

Density of Insect Galls in the Forest Understorey and Canopy: Neotropical, Gondwana or Global Patterns?

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Abstract Gall-forming insects reach highest diversity, abundance and survivorship on sclerophyllous vegetation. This pattern was recently reviewed and shown as a habitat rather than ecosystem effect. We tested the hypothesis that upper forest canopies are probably the best suitable habitat for gall-forming insects in any tropical vegetation, comparing the wet rainforest of Panama (Neotropical), and the subtropical forest of Australia (Australian). We further tested whether foliage/plant community traits could influence this gall distribution pattern, and we investigated the effect of host family size and evolutionary age. Foliage traits, leaf chewing herbivory, and gall abundance and survivorship were measured using vertical cylindrical transects from the understorey to the canopy. In both Panama and Australia, leaf sclerophylly increased significantly with sampling height, while free-feeding herbivory decreased inversely. Gall distribution and survivorship responded significantly to sclerophylly, but distribution between understorey and canopy varied between study sites. The probability of gall survivorship increased with increasing leaf sclerophylly as death by fungi, parasitoids or accidental chewing were greater in the non-sclerophyllous vegetation in the understorey of both study sites. However, number of galls, proportion of infected sampled plants, and proportion of host species against total sampled species were all greater in Panamá than in Australia.

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On the other hand, the Australian forest had a fauna much more concentrated on fewer hosts, with 80 % of galls infesting six host species. The present study supports the existence of a global positive effect of sclerophylly on gall establishment and survivorship in the upper canopy of tropical and subtropical forests.

Keywords Canopy • Gall density • Leaf herbivory • Sclerophyllous habitats • Forest vertical distribution

8.1 Introduction: Galls in Forests

Galls are well known endoparasitic specialist herbivores related to highly sclerophyllous plants, thus a typical sun-love interaction. Seminal work of Fernandes and Price (1988, 1992) demonstrated that differential death by fungi and parasites, greater in shadowed and mesic compared to sunny and xeric sclerophyllous vegetations, is a likely mechanism driving the gall species distribution pattern. More recently, Mendonça (2001) added an evolutionary layer to this debate, proposing an ingenious evolutionary mechanism to explain the diversification of gall species based on the ecosystem-level synchrony of leaf flush. He predicted increasing speciation rates due to insect survival after mistaken oviposition, a likely event if all plants produce young leaves at the same time and insects have early oviposition to avoid hard tissues and thus facilitate the development of the gall tumour. Mendonça's hypothesis complements the harsh environment (Fernandes and Price 1988) and sclerophylly hypotheses (Fernandes and Price 1992). The former explains a mechanism of speciation and the latter of survivorship in sclerophyllous synchronous ecosystems. When considered together, these hypotheses help to explain why the highest gall diversity occurs in the Mediterranean-type vegetations, like the Brazilian cerrado (Price et al. 1998).

However, 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, bringing to evidence a previously unexpected relation of this unique interaction with a very wet ecosystem. Furthermore, a significant amount of this diversity was detected by a yearly sampling protocol which measured the variation in gall species richness and abundance following each host-plant's leaf-flush (Medianero and Barrios 2001; Medianero et al. 2003). In Panama, no synchrony of leaf flush was observed at all, but gall diversity was among the highest ever found, thus contradicting the predictions of Mendonça (2001).

On the other hand, comparative analyses of the distribution of galls between xeric (upper canopy) and mesic (understorey) habitats within the forest seem to corroborate Fernandes and Price's (1992) prediction: a positive gradient between gall diversity and vegetation sclerophylly may exist. Nevertheless, even though the accepted mechanism to explain greater gall mortality in mesic over xeric habitats is apparently correct at the branch/leaf scale (Ribeiro and Basset 2007), it was first developed based on of a comparison between forest understorey and cerrado

canopies, thus lack a proper vegetation-habitat control (reviewed in Ribeiro 2003). Indeed, Medianero et al. (2003, 2010) found that a humid closed rainforest on the Caribbean coast of Panama (San Lorenzo Protected Area) was richer in gall species than the dry semi-deciduous forest on the Panamanian Pacific coast (Parque Metropolitano). Mostly important, both forests were richer in galls in the canopy than in the understorey. Hence, the actual eco-physiology of the habitat (forest understorey vs. cerrado canopy) within which the galls live is more relevant to the pattern than the existence of a mesic or xeric state of the plant community as a whole. Hence, the present global estimate of 130,000 gall species from Espírito-Santo and Fernandes (2007), although accounting for previous bias in the literature, such as lesser studies in the canopies than in easier accessible vegetation in temperate or tropical latitudes, may have missed within-ecosystem habitats comparisons.

Despite the positive response to sclerophyllous habitats, wherever galls occur, they are restricted to very few host species (Espírito-Santo and Fernandes 2007; Ribeiro and Basset 2007). Why so few plant taxa across biomes are suitable hosts for gall species is so far an unanswered question. For instance, Ribeiro and Basset (2007) observed galls on few tree species (22 % out of 73 tree/liana sampled species), from which 50 % had congeners or were also found (31 %) in the Brazilian cerrado. Both Price (1977) and Fernandes (1992) have proposed that gall diversity follows plant family size, but neither of these authors actually discussed evolutionary constraints to gall species distribution related to the life history of the host. Likewise, little have been done in order to understand what are the actual constraints to gall invasion success into most of host taxonomic groups, neither if this is a recent or old evolutionarily phenomena:

- how much of the Neotropical gall diversity resulted from local adaptive radiation in association with continuous sclerophyllous habitats, thus with wide and abundant host species distribution? Conversely,
- how much of such biodiversity was caused by an older Gondwana evolutionary history, which may influences gall species distribution in Neotropical, Cape Africa or Australasian regions?

This chapter revisited previous data obtained by the canopy-understorey cylinder transects protocol (Ribeiro and Basset 2007; Ribeiro et al. 2012), and add a new analytical approach in comparing the gall abundance distribution and survivorship between understorey and canopy of (a) a Neotropical wet rainforest, in Panama; and (b) an Australian subtropical rainforest (part of the Gondwana Rainforests of Australia), in Queensland. We explore the hypothesis that sclerophylly effect on gall distribution, previously demonstrated in the Neotropical region, is a general phenomenon, likely to be found in other regions, and is more important than other ecologic or evolutionary causes of gall abundance and distribution. Hence, besides testing the effect of leaf height and sclerophylly on gall distribution, we compared the forests foliage density and vertical distribution. In addition, we investigated whether gall diversity is restricted to few host species that belong to large pan-tropical or pre-Gondwana plant families.

8.2 Methodology

The IBISCA Project and global comparisons in insect diversity – IBISCA (Investigating Biodiversity of Insects in Soil and Canopy) is an international project with the goal of performing simultaneously several arthropod sampling protocols, targeting particular speciose taxonomic groups, and yielding adequate data to compare the fauna from the soil to the canopy (details in Basset et al. 2007, 2012; Kitching et al. 2012). So far, expeditions were conducted in San Lorenzo Protected Area, Panama, Lamington Park, Australia, Santo Island, Vanuatu, and Auvergne County, France.

This Chapter focus on San Lorenzo and Lamington Park. Details on each study site and methodology are found in Basset et al. (2007), Ribeiro and Basset (2007), Kitching et al. (2012) and Ribeiro et al. (2012). To study galls, parasites and herbivory, a new methodology was developed, which generates a comparable number of searched leaves in same space volume from top canopy to understorey. Such procedure, the canopy-understorey pin-cylinder transect (hereafter cylinder; Ribeiro and Basset 2007), allows a direct comparison of different forests by using a same volumetric sample unit. A different amount of understorey-canopy cylinders were set in each study site to adjust to the general sampling design of each IBISCA project. In San Lorenzo, five sites were sampled with one understorey and three canopy cylinders in each, and in Lamington Park four altitudes were each surveyed with one understorey and four canopy transect. Both study sites were sampled during two distinct seasons: August 2003 (rainy season) and May 2004 (end of the short dry season), in Panama; in October 2006 (early wet season) and March-April 2007 (early dry season), in Australia. A short description of the method, which is detailed in Ribeiro and Basset (2007) and Ribeiro et al. (2012), is presented below.

8.2.1 *Sampling Protocol: The Pin-Cylinder Transect*

The canopy cylinder transect is a cylindrical transect which started at the upper canopy and finished at 3 m above the ground. For the understorey cylinder transect, it followed along an equivalent horizontal transect of 20 m in Lamington and 30 m in San Lorenzo (the average height of these forests, respectively) parallel to and 10 cm above the soil, thus preventing sampling seedlings. In each transect, a ‘sample’ consisted of a branch or continuous groups of leaves within the cylinder. 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 taken from counting all leaves with more than 10 % of leaf area lost, estimated visually. Since this figure represents global average leaf area loss in tropical wet forests, leaves scored above this average may be considered “substantially damaged” (Coley and Aide 1991) and the proportion of damaged/total leaves per strata resulted in our estimate of free-feeding herbivory. Healthy leaves were collected for an 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 imperfections, were collected and frozen. Galls were opened in the laboratory to evaluate if they were alive or dead and if dead, the cause of death. We analysed the following gall categories: (a) all galls (including galls with live and dead insects; hereafter 'live' and 'dead' galls for sake of brevity); (b) only galls with live larvae; (c) recently hatched galls; and (d) galls with larvae that had died recently by fungal attack (recognized by rotten larvae or the presence of mould) or parasitoid attack (identified by the presence of the parasitoid ecdysis or several small asymmetric apertures in the gall, along with wastes inside).

8.3 Contrasting Foliage and Gall Distribution in the Panamanian San Lorenzo Forest and in the Australian Lamington Park

The Panamanian forest had substantially more plants in the understorey than in the canopy, but similarly more foliage in the opposite direction (8.5 times more, Table 8.1). Contrastingly, Lamington subtropical forest had only 50 % more plants in the understorey compared with the canopy, and only 2.5 more leaves in the canopy (Table 8.1). These figures reflect a much denser and entangled forest in Lamington than in San Lorenzo, which had 2.5 plant species per cylinder against 1.3 species in the latter. Hence, it is as if the tropical Panamanian forest was shaped by the top, with the upper canopy species shadowing down the rest of the forest, thus resulting in empty spaces within the forest.

8.4 San Lorenzo Forest Gall Distribution

8.4.1 *Gall Distribution Among Tree Species*

Galls were present only in 47 samples and 16 (out of 73) identified host species (Ribeiro and Basset 2007). Overall, 32 gall species were collected, including 59 % of which occurred exclusively in the canopy, 28 % only in the understorey, and 12.5 % found in both habitats. We noted that 81 % of our gall host plants at San Lorenzo have either congeners (50 %) or are present (31 %) in the Brazilian cerrado (Table 8.1), where gall diversity is one of the highest in the world (Price et al. 1998).

Scaling down to leaf level, Ribeiro and Basset (2007) surveyed in average 21,997 leaves per year, of which 2.4 % bore galls in the wet season 2003 and 5.5 % by the end of the dry season, although restricted to fewer trees. However, a similar number of galls were sampled in the two seasons (average 2,507 galls), with 15.6 % of galls

Table 8.1 Canopy and understorey plant parameters, and gall versus chewing herbivory infestation obtained by understorey-canopy cylinder protocol, in San Lorenzo National Park, Panama, and Lamington National Park, Australia

Forest/gall parameter	San Lorenzo	Lamington park
Plant diversity	73 plant species	72 plant species
	50 genera	61 genera
	31 families	33 families
	231 sampled plants	329 sampled plants
Plant/foilage distribution	7.3 more plants in the understorey than canopy	1.5 more plants in the understorey than canopy
	8.5 more leaves in the canopy than in the understorey	2.5 more leaves in the canopy than the understorey
Total sampled leaves	22,155 sampled leaves	43,980 sampled leaves
Mean chewing herbivory	20 % damaged	35 % damaged
Numbers of host species	16 species	29 species
	22 % of total plant species	40.2 % of total plant species
Mean proportion of infected leaves per galls per year	2.4 % infected by galls	42 % infected by galls
Mean sampled galls per year	2,540 galls	7,447 galls
Gall distribution and host species specifics	31 % of galled host species are present in the cerrado	2006 – 80 % of these galls were concentrated in six host species: <i>Argyrodendron actinophyllum</i> , <i>Argyrodendron trifoliolatum</i> , <i>Arytera divaricata</i> , <i>Caldcluvia paniculosa</i> , <i>Melodinus australis</i> , <i>Orites excelsa</i>
	50 % of galled species have congeneric cerrado species	2007 – 65 % of galls on <i>Ficus watkinsiana</i> 18 % on <i>Argyrodendron trifoliolatum</i> 10 % on <i>Arytera divaricata</i> <i>Arytera divaricata</i> – young saplings inflated the number of galls in the understorey

with live larvae in wet season against 5.4 % by the end of the dry season. Leaves substantially damaged by free-feeding herbivory were 20 and 17 % of leaves surveyed in the wet and dry seasons, respectively.

8.4.2 *Gall Density, Sclerophylly and Leaf Chewing Distribution*

Regardless of plant taxonomy, leaf sclerophylly increased significantly with sampling height (Fig. 8.1a). The regression supporting such pattern was not affected by sites, or by the distribution of foliage at different canopy strata (Ribeiro and Basset 2007).

Although there was a high variation in sclerophylly (some understory leaves being as tough as canopy leaves), canopy leaves were nearly twice more sclerophyllous than understory leaves. Leaf sclerophylly affected insect herbivory more significantly than foliage density, but in contrasting directions for gall-forming and free-feeding chewing insects. Although the absolute number of chewed leaves was proportional to the total number of leaves available, thus increasing with height, the proportion of chewed leaves decreased significantly with height. This pattern was similar in both sampling seasons (Fig. 8.1b). On the other hand, sclerophylly affected gall density positively, an effect more important than sample height, and more relevant to gall survivorship than oviposition patterns. The average number of live galls collected in the canopy was 13 times greater than in the understory, a pattern consistent across sites and sampling years (Ribeiro and Basset 2007, Fig. 8.1c). Further, there was a negative relationship between leaf sclerophylly and the proportion of dead galls.

8.5 Lamington Forest Gall Distribution

8.5.1 *Gall Distribution Among Tree Species*

In the early wet season, we sampled 59 species of trees and shrubs, from among which 25 species had galls (42 % of total). Thirty-five percent of individual sampled plants had galls, reflecting a great concentration of galls on a relatively few hosts. A total of 4,089 galls were sampled in the year out of 61,107 sampled leaves (Table 8.1). From the total of sampled gall in the wet season, 80 % were concentrated in six host species: *Argyrodendron actinophyllum* Bailey (Edlin), *Argyrodendron trifoliolatum* F. Muell. (Malvaceae), *Arytera divaricata* F. Muell. (Sapindaceae), *Ackama paniculosa* (F. Muell.) Engl. (Cunoniaceae), *Melodinus australis* (F. Muell.) Pierre (Apocynaceae) and *Orites excelsa* R. Br. (Proteaceae). For the dry season, 65 % of those were collected in only three individual branches of a single *Ficus watkinsiana* F. M. Bailey (Moraceae) (an average of 16.6 galls per leaf were sampled). *Argyrodendron trifoliolatum* had 18 % of the remaining galls and *A. divaricata* accumulated 10 %. A gall morphospecies never occurred in different host species and, mostly, hosts held one to two gall morphospecies. 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 galls observed.

8.5.2 *Gall Density, Sclerophylly and Leaf Chewing Distribution*

A strong positive correlation between leaf height in the canopy and sclerophylly existed in the Lamington forest (Fig. 8.1d), consistent across all altitudes. In the wet season, both total and live galls showed the same distribution pattern, that is, a

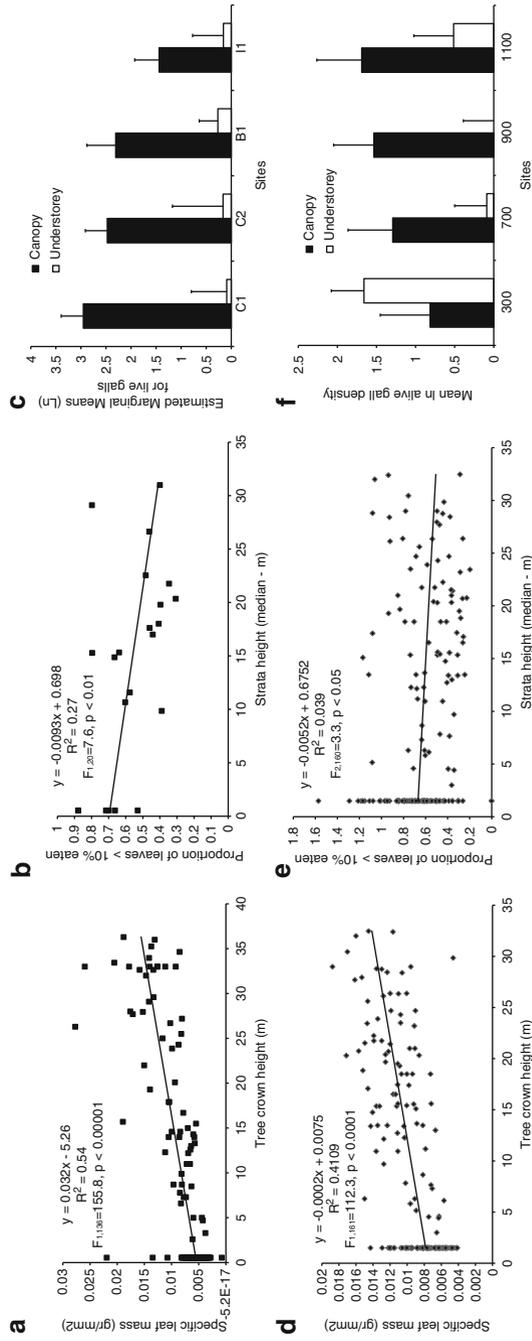


Fig. 8.1 Changes in sclerophylly (specific leaf mass), chewing herbivory (proportion of leaves with leaf area lost >10%) and gall survivorship (ln alive galls) in the understorey and canopy of San Lorenzo, Panama (A) and Lamington, Australia (B) Parks

higher density in the canopy than in the understorey. For both total and live galls, altitude and “canopy x understorey” habitats interacted significantly (mixed ANOVA model: Total; $F_{1,63}=3.57$, p , 0.01; Live galls; $F_{1,47.3}=3.18$, $p<0.03$, Table 8.1, Fig. 8.1f), due to a similar density of galls in the two habitats at 300 m, in contrast to all other altitudes, where galls predominated in the canopy. However, it is important to note that the high understorey gall density at 300 m was caused by a specific infestation of three sampled saplings of the canopy tree *Arytera divaricata* and that 19 % of galls found on these hosts were dead. Hence, a clear confounding with a super-host species effect. Although no statistical difference was found when comparing the total galls in the canopy and the understorey at any site, above 300 m no live galls were found in the understorey (S.P. Ribeiro and R.L. Kitching, unpublished data).

There was a significant response in leaf chewing herbivory with altitude (Type III mixed ANOVA, $F_{1,160}=3.98$, $p<0.001$). As expected, lower, warmer altitudes had more leaf-chewing herbivory activity, with 300 and 700 m recording the highest rates, 900 m an intermediate level of herbivory and a significantly lower mean herbivory rate at the 1,100 m sites (Least Significant Difference post-hoc test, $p<0.0001$). However, no direct sclerophylly effect was found (Multiple regression, t-test on Beta $t=0.73$, $p>0.05$). Nevertheless, chewing decreased significantly with forest height, reflecting somehow a pattern indirectly related to habitat sclerophylly, and inverse from that found for gall (Fig. 8.1e). Regardless a low coefficient of determination, the robustness of the sample size allowed the detection of this trend, even though further explanations are needed for the huge overdispersion of chewing in the forest. An obvious factor affecting the pattern was the mountain altitude, as described before. Still, when comparing all leaf herbivory from understorey and canopy, a significantly higher leaf area lost rate was found for the former (t-test $t_{172; 0.05}=3.27$, $p<0.001$).

8.6 Global Pattern Versus Biographic Idiosyncrasies: The Role of Gall Host Taxonomy and Phylogeographic Evolution

Few studies have explored patterns of herbivory distribution based on large samples actually randomized at the scale of the leaf. The use of the canopy-understorey cylinder allowed a proper comparative study on gall distribution between different forests and habitats. Before, a pioneer study from Price et al. (1998) produced a reliable global comparison in gall diversity among ecological communities, showing a strong positive response to sclerophyllous ecosystems. However, fine scale gall ecological responses that may have produced the global pattern were not properly explored, especially in comparisons between habitats within a forest community. Access to high canopies using really comparative sample protocol was needed to provide proper hypotheses test (Ribeiro 2003; Fleck and Fonseca 2007).

The Panamanian San Lorenzo and the Australian Lamington IBISCA sites presented a very similar number of plant species within the cylinders (72 in Australia compared with 73 in Panama). Such similarity suggests that the number of branches and species found in the same forest volume may differ little between these two ecosystems, despite a much greater leaf density and seasonal variation in Australia (mean values: 43,980 in Australia against 21,997 in Panama). The number of galled plant species in Australia, however, was nearly twice than found in Panama, even though 80–93 % of the gall density was concentrated in just seven host species and caused by an estimated number of only eight species of gall insects, found on those particular hosts.

The fact that Lamington forest was in average a more sclerophyllous vegetation than San Lorenzo and had the double number of galled tree species, suggest the importance of overall plant community sclerophylly in gall establishment and evolution. Such sclerophyllous trait may well relate to the widespread number of gall species in other ecosystems such as the Brazilian cerrado (Fernandes and Price 1992; Ribeiro et al. 1999).

Finally, the prediction from Fernandes (1992) that most frequently attacked and densely infested host species belong to large pantropical families was supported only for Lamington forest, where galls were found in Malvaceae (*Argyrodendron*), Moraceae (*Ficus*), Sapindaceae, Apocynaceae and Proteaceae. All these families have more than 60 genera and some (Moraceae) have more than 1,000 species. *Ackama paniculata* was the only exception to this pattern, belonging to the small, however primitive (pre-Gondwana) Cunoniaceae family which contains only 25 genera. Another interesting case to note is the galled Proteaceae *Orites excelsa*. This genus has a gall fossil register from the early Cenozoic and is also found in all south continents. Therefore, gall species distribution may have responded to its early radiation, from 115 to 100 million years ago, just before the split of Gondwana (Larew 1986; Tahvanainen and Niemela 1987).

Nevertheless, this pattern was not supported by the Panamanian data (Medianero et al. 2003; Ribeiro and Basset 2007), where most of galls where on species belonging to small families, and thus appears not to be a fundamental mechanism driving gall distributions worldwide. A strongly constrained evolutionary history of the gall-forming guild, related to a restricted number of host species (see Veldtman and McGeoch 2003), may better define a global pattern. Through analysis of the fossil record, Larew (1986) has shown a significant constancy in the gall fauna associated with a number of host species from the late Miocene-Pliocene, 20–13 million years ago. In addition, when analysed at the community level, following random sampling in the vegetation, we found that galls infected only 22 % of sampled tree species in San Lorenzo National Park, and 40.2 % in Lamington Park.

8.7 Conclusions

Unknown evolutionary constraints appear to restrict gall-inducing insects from spreading to the whole of the local flora. Although gall taxa diversification seem to respond to host range in an evolutionarily long time (Hardy and Cook 2010),

radiation after host invasion may be more related to host species life history and ecology rather than to any taxonomic or biochemical traits. For instance, the greater expectation of finding galls in a plant from a large family could be just a neutral consequence of the sheer size of the family. One may suppose that in a large plant family at least some species will have a life history that matches gall adaptation and developmental demands, and thus increases the chance that indeed those plants will be surveyed by most of sampling methods (examples in Santos et al. 2011). Even authors that have been finding a strong relationship between family size and gall diversity in cerrado, such as Araújo (2011), have clearly posed that the event is host specific within a large family, and that has actually little echo at the genera level, for instance.

These life history components favourable to gall invasion are likely to be related to leaf quality/sclerophylly and the subsequent effects on risk of mortality, caused by fungi, parasitoids, or accidental chewing by herbivores. The latter effect was first proposed by Ribeiro and Basset (2007) and is also partially supported by Lamington data, which showed a substantially higher leaf area lost in the understorey compared with the canopy, where most of the galls were found.

Our work filled up a few gaps in cross-ecosystems/continents data, at a scale that allowed us to support or reject some unanswered hypotheses on galls species distribution patterns. Fleck and Fonseca (2007) listed flaws and deficiencies of 13 classic hypotheses on insect diversity distribution when applied to gall species. We may suggest that “taxonomic isolation”, “soil fertility”, “plant species richness” or “resource concentration” are unlikely to explain gall distribution. In addition, the lack of data on tall tropical forest galls jeopardizes previous negative conclusions on the “architecture complexity” hypothesis. In fact, the latter may be a complementary explanation to the “higrothermal/sclerophylly stress”, the one our data corroborate most, along with the Price’s (1994) “phylogenetic constraint” hypothesis, not explored by Fleck and Fonseca (2007).

In conclusion, micro-habitat harshness and leaf sclerophylly determine gall insects’ oviposition preferences and/or survivorship (Fernandes and Price 1988, 1992; Ribeiro and Basset 2007), although in Lamington National Park these mechanisms were partially masked by a strong host specific association that constrained gall distribution, as well as the strong altitudinal factor. Comparison with San Lorenzo humid closed rainforest suggests the likely existence of a sclerophylly rate threshold above which galls tend to succeed better and spread in the plant community.

Nevertheless, specific evolutionary histories play an equally important role in the global patterns of local gall species richness and abundance. Idiosyncrasies ought to be related to biogeographic regions, and an isolated continent as Australia was indeed expected to reflect Gondwana events. On the contrary, the Neotropical region seems to be mostly influenced by a high number of widely distributed host species, which have a biogeographic range across biomes and sufficiently connected by xeric/canopy habitats.

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