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Vegetation traits and herbivory distribution in an Australian subtropical forest

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ABSTRACT

We tested the hypothesis that leaves in the canopy should have higher sclerophylly indices compared with understorey leaves, which should, along with other physical foliage traits, allow greater gall-forming insect survivorship in the canopy and result in higher leaf-chewing damage in the understorey. The study was conducted in the subtropical rainforest of Lamington National Park, Queensland, Australia. Along an altitudinal gradient, four independent canopy pin-transects and one equivalent, horizontal understorey pin-transect (20 metres long) were conducted at each of four altitudes, 300, 700, 900 and 1100 m above sea level (a.s.l.). Each discrete layer (stratum) of foliage within the 1 m diameter pin-transects was considered a sample. From each sample, various leaf and meristem measurements were taken, and the number of damaged leaves was counted. Healthy leaves were also collected for analysis of specific leaf mass, an indirect measure of sclerophylly. All vegetation resources were more abundant in the canopy than in the understorey, and also increased from lower to higher altitudes. In the canopy, leaf density increased steadily from 300 to 1100 m sites, but in the understorey 300 and 900 m had denser foliage than 700 and 1100 m. Young leaves were more available in the canopy than the understorey. However, the sites at 900 and 1100 m had as many young leaves in the understorey as 300 m sites had in the canopy. The ratio of young/mature leaves increased with altitude, with no difference between understorey and canopy. Leaf area did not vary between canopy and understorey. Active meristems were found in greater numbers in the canopy. A significant increase in sclerophylly with increasing canopy stratum height was found. Comparing altitudes, 300 and 1100 m sites had more active meristems than those at 700 and 900 m. Out of 72 plant species, 29 presented galls of which the greatest densities were concentrated on seven host species. Herbivory was more intense at lower altitudes, suggesting that micro-climate and host specificity may drive the insect distribution patterns ❒ *canopy-understorey vegetation gradient, gall density, leaf herbivory, gall super hosts, Lamington National Park, sclerophyllous habitats.*

Herbivorous insect species diversity and population parameters are affected by the quality and distribution of their food resources, in particular leaves. Nevertheless, little has been done to describe forest canopy traits at the scale which is relevant for herbivores: the foliage. Leaf area, spatial distribution, density and sclerophylly may be measured, along with the distribution of damaged leaves, and thus produce direct information on how leaf traits affect the distribution of herbivory. Recently Ribeiro and Basset (2007) showed the importance of sclerophylly and leaf density for gall-forming and leaf-chewing herbivory. The positive response of galls to increasing sclerophylly with canopy height and an accompanying inverse response of leaf-chewing seem to be strong ecological patterns, likely to be repeated in a variety of distinct forest types.

Gall-forming insect species are highly specialist endophagous insects. The mechanisms by which their larvae interact with leaves have been the focus of many ecological studies and of a number of important hypotheses (Price 1994; Price *et al.* 1998; Mendonça 2001). Gall insects manipulate the leaf tissues, inducing nitrogen-richer cells to grow, surrounding the larvae. As a consequence, this guild strongly contrasts with free-feeding, leaf-chewing herbivores. Gall species are specialists and adapted to low nutritional leaves, whilst leaf chewers tend to be generalist species, closely dependent on the natural nutrient content of the host leaves (Coley *et al.* 1985; Herms & Mattson 1992; Novotny & Basset 2000; Novotny *et al.* 2002). Recent studies on gall diversity in Panama have shown a substantially larger number of galls in the canopy of tropical forests than in any other ecosystem (Ribeiro & Basset 2007). These authors demonstrated that the upper canopy is a sclerophyllous and harsh environment compared to the understorey, thus favourable for gall survivorship.

Although the distribution of gall-forming species is considered to be strongly related to sclerophylly, it is also highly correlated with a limited number of host taxa that have galls in each ecosystem, or within a habitat in each ecosystem. For instance, although gall populations were larger in the canopy compared to the understorey, galls were only found on 16 plant species in San Lorenzo Park, Panama, representing only 22% of sampled tree species (Ribeiro & Basset 2007). Both Price (1977) and Fernandes (1992) proposed that gall diversity is positively related to plant family size (i.e. the number of species in families), but neither author actually discussed how the evolutionary constraints that restrict gall-forming species to so few host choices may affect the global pattern of gall species distribution.

In addition, until Ribeiro and Basset (2007) there was no methodology available to compare gall abundance or leaf herbivory in a way that compensates for differences in vegetation densities along vertical gradients in forests. A sampling protocol that explicitly accounts for vegetation density in comparable habitat volumes not only allows the adequate comparison of herbivory levels, but also enables proper quantification of the distribution of vegetation within and between sites and habitats.

The present work describes the variation in forest foliage traits, such as leaf strata (discrete layers of foliage), leaf density, active meristem density and leaf sclerophylly, between habitats and along an altitudinal gradient in a subtropical, mesic, cloud forest in south-eastern Queensland. We also examine how gall density and herbivory is distributed from the understorey to the canopy, along the same altitudinal gradient.

MATERIALS AND METHODS

Study sites and canopy access. Research was conducted in subtropical rainforest in Lamington National Park, Queensland, Australia. The park has an area of 20 590 ha, and belongs to the Gondwana Rainforests of Australia World Heritage Area. It has an altitudinal gradient ranging from around 200 m to 1150 m above sea level (a.s.l.). The rainforest of the highest elevations is simple microphyll fern forest dominated by *Nothofagus moorei* (Fagaceae). Climate is seasonal, with most of the annual rainfall (1800 mm) occurring in the summer months (between November to March). In the winter the temperature can fall as low as 0° C overnight (see Strong *et al.* 2011). Sampling was undertaken as part of the larger IBISCA-Queensland Project described in Kitching *et al.* (2011). This project provided the framework for this study and established a series of four permanent plots (A-D) at each of five altitudinal categories (300, 500, 700, 900 and 1100 m a.s.l.). Due to difficulties with site access and associated safety constraints for sampling with single rope climbing techniques, the 500 m altitude sites could not be used in this project. All other altitudes were sampled.

Samples were taken in October 2006, during the early wet season, and again in March-April 2007, in the early dry season. This was an exceptionally dry period, with rainfall ranging from 200-300 mm in the October sampling period, and from 100-200 mm in April, in both cases below the historic mean precipitation (Bureau of Meteorology, Qld Climate Service Centre: http://www.bom.gov.au/climate/).

Sampling protocol – the pin-cylinder transect. Vegetation traits and herbivory were measured, and galls sampled, on all leaves within a volumetric cylinder space of one metre in diameter, settled in both vertical and horizontal sections of the forest. For the 'canopy-pin transect', each cylinder transect started at the upper canopy and finished at three metres above the ground. For the 'understorey-pin transect', it followed an equivalent horizontal transect of 20 m (the average height of this forest) parallel to and at 10 cm above the soil surface, thus preventing sampling seedlings. This method is similar to the pin-quadrat method used in phytosociological surveys of grasslands (Borges & Brown 1999), but instead of counting leaf touches, we counted leaves and galls found inside this cylindrical volume. Within each transect, a sample was taken as a discrete layer of foliage, i.e. a continuous group of leaves separated by a distinct gap from the next group, hereafter called a leaf stratum (see details in Ribeiro & Basset 2007). Four independent canopy pin-transects (one per plot) and one horizontal understorey pin-transect were conducted per altitude (300, 700, 900 and 1100 m a.s.l.). The understorey pin-transects were set in the plots 300C, 700A, 900B, and 1100C, by random choice.

From each sample, the total number of leaves, the number of young leaves, the number of buds and active meristems and the number of damaged leaves were counted. Leaf herbivory was estimated by counting all leaves with more than 10% of the leaf area lost, estimated visually. Since this figure represents the global average leaf area loss in tropical wet forests, leaves scored above this average may be considered 'substantially damaged' (Coley & Aide 1991), and we used the proportion of damaged/total leaves per stratum as our estimate of free-feeding herbivory. Healthy leaves were collected for analysis of specific leaf mass, an indirect measure of sclerophylly. Specific mass per leaf area unit (Cooke *et al.* 1984) was obtained by dividing leaf dry weight by area, using mature leaves collected in 2006. To estimate gall densities, all leaves in a sample with galls, or any gall-like imperfection, were collected, counted and frozen for future analyses. Detailed analyses of the causes of mortality of galls will appear elsewhere.

Statistical analyses. The effects of altitude and forest habitat (understorey versus canopy) on vegetation traits and herbivory were tested in a mixed ANCOVA model, with sample sites set as random factors and altitude as a covariate, or with bifactorial models, taking altitude as fixed factors in interaction with habitat. The model choice depended on the hypothesis and the assumed necessity to explicitly incorporate the site variation in the model – first option – or to test variance between individual altitudes rather than altitude as whole – second option. In these analyses, the mean canopy pin transect data were compared with the understorey pin transect data. Some dependent variables were ln(x+1) transformed, to satisfy the assumptions of normality. Proportion of damaged leaves was transformed by the arsine of the square root. All models were analysed using in SPSS 17.0.

RESULTS

Forest vegetation traits and herbivory distribution. All vegetation resources were more abundant in the canopy than in the understorey, and also increased from the lower to the higher altitudes (Figs 1, 2). The particulars are worthwhile exploring.

*Foliage volume and young leaves***.** Total leaves, as expected, were much denser in the canopy than in the understorey (ANOVA, $F_{1;160} = 182.5$, $p<0.0001$, Fig. 1). Although leaf density in the canopy increased steadily from 300 m to 1100 m, in the understorey leaf density did not vary substantially between altitudes, resulting in a significant interaction between these factors (ANOVA $F_{3;160} = 3.4$, $p < 0.05$, Fig. 3). Young leaves were more available in the canopy than in the understorey, but the difference was marginally significant ($p < 0.07$) due to a stronger interaction between habitat and altitude: the plots at 900 and 1100 m showed as many young leaves in the understorey as in the canopy of plots at 300 m (ANOVA $F_{1;150} = 9.6$, $p < 0.01$, Figs 2, 3). The understorey at 300 and 700 m had the lowest amounts of young leaves. Interestingly, the ratio of young to mature leaves increased consistently with altitude, with no difference between understorey and canopy ($y = 0.00018$; $r^2 = 0.48$, $p < 0.0001$; effect of habitat – t-test = 1.6, $p = 0.113$, Fig. 3). On the other hand, leaf area did not vary between canopy and understorey, and was greater at 300 and 700 m than at other altitudes (LSD, $p < 0.05$). This result reflects larger leaves in the understorey than in the canopy, but also a substantially large variation in the data (Fig. 4).

Finally, there was little variation in the number of leaf strata. The mean number of strata for all transects was 5.4, and the 900 m altitude had the greatest number (mean = 7.25) and the only forest with eight strata (in three of the four transects). The minimum number of strata was three, found at 300 m and 1100 m.

*Buds and meristems***.** Active meristems, namely young vegetative and reproductive buds, flowers and fruits, comprise a very particular type of resource for herbivorous insects. Unequivocally, most of these resources were found in greater numbers in the canopy (ANOVA, $F_{1;160} = 141.3$, $p < 0.0001$, Fig. 4). Comparing altitudes, the 300 and 1100 m plots had more active meristems than those at 700 and 900 m sites (ANOVA, $F_{3;160} = 4.4$, $p < 0.04$, Fig. 4).

A strong positive correlation between leaf sample height in the canopy and sclerophylly was found ($y = 0.0075 + 0.00020$ [Median height]; $r^2 = 0.41$; $F_{1,161} = 112.3$, $p < 0.0001$ Fig. 5), consistent across all altitudes. Leaf area lost by chewing (estimated only for 2006) showed a significant negative response to canopy height, although there was no direct response to sclerophylly. However, the regression model explained low levels of the data variance ($y = 0.36 - 0.0052$ [median height]; $r^2 = 0.04$; $F_{2,160} = 3.3$, $p < 0.05$), even though leaf chewing was still significantly greater in the understorey than in the canopy (t-test$_{172}$ = 1.97, $p < 0.001$). Regardless of a greater availability of vegetation resources at the 1100 m plots, herbivory was more intense at the lower elevation plots ($F_{3,154} = 4.48$, $p < 0.005$).

Gall distribution among tree species. In 2006, we sampled 59 tree and shrub species (Appendix 1), of which 25 species (42%) had galls. Also, 35% of individual sampled plants had galls, reflecting a great concentration of galls in few hosts. A total of 4089 galls were sampled in this year, from 61 107 sampled leaves. Interestingly, 80% of these galls were concentrated on six host species (*Argyrodendron actinophyllum, Argyrodendron trifoliolatum, Arytera divaricata,*

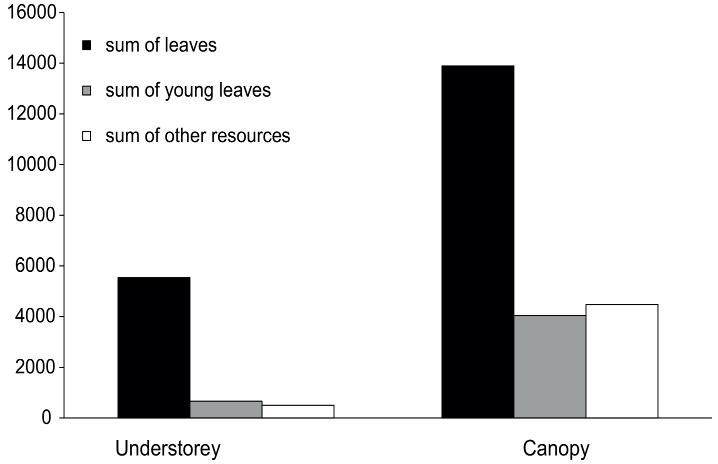

FIG. 1. Comparison of the total numbers of leaves, young leaves and other resources (buds + active meristems) sampled in the understorey and the canopy, summed across four elevations (300, 700, 900 and 1100 m a.s.l.) in Lamington National Park IBISCA-Qld plots. Understorey values are based on the sum of data from four pin-transects (one per plot). Canopy values are based on the sum of data from 12 pin transects (four per plot) divided by four.

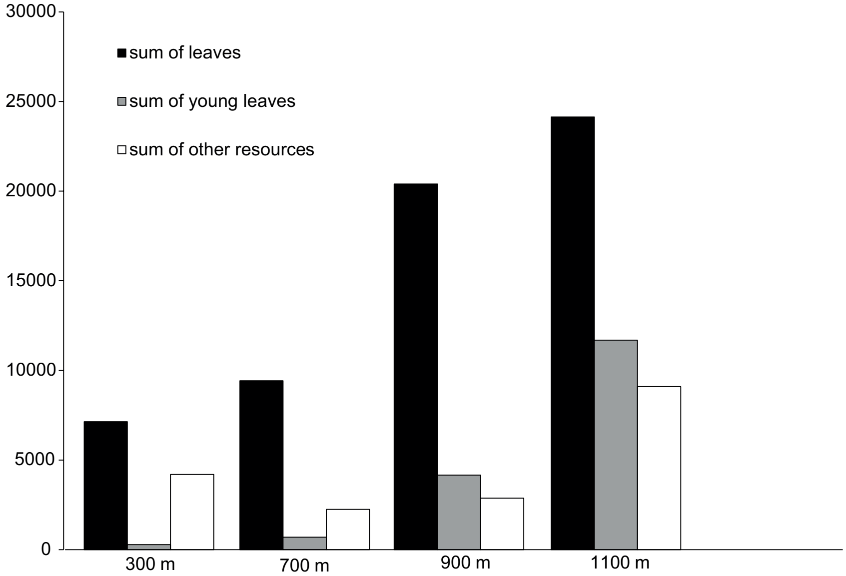

FIG. 2. Total numbers of leaves, young leaves and other resources (buds + active meristems) sampled from four different altitudes (300, 700, 900 and 1100 m a.s.l.) in rainforest at Lamington National Park. Each bar based on data from four canopy pin transects and one understorey pin transect.

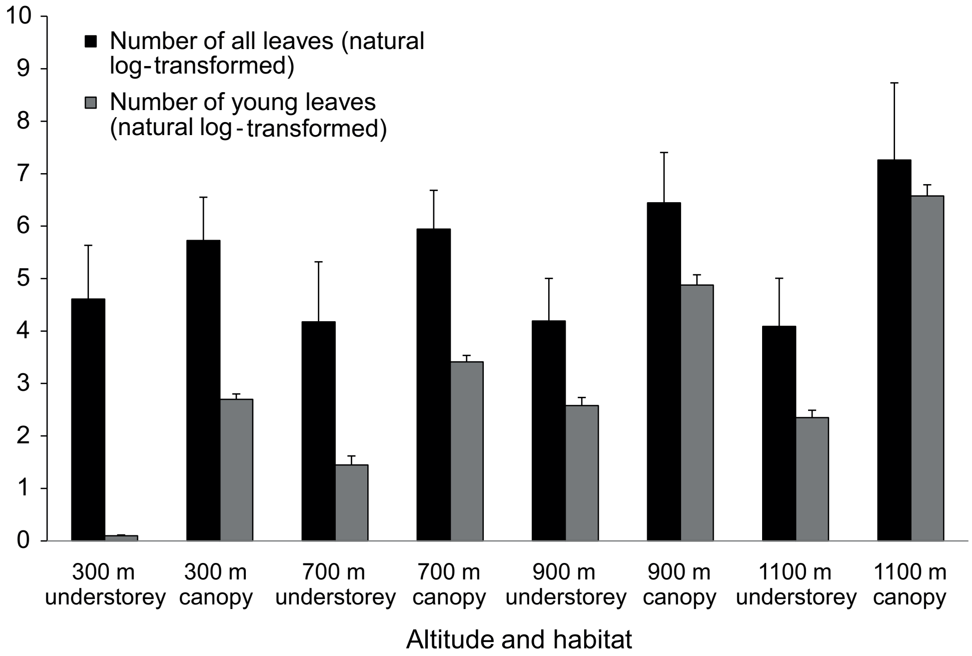

FIG. 3. Foliage traits, mean number of leaves (solid bars) and mean number of young leaves (shaded bars), both ln(x+1) transformed, in the understorey and canopy of rainforest within each of four altitudes (m a.s.l.) at Lamington National Park, Queensland.

Caldcluvia paniculosa, Melodinus australis, Orites excelsa).

In 2007, only 49 tree and shrub species were sampled, but 18% of these were new species not sampled in the 2006 survey, thus a total of 72 species were sampled (out of 329 plant individuals - 164 in 2006 and 165 in 2007), from which 40% (29 species) had some gall tumours. A total of 10 805 galls were sampled in 2007 from 26 854 sampled leaves. However, 65% of these were collected from only three individual branches of a single *Ficus watkinsiana* tree (an average of 16.6 galls per leaf). Of the remaining galls, 18% were from *Argyrodendron trifolialatum* and 10% from *Arytera divaricata*. Other galled plant species were the same as those from the 2006 collection. In summary, only seven species, or 9.7% of the total number of identified plants (and 24% of galled plant species), accumulated the majority of sampled galls.

Exceptionally, a high understorey gall density was observed at 300 m, caused by a specific infestation of three young individuals of the tree *Arytera divaricata*. However, 19% of the sampled galls on these hosts were dead. The much greater leaf density found in the wetter season in October 2006 seemed to substantially affect the gall density pattern, as most of the galled tree species were found in this year, compared to a much more concentrated density of galls on only one species, *Ficus watkinsiana*, in autumn 2007.

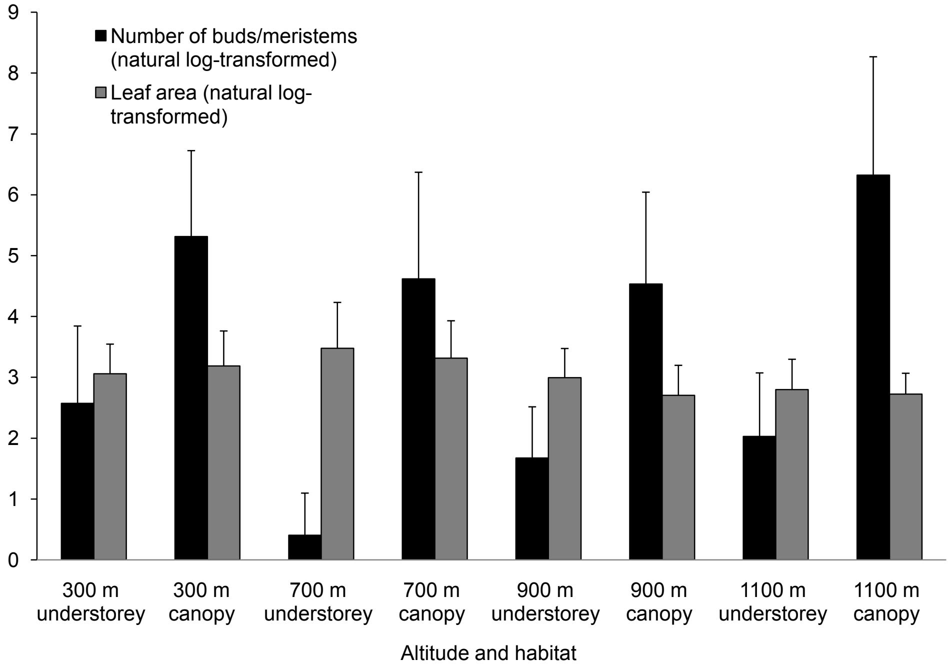

FIG. 4. Meristematic resources, mean number of buds and meristems (solid bars) and mean leaf area (shaded bars), both ln(x+1) transformed, in the understorey and canopy of rainforest within each of four altitudes at Lamington National Park, Queensland.

DISCUSSION

The *Nothofagus* forest at 1100 m showed a remarkably distinct amount of plant resources compared with all other altitudes. The larger amounts of resources available in these high altitude forests included leaves, young leaves and active meristems. Moreover, the average leaf sclerophylly for the understorey was lower at 1100 m compared to that at 900 m (LSD, $p < 0.03$). Nevertheless, the 1100 m plots showed the smallest proportion of chewed leaves. While gall insects responded closely to the presence of specific host species or sclerophyllous habitat (see below), free-feeding herbivores did not respond so directly to the general availability of vegetation resources. Conversely, the observed pattern of higher leaf chewing herbivory at 300 m may reflect some level of specificity, either in host species or in micro-climate. In addition, the 300 m plots had the second highest availability of vegetation resources in comparison with other elevations, and the substantial leaf damage observed at this altitude may be due to an optimum combination of climate and resources, thus resulting in high levels of insect herbivory. Additional IBISCA-Queensland data on the distribution and abundance of insect species may help elucidate the influence of vegetation traits on forest biodiversity.

A clear pattern of highly concentrated gall densities on few host species and few host individuals, along with an outbreak phenomenon in early autumn, defined the gall-former insect distribution at the study sites. In addition,

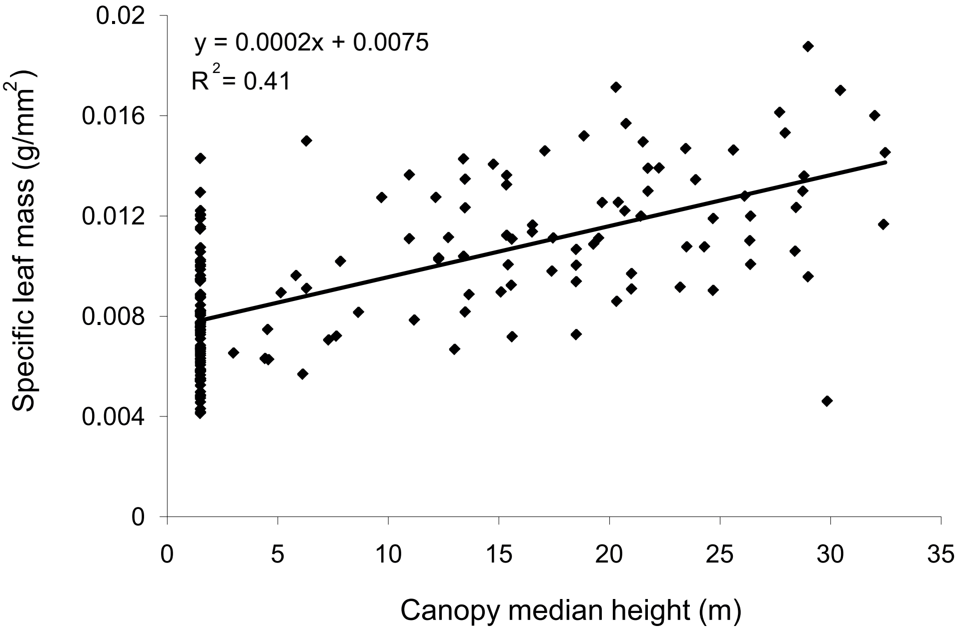

FIG. 5. Relationships between leaf sclerophylly (specific leaf mass) and sample height above the ground (canopy median height), based on multiple plant species sampled across four altitudes (300, 700, 900 and 1100 m a.s.l.) in Lamington National Park, Queensland.

the expected predominance of galls in the canopy compared to the understorey was observed in the 2006 spring sample, regardless of altitude. However, this pattern disappeared in 2007 due to a highly patchy distribution of galls on few trees, and the total absence of live galls in any understorey plant above 300 m (unpub. data). The much greater leaf density found in the wetter season in 2006 seemed to substantially affect the gall density pattern, as most of the galled tree species were found in this season, compared with a much more concentrated density of galls on only one species, *Ficus watkinsiana*, in the following early dry season. Therefore, the present work has shown an important non-synchronised pattern in gall distribution, clearly contrary to Mendonça's (2001) prediction, but providing strong support for the relative importance of the super host hypothesis (Price 1994; Mendonça 2007). As predicted by Fernandes (1992), the most frequently attacked and densely infested host species belonged to large pantropical families, such as Sterculiaceae (*Argyrodendron*), Moraceae (*Ficus*), Sapindaceae, Apocynaceae and Proteaceae, all with more than 60 genera, and some (Moraceae) with more than 1000 species. *Caldcluvia paniculata* was the only exception, belonging to the Cunoniaceae, a family with 25 genera. Another galled species of note is *Orites excelsa* (Proteaceae). This species has a fossil record from the early Cenozoic, and is found in all southern continents, probably because of a Gondwanan distribution (Larew 1986; Tahvanainen & Niemela 1987). Hence, we have evidence of galls successfully infesting both large and old plant families, a pattern only partially supported by Fernandes' (1992) data.

The Lamington rainforest showed a very strong and clear pattern of increasing

TABLE 1. Identified plant species sampled from canopy and understorey pin transects along an altitudinal gradient at Lamington National Park, Queensland and their occurrence at IBISCA-Queensland study plots (see Kitching *et al*. 2011 for plot details). * indicates those species with galls.

Plant species	**Plant family**	**IBISCA-Qld altitude/plots**
Acmena ingens	Myrtaceae	700A
Acmena smithii	Myrtaceae	900B
Acradenia euodiiformis *	Rutaceae	900C
Acronychia pubescens	Rutaceae	900D
Anthocarapa nitidula *	Meliaceae	900A; 700A
Aphananthe philippinensis	Ulmaceae	300B
Argyrodendron actinophyllum subsp. *actinophyllum**	Euphorbiaceae	300C; 700D; 900A
Argyrodendron trifoliolatum *	Euphorbiaceae	700A, B
Arytera distylis	Sapindaceae	300D
Arytera divaricata *	Sapindaceae	300C, D; 700A
Atalaya multiflora	Sapindaceae	300C
Atractocarpus benthamianus	Rubiaceae	1100C
Austrosteenisia glabristyla	Fabaceae	700B; 900C, D; 1100A
Baloghia inophylla *	Euphorbiaceae	700A, B, D; 900A
Brachychiton discolor	Malvaceae	300D
Caldcluvia paniculosa *	Cunoniaceae	900C; 1100A,C
Castanospermum australe	Fabaceae	300A
Cephalaralia cephalobotrys	Araliaceae	1100C
Cissus antartica *	Vitaceae	300B
Cissus sterculiifolia	Vitaceae	900B
Citronella moorei	Leptaulaceae	300A
Cleistanthus cunninghamii	Phyllanthaceae	300A, C; 700A
Cryptocarya obovata	Lauraceae	900B
Daphnandra apatela	Atherospermataceae	700A
Denhamia celastroides	Celastraceae	900B
Diospyros pentamera	Ebenaceae	700A, B; 900C
Diploglottis australis	Sapindaceae	700A
Doryphora sassafras	Atherospermataceae	1100C
Drypetes deplanchei	Putranjivaceae	700C; 1100C
Elattostachys nervosa *	Sapindaceae	700A

TABLE 1. cont…

Plant species	**Plant family**	**IBISCA-Qld altitude/plots**
Endiandra muelleri subsp. *muelleri**	Lauraceae	700A; 900D
Ficus macrophylla forma *macrophylla*	Moraceae	300C
Ficus watkinsiana *	Moraceae	300B; 900D
Flindersia australis *	Rutaceae	300 D
Gossia acmenoides *	Myrtaceae	300 C
Halfordia kendack *	Rutaceae	900B
Harpullia hillii	Sapindaceae	700A
Helicia gabriflora	Proteaceae	900A, B
Hodgkinsonia ovatiflora	Rubiaceae	300D
Litsea reticulata	Lauraceae	900 C
Lophostemon confertus *	Myrtaceae	300A; 700D
Melodinus australis *	Apocynaceae	700A; 900B, C, D; 1100A, C
Melodorum leichhardtii *	Annonaceae	300B,D
Myrsine subsessilis subsp. *subsessilis*	Myrsinaceae	1100C
Neolitsea australiensis	Lauraceae	700A; 900B
Nothofagus moorei	Notofagaceae	1100C, D
Orites excelsa *	Proteaceae	900B; 1100A, B, C
Pararistolochia laheyana	Aristolochiaceae	1100C
Planchonella australis	Sapotaceae	300C
Polyosma cunninghamii	Escallionaceae	900B; 1100D
Polyscias elegans	Araliaceae	700A
Pseudoweinmannia lachnocarpa *	Cunoniaceae	300B; 700C
Psychotria simmondsiana var. *simmondsiana*	Rubiaceae	1100C
Psydrax odorata	Rubiaceae	300C
Quintinia sieberi *	Quintiniaceae	1100B, C
Quintinia verdonii	Quintiniaceae	900B
Ripogonum album	Ripogonaceae	900B
Ripogonum discolor	Ripogonaceae	1100C
Ripogonum fawcettianum	Ripogonaceae	900D; 1100C
Sarcopteryx stipata	Sapindaceae	900B
Stenocarpus salignus *	Proteaceae	900B

TABLE 1. cont…

Plant species	**Plant family**	**IBISCA-Qld altitude/plots**
Streblus brunonianus	Moraceae	700A
Syzygium oleosum	Myrtaceae	1100C
Tasmannia insipida	Winteraceae	300C
Tetrastigma nitens *	Vitaceae	300B, C, D
Triunia youngiana *	Proteaceae	900B; 1100C
Trophis scandens subsp. *scandens* *	Moraceae	300B
Vitex lignum-vitae	Lamiaceae	300C
Wilkiea austroqueenslandica	Monimiaceae	900B
Wilkiea huegeliana	Monimiaceae	900B

sclerophylly with canopy height, in accordance with our predictions. Nevertheless, the effects of sclerophylly and sample median height were not significantly collinear when tested against gall density (unpub. data). As the galls are strictly related to their host plants, they track the host even though there might be more and different sclerophyllous leaves available in the ecosystem. Although micro-habitat harshness and sclerophylly have been shown to determine gall insects' oviposition preferences and/or survivorship (Fernandes & Price 1988, 1992; Ribeiro & Basset 2007), in Lamington National Park these mechanisms were partially masked by the idiosyncrasies of the very few super host species present in the area.

Finally, although most leaf chewing tended to occur in the understorey, a substantially high variation in the data may have resulted in lack of a direct relationship with sclerophylly. In addition to this scattered distribution of leaf chewing, we also observed that gall distribution did not predominate exclusively in the canopy, as predicted. Namely, the gall distribution pattern was affected by host specificity in the early dry season. Canopy sclerophylly was considered the mechanism behind both increasing gall density and decreasing leaf chewing herbivory (Ribeiro & Basset, 2007). However, one specific aspect about the Lamington forest must be emphasised. While wet tropical forests, such as that found in Panama, had leaf sclerophylly mostly varying from 0.0014 to 0.01 g/mm^2 in the understorey, at Lamington understorey sclerophylly consistently ranged from 0.004 to 0.0140 g/mm^2. Therefore, a relatively more sclerophyllous vegetation at ground level in Lamington may mask the predicted ecological response, namely an inverse distribution pattern in the leaf chewing and leaf galling herbivore guilds, which should be related to soft-hard leaf variation.

In conclusion, it seems necessary to generate a world-wide range of complementary studies covering overlooked ecosystems and habitats in terms of vegetation and herbivory parameters. The IBISCA research model (see Kitching *et al.* 2011) has enabled the opportunity to conduct insect studies across the globe in order to clarify questions such as those examined, related to insect species density and diversity in forest habitats.

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