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Species diversity and structure of phytophagous beetle assemblages along a latitudinal gradient: predicting the potential impacts of climate change

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Abstract. 1. Assemblages of phytophagous beetles on *Acacia* were examined along a 1150 km latitudinal gradient in eastern Australia to investigate the potential effects of climate change on insect communities. The latitudinal gradient was used as a surrogate for differences in temperature. Several possible confounding variables were held constant by selecting comparable sites and emphasising a single host-plant species.

2. Total species richness increased towards the tropics, but there were no significant differences among latitudes for average species density, species richness, Fisher's α, or average Chao-1 index.

3. Beetles sampled along the gradient were classified into four *climate change response* groups, depending on their latitudinal range and apparent host specificity: *cosmopolitan* species, *generalist feeders*, *climate generalists*, and *specialists*. These four groups might respond differently to shifting climate zones. *Cosmopolitan* species (22% of community, found at more than one latitude and on more than one host plant) may be resilient to climate change. *Generalist feeders* (16%, found only at one latitude but found on more than one *Acacia* species) may well feed on several species but will have to move with their climatic envelope. *Climate generalists* (6%, found only on *Acacia falcata* but found at more than one latitude) may be constrained by the host species' ability to either cope with the changing climate or move with it. Finally, *specialists* (55%, found only on *A. falcata* and at only one latitude) may be forced to move poleward concurrently with their host species, or go extinct.

4. The analyses indicate that community structure may be fairly resilient to temperature change. The displacement or local extinction of species, especially the species that are found at only one latitude and on only one host plant, however, may lead to significant changes in community composition.

Key words. *Acacia, Coleoptera, community structure, environmental gradient, insect herbivores, rare species, temperature.*

Introduction

Over the coming century, shifting climate zones will affect the distribution and abundance of many species, potentially leading to changes in the structure and composition of communities (Ayres & Lombardero, 2000; Hughes, 2000; Bale *et al.*, 2002). In Australia, there is little known about factors that currently determine the abundance and distribution of most species (Hughes, 2003), especially invertebrates, thus restricting our ability to predict how these species, and the communities they live in, will respond to a rapidly changing climate. One method for assessing community structure involves grouping species based on feeding style (Root, 1973). Classifying species into feeding guilds that are ecologically and evolutionary relevant

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(Simberloff & Dayan, 1991; Peeters *et al.*, 2001) allows comparisons and generalisations to be made about insects that are not possible using taxonomic groupings alone. Both feeding guild classification and classical taxonomic classification has been used in this study. Plant functional groups have been used extensively to determine responses to climate change based on their photosynthetic pathways, plant lifespan, above-ground biomass and stature, and geographical location (Bazzaz, 1990; Cammell & Knight, 1992; Landsberg & Stafford Smith, 1992; Paruelo & Lauenroth, 1995; Condit *et al.*, 1996; Diaz & Cabido, 1997; Cornelissen *et al.*, 2001; Dormann & Woodin, 2002; Epstein *et al.*, 2002; Richardson *et al.*, 2002). For herbivorous insects, the first comprehensive functional groupings in relation to climate change were developed by Landsberg and Stafford Smith (1992). This scheme was primarily developed to predict how a changing climate and host-plant traits would influence the outbreak of individual pest species, particularly forestry and crop pests. We have developed a complementary classification scheme to assess the potential impacts of climate change on arthropod functional groups, specifically within herbivore communities.

Environmental gradients are a useful tool for understanding the role of current climate in structuring insect communities (Harrison, 1993; Hodkinson *et al.*, 1999) and have been used as a surrogate for predicting responses to future climate change (Fielding *et al.*, 1999; Fleishman *et al.*, 2000). Both latitudinal and altitudinal gradients have been examined for this purpose. However, many of the studies assessing community structure among latitudes have compared samples that are fundamentally different not only in climate, but are also from varied habitats and evolutionary lineages, and have been assessed at different spatial scales (Moran & Southwood, 1982; McCoy & Rey, 1983; Basset, 1991; Price *et al.*, 1995; Majer *et al.*, 2001). Therefore differences in community composition found in these samples that are apparently associated with climate may be confounded with those resulting from other habitat variables. In the case of arthropod communities, for example, the effects of factors such as host-plant chemistry, phylogeny, and architecture are also known to be important determinants of community composition (Strong *et al.*, 1984; Armbruster, 1992; Anderson, 1993; Peeters, 2002). Further, many comparisons of community structure between tropical and temperate latitudes have been limited to one tropical and one temperate site and/or have used a range of sampling techniques, making generalisations difficult (Price, 1991; Holmes *et al.*, 1997).

In this study, a latitudinal gradient was used as a surrogate for a changing climate, specifically an increase in temperature. By identifying species richness patterns along the latitudinal gradient, and classifying species into *functional groups* in terms of their distribution among hosts and latitudes, hypotheses can be made about the possible responses of these groups to future climate change. It is recognised that a latitudinal gradient is not a perfect surrogate for future temperature shifts, most notably because photoperiod is a potential confounding variable (Whittaker & Tribe, 1996; Fielding *et al.*, 1999). However it is clear that the abundance and distribution of species have already been affected by anthropogenic climate change over the past few decades resulting in poleward shifts in the geographical ranges of a wide variety of taxa (e.g. Parmesan *et al.*, 1999; Crozier, 2002; Walther *et al.*, 2002; Root *et al.*, 2003). The impacts of these latitudinal shifts need to be understood. A targeted sampling regime using a focal host-plant species within a defined altitude and vegetation type will reduce many of the confounding factors that may influence results along latitudinal gradients.

The aim of this study was to examine the role of climate (and host-plant identity) in determining the structure and composition of an arthropod community. To overcome some of the limitations described above, this study focused on temperature as the main variable while holding other variables relatively constant. The community was sampled on a standardised set of host-plant species, growing in similar habitats and at the same altitude, at a number of replicate sites along an extensive latitudinal gradient. The primary focus was the phytophagous beetle community on a single host-plant species, *Acacia falcata*, although beetles from other, co-occurring phyllodinous *Acacia* species were also sampled.

Firstly, changes in community composition and community structure were assessed among latitudes and among host species. Beetle species were categorised into four *climate change response* groups (*cosmopolitan*, *generalist feeders*, *specialist feeders*, and *climate generalists*) based on their distribution across host-plant species and latitudes.

Secondly, changes in species richness along the latitudinal gradient were examined. This was assessed in terms of the total number of species collected among latitudes (site data pooled) and as the average number of species per site among latitudes. Increases in species richness from temperate latitudes toward the tropics are well documented for a range of organisms (Fischer, 1960; Rosenzweig, 1995; Gaston, 2000) although some exceptions are known (Owen & Owen, 1974; Eastop, 1978; Platnick, 1991; Price, 1991).

Thirdly, the role of rare species in determining diversity patterns and community composition was examined. Rare species make up a substantial component of all arthropod communities, but their role and importance in structuring broad community patterns among regions is not well understood (Price *et al.*, 1995; Novotny & Basset, 2000; Magurran & Henderson, 2003). Lawton (1991) predicted that there are more rare species within tropical than temperate regions, based on comparison of a birch forest in Britain with a rainforest site in Brunei. Dobzhansky (1950) observed that there were more rare plant species within a 1 ha plot in tropical forests than in the temperate forests of the transition zones of Sierra Nevada, California. Studies compiled by Price *et al.* (1995) also indicated rare species were more prevalent in tropical than in temperate communities. However, lack of consistency in sampling design, plant phylogeny, and habitat type can produce spurious trends. If rare species exert a stronger influence on the overall species assemblage towards the tropics, then their exclusion would alter the diversity trends apparent among latitudes, compared with datasets in which they are included. Therefore latitudinal trends in the data were examined with and without the inclusion of rare species.

Materials and methods

Sampling methods

Acacia falcata was chosen as the focal host species due to its extensive coastal distribution, spanning 1150 km along the east coast of Australia (9° of latitude). Four latitudes, spanning *A. falcata*'s entire coastal range were selected: Batemans Bay, New South Wales (NSW) (35°40′S, the most temperate latitude), Sydney, NSW (33°36′S), Grafton, NSW (29°44′S), and Gympie, Queensland (26°7′S, the most tropical latitude). At each latitude, three sites were selected where *A. falcata* was abundant (>100 individual plants) and the majority of plants were taller than 1.5 m (mature plant stature). All sites were open eucalypt forests and were at a similar altitude (less than 150 m). The distances between sites within latitudes ranged from 2 to 80 km. There was a reduction in average annual temperature of 4.3 °C from north to south, but no directional trend in precipitation: Sydney (the second-most southerly site) had a significantly lower precipitation compared to the three other latitudes (Andrew & Hughes, in press).

Arthropods were sampled seasonally for 2 years, from November 1999 (spring) to August 2001 (winter), a total of eight collections. At each site, at each collection time, 10 *A. falcata* 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. This standardised the sample area among the plants sampled at each site at each season. At sites with co-occurring phyllodinous *Acacia* species (Table 1), five individuals of each 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.

All beetles were identified to family and morphospecies. Beetle morphospecies were classified as phytophagous if the dominant feeding style within its family or superfamily was leaf feeding. Adult morphospecies were formally identified as separate species by expert taxonomists, and will hereafter be referred to as species. Larval specimens were classified to morphospecies and given a separate species code, since it is difficult to associate larvae with adults of the same species. All specimen and sample data were recorded and are stored in the Biota 1.6 database (Colwell, 1996).

Species were classified into four guilds: leaf beetles, weevils, larvae and *other*. Leaf beetles and weevils were placed into separate guilds due to their different feeding habits, evolutionary lineages and morphological characteristics (Lawrence & Britton, 1991; Elliott *et al.*, 1998; Peeters *et al.*, 2001). Leaf beetles included species within the families Cerambycidae and Chrysomelidae (superfamily Chrysomeloidea). Weevils included species within the families Attelabidae, Belidae, Brentidae, and Curculionidae (superfamily Curculionoidea). Larvae included individuals from any beetle family collected in the larval life-stage. Most individual larvae collected were classified within the Chrysomeloidea or Curculionoidea superfamilies and were assumed to be herbivores, but due to many having different feeding habits to their adult form (Lawrence *et al.*, 2000), they were classified into a separate guild. The *other* guild category included species from the families Buprestidae, Cantharidae, Mordellidae, Oedemeridae, Scraptidae, Scydmaenidae, and Tenebrionidae, which were pooled together due to their low abundances and irregular collection (4% of total abundance).

Statistical analysis

Both the density of phytophagous beetle species (the number of species per a specified number of samples) and species richness (the number of species present per a specified number of individuals) (Hurlbert, 1971; Gotelli & Colwell, 2001; Magurran, 2004) were assessed for collections from *A. falcata*. Total species richness (sites pooled within latitudes) was analysed using a *G*-test. Species density and Fisher's α (compared at 70 samples per latitude), and species richness (compared at 15 individuals beetles per site, based on the beetle

Table 1. Host plants sampled at each of four latitudes during this study.

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

abundance recorded at the site with the lowest abundance value) were compared 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, and Fisher's α values were calculated for each of 12 sites using EstimateS 5.0 (Colwell, 1997).

Estimates of the total number of species within the phytophagous beetle community within latitudes were made using the Chao-1 index in EstimateS 5.0 (Colwell & Coddington, 1994; Chao *et al.*, 2000). Chao-1 is a species richness estimator calculated over 1000 randomisations based on occurrences of singletons and doubletons. Comparative tests have identified Chao-1 as a robust species richness estimator (Coddington *et al.*, 1996; Foggo *et al.*, 2003).

The above statistical comparisons were also conducted 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* plant at one site during one sampling season. To assess the representativeness of phytophagous beetle communities on *A. falcata*, the proportion of beetle species on *A. falcata* compared with that of beetles on all *Acacia* species sampled per latitude was also calculated and compared among latitudes.

Community structure among latitudes was compared using a *G*-test, based on relative species richness within the four beetle guilds. A one-way MANOVA compared total species richness within guilds and among latitudes, using sites as replicates. Pillai's Trace was the test statistic used (Tabachnick & Fidell, 2001; Quinn & Keough, 2002).

Similarity of phytophagous beetle communities between adjacent latitudes (sites pooled within latitudes) were compared using two similarity measures: one a presence/absence based measure (Sorensen Incidence) and the other including an assessment of abundance (Morisita–Horn index) (Colwell & Coddington, 1994; Chao *et al.*, 2000; Gotelli & Colwell, 2001; Magurran, 2004). Both indices were calculated using EstimateS 5.0 (Colwell, 1997).

Results

Community composition

A total of 96 phytophagous beetle morphospecies were collected from 930 *A. falcata* shrubs at the 12 sites. Twenty-nine species were from the Curculionidae, 27 from the Chrysomelidae, three from the Cerambycidae, two each from the Belidae, Brentidae, and Buprestidae, and one each from the Attelabidae, Cantharidae, Mordellidae, Oedemeridae, Scraptidae, Scydmaenidae, and Tenebrionidae (Table 2). There were also 24 species of larvae, which were treated as separate species to the adult fauna.

Only two species, a weevil (Curculioninae sp. 1) and a leaf beetle (*Monolepta* sp. 1) were sampled at all four latitudes (Table 2 – group 1). Four species were sampled at the most temperate plus both mid-latitudes (group 2) and four species were sampled at the most tropical plus both mid-latitudes (group 3). Seven species (group 5) were sampled at only the two more tropical latitudes (Grafton and Gympie); most of these species had only one or two individuals collected at each latitude.

Sixty-nine species (72% of total species) were found only at one of the four latitudes (Table 2 – group 6). Fourteen species were found only at the most southerly latitude, Batemans Bay. The second-most southerly latitude (Sydney) had 15 species collected there and at no other latitude, the second-most northerly latitude (Grafton) had 12, and the most northerly latitude (Gympie) had 28.

A further 48 phytophagous beetle species were collected from eight phyllodinous *Acacia* species co-occurring with *A. falcata*, making a total of 145 species collected from all host plants sampled. Gympie had the highest total species richness (81 species), followed by Sydney (53 species), Batemans Bay (47 species), and Grafton (39 species). To assess the representativeness of the *A. falcata* beetle community among latitudes, the number of phytophagous beetle species collected from *A. falcata* at a latitude was divided by the total number of beetle species collected from all *Acacia* species at that same latitude. Representativeness of *A. falcata* beetle communities among latitudes from all samples collected varied among latitudes: Grafton had the highest proportion (0.92), followed by Batemans Bay (0.64), Gympie (0.63), and Sydney (0.60).

To assess the relative importance of climate and host plant on phytophagous beetle species distribution, species collected from *A. falcata* were placed into four classifications (Table 2 – climate change response group). Species found at more than one latitude and on more than one host-plant species were classified as *cosmopolitan* (20 species). The second group (*climate generalists*) were found only on *A. falcata*, but at one or more latitude (seven species). The third group (*generalist feeders*) were beetle species found only at one latitude, but on both *A. falcata* and at least one other host-plant species (21 species). The fourth group (*specialists*) were beetle species found only at one latitude and only on *A. falcata* (48 species).

Community structure

The relative numbers of beetle species within the four guilds (weevils, leaf beetles, larvae, and *other*) were compared to assess whether broad changes in community structure were evident along the latitudinal gradient. Species from all four guilds were found at all latitudes and there were no significant differences in the average species density within guilds among latitudes (Table 3, part a).

Relative beetle species richness within guilds also showed no significant differences in community structure among latitudes on *A. falcata* ($G_9 = 3.75$, $P = 0.927$). Leaf beetles generally contributed the most species to the total phytophagous beetle community ($\approx 38\%$ at each latitude), followed by weevils ($\approx 33\%$), larvae ($\approx 22\%$), and *other* ($\approx 7\%$).

Table 2. Abundance of phytophagous beetle 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 – see *Community structure* in the Results section for details.

				Latitudes			
Feeding guild	Climate change response group	Family	Species	Batemans Bay	Sydney	Grafton	Gympie
Group 1							
Weevil	*Cosmopolitan*	Curculionidae	Curculioninae sp. 1	2	11	1	5
Leaf beetle	*Cosmopolitan*	Chrysomelidae	*Monolepta* sp. 1	3	5	4	1
Group 2							
Leaf beetle	*Climate generalist*	Chrysomelidae	Chrysomelidae I	1	1	2	
Leaf beetle	*Cosmopolitan*	Chrysomelidae	Chrysomelidae G	3	1	5	
Larvae	*Climate generalist*		Larvae-018	1	2	1	
Weevil	*Cosmopolitan*	Attelabidae	*Autetobius* sp. 1	2	2	1	
Group 3							
Weevil	*Cosmopolitan*	Belidae	*Rhinotia* sp. 2		6	1	1
Weevil	*Cosmopolitan*	Curculionidae	Curculioninae sp. 8		4	1	2
Leaf beetle	*Climate generalist*	Chrysomelidae	Chrysomelidae J		2	2	1
Leaf beetle	*Cosmopolitan*	Cerambycidae	Cerambycidae E		1	2	1
Group 4							
Leaf beetle	*Climate generalist*	Chrysomelidae	*Arispoda* sp. 1	1	3		1
Leaf beetle	*Cosmopolitan*	Chrysomelidae	*Bruchidus* sp. 1	18		2	1
Leaf beetle	*Cosmopolitan*	Chrysomelidae	*Monolepta* sp. 3	1		16	17
Weevil	*Cosmopolitan*	Curculionidae	Entiminae sp. 4	26	1		
Weevil	*Cosmopolitan*	Brentidae	Apioninae sp. 1	1		1	
Leaf beetle	*Climate generalist*	Chrysomelidae	*Arispoda* sp. 4	1			1
Larvae	*Climate generalist*		Larvae-003	1			1
Larvae	*Cosmopolitan*		Larvae-020		2	1	
Leaf beetle	*Cosmopolitan*	Chrysomelidae	*Arispoda* sp. 2		1	1	
Weevil	*Cosmopolitan*	Curculionidae	Mesoptilinae sp. 3		1		1
Group 5							
Other	*Cosmopolitan*	Scraptidae	*Heteromastix* sp. 1			5	1
Weevil	*Cosmopolitan*	Curculionidae	Curculioninae sp. 15			2	8
Leaf beetle	*Cosmopolitan*	Chrysomelidae	*Ditropidus* sp. 2			2	2
Larvae	*Cosmopolitan*		Larvae-005			2	1
Weevil	*Climate generalist*	Curculionidae	Curculioninae P			1	1
Other	*Cosmopolitan*	Buprestidae	*Cisseis* sp. 1			1	1
Other	*Cosmopolitan*	Mordellidae	Mordellidae sp. 4			1	1
Group 6							
Weevil	*Generalist feeder*	Curculionidae	Curculioninae sp. 20	20			
Weevil	*Generalist feeder*	Curculionidae	Curculioninae sp. 7	7			
Leaf beetle	*Generalist feeder*	Chrysomelidae	*Ditropidus* sp. 4	3			
Larvae	*Specialist*		Larvae-035	2			
Weevil	*Specialist*	Curculionidae	Curculioninae sp. 12	1			
Weevil	*Specialist*	Curculionidae	Curculioninae sp. 17	1			
Weevil	*Specialist*	Curculionidae	Curculioninae sp. 9	1			
Weevil	*Specialist*	Curculionidae	Curculioninae sp. 3	1			
Weevil	*Specialist*	Curculionidae	Molytinae sp. 1	1			
Larvae	*Generalist feeder*		Larvae-012	1			
Larvae	*Specialist*		Larvae-013	1			
Larvae	*Specialist*		Larvae-021	1			
Larvae	*Generalist feeder*		Larvae-037	1			
Other	*Specialist*	Oedemeridae	Oedemerinae sp. 2	1			
Leaf beetle	*Specialist*	Chrysomelidae	*Ditropidella binotata*		10		
Leaf beetle	*Generalist feeder*	Chrysomelidae	*Trachyopthona* sp. 1		5		
Weevil	*Specialist*	Curculionidae	Entiminae sp. 2		2		
Larvae	*Generalist feeder*		Larvae-017		2		
Weevil	*Specialist*	Brentidae	*Cylas* sp. 1		1		
Weevil	*Specialist*	Curculionidae	Curculioninae Q		1		

Table 2. Continued

Feeding guild	Climate change response group	Family	Species	Latitudes Batemans Bay	Sydney	Grafton	Gympie
Weevil	*Specialist*	Curculionidae	Curculioninae sp. 10		1		
Weevil	*Specialist*	Curculionidae	Curculioninae sp. 14		1		
Weevil	*Specialist*	Curculionidae	Mesoptilinae sp. 1		1		
Leaf beetle	*Specialist*	Cerambycidae	Lamiinae sp. 3		1		
Leaf beetle	*Generalist feeder*	Chrysomelidae	*Arispoda* sp. 5		1		
Leaf beetle	*Specialist*	Chrysomelidae	Chrysomelidae K		1		
Leaf beetle	*Specialist*	Chrysomelidae	Chrysomelidae M		1		
Larvae	*Specialist*		Larvae-033		1		
Other	*Specialist*	Buprestidae	Agrilinae sp. 1		1		
Larvae	*Generalist feeder*		Larvae-023			11	
Larvae	*Specialist*		Larvae-024			6	
Larvae	*Specialist*		Larvae-039			6	
Weevil	*Specialist*	Curculionidae	Cyclominae sp. 2			1	
Weevil	*Specialist*	Curculionidae	Entiminae sp. 1			1	
Weevil	*Specialist*	Curculionidae	Entiminae sp. 7			1	
Leaf beetle	*Specialist*	Chrysomelidae	*Arispoda* sp. 3			1	
Leaf beetle	*Specialist*	Chrysomelidae	*Ditropidus* sp. 5			1	
Larvae	*Generalist feeder*		Larvae-008			1	
Larvae	*Specialist*		Larvae-011			1	
Larvae	*Specialist*		Larvae-022			1	
Other	*Specialist*	Scydmeanidae	*Hispelynus* sp. 1			1	
Weevil	*Generalist feeder*	Curculionidae	Entiminae sp. 5				6
Weevil	*Generalist feeder*	Curculionidae	Curculioninae sp. 6				3
Larvae	*Generalist feeder*		Larvae-001				3
Weevil	*Generalist feeder*	Curculionidae	Curculioninae sp. 19				2
Larvae	*Specialist*		Larvae-025				2
Larvae	*Generalist feeder*		Larvae-028				2
Weevil	*Specialist*	Belidae	*Rhinotia* sp. 1				1
Weevil	*Specialist*	Curculionidae	Cryptorhynchinae sp. 2				1
Weevil	*Specialist*	Curculionidae	Curculioninae sp. 11				1
Weevil	*Specialist*	Curculionidae	Curculioninae sp. 16				1
Weevil	*Specialist*	Curculionidae	Curculioninae sp. 21				1
Weevil	*Specialist*	Curculionidae	Cyclominae sp. 1				1
Leaf beetle	*Specialist*	Cerambycidae	Lamiinae sp. 2				1
Leaf beetle	*Generalist feeder*	Chrysomelidae	*Calomela augomela*				1
Leaf beetle	*Specialist*	Chrysomelidae	*Calomela ioptera*				1
Leaf beetle	*Specialist*	Chrysomelidae	Chrysomelidae F				1
Leaf beetle	*Specialist*	Chrysomelidae	*Diandicus* sp. 1				1
Leaf beetle	*Generalist feeder*	Chrysomelidae	*Dicranostoma pices*				1
Leaf beetle	*Specialist*	Chrysomelidae	*Ditrobidella* sp. 2				1
Leaf beetle	*Specialist*	Chrysomelidae	*Ditropidus* sp. 1				1
Leaf beetle	*Generalist feeder*	Chrysomelidae	*Geloptera* sp. 1				1
Leaf beetle	*Specialist*	Chrysomelidae	*Monolepta* sp. 5				1
Larvae	*Generalist feeder*		Larvae-004				1
Larvae	*Specialist*		Larvae-006				1
Larvae	*Generalist feeder*		Larvae-007				1
Larvae	*Specialist*		Larvae-031				1
Other	*Generalist feeder*	Cantharidae	*Chauliognathus* sp. 1				1
Other	*Specialist*	Tenebrionidae	Alleculinae sp. 3				1
Number of species				27	30	34	47
Number of unique species				14	15	12	28
Number of singleton species				17	17	20	36

Species diversity indices were calculated to compare similarity of phytophagous beetle assemblages between adjacent latitudes. The Sorensen Incidence diversity measure showed a consistent similarity in species composition between adjacent latitudes (Fig. 1a). The Morisita–Horn index indicated that similarity in species composition was higher

Table 3. Summary statistics table for multivariate analysis of variance (MANOVA). (a) Species density for the full dataset and (b) species density for the *common species* dataset are shown. Component guilds (weevils, leaf beetles, and larvae) analyses (one-way ANOVAS) are also shown. n.a., Not applicable.

(a) Species richness (full dataset)						
Latitude	d.f.	Pillai Trace	*F*	*P*		
	12,21	1.098	1.01	0.473		
Component guilds	d.f.	Pillai Trace	Weevils	Leaf beetles	Larvae	*Other*
	3,8	0.47	$P = 0.63$	$P = 0.66$	$P = 0.22$	$P = 0.09$
(b) Species richness (*common species* dataset)						
Latitude	d.f.	Pillai Trace	*F*	*P*		
	12,21	1.369	1.47	0.2126		
Component guilds	d.f.	Pillai Trace	Weevils	Leaf beetles	Larvae	*Other*
	3,8	0.21	$P = 0.78$	$P = 0.37$	$P = 0.34$	n.a.

between the more tropical latitudes (Gympie and Grafton) compared with that between the mid-latitudes (Grafton and Sydney) and that between the more temperate latitudes (Sydney and Batemans Bay) (Fig. 1a).

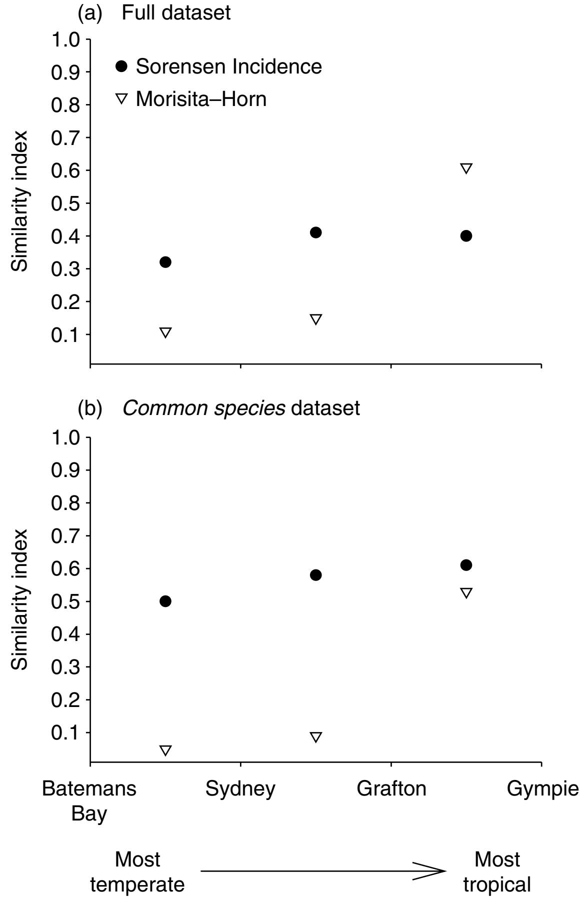


Fig. 1. Pairwise comparison of similarity of herbivore beetle species composition between adjacent latitudes (Batemans Bay and Sydney, Sydney and Grafton, Grafton and Gympie) using two different similarity indices: Sorensen Incidence and Morisita–Horn. (a) Full dataset, (b) *common species* dataset. Higher numbers indicate relatively higher similarity in composition among latitudes.

The two similarity measures also showed different trends for each of the individual guilds between adjacent latitudes (Fig. 2). The Sorensen Incidence index showed no consistent trends in community similarity from the more temperate to the more tropical zones (Fig. 2a). In contrast, the Morisita–Horn index showed both the weevils and leaf beetle guilds increasing in species similarity between adjacent latitudes towards the tropics, and larvae similarity decreasing towards the tropics (Fig. 2b). The *other* guild did not have any species in common between the two most temperate latitudes or between the two mid-latitudes.

Species richness along the latitudinal gradient

The number of beetle species collected at each latitude (sites pooled) was significantly different (Fig. 3a), being highest at the most tropical latitude (Gympie – 47 species) and decreasing towards the most temperate latitude (Batemans Bay – 27 species). Average number of beetle species per site within latitudes did not differ significantly among latitudes in terms of species density, Fisher's α, or species richness (Fig. 4a–c).

Species accumulation curves were used to assess the adequacy of sampling effort among latitudes (Fig. 5a). The rate of new species accumulating at each latitude (sites pooled) was relatively high at the most tropical latitude (Gympie), compared with the more temperate latitudes. An asymptote in species accumulation, however, had not been reached for any latitude after 2 years of sampling.

In order to estimate the number of phytophagous beetle species, the Chao-1 index (based on occurrences of singletons and doubletons) was calculated. This estimate indicated that 182 ± 35 phytophagous beetle species would be expected to be associated with *A. falcata*, i.e. approximately double the number of actual species sampled (96 species). For each individual latitude (sites pooled), the Chao-1 estimates for both the most tropical (Gympie, 175 ± 76) and most temperate (Batemans Bay, 94 ± 69) latitudes were still rising and exhibited high variation around the mean (Fig. 6a,d). In contrast, the Chao-1 index for both the mid-latitudes (Grafton, 45 ± 10 and Sydney, 57 ± 13) were relatively closer to asymptoting and exhibited a low level of variation around

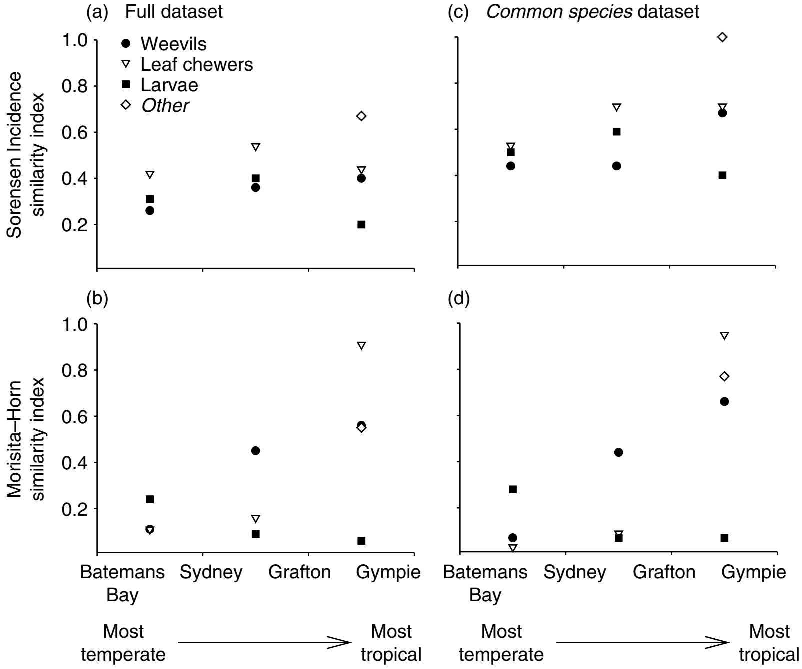


Fig. 2. Pairwise comparison of similarity of herbivore beetle guilds between adjacent latitudes (Batemans Bay and Sydney, Sydney and Grafton, Grafton and Gympie). Guilds include weevils, leaf beetles, larvae, and *other*. (a) Full data set compared using the Sorensen Incidence similarity index, (b) full data set compared using the Morisita–Horn similarity index, (c) *common species* dataset compared using the Sorensen Incidence similarity index, and (d) *common species* dataset using the Morisita–Horn similarity index. Higher numbers indicate relatively higher similarity in composition among latitudes.

the mean (Fig. 6b,c). The average Chao-1 index (based on the estimate at each of the three sites per latitude) showed no significant differences among latitudes (Fig. 4d).

To compare the adequacy of the sampling among latitudes, the number of species sampled per latitude (species density) was divided by the respective average Chao-1 value per latitude. Both the most tropical (Gympie) and most temperate (Batemans Bay) latitudes had a lower proportion of species sampled per estimated species richness (0.29 and 0.30 respectively) than the mid-latitudes (0.63 second most tropical latitude, Grafton, and 0.71 second most temperate latitude, Sydney).

Role of rare species

Single occurrence species were removed from the dataset and the analyses described above were repeated (the *common species* dataset – a total of 53 species compared with 96 for the full dataset). In terms of community structure, similar trends were found in the *common species* dataset as the full dataset (Table 3, part b), except that the *other* guild was absent from the two most temperate latitudes (Batemans Bay and Sydney). Relative beetle species richness within guilds showed no significant differences in community structure among latitudes on *A. falcata* ($G_9 = 7.70$, $P = 0.564$).

The similarity between species assemblages between adjacent latitudes was also assessed using both datasets. Both the Sorensen Incidence diversity measure and Morisita–Horn index showed consistent trends between both datasets when all species were assessed together (Fig. 1a,b) and when guilds were assessed separately (Fig. 2).

There was no significant decrease in total species richness among latitudes for the *common species* dataset when sites were pooled within latitudes (Fig. 3b). When the average number of species sampled per latitude was assessed, there were no significant differences among latitudes for average species density and the average Fischer's α value (Fig. 4e,f). In contrast, average species richness was significantly lower at the most temperate latitude, Batemans Bay, compared with the three more northerly latitudes (Fig. 4g).

In terms of species accumulation, the two more-tropical latitudes (Gympie and Grafton) accumulated species at a relatively faster rate than the two temperate latitudes (Sydney and Batemans Bay) (Fig. 5c). Compared with the full dataset (Fig. 5a,b), all four latitudes in the *common species* dataset were accumulating new species at a lower rate (Fig. 5c,d).

The estimated number of species (Chao-1 index) for the *common species* was constant for all four latitudes (i.e. mean estimate of species richness asymptoted and exhibited low variance about the mean) (Fig. 6e–h). The most tropical latitude was estimated to have the most species (49 species), followed by the second-most tropical (33 species), the most temperate (31 species), and the second-most temperate (24 species).

When species density of *common species* sampled per latitude was divided by the estimated mean number of species

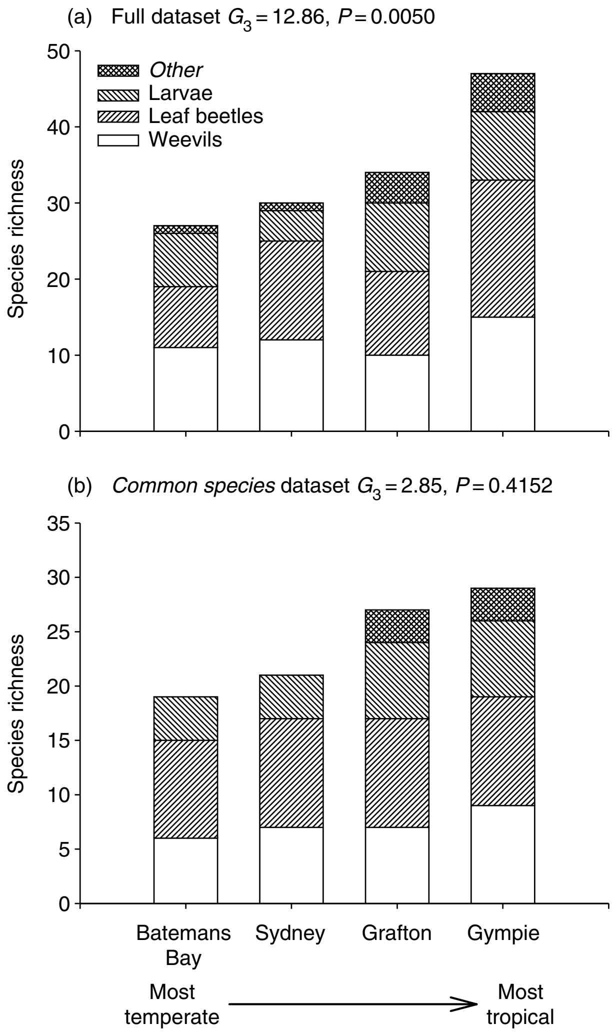


Fig. 3. Phytophagous beetle species richness at four different latitudes collected from *Acacia falcata*. (a) Full dataset, (b) *common species* dataset. Component guild richness also included: weevils, leaf beetles, larvae, and *other*. See Materials and methods for details.

(Chao-1 index) associated with *A. falcata* per latitude, the adequacy of sampling was better than that of the full dataset. Samples from the most tropical latitude were the most under-sampled (0.59), followed by the most temperate latitude (0.61), whilst the second-most temperate latitude (0.82), and the second-most tropical (0.88) were relatively well sampled.

Overall, the full species dataset (96 species) and the *common species* dataset (53 species) showed similar trends, but there were differences in terms of average species richness. Species accumulation and estimated number of species (and associated variation) among latitudes were different among datasets, with the *common species* dataset having lower richness at all latitudes and having curves that were relatively closer to asymptoting compared to the *common species* dataset.

Discussion

The classification of beetle species into different groups depending on their distribution among latitudes and host-plant species enables hypotheses to be generated as to their response to future changes in climate, assuming that host-plant distributions will generally move polewards over the coming century. Species that are *cosmopolitan* (in this study, defined as those found at more than one latitude and on more than one host plant: 20% of phytophagous beetle species on *A. falcata*) may be quite resilient to changes in local climate and changes in the distribution of hosts, and will survive *in situ* and/or could move with the host plant and potentially expand their range. *Generalist feeders* (defined here as species found only at one latitude but collected from more than one *Acacia* host-plant species: 21% of species) may be constrained by climate, having to move with a changing climatic zones but being able to feed on multiple host-plant species. *Climate generalists* (defined here as species found only on one host species, but at more than one latitude: 7% of species collected) may be constrained by their host's ability to cope with the changing climate, only moving into new areas once the host plant has colonised. Finally, *specialists* (defined here as species found only on one host species and one latitude: 50% of species) will have to move polewards with a changing climate and stay on the single host species in order to survive.

The finding that overall community structure, in terms of the guild assignations used, was quite consistent among latitudes also has implications for predicting future climate change impacts. The relative number of species within guilds was consistent among latitudes, independent of species composition. This indicates that even though many species may be displaced by climate change, the overall community structure of the phytophagous beetle communities may be resilient.

Trends among latitudes

Detection of a latitudinal trend in the number of species was dependent on the methods used. When all sites within latitudes were pooled, total species richness increased, as expected, towards the tropics. However there was a high level of variation between sites within latitudes, despite samples being collected from the same host plant and from comparable habitats. As a result, when species richness was averaged across sites within latitudes and compared among latitudes, the trend towards the tropics disappeared. This indicates that methods used to assess diversity along gradients strongly influence the patterns seen.

Total species richness appears to be consistently higher in the tropics than in more temperate zones. Similar trends have been identified for a range of other taxa including bats, mammalian quadrupeds, herpetofauna, termites, coastal fish, and fossil formanifera (Rosenzweig, 1995). The finding that the total richness of phytophagous beetle species

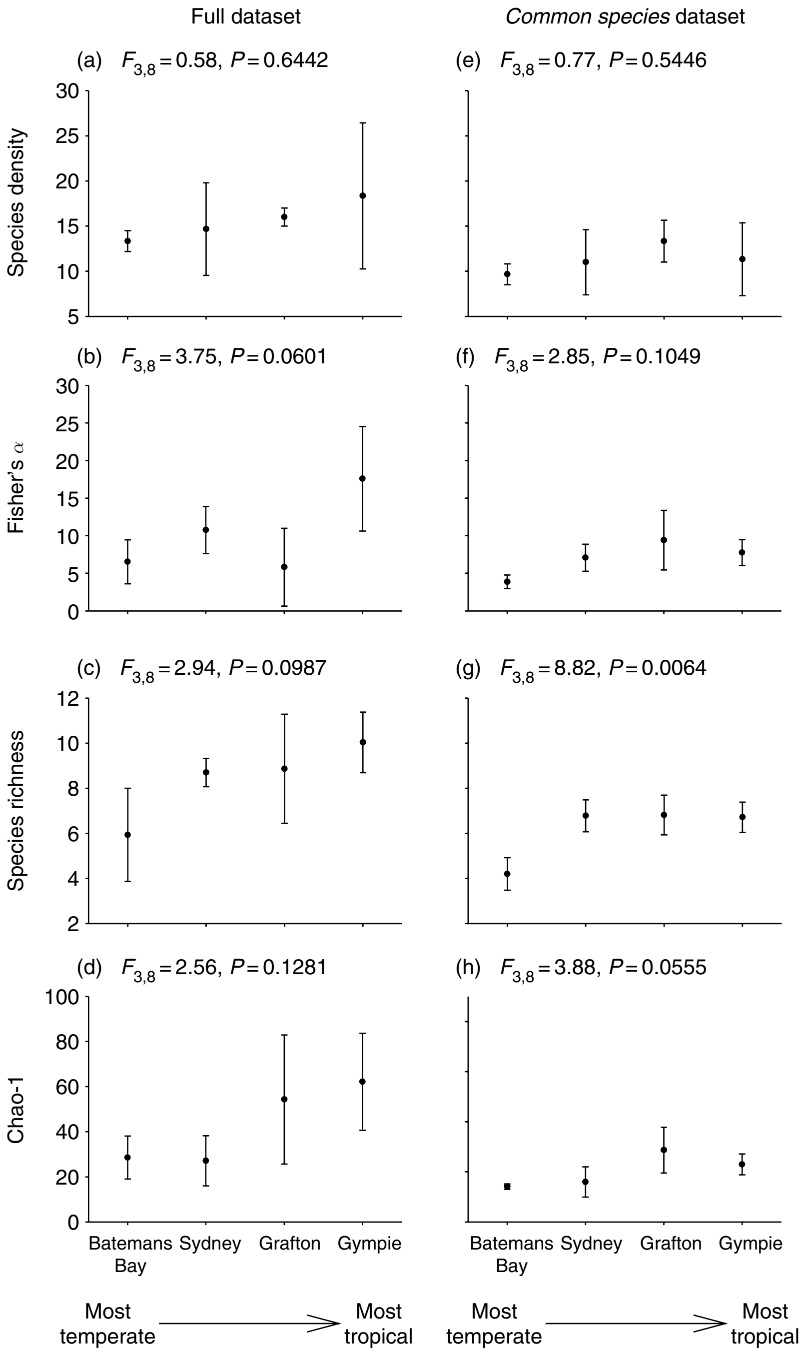
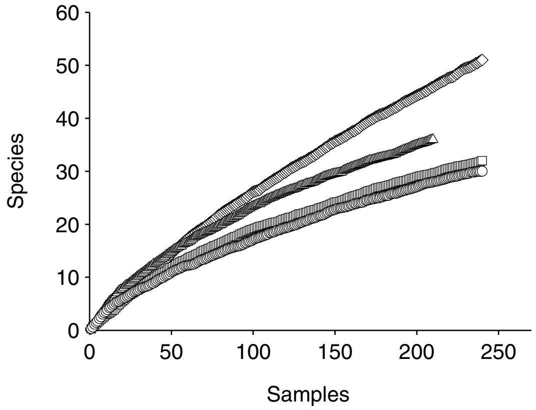


Fig. 4. Changes in phytophagous beetles at four different latitudes collected from *Acacia falcata*. From the full dataset: (a) species density (based on 70 samples per site), (b) Fisher's α, (c) species richness (based on 15 individuals per site), and (d) Chao-1 species richness estimation. From the *common species* dataset: (e) species density (based on 70 samples per site), (f) Fisher's α, (g) species richness (based on 15 individuals per site), and (h) Chao-1 species richness estimation. Means (± SD) ($n = 3$) per latitude are shown.

among latitudes decreased, when sites were pooled, from the more tropical latitudes towards the more temperate zone is also consistent with several other studies on beetle assemblages. Stork (1997) found higher species diversity in tropical beetle samples compared with temperate ones, in collections at the Natural History Museum (London). In a comparison of beetle species richness on different host-plant genera, Southwood *et al.* (1982), found higher beetle species richness on four out of five host-plant genera (*Betula*, *Buddleia*, *Robinia*, and *Salix*) in the more tropical region

(a) Full dataset



(b) *Common species* dataset

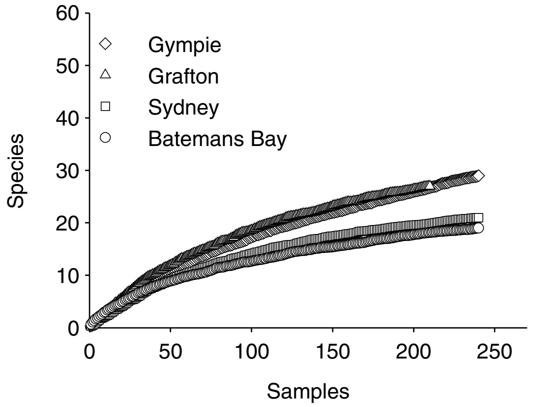


Fig. 5. Species accumulation curves for phytophagous beetles at four different latitudes (most temperate Batemans Bay, Sydney, Grafton, and most tropical Gympie) collected from *Acacia falcata*: (a) full dataset; (b) *common species* dataset.

(South Africa) compared with the more temperate region (U.K.). During insect surveys on bracken (*Pteridium aquilinum*), one of the most widespread plant species, beetles were found only on plants from tropical sites in Papua New Guinea, and not in the more temperate sites within New Mexico, U.S.A., Sydney, Australia, and a variety of sites in South Africa and Britain (Lawton, 1984; Compton *et al.*, 1989; Shuter & Westoby, 1992). At the regional scale within a continent, North American species of *Epicanta* (Coleoptera: Meloidae) show a strong gradient in species richness, being lowest in the prairie region of central North America, and highest in northern Arizona (Kerr & Packer, 1999).

At a finer scale of resolution, it was found that the average number of phytophagous beetle species among latitudes (average per site) did not significantly differ in terms of species richness, species density, and Fisher's α in the full dataset. Other studies of arthropod faunas have also found increases in species diversity towards the more tropical latitudes when sites are pooled, but no significant changes in average species diversity among latitudes (average per site). Price *et al.* (1995), noted that total species richness of lepidopteran larvae on *Erythroxylum* was higher in tropical Cerrado in central Brazil than on other savanna vegetation in Arizona, U.S.A., but that there was no difference between species richness per individual tree between latitudes. For other taxa, such as vascular plants, species richness at the 0.1-ha scale was similar among latitudes in each of savanna woodland, sclerophyll woodland, and coastal dune vegetation in Australia (Rice & Westoby, 1983; Specht, 1988). For invertebrates collected in pitcher plants along a latitudinal gradient across North America, there was no significant change in species diversity per site among latitudes (Buckley *et al.*, 2003). Comparisons of communities within similar habitats between latitudes have found species diversity to be consistent, a finding further supported by this study.

Changes in species diversity within taxa along environmental gradients, such as latitudinal gradients, are in part associated with changes in resource availability (Rotenberry, 1978; Shmida & Wilson, 1985; Stevens & Willig, 2002). Most studies that have assessed changes in diversity along latitudinal gradients have taken samples from a variety of habitats and have tended to sample from comparatively more heterogeneous habitats towards the tropics than when sampling from more temperate habitats (Stevens, 1989; Kaufman & Willig, 1998). It is believed that only two previous studies have assessed diversity patterns along latitudinal gradients from comparable habitat. Davidowitz and Rosenzweig (1998) assessed species richness of American grasshoppers (Acrididae) from published distribution maps in a single habitat (prairie grassland) between latitudes. They found grasshopper species richness was highest at mid-latitudes (35°N), which included areas with more preferred (grassy) habitat. The second study, by Progar and Schowalter (2002), assessed canopy arthropods on Douglas fir (*Pseudotsuga menziesii*) along a 270-km latitudinal/precipitation/altitudinal gradient in the Pacific north-west of the U.S.A. They found that arthropod associations (based on abundance of taxa) varied with latitude, precipitation, and tree age (some trees sampled were up to 500 years old). Unfortunately, they did not assess community structure along the entire latitudinal range of the host species (Douglas fir range extends from south-east Alaska to northern California). In the present study, species similarity of phytophagous beetle assemblages among latitudes did not show any consistent change towards the tropics. The samples in the work reported here were taken from the same host-plant species in similar habitat types at equivalent altitudes, minimising habitat heterogeneity. However, similarity between the two more tropical latitude comparisons (Grafton and Gympie) was higher than between the more temperate latitude comparisons (Grafton and Sydney; Sydney and Batemans Bay). This is probably due to the seven species found only at both Grafton and Gympie (Table 2 – group 5), and *Monolepta* sp. 3 that was found at three latitudes, but in high abundance at Grafton and Gympie (Table 2 – group 4).

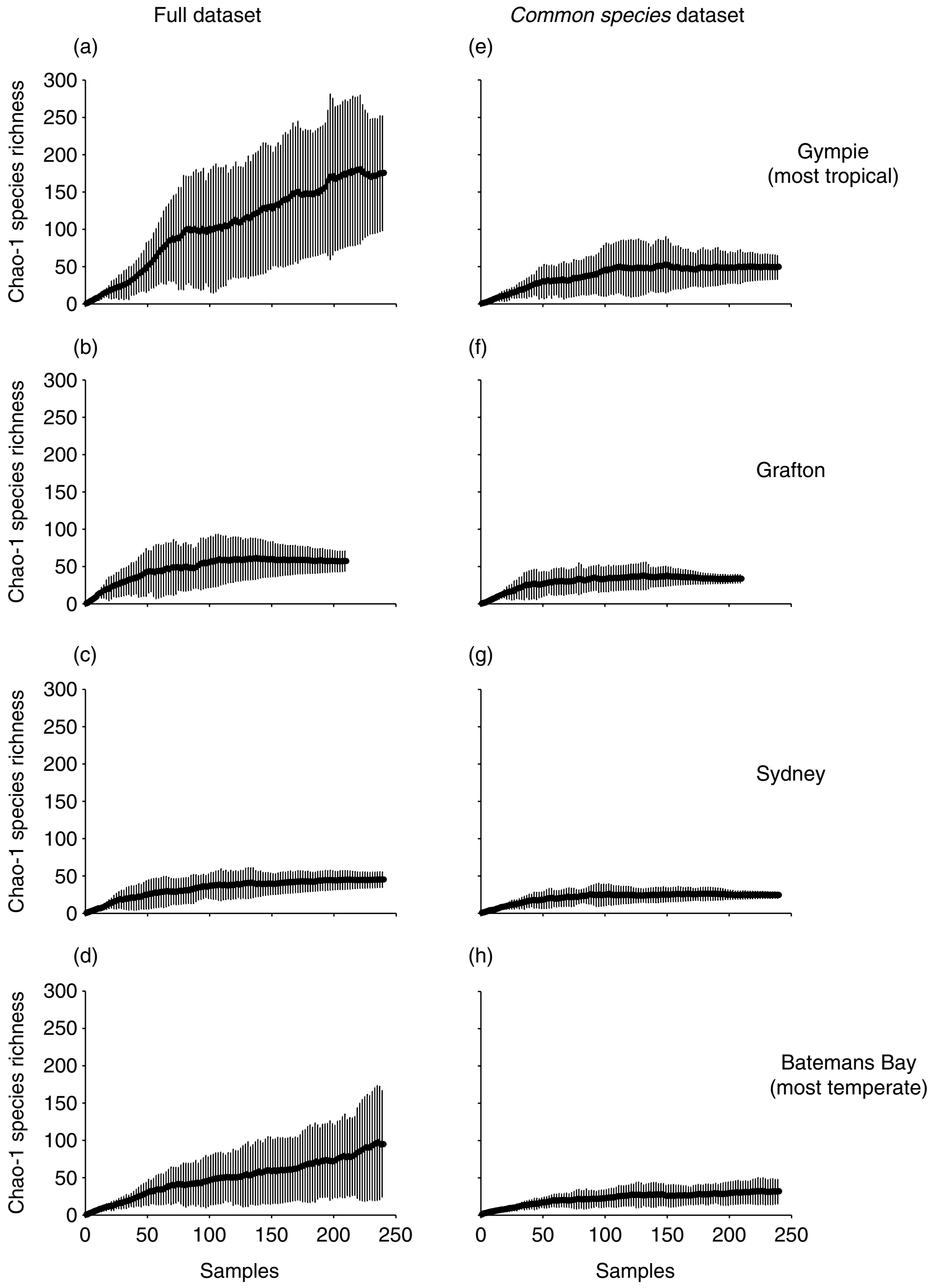


Fig. 6. Chao-1 species estimation (± SD; 50 randomisations) at four different latitudes for phytophagous beetles collected from *Acacia falcata*. (a)–(d) Full dataset; (e)–(h) *common species* dataset. See Materials and methods for details.

Role of rare species

In spite of problems with specifically defining what a rare species is (Gaston, 1994), many diversity studies have found that rare species make up a high proportion of the overall species richness (Basset, 1993; Fensham, 1994; Bürki & Nentwig, 1997; Sárospataki, 1999; Novotny & Basset, 2000; Magurran & Henderson, 2003). In this study, rare species (defined here as those sampled from only one tree at one site at one sampling time) contributed 43 species out of the total of 96 (45%) species collected from *A. falcata*.

Rare species are thought to contribute more to diversity at tropical latitudes than at temperate latitudes (Coddington *et al.*, 1996). This study indicates that rare phytophagous beetle species do appear to have a large role in determining changes in community structure among latitudes; there were more rare species in total in the tropical latitudes, supporting Coddington *et al.*'s (1996) assessment. Different trends were found between the full dataset and the *common species* dataset (rare species excluded) for total species richness and average species richness (sites averaged) among latitudes. Other studies do not support a strong influence of rare species among latitudes, e.g. ichneumonid wasps showed variable responses in the proportion of single occurrence species in samples from two tropical and two temperate sites (Owen & Owen, 1974). Rare and common species of New World bats also show similar patterns along a latitudinal gradient (high richness towards the tropical latitudes) (Stevens & Willig, 2002).

When the *common species*–sample curves were compared in this study, total species per latitude were relatively closer to asymptoting for all four latitudes compared with the full dataset after 2 years of sampling. Similar trends were found for leaf-chewing beetle species associated with 15 *Ficus* species near Madang, Papua New Guinea (Basset *et al.*, 1997). In this study, the total species–sample curve was increasing after 324 species were collected, but when rare species (less than five individuals) were excluded, the accumulation curve asymptoted at around 80 species. The overall conclusion is that rare species contribute significantly to species diversity within sites and among latitudes, and their influence needs to be taken into account when assessing diversity patterns along environmental gradients.

Estimated total species richness

The species richness estimator used (Chao-1) is one of a variety of species estimators available (Colwell, 1997; Chiarucci *et al.*, 2003). Different studies have reached varying conclusions about the merits of each estimator (e.g. Colwell & Coddington, 1994; Chazdon *et al.*, 1998; Toti *et al.*, 2000; Hofer & Bersier, 2001; Chiarucci *et al.*, 2003). The Chao-1 index has performed well compared with other species richness estimators in temperate forests (Coddington *et al.*, 1996). It was found that the Chao-1 index calculated for both the most tropical latitude and the most temperate latitude was highly variable (high variation around the mean), compared with the index calculated for the two mid-latitudes. However, in the *common species* dataset, all four latitudes produced Chao-1 estimate curves that had low variation around the estimated mean.

There were no significant differences among latitudes when average Chao-1 indexes were compared, both for the full dataset and *common species* dataset. This trend was similar to the average species richness, density, and Fisher's α among latitudes. This supports the view that *within* a habitat type among latitudes, average species diversity (average of sites within latitudes) does not increase directionally towards the tropics.

Potential impacts of climate change

Over the past century, there has been a global increase in temperature of $0.6 \pm 0.2\,^{\circ}\mathrm{C}$ (IPCC, 2001). Organisms have already shown clear responses to these climatic changes (Walther *et al.*, 2002), including poleward latitudinal shifts in distribution (Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Root *et al.*, 2003). Climate models have predicted that by 2100, temperatures will rise between 1.4 °C and 5.8 °C globally (IPCC, 2001). In Australia, increases in mean temperatures will occur at all latitudes (CSIRO, 2001), shifting climate zones southwards towards the poles. These climatic changes are predicted to have a relatively greater impact on species at higher latitudes (Bale *et al.*, 2002).

An understanding of how communities will respond to these changes is needed. Community level responses to climate change cannot be predicted from physiological experiments or from field collected data on individual herbivore species and their associated host plants (Ayres, 1993; Harrington *et al.*, 1999). In this study, the focal host-plant species (*Acacia falcata*) already extends through a range of latitudes and considerable variation in mean annual temperature (Andrew & Hughes, in press), and may therefore be pre-adapted to cope with temperature change in the future (Bale *et al.*, 2002). However, the phytophagous insect species associated with this host plant may not be as resilient to a changing climate. One of the most important findings in this study is that even though rare species are more species rich towards the tropics, they contribute significantly to the community composition of the phytophagous beetle assemblage at all latitudes. The ability of these individual species to adapt to a warmer and more variable climate, especially if they are already climatically restricted, will determine the level of species displacement and extinction by climate change (Davis *et al.*, 1998; Bale *et al.*, 2002).

Community structure, in terms of species richness and diversity in the four guilds defined in the work reported here, was consistent among latitudes, implying that it may be fairly resilient to temperature change. However, the displacement or local extinction of species, especially the species that are found at only one latitude and on only one host species, may lead to significant changes in community composition.

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