

Potential host colonization by insect herbivores in a warmer climate: a transplant experiment

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Abstract

We conducted a transplant experiment to investigate the potential colonization of a plant species by insect herbivores under a warmer climate. *Acacia falcata* seeds collected from four latitudes, encompassing the current coastal range of the species (1150 km), were grown in the same soil type and climatic conditions in a glasshouse. Plants were then transplanted to two sites, 280 km north of *A. falcata*'s current coastal range; the transplant sites were 1.2 and 5.5 °C warmer than the northernmost and southernmost boundaries of the species' current range, respectively. We compared the structure and composition of the herbivorous Hemiptera and Coleoptera communities on the transplants (i) to that of *A. falcata* within its current distribution, (ii) to a closely related *Acacia* species (*Acacia leptostachya*) that naturally occurred at the transplant sites, and (iii) among the *A. falcata* transplants originating from seeds collected at different latitudes. Herbivory on *A. falcata* was also compared between the transplants and the current distribution, and among transplant originating from different latitudes. Thirty species of externally feeding herbivorous Coleoptera and Hemiptera were collected from the transplanted *A. falcata* over a period of 12 months following transplantation. Guild structure of this herbivore community (based on the proportion of species within each of seven groups based on taxonomy and feeding style) did not significantly differ between the transplants and that found on *A. falcata* within its natural range, but did differ between the transplants and *A. leptostachya*. Rates of herbivory did not significantly differ between the transplants and plants at sites within the natural range. There were no significant differences in herbivore species richness or overall rates of herbivory on the transplants originating from different latitudes. In conclusion, host plant identity was apparently more important than climate in influencing the structure of the colonizing herbivore community. If this result holds for other plant–herbivore systems, we might expect that under a warmer climate, broad patterns in insect community structure and rates of herbivory may remain similar to that at present, even though species composition may change substantially.

Keywords: *Acacia*, Australia, climate change, Coleoptera, community structure, Hemiptera, phytophagous insect, transplant experiment

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Introduction

Global temperatures have increased approximately 0.6 °C over the past century and climate models predict increases of 1.4–5.8 °C by 2100 (IPCC, 2001). The abundance and distribution of species has already been affected by anthropogenic climate change over the past

few decades with poleward shifts in geographical ranges documented for a wide variety of taxa (e.g. Parmesan *et al.*, 1999; Crozier, 2002; Walther *et al.*, 2002; Root *et al.*, 2003). Individualistic responses of species to current and future changes, especially differential migration rates, will result in the progressive decoupling of present day ecological interactions, together with the formation of new relationships, potentially leading to profound changes in the structure and composition of present day communities (Hughes, 2000; Harrington *et al.*, 2001).

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In this study, we investigated how the relationship of herbivorous insects and their host plants may change under a warmer climate. We focused on herbivorous insect communities for several reasons. First, insect herbivores comprise a significant portion of global biodiversity, representing about a million of the 1.75 million described species (e.g. Jones & Lawton, 1991; Price, 2002). Second, herbivores have significant impacts on productivity, decomposition, nutrient-cycling and other important ecosystem-level processes (e.g. Kremen *et al.*, 1993). Third, many insect herbivores are highly mobile, and may, therefore, be expected to migrate rapidly in response to shifting climate zones. If the migration rates of their host plants lag behind, a reasonable expectation given what is known about plant dispersal rates under past climate changes (Huntley & Webb, 1989; Webb, 1992), we might expect herbivores to colonize new plant species and conversely, for host species to be subject to new suites of herbivores within their current range in the short to medium term.

Transplant experiments offer a powerful method of testing hypotheses about how species and communities will be affected by future climatic changes although there are relatively few published studies using this technique (but see Wieder & Yavitt, 1994; Hobbie & Chapin, 1998; Shaw & Harte, 2001; Bruelheide, 2003). CSIRO climate models project a 1–5 °C warming along the east coast of Australia over the next 70 years (CSIRO, 2001). We investigated whether broad changes in herbivore community structure and/or composition will occur as the climate warms, by transplanting a host plant species to locations subject to mean annual temperatures 1.2 °C higher than at the species' current warmest boundary and 5.5 °C higher than at its coolest edge. We then compared the structure and composition of the herbivorous insect community that colonized the transplants (i) to that of the host plant species within its natural range and (ii) to a congeneric plant species that grew naturally at the transplant latitude. This experiment, therefore, tested whether characteristics of herbivorous communities on a host species *in situ* under a warmer climate may be predicted by their present day structure and composition or alternatively, by those on related plants in warmer environments.

We also investigated whether the herbivore community and rates of herbivory were affected by the latitudinal origin of the transplants. Ecotypic variation in traits such as foliage chemistry and phenology might be expected in a species with such a broad range (in this case encompassing 4.3 °C mean annual temperature) (Hodgkinson & Quinn, 1978; Roberds *et al.*, 1990; King *et al.*, 1995; Klingaman & Oliver, 1996), which in turn might be expected to affect the assemblage of herbivores and the damage that the plants may incur. Herbi-

vore assemblages and herbivory rates were compared among transplants originating from seed collected from four latitudes encompassing the natural coastal range of the focal host plant species.

The questions we addressed were:

1. Are herbivore communities structured differently on a host plant species in a warmer climate compared with those in the host's natural range?
2. Do rates of herbivory differ between a host plant species in a warmer climate compared with those in the host's natural range?
3. Does host plant ecotype influence herbivore community structure and herbivory in a warmer climate?

Methods

Host plant species

We focused on the host plant *Acacia falcata* Willd., a phyllodinous species (Family Fabaceae, subgenus Phyllodinae, section Phyllodineae) with an extensive latitudinal distribution along the east coast of Australia. The coastal distribution (at altitudes of <150 m) of *A. falcata* ranges from south of Moruya, New South Wales (NSW) (35°53'S) to Tairo, Queensland (Qld) (25°45'S), a distance of 1150 km (Fig. 1). *A. falcata* also

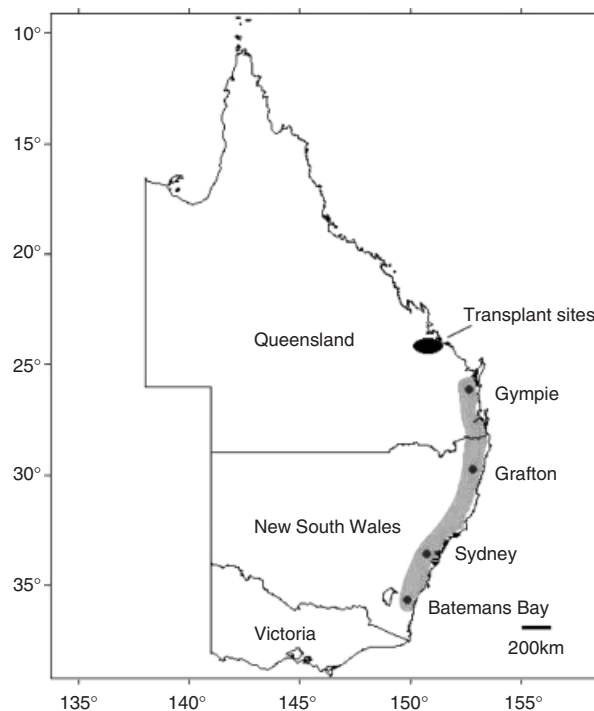


Fig. 1 Location of transplant sites in relation to the coastal distribution of *Acacia falcata* along the east coast of Australia and latitudes sampled within its range.

occurs inland at higher altitudes from Bundara, NSW (30°17'S) to Atherton, North Queensland (17°22'S). We have previously characterized the arthropod communities on *A. falcata* throughout its coastal range in terms of the abundance and biomass of insect feeding guilds (Andrew & Hughes, 2005a), species diversity of phytophagous Coleoptera (Andrew & Hughes, 2004), and Hemiptera (Andrew & Hughes, 2005b), and the rates of herbivory (Andrew & Hughes, 2005c).

Seeds of *A. falcata* were collected in November 1999 from three sites at each of four latitudes encompassing the natural coastal range of the species (Fig. 1). The southern-most latitude used for seed collection was Batemans Bay, NSW (35°40'S, 150°20'E), followed by Sydney, NSW (33°36'S, 150°52'E), Grafton, NSW (29°44'S, 152°58'E) and the northern-most latitude, Gympie, Qld (26°7'S, 153°11'E). This range spans 4.3 °C mean annual temperature.

Seeds collected at different sites within latitudes were pooled and then treated with boiling water to promote germination. Once germinated, seeds were planted in sterilized potting mix in 5 cm diameter tubes and moved into a glasshouse at Macquarie University. Plants were transferred to 20 cm diameter pots once their roots were well developed and then grown for 1 year. A slow-release fertilizer (Osmocote® for Australian native plants, Baulkham Hills, NSW, Australia) was added to the potting mix three times according to the manufacturers' instructions: at the initial potting into 5 cm pots, during repotting into 20 cm pots, and 6 months later. Plants were watered twice daily for 5 min using an automated mist-spray sprinkler system and were subject to natural photoperiod.

In November 2000, the 1 year old plants were placed outside the glasshouse to acclimatize to natural weather conditions for 2 months. During this period, they were watered three times weekly. Most plants were over 2 m tall by this time and were subsequently cut back to 50 cm before transplantation.

Study sites

In February 2001, 160 plants were transplanted to two 20 m² sites, 27 km apart: Dan Dan (24°10'51"S, 151°05'16"E) and Calliope (23°57'04"S, 151°10'55"E) near Gladstone, central Queensland (Fig. 1). These sites, collectively known as the 'transplant latitude' hereafter, are approximately 280 km north of the northernmost coastal boundary of *A. falcata* (Gympie). Both transplant sites were open eucalypt woodland with 10–30% canopy cover, with easterly aspect on clay soils. Mean annual temperature at the transplant sites was 21.4 °C, compared with that for Gympie (20.2 °C), Grafton (18.3 °C), western Sydney (16.9 °C) and Batemans Bay (15.9 °C)

(BIOCLIM 5.0, Busby, 1991). Based on BIOLCLIM 5.0, the mean annual precipitation at the transplant sites was 919 mm, which is lower than Gympie (1104 mm), Grafton (1118 mm) and Batemans Bay (1145 mm), but higher than western Sydney (838 mm).

Both transplant sites were fenced to exclude vertebrate herbivores. Eighty plants (20 plants from each of the four latitudes of origin) were randomly planted at each site at 1.5 m intervals in a 16 m × 16 m grid, with a 2 m buffer from the fence. Plants were watered for 3 days after transplantation. Ten of the 160 trees (from various latitudes) died during the 12-month monitoring period after transplantation.

Five soil samples (8 cm diameter × 13 cm depth, 653 cm³) were taken per transplant site, bulked, dried and sieved through 1 mm mesh. Total soil nitrogen for each site was assessed using a LECO CHN-2000 analyser (Leco Corporation, St Joseph, MI, USA) and total phosphorus using ICPOES Method # 113 (Anonymous, 2000). Total N and P for the transplant sites (Dan Dan total N: 0.11% w/w, total P: 220 mg kg⁻¹; Calliope: total N: 0.07% w/w, total P: 240 mg kg⁻¹) was similar to the range found at sites within *A. falcata*'s natural distribution (range total N: 0.07–0.20% w/w, total P: 74–237 mg kg⁻¹) (Andrew & Hughes, 2005c).

Herbivore community structure

Arthropods on the transplants were sampled in May 2001, November 2001 and February 2002. At each site, at each sampling time, five *A. falcata* plants from each collection latitude were haphazardly selected and sprayed with 0.6% pyrethrum/water solution in the morning on low-wind days, a total of 120 samples. All arthropods that fell onto two collecting trays (50 cm × 30 cm) placed beneath the plants were transferred into vials containing 70% ethanol for storage. Collections were also made using the same methods on an equivalent number of *A. leptostachya* Benth. (subgenus Phyllodinae, section Juliflorae), at both transplant sites at each sampling period. After the February 2002 sample, all transplanted shrubs were destroyed, pre-flowering, to comply with scientific licensing conditions.

All Coleoptera and Hemiptera were identified to family and morphospecies. Adult morphospecies were formally identified as separate species by expert taxonomists. Only species classified as phytophagous were used in this study. Larvae and nymphs were excluded from the analysis because it is extremely difficult to associate juveniles with adults of the same species in preserved collections.

The Coleoptera and Hemiptera were classified into functional guilds according to their different feeding

habits, evolutionary lineages and morphological characteristics (Lawrence & Britton, 1991; Elliott *et al.*, 1998; Peeters *et al.*, 2001). Coleoptera were divided into leaf-chewers (species within the families Cerambycidae and Chrysomelidae: superfamily Chrysomeloidea) and weevils (species within the families Attelabidae, Belidae, Brentidae and Curculionidae: superfamily Curculionoidea). Hemiptera were divided into five guilds: phloem hoppers, phloem bugs, mesophyll hoppers, mesophyll bugs and xylem hoppers. Classification into each guild was based on the feeding habit and taxonomic relationship of each species as reported in CSIRO (1991), Peeters *et al.* (2001), Andrew & Hughes (2004, 2005b) and from expert taxonomist advice (G. Cassis, M. Fletcher and G. Taylor). Phloem hoppers feed on phloem sap and were identified from the suborder Auchenorrhyncha including leafhoppers (most Cicadellidae subfamilies) and planthoppers (Fulgoroidea). Phloem bugs also feed on phloem sap and comprised species from the suborder Sternorrhyncha including psyllids (Psylloidea), aphids (Aphididae) and white flies (Aleyrodidae). Mesophyll hoppers feed on mesophyll fluid and were identified as leafhoppers from the suborder Auchenorrhyncha, family Cicadellidae, subfamily Typhlocybinae. Mesophyll bugs also feed on mesophyll fluid and included species from the Heteroptera (true bugs). Xylem hoppers feed on xylem fluid and comprised species from the suborder Auchenorrhyncha including froghoppers (Cercopidae) and leafhoppers from the family Cicadellidae, subfamily Cicadellinae.

Owing to the low number of herbivore species per shrub sampled, individual shrubs were pooled within latitudes of origin and for both transplant sites and three sampling times. G-tests were used to compare the proportion of species within guilds on the transplanted *A. falcata* to (i) a previously collected data set of arthropods from *A. falcata* throughout its natural range, sampled seasonally for 2 years (930 plants) (Andrew & Hughes, 2004, 2005b) (hereafter referred to as the *full* data set, (ii) *A. falcata* plants from a subset of the current range, standardized to equivalent sample seasons and total number of individual plants as the transplanted plants (hereafter referred to the *standardized* data set) and (iii) the congeneric host species native to the transplant sites, *A. leptostachya*.

For the *standardized* data set, we used collections from 30 randomly chosen shrubs from each of the four latitudes (Batemans Bay, Sydney, Grafton and Gympie) from three of the eight seasonal samples made between November 1999 and February 2001 (November 2000, February 2001 and May 2001), a total of 120 samples.

We used a G-test to compare total species richness, and richness within the two herbivore taxa (Coleoptera

and Hemiptera) among transplants originating from seeds collected at different latitudes (data collected from the two transplant sites were combined).

Owing to the different number of samples made between those along the latitudinal gradient and the transplant latitudes, species richness comparisons were also plotted as a function of the number of individuals collected (Gotelli & Colwell, 2001; Andrew & Hughes, 2005b). Accumulation (rarefaction) curves were generated to compare the species richness between *A. falcata* transplant shrubs and *A. falcata* plants within the natural range using ESTIMATE S 5.0 (Colwell, 1997). Species accumulation curves were standardized by comparing the number of species per 119 individuals (the lowest number collected from *A. falcata* at any of the latitudes or transplants). *A. falcata* samples used for this comparison were taken only from the *standardized* data set.

Herbivory assessment

An assessment of rates of herbivory was made on the transplanted shrubs following the protocols outlined in Andrew & Hughes (2005c). Briefly, herbivore damage was assessed over a 12-month period, from February 2001 to February 2002. Five expanding phyllodes on one branch from each of five plants from each of the four latitudes were sequentially numbered using a water-based permanent pen. Images of each phyllode were taken *in situ* using a digital camera. Three different types of herbivore damage (chewing, sap-sucking and mining) were identified and the area missing, relative to total phyllode area was assessed using IMAGE J software (Rasband, 2003).

To assess differences in herbivory among the four latitudes of origin, chewing, sap-sucking and mining herbivory per phyllode was measured over 12 months, from February 2001 to February 2002. Herbivory was compared both among latitudes of origin and transplant sites by a two-way multivariate analysis of variance (MANOVA), with plants originating from each of the four latitudes used as replicates (rates for individual phyllodes were averaged within plants) using DATADESK[®] 6.1, (Data Description Inc., Ithaca, NY, USA) (Velleman, 1997). Pillai's trace was the test statistic used (Tabachnick & Fidell, 2001; Quinn & Keough, 2002).

To compare rates of herbivory at the transplant latitudes to those in the natural distribution, an average percentage herbivory for each damage type (chewing, sap-sucking and mining) at each transplant site was compared with a subset of a previously collected data set (Andrew & Hughes, 2005c) over a comparable 12-month period (February 2001 to February 2002). Average percentage herbivory per site, within each of the four natural distribution latitudes and the transplant

latitude, were used as replicates (rates for individual phyllodes and plants were averaged). Percentage herbivory among the latitudes and transplants was compared using a one-way MANOVA using DATADESK® 6.1. Pillai's trace was the test statistic used. By pooling samples across leaves and sites within latitudes we have taken into account much of the variation that occurs within latitudes. This does reduce the statistical power of these analyses but we believe that this method is appropriate for the questions addressed.

A priori power calculations were carried out for each of the hypotheses being tested. Analyses were calculated using GPOWER (Erdfelder *et al.*, 1996) with Cohen's (1988) 'medium' effect size conventions used.

Results

Herbivore community structure

Eleven species of adult Coleoptera were collected from the transplanted shrubs: five from the Curculionidae, four from the Chrysomelidae and two from the Brentidae. Nineteen species of adult Hemiptera were collected: seven species from the Cicadellidae, three each from the Alyrodidae and Psyllidae, and a single species each from the Aphididae, Issidae, Lygaedae, Meenopliidae, Membracidae and Miridae.

Of the 30 species collected on the transplants, only five species were collected from previous samples of *A. falcata* within its natural range: four Hemiptera and one Coleoptera species (Table 1 – species in bold). Of these, *Aphid* sp. 4 and *Calomela ioptera* were common at both transplant sites. The three other species were sampled only once: *Acizzia* sp. 1 and *Zygina ipoloo* were sampled only at Calliope, while *Acizzia* sp. 2 was sampled only from Dan Dan.

Eight herbivore species, six Hemiptera and two Coleoptera, were collected from *A. leptostachya* (compared with 30 for the transplanted *A. falcata*). All eight species were also found on the transplants (Table 1).

Six feeding guilds were found on the transplants, compared with seven for the full data set sampled from the natural range of *A. falcata*: eight species of phloem hopper, seven species each of phloem bugs and weevils, four species of leaf beetle, two species of mesophyll bug and two species of mesophyll hopper. The seventh guild, xylem hoppers, was not found on the transplanted shrubs (but it should be noted that this guild was very sparse on *A. falcata* within its natural range as well). The proportion of species within each guild on the transplants was not significantly different from that of either the *full* data set collected ($G_6 = 7.50$, $P = 0.28$, power = 0.90), or the *standardized* data set ($G_6 = 9.3$, $P = 0.16$, power = 0.69) (Fig. 2). However, there were

significant differences between guild structure on the transplanted *A. falcata* and the co-occurring *A. leptostachya* ($G_6 = 20.22$, $P < 0.01$, power = 0.23): compared with the transplanted *A. falcata*, *A. leptostachya* had a higher proportion of phloem bugs and mesophyll hoppers but a lower proportion of phloem hoppers and no mesophyll bugs. It should be noted, however, that the fauna of *A. leptostachya* was rather depauperate, so this comparison should be treated with some caution.

We compared species accumulation curves between the transplants and plants from the four latitudes within the natural distribution of *A. falcata* (Fig. 3). The transplants had a lower species accumulation at an equivalent number of individuals ($n = 119$) compared with collections from Sydney, Gympie and Batemans Bay but a higher number of species compared with Grafton.

Thirteen species were common to more than one transplant site (Table 1 – Group A). Eight species were found at both sites, while two species were found only at Dan Dan, and three were found only at Calliope. Two species dominated the herbivore community (Fig. 1), *Alcidodes bulbo* and *Aphid*-4. Together, these comprised 58% of the abundance of individual herbivores sampled. Seventeen species were *rare*, being collected from one plant at only one collection time (Table 1 – Group B).

Herbivory

There were no significant differences in the overall rates of herbivory on *A. falcata* between the transplant location and the natural distribution latitudes (Table 2a, Fig. 4) and for two of the three component herbivory types, chewing and sap-sucking herbivory (Table 2b). Mining herbivory was significantly lower at the transplant sites ($0.55 \pm 0.29\%$) compared with Gympie ($5.86 \pm 2.34\%$) (Table 3b).

Comparison between host plant latitudes of origin

There were no significant differences in either the total number of species (Hemiptera and Coleoptera combined) ($G_3 = 2.1$, $P = 0.55$, power = 0.24), or for either order compared separately (Coleoptera: $G_3 = 0.78$, $P = 0.85$; Hemiptera: $G_3 = 1.90$, $P = 0.59$, power = 0.15) on the transplants originating from the four different collection latitudes.

There were no significant differences in the overall rate of herbivory among *A. falcata* plants from different latitudes of origin, nor among the component types of herbivory (Table 3). Similarly there was no significant difference in the overall rate of herbivory among transplant sites, however, there was a significantly higher

Table 1 Abundance of phytophagous Coleoptera and Hemiptera collected from *Acacia falcata* transplants (latitudes of origin pooled) and *Acacia leptostachya* plants (native to sites) at two sites (Calliope and Dan Dan) near Gladstone, central Queensland

Feeding guild	Family	Herbivore species	<i>Acacia falcata</i>		<i>Acacia leptostachya</i>	
			Dan Dan	Caliope	Dan Dan	Calliope
<i>Group A</i>						
Phloem bug	Aphididae	Aphid-4	17	27		2
Phloem hopper	Cicadellidae	Cicad-T2	10	1		
Leaf beetle	Chrysomelidae	<i>Calomela ioptera</i> (Baly)	8	8		
Phloem bug	Alyrodidae	Alyrod-T1	8	5	2	
Weevil	Brentidae	<i>Apion</i> -T1	3	6	1	
Phloem hopper	Cicadellidae	Cicad-T1	2	1	1	
Phloem hopper	Membracidae	Membr-T1	1	1		
Mesophyll bug	Lygaeidae	Saldid-3	1	1		
Phloem hopper	Cicadellidae	Cicad-T1	3			
Mesophyll hopper	Cicadellidae	Cicad-T3	2			
Weevil	Brentidae	<i>Alcidodes bubo</i> (Fabricius)		76		1
Weevil	Curculionidae	Curc-T2		6		
Phloem bug	Psyllidae	<i>Acizzia</i> sp. 1		2	1	13
<i>Group B</i>						
Phloem hopper	Cicadellidae	<i>Mapochiella rotundata</i>	1			
Leaf beetle	Chrysomelidae	Chry-T1	1			
Weevil	Curculionidae	Curc-T4	1			
Phloem bug	Psyllidae	Acizz-T1	1			
Mesophyll hopper	Cicadellidae	<i>Zygina ipoloa</i> (Kirkaldy)	1		1	
Phloem hopper	Meenoplidae	Meeno-T1	1			
Phloem bug	Psyllidae	<i>Acizzia</i> sp. 2	1			
Phloem bug	Alyrodidae	Alyrod-4	1			
Mesophyll bug	Miridae	Mirid-T1	1			
Weevil	Curculionidae	<i>Neolaemosaccus</i> -T5		1		
Phloem hopper	Cicadellidae	Cicad-T2		1		
Leaf beetle	Chrysomelidae	<i>Rhyparida</i> sp. 2		1	1	1
Leaf beetle	Chrysomelidae	Chry-T5		1		
Phloem bug	Alyrodidae	Alyrod-T3		1		
Weevil	Curculionidae	<i>Nanophyes</i> -T3		1		
Phloem hopper	Issidae	Issid-T1		1		
Weevil	Curculionidae	Curc-T6		1		
Number of species			19	19	6	4

Component feeding guilds and family associations are also included. Species in bold were also found on *A. falcata* within its current coastal distribution (see 'Results' for details). Group A species were common to more than one plant at more than one collection time. Group B species were *rare*, being collected from one plant at only one collection time.

amount of sap-sucking herbivory at Calliope ($1.44 \pm 1.69\%$) compared with Dan Dan ($0.47 \pm 0.79\%$). There were no significant interactions between latitude of origin and transplant site. It should be noted that across both sites, the rates of herbivory ranged from 1.9% to 88.7% per plant for phyllode chewing, 0% to 7.05% per plant for sap-sucking, and 0% to 6.7% per plant for phyllode-mining.

Discussion

Climate change will have profound impacts on most species and communities over the next century and

beyond. Predicting both the magnitude and direction of these impacts for even single, well-studied species is difficult, and for whole suites of interacting species even more so (Voigt *et al.*, 2003). Most predictions made to date have come from either small-scale experiments in which factors such as temperature and CO₂ have been manipulated (e.g. Diaz *et al.*, 1998; Dury *et al.*, 1998; Buse *et al.*, 1999; Johns & Hughes, 2002), bioclimatic modelling (e.g. Woodward & Rochefort, 1991; Brereton *et al.*, 1995; Hughes *et al.*, 1996; Kadman & Heller, 1998; Hoegh-Guldberg, 1999; Beaumont & Hughes, 2002), field studies along environmental gradients (e.g. Hill & Hodkinson, 1992; Harrison, 1993; Whittaker & Tribe,

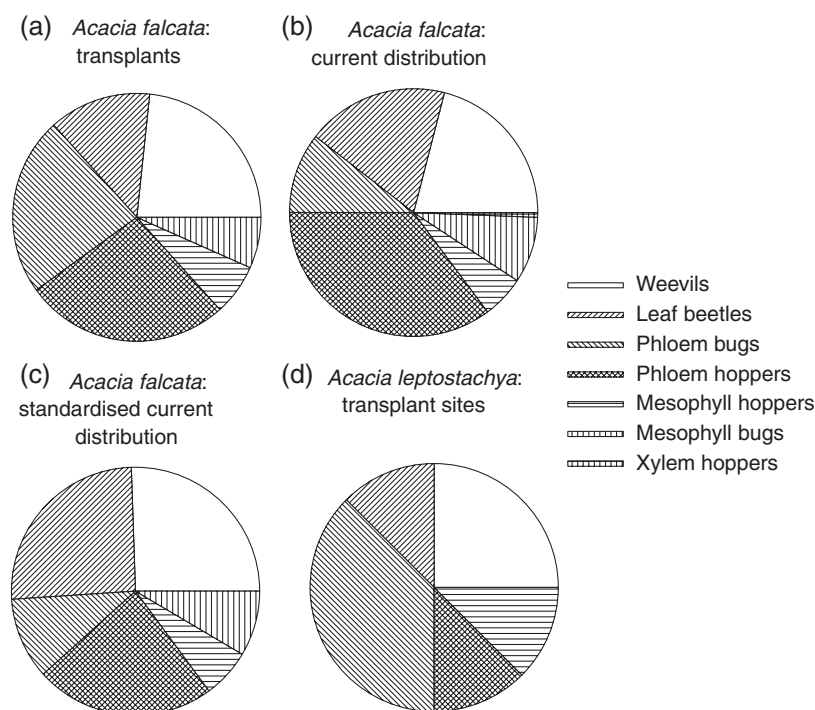


Fig. 2 Herbivore guild composition on (a) transplanted *Acacia falcata* (b) *A. falcata* from its current range based on all samples collected (Andrew & Hughes, 2004, 2005b), (c) *A. falcata* in current range based on an equivalent number of plants sampled as the transplants and (d) *Acacia leptostachya*, the native host plant at the transplant sites.

1996; Fielding *et al.*, 1999; Hodkinson *et al.*, 1999; Fleishman *et al.*, 2000; Andrew & Hughes, 2004, 2005b), and long-term studies at a few sites (e.g. Woiwod, 1997; Voigt *et al.*, 2003). Transplant experiments offer a useful complement to these approaches and can be used to address broad questions about how communities might be structured and composed in the future.

In this study, we found that the herbivore assemblage collected from transplanted shrubs had a similar guild structure to that of the host within its current geographic range and was significantly different from the assemblage on a congeneric species at the transplant site. This suggests that community structure, based on the relative number of species in the guilds we identified, may be influenced more by the particular characteristics of the host plant species (be they chemical or physical) than by climate. The somewhat depauperate herbivore fauna on *A. leptostachya* compared with *A. falcata*, however, means that differences in guild structure between hosts at the transplant sites need to be interpreted with some caution.

The insect assemblages we collected included adult representatives from the major feeding guilds also found within the natural range of *A. falcata*, except for xylem feeders. Adult xylem feeders were also rare in the main range of *A. falcata* (sampled only at Batemans Bay – the most temperate latitude), and their

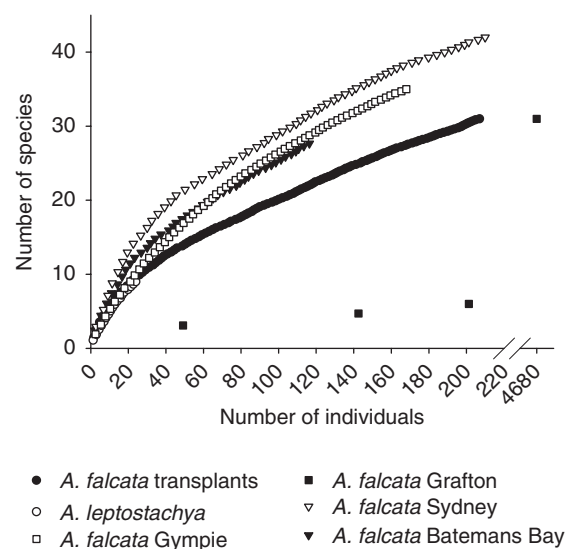


Fig. 3 Rarefaction curve (Coleman curve) of species collected from *Acacia falcata* at the transplant sites and *Acacia leptostachya*, native to the transplant sites and *A. falcata* at each of four latitudes in its current distribution, per number of individuals collected, from the *standardized* data set. See 'Methods' for sampling details.

absence from the data set may be due to them being collected only as nymphs (which were not assessed in this study).

Table 2 Summary table of MANOVA statistics (a) rate of herbivory among the transplant latitudes and latitudes in the natural distribution of *A. falcata* and (b) ANOVA statistics for component herbivory types

Variable	df	Pillai trace		Approx F		P		Power
<i>(a)</i>								
Latitude	12, 24	1.34		1.61		0.15		0.25
		Chewing		Sucking		Mining		
Variable	df	F	P	F	P	F	P	Power
<i>(b)</i>								
Latitude	4, 8	0.47	0.76	1.84	0.22	3.84	0.05	0.25

Significant values in bold. *A priori* power calculations included.

Of the 30 species of herbivorous Coleoptera and Hemiptera collected on the transplanted *A. falcata*, only five were found on *A. falcata* within its current range. The four hemipterans, *Acizzia* sp. 1, *Acizzia* sp. 2, Aphid sp. 4 and *Zygina ipoloea* were cosmopolitan in distribution in the natural range (i.e. found at more than one latitude and on other, co-occurring acacias) (Andrew & Hughes, 2005b). *Calomela ioptera* (Coleoptera), was identified as a *specialist species* in the natural range being only found on one plant at Gympie at one sampling time (i.e. rare) (Andrew & Hughes, 2004), but was relatively common on transplants: this species is also known to feed on a range of *Acacia* species along the east coast of Australia (Reid, 1989).

The transplantation of *A. falcata* into a warmer climate, therefore, demonstrated that a suite of new insect herbivore species may colonize *A. falcata* within its current range over the coming century, assuming the plant's most tropical boundary does not move poleward at the same pace as the insects. Changes in composition within transplanted plant communities have previously been found (e.g. Bruelheide, 2003) but to our knowledge there have been no other published studies in which insect communities on transplanted plants have been assessed.

The number of species that colonized the transplanted *A. falcata* over 12 months was lower than that found at three of the four latitudes within the natural range. Grafton had a low species accumulation when plotted against abundance to other latitudes and the transplant sites, due to samples being dominated (96% of total abundance) by a single herbivore species: *Acizzia* sp. 2 (Andrew & Hughes, 2005b). The transplanted shrubs used in this study were younger and smaller than those sampled within the natural range of *A. falcata* in our previous studies (N. R. Andrew & L. Hughes, unpublished data). It might have been anticipated, therefore, that the transplanted *A. falcata*

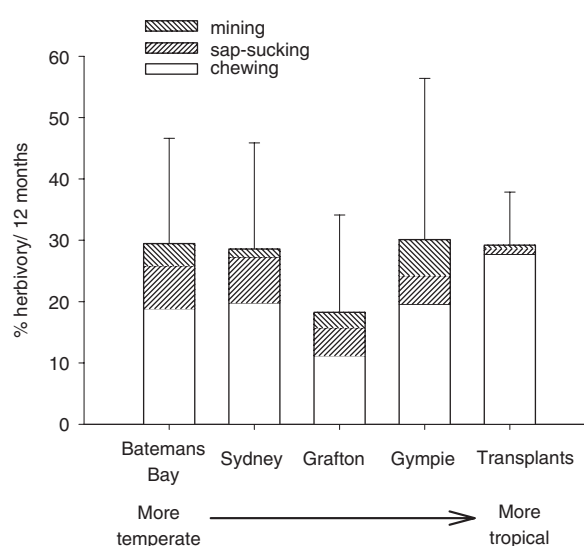


Fig. 4 Average rate of phyllode herbivory (\pm SD) including chewing, sap-sucking and mining on *Acacia falcata* at four latitudes in its natural coastal distribution and the transplant latitude.

would have a more depauperate herbivore community compared with that of the more architecturally complex *A. falcata* shrubs within the natural range (Leather, 1986). Our finding that the guild structure of the transplants did not differ significantly between the transplants and either the full data set of arthropods sampled within the natural range, or the data set subsampled to equivalent sample size, indicated that the differences in size between the plants had little effect on the community collected. Furthermore, we found that the community collected on *A. leptostachya*, which is a small tree (up to 4 m in height) was actually lower in species richness than the transplanted *A. falcata* shrubs.

We found no differences in the diversity of herbivore species among *A. falcata* transplants grown from seeds

Table 3 Summary of MANOVA statistics (a) Rate of herbivory on *A. falcata* among different latitudes of origin and (b) ANOVA statistics for component herbivory types. *A priori* power calculations included

Variable	df	Pillai trace	Approx <i>F</i>	<i>P</i>	Power			
<i>(a)</i>								
Latitude	9,84	0.30	1.04	0.42	0.82			
Site	3,26	0.22	2.46	0.09	0.93			
Latitude * site	9,84	0.35	1.37	0.21	0.82			
		<u>Chewing</u>		<u>Sucking</u>		<u>Mining</u>		
Variable	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	Power
<i>(b)</i>								
Latitude	3,28	0.46	0.71	2.32	0.10	0.74	0.54	0.46
Site	1,28	2.47	0.13	5.63	0.02	1.01	0.32	0.66
Latitude * site	3,28	1.57	0.22	0.62	0.61	2.25	0.10	0.46

collected at different latitudes. While many of the herbivores collected from the transplants were unique to plants originating from one latitude, all were singleton occurrences. Their presence on plants from one particular latitude was therefore, likely to be due to the lack of sampling rather than a preference for transplants from a particular latitude.

There were no significant differences in the rate of herbivory on *A. falcata* among latitudes of origin. There was also no significant difference in the rate of herbivory within the natural range and between the transplanted *A. falcata*. This is in contrast to studies that have concluded that herbivory increases towards the tropics for a range of plant species and habitats (Dyer & Coley, 2002). The most specialized type of herbivory, mining, was significantly lower on the transplanted shrubs compared with only the most northerly latitude (Gympie). We expected a lower rate of mining herbivory at the transplant latitude due to the short period of time miners had to adapt to a new host plant species, compared with rates of mining herbivory in the natural distribution. Rates of herbivory of a more general nature (chewing and sap-sucking) did not change significantly between the transplants and the natural distribution of *A. falcata*. This is possibly explained by generalist herbivores taking less time to adapt to a novel host plant compared with specialist herbivore feeders. Interestingly Bruelheide (2003), found herbivory by a generalist slug increased on plots of montane meadow translocated from high altitude to low altitude. A more detailed analysis of which specific taxa were causing the most chewing damage (in our case Coleoptera or Orthoptera) would be interesting, but was outside the scope of this study.

In summary, we found that guild structure of herbivorous Hemiptera and Coleoptera was similar between host plants transplanted to a warmer climate and the same host species within its current range. The overlap in actual insect species identity between the transplants and the current range, however, was quite low. Similarly, rates of herbivory were similar on *A. falcata* in a warmer climate compared with populations within its natural range. If these results can be generalized to other plant hosts, we might predict that as climate zones shift poleward and mobile organisms like flying insects respond by migrating to stay within their current climatic envelope, plants will be colonized by new herbivore species within similar guilds to those currently supported. Changes in the composition, but not necessarily the structure, of these new communities may, therefore, result. Damage to the plants (as measured by rates of herbivory) by these new suites of herbivores might also be similar in a warmer climate. Similar types of experiments in other regions and for other host species will be needed to test these predictions.

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