94	0.1731	14.60	0.0006	0.04	0.8349	0.60	0.4433
Scavengers	1, 32	0.20	0.6581	0.33	0.5677	0.30	0.5871	5.56	0.0247	2.44	0.1291	1.16	0.2890	0.30	0.5856
Various	1, 32	0.51	0.4816	1.20	0.2823	0.00	0.9453	0.13	0.7206	278.51	<0.0001	0.17	0.6827	1.76	0.1935

Sampling times (two summer, two winter) pooled. Significant sources of variation are in bold.

Table 7. Summary table of one-way ANOVA for carnivore and herbivore (a) log₂ absolute abundance (b) log₂ absolute biomass (c) relative abundance (d) relative biomass; and (e) ratio carnivore/herbivore abundance and biomass. Analyses based on seven *Acacia* host species comparisons at individual sites

Factor	d.f.	Batemans Bay				Sydney				Gympie					
		Site 1		Site 2		Site 1		Site 2		Site 1		Site 2			
		<i>A. stricta</i> F-ratio	<i>P</i>	<i>A. falcata</i> vs. <i>A. bimerata</i> F-ratio	<i>P</i>	<i>A. falcata</i> vs. <i>A. longifolia</i> F-ratio	<i>P</i>	<i>A. falcata</i> vs. <i>A. leiocalyx</i> F-ratio	<i>P</i>	<i>A. falcata</i> vs. <i>A. concurrens</i> F-ratio	<i>P</i>	<i>A. falcata</i> vs. <i>A. concurrens</i> F-ratio	<i>P</i>		
(a) Absolute abundance															
Carnivores	1,31	13.63	0.0008	7.02	0.0124	13.31	0.0009	22.21	<0.0001	11.79	0.0018	4.09	0.0519	0.69	0.4129
Herbivores	1,31	9.31	0.0046	17.36	0.0002	3.73	0.0624	17.79	0.0002	10.85	0.0026	13.92	0.0008	0.13	0.7171
(b) Absolute biomass															
Carnivores	1,31	6.41	0.0164	25.26	<0.0001	24.55	<0.0001	17.21	0.0002	16.76	0.0003	7.00	0.0126	0.35	0.5555
Herbivores	1,31	4.03	0.0532	9.11	0.005	1.60	0.2150	13.37	0.0009	26.23	<0.0001	21.16	<0.0001	1.58	0.2182
(c) Relative abundance															
Carnivores	1,31	0.03	0.8750	0.11	0.7424	2.21	0.1465	2.40	0.1313	0.06	0.8116	0.14	0.7085	1.14	0.2929
Herbivores	1,31	4.25	0.0472	1.36	0.2526	0.01	0.9399	4.57	0.0402	0.39	0.5366	1.77	0.1936	5.03	0.032
(d) Relative biomass															
Carnivores	1,31	1.07	0.3094	0.1	0.7533	0.51	0.4809	0.61	0.4397	0.95	0.3375	8.73	0.0058	0.25	0.6205
Herbivores	1,31	1.28	0.2662	0.16	0.6962	0.00	0.9844	5.42	0.0263	7.12	0.0123	9.99	0.0034	3.27	0.0798
(e) Ratio carn/herb															
Abundance	1,31	0.07	0.7931	0.96	0.3351	0.00	0.9592	0.84	0.3660	1.56	0.2221	2.97	0.0948	0.69	0.4129
Biomass	1,31	0.54	0.4669	0.76	0.3891	0.82	0.3731	0.13	0.7194	2.00	0.1664	5.15	0.0302	0.03	0.8534

Sampling times (two summer, two winter) pooled. Significant sources of variation are in bold.

south gradient in abundance or biomass either for the arthropod community as a whole, or within the component feeding groups. There are few studies that have previously assessed feeding group structure along latitudinal gradients that are directly comparable. Progar and Schowalter (2002) assessed arthropod communities along a relatively short latitudinal gradient (270 km) and found that herbivores increased in abundance towards the tropics, while predators and fungivores decreased, with precipitation and elevation also influencing the results. Ants have previously been found to be more abundant compared with herbivores in tropical rainforests (Davidson *et al.* 2003), but we found no evidence for this in the present study (Fig. 2) although our sampling from a single habitat may not be directly comparable.

During both winter sampling periods at Grafton, two sites had a 10-fold increase in the sapsucking population (predominately psyllids) compared with the other seasons sampled. Sapsucking insects have also been found to be highly abundant and highly variable among sampling times in other studies (Moran & Southwood 1982; Root & Cappuccino 1992; Fensham 1994a; Basset & Novotny 1999). Abundance-size relationships for different clades of Hemiptera have shown negative linear relationships, indicating that smaller sized species tend to be more abundant (Hodkinson & Casson 2000). This is true of the most abundant species collected in this study: a psyllid (*Acizzia* sp. 8) collected at Grafton, that weighed 0.0532 mg (dry weight) per individual (compared with an average of 2.71 mg per individual for the overall sample), fluctuated between one and 770 individuals per tree. Root (1973) found seasonal differences in herbivorous insect communities feeding on experimental plots of collards (*Brassica oleracea*), and similarly found that sapsuckers were highly abundant but low in total biomass. Gaston and Lawton (1988) predicted that highly abundant species will tend to be small and have wide population fluctuations. Size-abundance relationships between species along the latitudinal gradient in this study will be assessed in more detail in future articles.

Further studies that compare arthropod community structure along the entire latitudinal distribution of a single host plant in comparable habitat are needed to determine if the trend of consistent abundance and biomass holds for other host plant species and in other regions worldwide. This information will enable a greater understanding of arthropod community structure along environmental gradients.

Ratio of carnivores to herbivores along the latitudinal gradient

We found that carnivore biomass showed a weak latitudinal trend, decreasing towards the temperate

latitudes, and that both carnivore and herbivore abundance showed a peak at Grafton (the second most tropical site). Relative abundance and biomass of both groups was consistent along the gradient, as was the ratio of carnivores to herbivores. As carnivores are an important source of herbivore mortality (Forkner & Hunter 2000; Moon & Stiling 2002), these findings indicate that the potential for carnivores to control herbivore populations may not vary along the gradient. Basset (1993) found approximately 30% of the relative abundance of arthropods associated with subtropical rainforest trees were carnivores, and approximately 35% herbivores. In comparable habitat from this study (Gympie, the most tropical site), carnivores comprised 26% of the relative abundance and herbivores 28%.

Herbivore damage on plants is directly related to the total abundance and biomass of associated herbivores (Morrow 1977; Elliott 1978; Fox & Morrow 1983; Landsberg & Cork 1997). We found that the biomass of herbivores, and that of the component herbivorous feeding groups, did not vary significantly along the latitudinal gradient. Abundance was also consistent along the gradient for herbivores as a whole and for the chewers group (sapsuckers were variable because of the peak in abundance in Grafton). From these data, we would predict that herbivore pressure along the latitudinal gradient would also be fairly consistent. This is in conflict with the widely held generalization that herbivore pressure increases towards the tropics (Coley & Aide 1991; Marquis & Braker 1994), based on data collected from a few sites, primarily in the USA and central/south America. A re-examination of this generalization incorporating more recent studies (e.g. Lowman 1984, 1985; Ohmart & Edwards 1991; Fensham 1994b; Landsberg & Cork 1997; Arturi *et al.* 1999; Jackson *et al.* 1999; Howlett & Davidson 2001; Andrew & Hughes 2005) may be timely.

Comparisons between host species

The majority of comparisons (68%) of arthropod community structure between host plant species and among latitudes were not significantly different. This suggests that there are consistencies in community structure, when measured in terms of abundance and biomass within feeding groups, between congeneric host species. Host species phylogeny did not appear to influence the arthropod community structure at the feeding group level, however, host plant chemistry and mechanical defences of individual host plant species may be responsible for the differences in group structure between host plant species at individual sites (Peeters 2002a,b).

We found that the relative abundance and biomass of carnivores was consistent across most host species comparisons, as was the ratio of carnivores to herbi-

vores between congeneric host species within sites. The relative abundance and biomass of herbivores was not significantly different in three of the seven host species comparisons. Studies of predator to prey ratios based on species richness in a range of freshwater, marine and terrestrial systems have also shown consistency in trophic structure (Jeffries & Lawton 1985; Warren & Gaston 1992; Kruger & McGavin 2001). However, Moran and Southwood (1982) found that the relative abundance and biomass of carnivores and herbivores, as well as carnivore to herbivore ratios, varied between species of *Salix* in Britain. While it is clear that predators and parasites will have variable impacts on different herbivore species (Hawkins *et al.* 1997; Sih *et al.* 1998; Price 2003), identifying a consistent carnivore: herbivore ratio (in relation to abundance and biomass) can assist in determining the overall impact that herbivores will have on their host plant, and the ability of carnivores to reduce this impact (Hairston *et al.* 1960).

Implications for predicting community response to climate change

In Australia, annual average temperatures have increased 0.8°C since 1910 (Collins 2000). Climate models predict increases in temperature of 1–6°C in some areas of eastern and inland Australia by 2070 (CSIRO 2001). At a regional level, changes in temperature and precipitation will potentially have profound impacts on all ecological communities.

In this study we have examined community structure along a latitudinal gradient as a predictive tool for understanding the potential impacts of climate change. In doing this we have made some implicit assumptions. First, we have assumed that the change in temperature along a latitudinal gradient can be used as a surrogate for potential changes in temperature over the coming century. We used a targeted sampling regime using a focal host plant species within a defined vegetation type to reduce many of the confounding factors that may influence results along latitudinal gradients, but our design has not removed all potential confounding factors. One environmental factor that covaries with latitude is photoperiod. Previous studies have dealt with this issue by examining altitudinal, rather than latitudinal gradients (Whittaker & Tribe 1996, 1998; Fielding *et al.* 1999). However, species do not necessarily exhibit the same constraints in distribution along altitudinal and latitudinal transects (Bird & Hodkinson 1999), and therefore, we cannot necessarily predict latitudinal distributions of species and community structure via trends identified from altitudinal studies. Our second assumption is that increasing temperature will be the most important factor influencing insect abundance and diversity patterns

(Dobson 1996; Speight *et al.* 1999; Bale *et al.* 2002). We acknowledge that changes in factors such as precipitation will also be an important influence on species distributions in the future. At present, however, confidence about the magnitude and direction for future changes other than temperature is low (CSIRO 2001).

Understanding patterns in community structure at the level of feeding group allows generalizations to be made about the impacts of climate change at a variety of locations and latitudes. Our results indicate that the overall group structure of arthropod communities on host plants such as *Acacia* species, may not alter greatly as a direct result of shifting climate zones, even though species composition within feeding groups will undoubtedly change. One consequence of stable structure in arthropod communities may be that herbivore pressure on plants may also be relatively stable, although the direct impact of elevated CO₂ on foliage quality and consumption rates (e.g. Dury *et al.* 1998; Roth *et al.* 1998; Smith & Jones 1998; Peters *et al.* 2000; Johns & Hughes 2002) may add further complexity.

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