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The IBISCA-Queensland Project

Predator pressure, herbivore abundance and plant damage along a subtropical altitudinal gradient

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ABSTRACT

Climate change is predicted to not only cause shifts in the latitudinal and altitudinal distribution of species, but also changes in trophic interactions. Studying changes in herbivory and herbivore and predator pressure along altitudinal gradients may assist our understanding of the complex trophic interactions and their responses to future climate change. As part of the IBISCA-Queensland Project, we tested the hypothesis that ant predation pressure influences the abundance of herbivores which in turn influences herbivory in the understorey of subtropical rainforest and that these relationships are modified by altitude. We used the occupancy of ants at tuna baits as a measure of predation pressure, herbivorous beetles as representatives of herbivores, and the extent of damage to mature leaves as a measure of herbivory. Ant predation pressure was the greatest at 300 m above sea level and declined with increasing altitude but only at ground level. In contrast, ant predation pressure on understorey foliage was not related to altitude and was always much lower than that on the ground. Neither altitude nor ant predation pressure at ground or understorey levels significantly influenced the abundance of herbivorous beetles. However, the species richness of herbivorous beetles significantly decreased with increasing altitude, and ground-level ant predation pressure negatively related to beetle species richness, after controlling for the effect of altitude. Levels of herbivory were not related to beetle abundance, whereas it was significantly negatively related to beetle species richness. This was however, opposite to our prediction that increased beetle species richness would increase leaf herbivory. Consequently, we found little evidence for the cascading effects of ants on herbivory in our study system. We suggest that future studies examine other groups of foliage-feeding insects such as lepidopteran larvae and Orthoptera, and the importance of other natural enemies, including parasitoids as well as non-specific predators. ❐ *elevation, Formicidae, Coleoptera, herbivory, predation.*

Arboreal insect assemblages within tropical ecosystems are dominated by ants in terms of both biomass and the number of individuals (Stork 1988; Hölldobler & Wilson 1990). Often the entire forest canopy fauna is dominated by large ant colonies (Stork 1991; Davidson 1997) many of which play a significant role in plant defenses by attacking invertebrate and mammalian herbivores and by interrupting encroaching vegetation (Huxley 1982). Although the role of ants as specialised predators is limited to some subfamilies and genera (Tobin 1991; Davidson 1997; Blüthgen *et al.* 2000; Dejean *et al.* 2000), a number of studies have demonstrated that ants represent important generalist predators of insect herbivores. For example, ants in lowland forests of New Guinea were responsible for 77% of the total predation of baits of live termites set on the foliage of *Ficus* plants (Novotny *et al.* 1999), while Floren *et al.* (2002), using caterpillars as baits in tropical lowland rain forest in Sabah, Malaysia, found that, on average, 85% of ant individuals in the canopy of trees were predacious. Further, using insecticidal fogging and direct observations, the latter study suggested that arboreal ants were responsible for an observed scarcity of less mobile arthropods in the rainforest canopy. Low numbers of less mobile holometabolous arthropods, such as lepidopteran larvae, were associated with ant dominance. In contrast, highly mobile hemi-metabolous nymphs occurred regularly and in large numbers on ant dominated trees (Floren *et al.* 2002).

Ant assemblages in tropical forests have markedly reduced species richness and abundance at higher elevations (Brown 1973; Fisher 1996; Bruhl *et al.* 1999). This upward depauperisation of ant assemblages along altitudinal gradients is anticipated to be associated with a decrease in predation pressure on herbivorous insects. It is of interest and significance, therefore, to investigate the rates of herbivory across an altitudinal gradient in relation to predation pressure due to ants.

Environmental gradients across latitude and altitude, in Australia and elsewhere, are increasingly being used as surrogate systems for predicting changes in arthropod assemblages in response to changing climatic conditions (Gutiérrez & Menéndez 1998; Bale *et al.* 2002; Andrew & Hughes 2004, 2005). In Australia, a rise in continental average temperature of ~0.8°C has already occurred since 1910 (Nicholls 2006). Our emerging understanding is that as temperatures rise, species are likely to shift their distributions from lower to higher altitudes, and polewards from lower to higher latitudes (Thomas *et al.* 2006). The consequences of such responses will have drastic impacts on existing biodiversity and the ecosystem services they provide (Walther *et al.* 2002).

This study investigated whether the extent of herbivory in understorey vegetation is related to the abundance and richness of insect herbivores, and whether these herbivores are in turn influenced by top-down impacts of predator pressure exerted by ants. We also tested whether these relationships are mediated by differences in altitude. Here we present preliminary results using herbivorous beetles as representatives of herbivores.

METHODS

Our study was carried out as part of the IBISCA-Queensland Project (Kitching *et al.* 2011) which established permanent survey plots along an altitudinal gradient at Lamington National Park, Queensland, Australia. Four replicated plots (20 m x 20 m quadrat) were established within each of five altitudinal zones, at approximately 300, 500, 700, 900 and 1100 m above sea level (a.s.l.). Plots were located within continuous forest spanning araucarian complex notophyll vine forest (300 m a.s.l.), warm subtropical complex notophyll vine forest (500 and 700 m), cool subtropical complex notophyll vine forest (900 m) and simple microphyll fern forest (1100 m) (Laidlaw *et al.* 2011). Long-term

monthly rainfall averages range from about 50 to 250 mm with most falling in summer (December-February) and rainfall increases with increasing elevation (Strong *et al.* 2011).

Ant predation pressure. To assess predator pressure we used the response of ants to food baits. Baits consisted of fragments of tuna (canned in oil) placed in a folded piece of tissue paper (5 cm x 5 cm). Baits were secured with stainless steel entomological pins onto a leaf or twig of an understorey plant ('foliage bait') or onto leaf litter or woody debris on the ground ('ground bait') beneath the foliage bait. A total of approximately 25 pairs (of tuna baits foliage and ground) were placed at random points within each study plot and exposed for 30 minutes (as per Novotny *et al.* 1999). The number of tuna baits attacked by ants was counted and voucher specimens of each ant morphospecies were collected and stored in 70% ethanol for later identification. Sampling was conducted in the austral spring of 2006 (6–24 October). In total, 970 tuna baits were set, 483 in understorey foliage and 487 at ground level across the five altitudinal zones. For logistical reasons, tuna baits were deployed at only two of the four survey plots at 700 m (700C and D, see Kitching *et al.* 2011).

Herbivore pressure in the understorey. The abundance of herbivorous beetles was used as a surrogate for herbivore pressure on understorey plant foliage. Beetles were sampled in the spring of 2006 (6-24 October), by beating 'vegetation' using a 1.5 m long beating stick and a 1 m^2 nylon sheet for collecting the falling material (see Ødegaard & Diserud 2011). 'Vegetation' included all structures including foliage and the trunks of large trees to thin branches, both living and dead. Each sample was obtained by beating all reachable vegetation on both sides of a 20 m long transect starting just outside the 20 m by 20 m standard IBISCA plots and walking in a straight line away from the plot. A forest area of approximately 3 x 20 m (60 m^2) and a forest volume of 60 m^2 x 3 m height (180 m^3) was covered by each sample. Ten samples (transects) were taken at each plot, all performed in different directions from the same starting point to prevent re-beating of the same area. Accordingly, a total of 200 samples was obtained (10 samples x 20 plots), but the 10 samples collected at each plot were pooled before analyses. Beetles were sorted to family and morphospecies. Although beetles representing various feeding guilds were collected (see Ødegaard & Diserud 2011), only herbivorous beetles were used for the present study. Both the total abundance and species richness of herbivorous beetles were recorded for each plot.

Measurement of foliage damage. Foliage damage due to herbivory within understorey vegetation was estimated from a random selection of leaves taken during spring (6-24 October) 2006. Leaf samples were collected from all four plots at each altitude, except at 700 and 900 m a.s.l. where only two and three plots were sampled respectively. At each plot, we randomly hand collected mature leaves of understorey vascular plants. Leaves from each plot were thoroughly mixed in a large cardboard box. Leaves were then picked from the box and progressively laid out flat, with the edges of individual leaves slightly separated, on a 48 cm x 48 cm square frame with a white background. Eight frames of leaves were compiled for each plot, giving a total of 136 frames across the five altitudinal zones, with between 16 to 70 individual leaves per frame.

Frames were photographed using an 8 megapixel digital camera and images imported into Adobe Photoshop version 6 (Adobe Systems Inc. 2001). Missing sections on the edges of leaves were reconstructed, based on the shapes of intact leaves of the same species. In addition to missing sections, leaf damage also included desiccated areas caused by leaf mining and leaf skeletonising larvae, and these areas were converted to white. Images were then contrasted to produce a black (undamaged leaf areas) and white (damaged leaf areas) image. ImageJ software (Rasband 2003) was used to measure both damaged leaf area and total leaf area (i.e. damaged and undamaged leaf area

combined). The proportion of leaf damage was calculated by dividing the damaged leaf areas by the total leaf areas summed across the eight frames per plot.

Data analysis. Initially we conducted analyses using altitude as a categorical variable. We first investigated differences in predation pressure (proportion of baits attacked) and species richness (number of species attracted to baits) of ants across the five altitudinal zones, using two-way ANOVA with altitude and stratum (ground versus understorey) as fixed factors. Herbivore pressure (abundance and species richness of herbivorous beetles) and understorey leaf damage were examined by analysis of covariance (ANCOVA) to test for the presence of top-down effects of predation pressure and herbivore pressure, in conjunction with the effect of altitude. Ant predation pressure was included as a covariate in the analysis of herbivore pressure, and herbivore pressure (as species richness or abundance of herbivorous beetles) as a covariate in the analysis of leaf damage. We assumed no interaction between the main factor (altitude) and the covariates. Due to the unequal number of replicated samples (ant data missing from some 700 m plots and leaf damage missing from some 700 and 900 m plots), type III sum of squares was used to calculate F statistics. When we found a significant effect of altitude, *post-hoc* pair-wise comparisons were made using Tukey's HSD tests.

We also conducted multiple regression analysis with altitude as a continuous variable, using the actual altitudes of the study plots (see Kitching *et al.* 2011 for these values). Separate analyses were conducted for five different response variables; ground-level ant predation pressure, understorey-level ant predation pressure, herbivorous beetle abundance, herbivorous beetle species richness and the proportion of damaged leaf area. Analyses of ant predation pressure (ground and understorey) included only altitude as an explanatory variable. Analyses of both beetle abundance and species richness included three explanatory variables; altitude, and ground and understorey ant predation pressure. Analysis of the proportion of leaf damage also included three explanatory variables; altitude, and herbivorous beetle abundance and species richness. A stepwise selection procedure, with P values of 0.05 for inclusion and 0.10 for exclusion, was used to construct the model which best explained the variation in each response variable.

Abundances of herbivorous beetles were log-transformed before analyses, but neither proportional (ant predation pressure and leaf damage) nor species richness of herbivorous beetles were transformed as they were approximately normally distributed without outliers. ANOVAs and ANCOVAs were conducted using the general linear model function, and regression analyses using the linear regression function within SPSS ver. 17 (2009).

RESULTS

Ant predation pressure. Across the five altitudinal zones, 271 of 487 (56%) baits at ground level were attacked by ants, while only 32 of 483 (7%) baits on understorey foliage were attacked. While we found significant effects of both altitude and stratum (ground versus understorey) on ant species richness and predation pressure, their interaction was also highly significant (Table 1). At ground level, we found the greatest number of ant species (mean 9.5) and the greatest proportion of baits attacked (mean 93%) at 300 m a.s.l. and the lowest at 1100 m (1.0 species, 6% of baits) (Fig. 1). However, in the understorey, neither species richness nor predation pressure differed significantly among altitudinal zones, although they were both lowest at 1100 m (Fig. 1). Linear regression confirmed these patterns, with a significant decrease in the proportion of ground-level baits attacked with increasing altitude (t = -5.95, correlation coefficient = -0.84, P<0.001), and no relationship between altitude and the proportion of foliage baits attacked.

TABLE 1. Summary results of ANOVA showing F and P values of altitude, stratum (ground versus understorey) and their interaction effects on ant species richness (number of ant species attracted to baits) and predation pressure (proportion of baits occupied by ants). Degrees of freedom for altitude, stratum, interaction and error are 4, 1, 4, and 26 respectively. Significant P values are shown in bold.

	Altitude		Stratum (ground vs understorey)		Interaction	
Dependent variable	F	P	F	P	F	P
Ant species richness	6.4	**0.001**	37.3	**<0.001**	4.0	**0.011**
Ant predation pressure	11.6	**<0.001**	82.5	**<0.001**	9.0	**<0.001**

TABLE 2. Summary results of ANCOVA showing F and P values of effects of altitude and covariate on abundance and species richness of herbivorous beetles and understorey herbivore damage (proportion of leaf area damaged by herbivores). Degrees of freedom for altitude and covariate are 4 and 1 respectively. Degrees of freedom of error term is 12 for herbivorous beetle abundance and species richness and 11 for herbivore leaf damage. Significant P values are shown in bold.

	Altitude		Covariate			
Dependent variable	F	P			F	P
Herbivorous beetle abundance	0.181	0.944	Ant predation pressure (ground)		**0.001**	0.973
	0.433	0.782	Ant predation pressure (understorey)		1.076	0.320
Herbivorous beetle species richness	7.057	**0.004**	Ant predation pressure (ground)		3.882	0.072
	4.186	**0.024**	Ant predation pressure (understorey)		**0.046**	0.834
Herbivore leaf damage	1.809	0.197	Herbivorous beetle abundance		0.976	0.344
	0.707	0.604	Herbivorous beetle species richness		0.461	0.511

Herbivory pressure. Beating understorey vegetation yielded a total of 4854 beetles representing 604 species. Herbivorous beetles represented 1212 individuals (25% of total) from 132 species (22%). The mean abundance of herbivorous beetles was greater at the highest altitudes (900 and 1100 m) (Fig. 2a). However, ANCOVA analysis found no significant relationship between altitude, nor the covariates (ant predation pressure at ground or understorey level), and the abundance of herbivorous beetles (Table 2). In contrast, the species richness of herbivorous beetles was significantly related to altitude (Table 2) with fewer herbivorous beetle species at higher altitudes (Fig. 2b) in spite of their higher abundances. Neither ground nor understorey ant predation pressure were related to herbivorous beetle species richness (Table 2).

Simple scatter plots between the covariates (ant predation pressure at the ground and in the understorey) and herbivorous beetle abundance and species richness showed no apparent relationships, consistent with the results of ANCOVA (Fig. 3).

Stepwise multiple linear regression selected none of the explanatory variables for herbivorous beetle abundance. In contrast, species richness of herbivorous beetles was significantly negatively associated with increasing altitude (t = -4.72, $P<0.001$). After controlling for the effect of altitude, beetle species richness was also negatively related to ant predation pressure on the ground (t = -3.52, P = 0.003) but not on understorey vegetation.
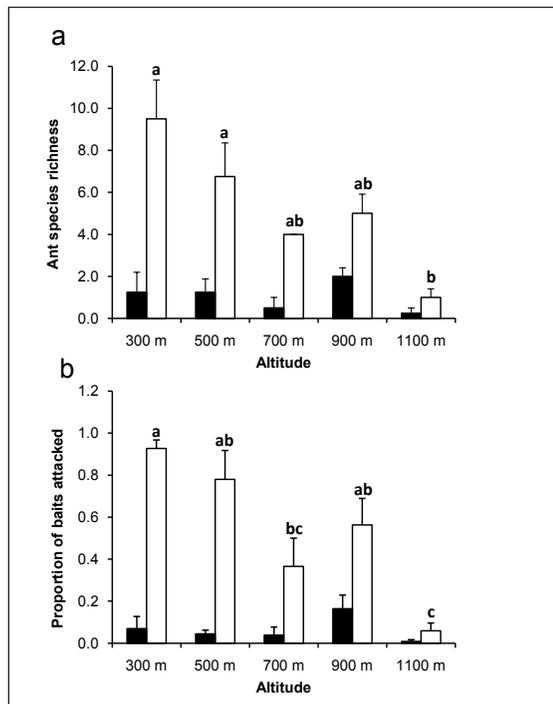
FIG. 1. Mean (+SE) proportion of tuna baits on understorey foliage (solid bars) and at ground level (open bars) attacked by ants within 30 minutes of exposure across five altitudinal zones (300, 500, 700, 900 & 1100 m a.s.l.). Results of post-hoc Tukey tests are shown with different letters indicating significant differences between altitudinal zones.

Herbivore damage of understorey leaves. A total of 5584 leaves was collected from the understorey across the five altitudes, representing 191 109 cm^2 of foliage including 9128.6 cm^2 lost to herbivory. The foliage area lost to herbivory within plots ranged between 2.54 and 9.37%. Although mean leaf damage was lowest at 300 and 700 m (Fig. 4), ANCOVA failed to detect significant altitudinal differences (Table 2). ANCOVA also failed to detect any significant effects of the covariates (abundance or species richness of herbivorous beetles) on the proportion of leaf damage (Table 2). In contrast, multiple regression found that the proportion of leaf damage was significantly negatively related
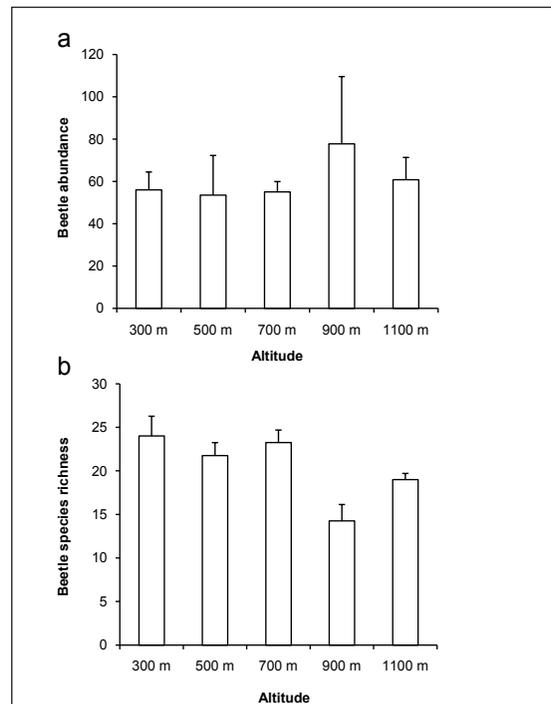

FIG. 2. Mean (+SE) abundance (a) and species richness (b) of herbivorous beetles collected from understorey vegetation across five altitudinal zones (300, 500, 700, 900 & 1100 m a.s.l.).

to herbivorous beetle species richness (t = -2.34, P<0.034). However, this relationship was not consistent within each altitudinal zone (Fig. 5).

DISCUSSION

Ant predation pressure. In tropical forests, ant species richness and abundance are generally reduced at higher altitude (Brown 1973; Fisher 1996; Bruhl *et al*. 1999). Similarly we found a significant reduction in ant species richness and predation pressure (proportion of baits occupied by ants) with increasing altitude. However, this was apparent only for epigaeic ants, and ant species richness and predation pressure in the understorey were much lower than on the
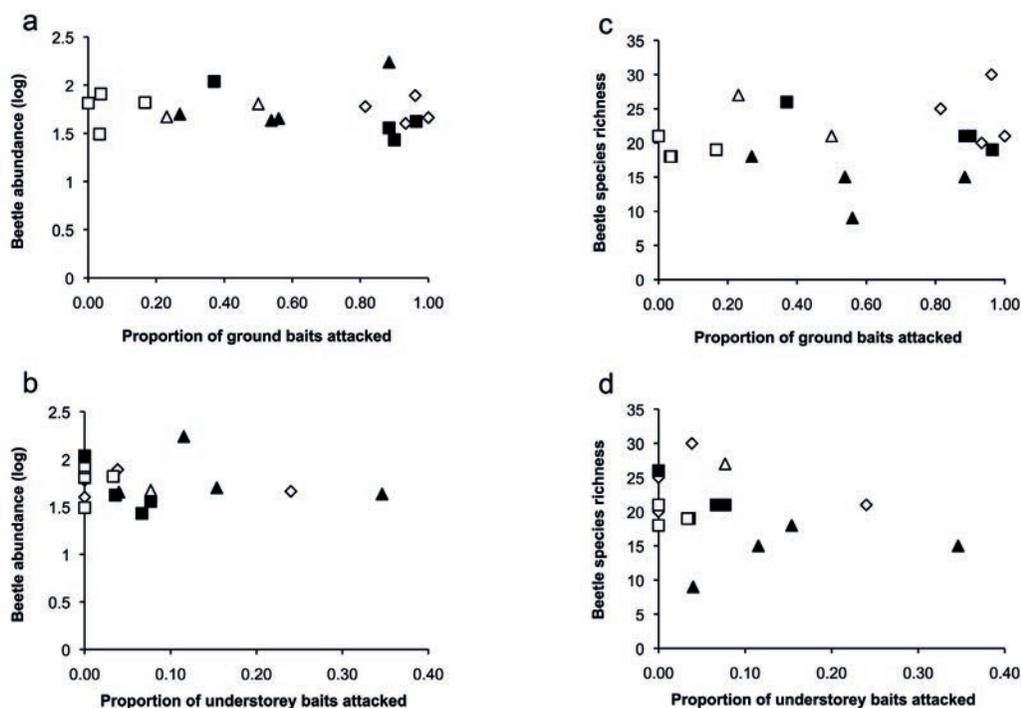
FIG. 3. Relationships between ant predation pressure (proportions of baits attacked) and herbivorous understorey beetles across altitude (◇, 300 m; ■, 500 m; △, 700 m; ▲, 900 m; and □, 1100 m a.s.l.). Beetle abundance was plotted against both proportion of baits attacked on the ground (a) and on understorey foliage (b). Similarly beetle species richness was plotted against baits attacked on the ground (c) and in the understorey (d).

ground, with no significant differences across altitudes (most plots having less than 6% of tuna baits occupied by ants). The low level of ant activity in the understorey observed in this study is in agreement with previous studies that have found low abundance and species richness of arboreal ants in Australia's subtropical rain-forests (Majer 1990; Majer *et al.* 2001).

This low observed ant predation pressure in the understorey, especially at lower altitudes, contrasts with lowland tropical forests where abundances of predatory ant species on trees are usually very high. For example, in lowland rainforest in Sabah, Malaysia, ants average 60% of all arthropods of a tree community (Floren & Linsenmair 1997) and on average 85% of ant
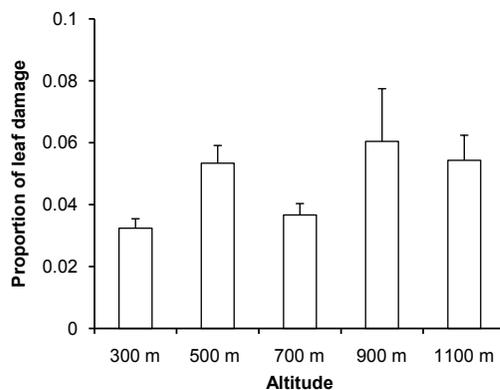

FIG. 4. Mean (+SE) herbivore damage (proportion of leaf area damaged) on understorey plant foliage across five altitudinal zones (300, 500, 700, 900 & 1100 m a.s.l.).
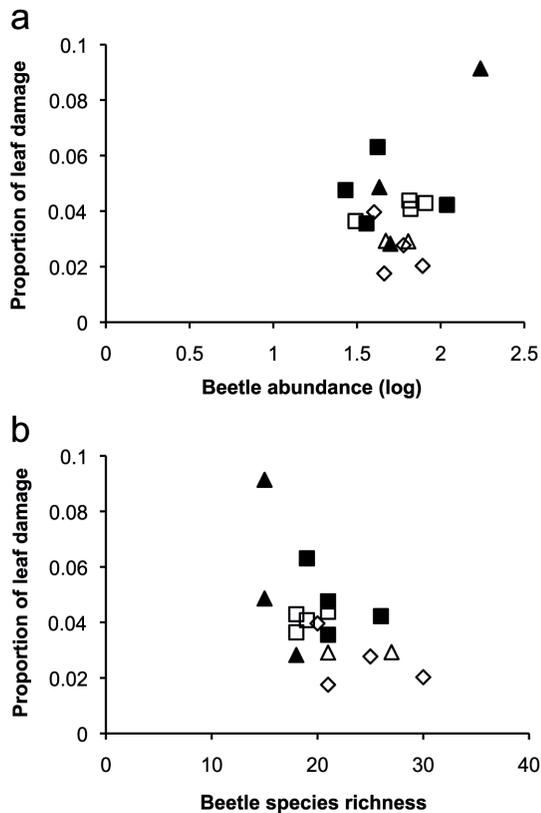
a

b

FIG. 5. Relationships between understorey leaf damage and herbivorous understorey beetles across altitude (◇, 300 m; ■, 500 m; △, 700 m; ▲, 900 m; and □, 1100 m a.s.l.). The proportion of leaf area damaged was plotted against the abundance (a) and species richness (b) of beetles.

individuals per tree are predacious (Floren *et al*. 2002). However, there can be substantially less ants in the understorey compared to the canopy, for example in rainforest in Cameroon ant density in the understorey can be ten times less than in the canopy (Basset *et al.* 1992). This reduced abundance in the understorey is reflected in reduced predation pressure as Olson (1992) recorded predation rates of 26% in the understorey compared to 75% in the canopy in primary rainforest in Cameroon. This

understorey predation rate is similar to that in the understorey of rainforest in Papua New Guinea where Novotny *et al.* (1999) found that during the day, 32% of tethered termites on fig foliage were attacked by ants within 30 minutes. Even though ant predation pressure in the understorey of tropical forests is lower than in the canopy, it still appears to be much greater than predation pressure in the understorey of subtropical rainforest in our study area.

We suspect that the extremely low predation pressure observed in this study is plausible, although it could be argued that it was due to short-comings in our sampling methods. First, tuna baits were placed only within the 20 x 20 m IBISCA-Qld plots, and large colonies of ants that may be nesting within larger tree trunks or canopy foliage may not have been sampled. Second, a bait exposure time of 30 minutes may be too short for subtropical arboreal ants to discover them (although it was sufficient for ground baits to attract large number of ants). Third, the study was conducted only during daylight hours thus excluding nocturnal predatory ant species. The third issue, however, may not be relevant as similar studies in tropical forests have shown that predatory ant activity is higher during the day (e.g. Novotny *et al.* 1999). Despite these issues, we believe that our results are best explained by a lack of dominant ant species (see Majer 1990) which are typical of tropical lowland rainforest and which substantially contribute to the high abundances of ants in these ecosystems.

Herbivory pressure. Although we anticipated some effect of ant predation pressure on herbivores, we did not find strong evidence supporting this hypothesis. The only significant relationship that we found was a negative influence of ground-level ant predation pressure on beetle species richness, after controlling for the effect of altitude. Although this may suggest that some species of herbivorous beetles are susceptible to increased levels of ant activity at ground-level, overall beetle abundance was

unaffected by ground- or understorey-level ant predation pressure.

Given that we observed very low ant activity in understorey vegetation, the lack of a relationship between understorey ant predation pressure and herbivorous beetles is not all that surprising. In addition, adult herbivorous beetles that we used to represent herbivores may not be particularly sensitive to ant predation even if predation pressure had been more intense than observed. Many herbivorous beetle species have differing larval and adult feeding strategies (Reid 2006), which may reduce the extent of direct interactions with predacious ants on the ground and foliage. In addition, more mobile herbivores such as adult beetles and other winged insects such as stick insects and orthopterans, may not be particularly vulnerable to ant predation. Ant predation may have a stronger impact on the less mobile larvae of beetles or moths and butterflies.

Herbivore damage of understorey plant leaves.
We found no significant effect of altitude on the extent of leaf damage. The observed pattern was rather idiosyncratic, with lower herbivore damage observed at 300 and 700 m and greater damage at 500, 900 and 1100 m a.s.l. The extent of leaf damage across the altitudinal zones did not coincide with observed patterns of abundance and species richness of herbivorous beetles. We found fewer beetle species at higher altitudes, but greater herbivory was observed there. Similarly, multiple regression detected a significant negative relationship between the species richness of herbivorous beetles and the proportion of leaf damage. We initially anticipated that increased herbivore pressure would result in greater levels of leaf damage, but the observed pattern was opposite to our expectation. The basis for the observed inverse relationship between beetle richness and levels of herbivory is unclear, but our results should be interpreted carefully as adult beetles are not the only insects causing leaf damage. In addition, most beetle species with foliage feeding adults belong to the subfamily Chrysomelinae (Chrysomelidae) and the broad-nosed weevils (Curculionidae), and these beetles were rare and species poor within our study sites at Lamington National Park (Ødegaard, personal observations).

Our results also require careful interpretation due to the way we measured leaf damage. Our leaf sampling involved the random collection of damaged and undamaged leaves still attached to plants. Consequently our measure of leaf damage did not account for leaves that were fully consumed or abscissed due to herbivory, potentially causing underestimation of herbivory. Ideally herbivore damage should be measured over the entire life span of each leaf (e.g. Lowman 1987). In addition, measuring leaf damage is complicated by leaf longevity. As leaves age they generally become less palatable to herbivores and most damage is sustained within a short period of time when the leaf is young (Coley 1980, Lowman 1985). This complicates trying to relate leaf damage of mature leaves with herbivore pressure. As leaf longevity increases there is more potential for a temporal mismatch between herbivore pressure at the time of sampling and herbivore pressure experienced when leaves were damaged.

We initially hypothesised that ant predation pressure would influence the herbivore pressure which in turn would influence the extent of leaf damage in the rainforest understorey and that these relationships would be modified by altitude. Specifically arboreal ant abundance was expected to decline with increasing altitude, ultimately resulting in an increase in herbivory with increasing altitude. However, we found very little evidence for the cascading effects of ants on herbivory in our study system, the subtropical rainforest of south-eastern Queensland. This may largely result from the depauperate arboreal ant fauna of these forests, across all altitudes. Predatory arboreal ants are much more abundant in tropical forests, where a similar study may shed more light on the role of altitude in modifying the influence of ants on herbivore dynamics. Our study begs the question of what drives herbivore

dynamics in subtropical rainforest. We suggest that future studies examine other groups of foliage-feeding insects such as lepidopteran larvae and Orthoptera, and the importance of other natural enemies of herbivores, including parasitoids as well as other non-specific predators.

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