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Gall-forming insects in a lowland tropical rainforest: low species diversity in an extremely specialised guild

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Abstract. 1. Gall-forming insects are a guild of endophages that exhibit a high level of fidelity to their host plants, however, their level of host specificity is seldom explicitly tested.

2. Gall-forming insect taxa from 32 species of woody tropical plants with resolved phylogenetic relationships were collected and reared, representing 15 families from all the major clades of angiosperms, at three lowland rainforest locations in Madang, Papua New Guinea (PNG).

3. More than 8800 galled plant parts were collected from 78 gall morphospecies at an average of 2.4 per host plant. Total species richness at the sampling sites was estimated to be 83–89. All but one morphospecies were monophagous resulting in an effective specialisation of 0.98.

4. Specific leaf weight, foliar nitrogen, the presence of latex, and the successional preference of plant species all gave a phylogenetic signal, but only plant successional preference influenced the species richness of galls on analysis of phylogenetically independent contrasts. Gall species were distributed randomly among host plant species and showed no preference for any particular plant lineage. Furthermore, most gall-forming taxa were evenly dispersed across the host plant phylogeny.

5. In the tropical rainforests of New Guinea, gall-forming insects are ubiquitous but occur in species-poor assemblages. Local species richness is closely tied to the diversity of angiosperms owing to very high host specificity.

6. Finally, galler species richness data from the literature across habitats and latitudes were compared and suggest that tropical rainforests may be richer in galls than previously acknowledged.

Key words. Gall-forming insects, host specificity, Papua New Guinea, sclerophylly, species richness, tropical rainforests.

Introduction

Gall-forming insects are a highly specialised group of endophages, employing a life strategy that has evolved independently many times among and within six insect orders (Stone & Schönrogge, 2003). Their high level of specialisation, with perhaps around 90% of all gall-forming species strictly monophagous (Carneiro *et al.*, 2009a; Raman, 2010), is often presupposed and it is commonplace in community studies that a unique combination of gall morphotype and host plant species is an acceptable proxy for the galling insect species (Price *et al.*, 1998; Blanche, 2000; Cuevas-Reyes *et al.*, 2003; Raman *et al.*, 2005; Shorthouse *et al.*, 2005; Carneiro *et al.*, 2009a). At local scales, the aforementioned assumption is generally vindicated, but we know, regionally at least, that many species form galls on closely-related congeneric hosts and are thus not true monophages, for example, gall midges on *Salix* (Redfern & Shirley, 2011) and oak gallwasps (Stone *et al.*, 2009).

Globally, there could be in the order of 130 000 species of insect gall (Espirito-Santo & Fernandes, 2007), roughly a 10-fold increase from the number of known species reported by Mani (1964), and the majority of undescribed species await discovery at tropical and subtropical latitudes (Espirito-Santo & Fernandes, 2007). As a general rule, herbivorous insect diversity

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increases with plant species richness and reaches its peak in the humid tropics (Lewinsohn & Roslin, 2008). In contrast, however, the peak of gall-forming insect species richness appears to lie within subtropical and warm temperate latitudes (23–38°N or S), where xeric habitats and scleromorphic vegetation are common, rather than in equatorial rainforests (Price *et al.*, 1998).

The hygrothermal stress hypothesis (Price *et al.*, 1987; Fernandes & Price, 1988, 1991), which could explain the observed patterns in Price *et al.* (1998), states that gallers are more successful in dry or stressed habitats on vegetation with long-lasting and scleromorphic plant modules (Price *et al.*, 1998). Both high specific leaf weight (SLW) and low foliar nitrogen concentration, which correlate with plant leaf toughness and longevity, are both features of sclerophyllous vegetation (Turner, 1994) and could affect galler species richness. However, support for (Fernandes & Price, 1988; Price *et al.*, 1998; Yukawa *et al.*, 2001; Lara *et al.*, 2002; Uechi *et al.*, 2003; Carneiro *et al.*, 2005) and against (Wright & Samways, 1998; Blanche, 2000; Veldtman & McGeoch, 2003) the hygrothermal stress hypothesis comes mainly in the form of comparisons of gall species richness between xeric and mesic sites and plant traits themselves are rarely measured. Exceptions are Ribeiro and Basset (2007), who found that tropical rainforest vegetation with a higher SLW had greater gall survivorship and species rich communities, and Bairstow *et al.* (2010) who found that the C : N ratio was the factor that best explained galler richness across a climatic gradient of *Acacia* spp. in Australia. Conversely, wet tropical rainforests potentially present adverse conditions for gall inducers, where higher mortality rates may be mediated by enemy parasitoids and endophytic fungi (Price *et al.*, 1998). Several studies, however, suggest that gall species richness in rainforest habitat is relatively underestimated (Medianero *et al.*, 2003; Hanson & Gomez-Laurito, 2005; Ribeiro & Basset, 2007; Nieves-Aldrey *et al.*, 2008).

The presence of plant exudates such as latex have been shown to act as a potent defence that can reduce herbivore abundance (Agrawal & Konno, 2009; Whitfeld *et al.*, 2012), but it is unclear how this trait may affect gall-forming insects specifically. Gallers are able to concentrate nutrients and redirect potentially harmful secondary plant compounds to outer gall tissues (Hartley, 1998; Price *et al.*, 1998; Allison & Schultz, 2005; Tooker *et al.*, 2008), but are they able to overcome the defences of latex-bearing plants?

The successional preference of plant species in Papua New Guinea (PNG) has been shown not to affect the species richness of some herbivorous insect guilds (Leps *et al.*, 2001; Dem *et al.*, 2013), whereas cell-sucking herbivores were richer in plants from early successional vegetation (Baje *et al.*, 2014). The plant vigour hypothesis (Price, 1991) suggests that gall formers might prefer early successional vegetation because they require meristematic (new growth) plant tissue for oviposition and subsequent gall formation, which should be in abundance in secondary vegetation types, but there is only limited support for this notion by Fernandes *et al.* (2010), who found galling insects to be richer in restored secondary rainforest stands compared with primary forest.

Galling insects and their host plants are a suitable model system in which to explore the ecological determinants of host specificity and species richness because the sessile and persistent nature of plant galls permits ease of sampling – even after the inducing insects have departed – and is implicit proof of the feeding interaction. Our study may be, to the best of our knowledge, the first to examine the community ecology of gall-forming insects in the Old World tropics.

Our main objectives were (i) to measure the host specificity and species richness of the sampled gall insect community, with the prediction that effective specialisation would be greater than 90%; (ii) to compare our data with a similar dataset for leaf miners, with the expectation that gallers would be more specialised but similarly rich in species; (iii) to use available plant trait data to test the hypothesis that the number of galling species would be significantly greater on plant species with relatively high SLW and/or low foliar nitrogen concentrations, based on the predictions of the hygrothermal stress hypothesis; (iv) to use the available plant trait data to test the null hypotheses that successional preference, local abundance, presence of latex, maximum plant size, and wood density would not have any significant effect on gall species richness; (v) to test the null hypothesis that distinct groups of galling taxa would be randomly distributed (i.e. not clustered or overdispersed) across the phylogeny of our target plant species; and (vi) to compare the number of gall-forming insect species per host plant species observed in this study to other data from the literature, predominantly from tropical latitudes, in order to contextualise our data and to aid in a general discussion of gall richness across the tropics.

Materials and methods

Host plant taxa

In this study, we used the same sampling design as one employed in previous studies of PNG herbivorous insect guilds (Novotny *et al.*, 2010), thus enabling cross-guild comparisons to be made if applicable. The method was created to measure the full range of possible host specificity levels from monophagy to polyphagy by sampling with equal effort host plant families from all the major lineages of flowering plants – gymnosperms, magnoliids, monocots, rosids and asterids – as per the Angiosperm Phylogeny Group (APG III, 2009). Thirty-two species of locally common woody plants from primary and secondary lowland rainforest were selected for the study of their gall-forming insect herbivores. These included four species of *Ficus* and one species of *Artocarpus* (Moraceae), three species of *Macaranga* and two species from other genera of Euphorbiaceae, three species of *Psychotria* and two species from other genera of Rubiaceae, two species each of *Syzigium* (Myrtaceae), *Celtis* (Cannabaceae), and *Tabernaemontana* (Apocynaceae), species from two genera each of Malvaceae and Agavaceae (Asparagaceae), as well as a single species each from seven other families.

For the plant species in question, their phylogenetic relationships were known, and a suite of plant traits and characteristics had been previously measured. These characteristics were obtained from 50 forest plots of $20 \times 20\,m^2$ each (2 ha in total) among the three sites also sampled in this study. The characters measured – local abundance, successional optimum, maximum individual size, wood density, specific leaf weight, and foliar nitrogen – are known or hypothesised to be important factors structuring folivorous herbivore communities as determinants of resource quantity and quality (Kennedy & Southwood, 1984; Basset & Novotny, 1999; Whitfeld *et al.*, 2012). All individuals with a diameter at breast height (DBH) > 1 cm from the focal species were surveyed in both primary and secondary forest plots (Baje *et al.*, 2014). Additionally, we used a dataset on PNG leaf miners (Novotny *et al.*, 2012), using the same methodology and locations, and which shared 30 host plant species with this study.

Study area and sampling

The study was carried out in the vicinity of Madang, Madang Province, Papua New Guinea. Sampling took place near the villages of Baitabag, Mis, and Ohu (145°41–7 E, 5°08–14 S, 0–200 m asl), which are each surrounded by approximately 200 ha of mixed secondary and primary rainforest. The mean annual rainfall in the Madang area is 3558 mm with minor seasonal variation and the mean air temperature is 26.5 °C, varying little throughout the year (McAlpine *et al.*, 1983).

Fieldwork was carried out in the period August 2010–March 2011. At each site, two collectors, working independently, spent two 8-h days per week hand-collecting galls from the accessible foliage of target host plants. Roughly 15–25 individual plants belonging to each of three host species were searched on a typical collection day, representing approximately 5.3 h of searching for galls per plant species. A single sampling unit was the collection of galls from a single host plant species by two collectors at a particular site on a particular day.

In total, all plant species were sampled 13 times. Effort was made to spread the sample dates of each host plant species so that they were separated by roughly equivalent time intervals across the entire project, in order to mitigate for any seasonal effects. Gall abundance was measured as the number of plant organs galled (i.e. the number of galled leaves, stems, petioles etc.), quantitatively from one to 10, and then categorised as either 11–100 or > 100. Only galls formed by, or strongly suspected to be formed by, insects were included in the study.

Collected galls were morphotyped according to gall morphology within host plant, photographed, and reared in clear plastic bags for a period of 1 month. Galled material was added to each rearing bag so that it was roughly one-third full in order to minimise condensation and to not impede the observation of eclosed insects. A limit of six rearing bags per morphospecies per sample unit was imposed to keep collections to a manageable amount, and any remaining material discarded. Rearing bags were checked for emergent insects every 1–2 days.

All eclosed insect specimens were transferred to vials of 95% EtOH for storage, except for lepidopterans, which were pinned. In addition to rearings, random dissections of gall morphospecies were carried out to aid in identification of the gall-formers. All galls for each host species were then morphotyped according to gall morphology using the images taken for each sample. Galls of a similar morphology on different organs of the same host plant were assumed to be the same species of inducer. Finally, for galls were reared or dissected material was sufficient, gall inducers were morphotyped across all samples and hosts assuming polyphagy within their respective gall-forming taxa (Cecidomyiidae, Hemiptera, Hymenoptera, Thysanoptera, and Lepidoptera) using either or both of the following species concepts: (i) the comparative morphology of adult and/or immature stage insects and (ii) the analysis of DNA barcode sequences, according to the 2% sequence divergence threshold (K2P distances).

Statistical analysis

Data from the three sampling locations were pooled for all analyses. Species' accumulation curves and species' estimator functions were produced using EstimateS (Colwell, 2013). As we did not record the exact number of individual galls (unless <=10), and because galls are mostly gregarious by nature, we used incidence-based rather than abundance-based estimators. Because many tropical herbivores are clade specialists (Weiblen *et al.*, 2006), the mean number of galling insect species among the major host plant clades – Rosids I, Rosids II, Asterids, and a paraphyletic 'Basal' clade comprising taxa basal to the Rosid-Asterid clade, including basal Eudicots, Monocots, and Magnoliids and Gymnosperms – were compared with a standard ANOVA for both this study and data from Indonesia (Docters van Leeuwen-Reijnvaan & Docters van Leeuwen, 1926). ANOVA was also employed to test for any effect of seasonality on gall species richness across the sampling period. The data were split evenly into three periods: the first 9 weeks, middle 10 weeks, and final 10 weeks of sampling that correspond with 'dry', 'post dry' and 'wet' seasons, respectively (although 'post dry' and 'wet' are no different climatically).

Host specificity was quantified as effective specialisation F_T, as termed by May (1990), such that $F_T = S_T/(S_{Tavg} \times T)$, where T is the number of host plant species, S_T the number of insect species on T hosts, and S_{Tavg} the mean number of insect species per host (Odegaard *et al.*, 2000).

The distribution of the number of insect species on each plant species was tested against the Poisson distribution. If not siginificantly different, it would suggest that plant colonisation events by galling species were mutually independent and so not influenced by the other galling species present.

The presence or otherwise of a phylogenetic signal among the plant traits and characteristics (including the number of leaf miner species, S_m) was ascertained by measuring the K statistic in the R package *Picante* (Kembel *et al.*, 2010), which yields a P-value based on 999 randomisations of trait values across the phylogeny compared with expected values under the Brownian motion model of evolution. The presence or absence of latex was measured as D, an alternative statistic better suited to binary data (Fritz & Purvis, 2010), in the R package *Caper* (Orme *et al.*, 2013). A generalised least squares analysis was adopted to measure the significance of plant characteristics on galler species richness. Analyses were conducted both with (PGLS; R package *caper*) and without (GLS) phylogeny as a covariate, the former being analagous with phylogenetically independent contrasts analysis (PICs) as long as the specified correlation structure was the Brownian model, as was the case. We analysed the effect of each plant trait on galler richness individually, rather than fitting all traits in a model to be simplified, because reduced versions of the phylogeny ($n = 25–32$) needed to be used for some plant traits owing to missing values. The response variable, the number of galling species, was square root transformed.

The dispersion of grouped gall-forming taxa (Cecidomyiidae, Hemiptera, etc.) with respect to host plant phylogeny was also assessed using the freely available software package Phylocom (Webb *et al.*, 2008). The host plant phylogenetic topology was constructed based on the phylogeny in Weiblen *et al.* (2006), which shared 23 of the 32 species in this study, and the Angiosperm Phylogeny Group (APG III, 2009). An ultrametric tree was created using Branch Length Adjustment in Phylocom and the estimated lineage ages given in Wikstrom *et al.* (2001) (see Appendix S2 and Table S2, Document S1). We followed the procedure used by Weiblen *et al.* (2006) that yields results based on two indices, the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) (Webb, 2000), rankings that can be tested for significance, based on 2999 randomisations.

Fisher's exact tests were used on 2×2 contingency tables to test whether or not the colonisation status (colonised or not colonised) of galling species was affected by (i) the host species' preference for primary ($SI \geq 50$) or secondary ($SI < 50$) forest, or (ii) the presence or not of latex in the host species.

In order to compare the species' richness observed in this study with that of other studies of tropical gall insects, data were collated from 16 tropical or subtropical studies (Table 2). The studies were selected based on latitude (between 30°N and 30°S of the equator) and provided they gave the necessary information, i.e. the number of host plant species bearing galls and the total number of insect gall species. We categorised 'local' studies as those whose spatial extent of sampling was in the order of $100\,\mathrm{km}^2$ or less, and 'regional' as those with spatial extent in the order of $1000\,\mathrm{km}^2$ or more. A temperate study from Great Britain was included for comparison only and was not included in the analysis.

All data analyses were carried out using the R statistical software package (R Core Team, 2013) unless otherwise stated.

Results

Host specificity

More than 8800 galled plant parts (leaves, stems, fruits, etc.) were collected and a conservative estimate of 8150 parts reared during the course of the study, representing vastly more individual galls. The project yielded 78 morphospecies on 32 target host plants at an average of 2.4 species per host species (Fig. 1). A subset of 28 morphospecies with unknown gall former were removed from host specificity analyses, leaving $n = 50$ morphospecies (Tables S3 and S4, Document S1). Just a single species of agromyzid fly was found to gall more than one host, those of closely related congenerics *Ficus wassa* and *F. copiosa*, detected by traditional taxonomy and confirmed by DNA barcoding (Figures S3 and S4, Document S1). Thus, effective specialisation, F, was 0.98 ($T = 32$, $S_T = 50$). Most galls were formed on leaves (55) and stems (14), and the others on petioles (3), combinations of leaves and stems (2), leaves and petioles (1), and leaves, petioles and stems (1), and one each on seeds, flowers and leafsheaths. Throughout the remainder of the manuscript, it is assumed that when talking about galls, *morphospecies* and *species* are synonymous.

Species richness

From 78 species, the richness of galls ranged from 0 to 6 species (median 2) per plant species. Four host species were not colonised by any galls (Fig. 1). Given the total gall assemblages observed per focal host species across the entire project, the average gall assemblage per host per sample was always a fraction, and, in the majority of cases, less than half of the available species pool (Fig. 1). There was no significant difference between the mean gall species richness of three consecutive periods of sampling, the first of which corresponds to a dry season (ANOVA, $F_{2,26} = 2.109$, $P = 0.142$).

The observed sample-based rarefaction curve appears to be near-asymptotic (Fig. 2a), indicating that the sampling duration was sufficiently long as to include most of the gall community on these hosts. The incidence-based species estimators giving the lowest and highest estimates were selected for illustration, predicting total community species pools of 83 (Bootstrap) and 88.7 (Jacknife 2) respectively, thus our observed gall community potentially represents 88–94% of the total gall community (Fig. 2). The accumulation of gall species with increasing number of plant species produces a straight line as a result of high host specificity (Fig. 2b). Using the number of angiosperm species with $DBH > 5\,\mathrm{cm}$ found in primary lowland PNG rainforests, and assuming all gall-formers were monophagous, the number of galling insect species predicted by extrapolating our data would be 528 from 220 host species in 1 ha, and 1027 from 428 species in 50 ha (Wanang CTFS 50 ha plot; G. Weiblen, pers. comm.). It should be noted, however, that the extrapolations are based on locally common plant species that are likely to host relatively higher numbers of gall species than locally rare host species and, therefore, a small overestimation should be expected in the results.

Gall species were distributed randomly among host plants (Poisson; $\chi^2_6 = 8.63$, $P > 0.05$) as a whole (Figure S1a, Document S1), but taken on their own, cecidomyiids (Figure S1b, Document S1) fitted a more clumped or aggregated distribution (Negative binomial; $\chi^2_6 = 4.30$, $P > 0.05$), colonising exactly half the number of studied plants.

There was no significant difference in the mean number of galling insect species among plant clades in this study (Fig. 3; ANOVA, $F_{3,28} = 1.137$, $P = 0.35$). This was also the case for Indonesian gall data extracted and analysed for comparison from Docters van Leeuwen-Reijnvaan and Docters van Leeuwen (1926) (Fig. 3; $F_{3,363} = 2.033$, $P = 0.11$).

The phylogenetic dispersal of most gall-forming taxa were neither significantly clustered nor overdispersed across the host plant phylogeny either in terms of NRI or NTI (Fig. 4; Cecidomyiidae $P = 0.75$ and $P = 0.91$ for NRI and NTI, respectively; Hemiptera $P = 0.42$ and $P = 0.50$; Hymenoptera $P = 0.30$

Table 1. Phylogenetic signal (PS) of plant traits and effects of plant traits on gall-forming insect species richness with (PGLS, phylogenetically generalised least squares) and without (GLS, generalised least squares regression) phylogenetic considerations (n = no. of plant species in the phylogeny) from lowland rainforest sites in New Guinea.

Variable	n	d.f.	K or D*	F	P	Adjusted r^2
Successional index (SI)	32	30				
PS			0.371		**0.031**	
GLS				4.549	**0.041**	
PGLS				5.326	**0.028**	0.138
Specific leaf weight (SLW)	32	30				
PS			0.486		**0.002**	
GLS				5.705	**0.023**	
PGLS				3.860	0.059	0.067
Latex (L)	32	30				
PS			−1.331*		**0.024**	
GLS				0.628	0.434	
PGLS				1.577	0.219	0.018
Diameter at breast height (DBH)	28	26				
PS			0.162		0.692	
GLS				0.131	0.720	
PGLS				1.825	0.188	0.056
Average basal area (BA)	25	23				
PS			0.095		0.877	
GLS				0.002	0.965	
PGLS				3.917	0.060	0.166
Wood density (WD)	25	23				
PS			0.359		0.080	
GLS				1.526	0.229	
PGLS				0.401	0.533	−0.003
Foliar nitrogen (N)	25	23				
PS			0.457		**0.016**	
GLS				5.586	**0.027**	
PGLS				3.221	0.086	0.078
Leaf miner species (S_m)	30	28				
PS			0.352		0.054	
GLS				1.221	0.279	
PGLS				0.276	0.603	0.010

K = Blomberg's K statistic, a measure of phylogenetic signal. D = measure of phylogenetic signal for binary data (see Methods). An asterisk * denotes a D statistic was used as opposed to K. Statistically significant results are displayed in bold type.

and $P = 0.44$; Lepidoptera $P = 0.40$ and $P = 0.40$; Thysanoptera $P = 0.82$ and $P = 0.82$). However, Agromyzidae were significantly clustered (NRI and NTI $P < 0.01$) on a portion of the Rosids I clade comprising Moraceae and Cannabaceae.

Plant species successional index (SI), SLW, the presence of latex, and foliar nitrogen all exhibited a significant phylogenetic signal when compared against null expectations (Table 1; $P < 0.01$ for SLW, otherwise $P < 0.05$). Successional index, specific leaf weight, and foliar nitrogen were also significantly correlated with the species richness of gall insects (Table 1; $P < 0.05$), but only the successional index of host plant species had a significant effect on the analysis of phylogenetically independent contrasts (Table 1; $P < 0.05$), explaining 14% of the variation in gall species richness. In this study, therefore, the effect of plant phylogeny accounted for most of the observed correlations with gall species richness, but insect gallers were more speciose on plant species that preferred primary rainforest. However, the successional index (SI) of plant species did not influence whether or not they were colonised by a galling insect (Fisher's exact test, $P = 1$).

The presence of latex in host plants resulted in significantly reduced colonisation by Cecidomyiidae (Fisher's exact test, $P < 0.05$; Figure S2b, Document S1), but not when all galling taxa where considered ($P = 1$; Figure S2a, Document S1).

In our analysis of tropical gall data from the literature (Table 1, Fig. 5), the average number of gall species per host plant species was 1.56. The regression line was forced through the origin ($r^2 = 0.996$, $F_{1,15} = 3932$, $P \ll 0.001$) and shows a robust linear relationship.

Discussion

Host specificity

Based on this study, the gall-forming insect community is the most specialised of 12 herbivorous insect guilds studied thus far in PNG lowland rainforests (Novotny *et al.*, 2010, 2012), followed by leaf suckers and leaf miners (Novotny *et al.*, 2010; Baje *et al.*, 2014). Effective specialisation was apparently higher, considering the disparity in sample sizes, than for Neotropical

Table 2. The mean number of gall-forming insect species per galled host plant species recorded from selected tropical studies and one temperate study for comparison. A habitat type of 'other' denotes habitats other than wet tropical rainforest.

Region	Reference	Sampling	Spatial scale	Habitat types	Insect gall species	Host plant species	Mean gall spp. per host sp.
Mexico	Cuevas-Reyes *et al.* (2004)	Architectural census	Local	Other	38	38	1
Indonesia	Yukawa and Partomihardjo (1997)	Non-systematic collecting (21-day period)	Regional	Wet tropical rainforest	16	15	1.07
Indonesia	Docters van Leeuwen-Reijnvaan and Docters van Leeuwen (1926, 1941)	Non-systematic collecting (18-year period)	Regional	Mixed	1136	988	1.15
Panama	Nieves-Aldrey *et al.* (2008)	Timed transects (1 h)	Regional	Wet tropical rainforest	50	42	1.19
Costa Rica	Hanson and Gomez-Laurito (2005)	Non-systematic collecting (10-year period)	Regional	Mixed, but mostly wet tropical rainforest	896	711	1.26
Brazil	Santos *et al.* (2011a)	Timed transects (3 h)	Regional	Other	64	48	1.33
Brazil	Mendonca *et al.* (2010)	Timed transects (1.5 h)	Local	Other	104	75	1.39
Brazil	Dalbem and Mendonca (2006)	Timed transects (1.5 h)	Local	Other	127	84	1.51
Brazil	Goncalves-Alvim and Fernandes (2001)	Architectural census	Regional	Other	125	80	1.56
Brazil	Santos *et al.* (2011b)	Timed transects (3 h)	Regional	Other	80	49	1.63
Brazil	Carneiro *et al.* (2009b)	Architectural census (woody plants only)	Regional	Other	239	140	1.71
Brazil	Fernandes *et al.* (1997)	Timed transects (1 h)	Regional	Other	236	134	1.76
Brazil	Coelho *et al.* (2009)	Timed transects (1 h)	Local	Other	90	50	1.8
Brazil	Maia and Fernandes (2004)	Timed transects (8 h)	Local	Other	137	73	1.88
Panama	Ribeiro and Basset (2007)	Canopy crane	Local	Wet tropical rainforest	32	16	2
PNG	This study	32 targeted host plant species	Local	Wet tropical rainforest	78	28	2.79
G.Britain	Cornell and Kahn (1989)	Long-term data	Regional	Other	184	33	5.58

*Non-insect galls and plant species hosting only non-insect galls were subtracted.

cecidomyiids (Carneiro *et al.*, 2009a) and 90% generally for galling insects (Raman, 2010), providing further evidence that the combination of gall morphology and host plant identity are an acceptable proxy for the inducing insect species, as has long been considered acceptable among gall researchers (Blanche, 2000; Raman *et al.*, 2005; Shorthouse *et al.*, 2005; Carneiro *et al.*, 2009a; Fernandes *et al.*, 2010).

There can be no doubt that in tropical rainforests, as in other habitats, galling insect specialisation is very high. Whether or not it is higher than in other regions, e.g. Europe, is difficult to say because our knowledge of the tropical gall fauna is clearly insufficient. Co-occurring congeneric plant species are a substantial component (~50%) of PNG rainforests that tend to reduce levels of herbivore specialisation (Novotny *et al.*, 2010), but with two-thirds of our gall species being found on 16 congeneric host species, the single oligophagous galler in our study confirms the rarity of this kind of interaction for gallers.

Species richness and host plant characteristics

We found 78 species of gall-forming insect distributed randomly on 32 host plant species in a lowland tropical rainforest in PNG. The Poisson distribution suggests that species probably colonise plant species independently, which was also the case for mesophyll suckers, leaf miners, and exposed chewers, all low diversity folivorous insect guilds in PNG (Novotny *et al.*, 2012). With an average of 2.4 species per host plant species, species richness is also comparable with PNG leaf miners (2.3) and mesophyll suckers (1.1) (Novotny *et al.*, 2010, 2012; Baje *et al.*, 2014). Additionally, gallers showed no special preference for any particular angiosperm lineage, all of which suggests that insect galls in the lowland rainforests of New Guinea should be ubiquitous but occur in species-poor assemblages.

Galling taxa in this study were generally cosmopolitan in that they were not significantly restricted to any single part of the host plant phylogeny, but with one exception. All three species of Agromyzidae (Diptera) were found clustered in the rosids I clade encompassing the families Moraceae and Cannabaceae. The ~40 species of galling agromyzid with known host plant species mainly colonise Asteraceae, Salicaceae, and Fabaceae (Dempewolf, 2005). Asteraceae are mainly herbaceous and so not really pertinent to the discussion, but Salicaceae and Fabaceae belong to the same rosids clade as the species in our study, so our data may possibly reflect the wider situation for galling Agromyzidae. Lepidoptera and Thysanoptera, however, contain more galling species globally, and on a greater range of host plant species, which may explain their phylogenetic dispersion.

We found no support in this study for the hygrothermal stress hypothesis. Both SLW and foliar nitrogen concentration did not significantly affect gall species richness when the plant phylogeny was taken into account. Gall richness was positively related to the SI of host plants in that plant species more commonly found in primary forests hosted more galling species,

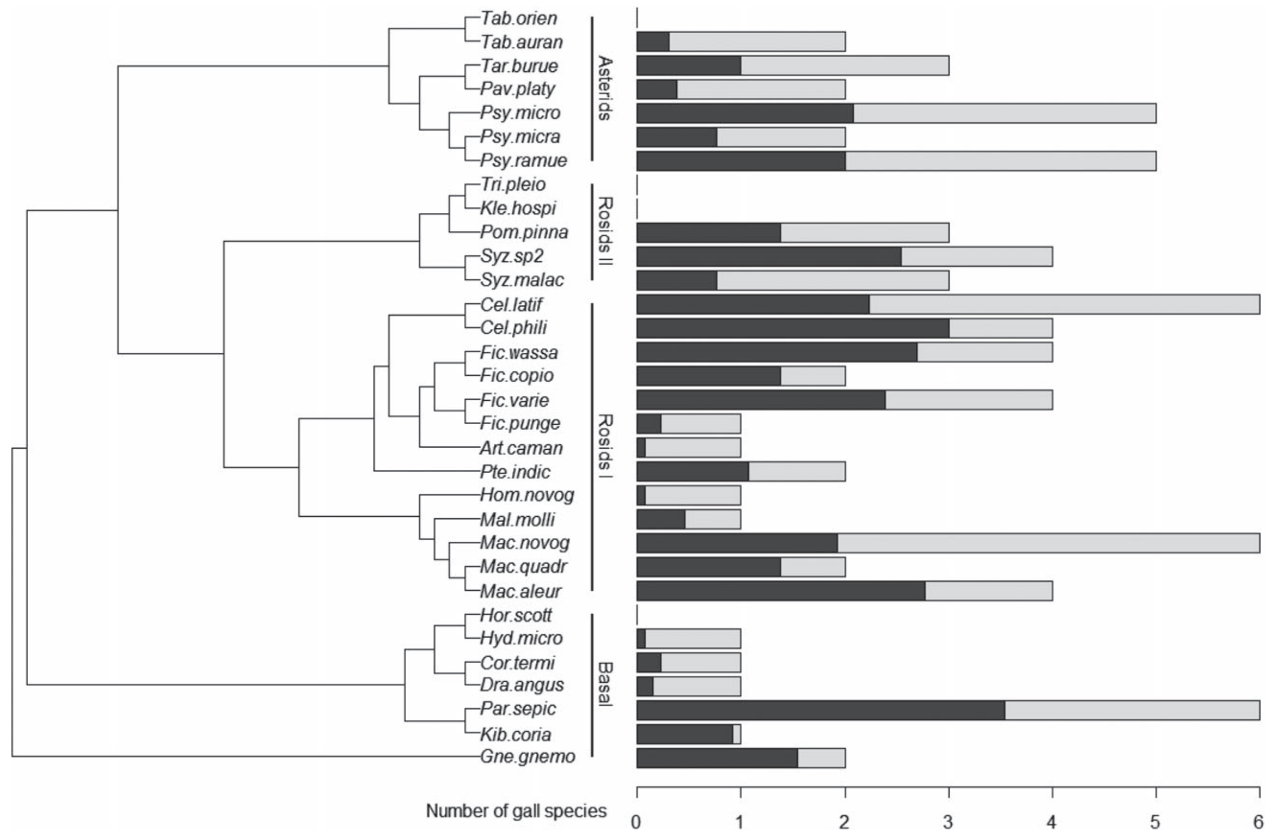

Fig. 1. Phylogram for 32 woody host plant species from lowland rainforest, Papua New Guinea (PNG), with annotated plant clades and corresponding gall species richness (total bar height). Average gall species yields per sample, based on 13 samples, are shown as dark bars.

and thus the hypothesis that SI would have no effect is rejected. This result contrasts with two other PNG studies where plant SI was not correlated with the species richness of leaf-chewing or sap-sucking herbivores (Leps *et al.*, 2001), and one in Amazonia where restored rainforest stands of typical secondary vegetation age (~10–18 years) were found to be richer in galling insect species than were primary rainforest patches (Fernandes *et al.*, 2010). From another PNG study, preliminary data suggests that there are more species of gall per angiosperm species in secondary than in primary montane rainforest plots (P. Butterill, unpublished). Our result, therefore, is surprising and could reflect other characteristics of the plant species, such as their phenology or growth strategy, rather than their successional preference *per se*.

We found no correlation between plant species that exude latex and gall species richness, either with or without phylogenetically independent contrasts, although latex production gave off a strong phylogenetic signal among our host species. Our results suggest that this trait is not important for galling insects and that the potentially harmful effects of latex can be bypassed. Sternorrhynchan gallers (Hemiptera), for example, may avoid contact with latex owing to their intercellular feeding mode (Agrawal & Konno, 2009), but it is less clear how other galling taxa might do so. On latex-producing plants, cecidomyiid gall midges colonised a significantly smaller proportion of species than on those where latex was absent, perhaps as a result of difficulties ovipositing into buds on these plants. However, the notion is not supported by Indonesian gall data where 21 out of 39 *Ficus* species (Moraceae) hosting galls were colonised by at least one cecidomyiid, and *Antiaria toxicaris* (Moraceae) hosted eight species of cecidomyiid gall.

How speciose are gallers in wet tropical rainforests?

One feature of most galling insect studies is that they only include plant species that host at least one gall, and so the number of host plant species with no galls (null hosts) has not been reported. In the datasets we compared, the average number of gall species per galled plant species is highly consistent, with the figure for PNG being the highest among the datasets with the exception of Great Britain. Our focus on locally common woody host species and sampling method likely explain, at least in part, the slightly higher values observed for PNG. First, locally common host species are more likely to host a greater number of gall species and, second, most surveys of tropical gall insects are based on either timed transects and architectural censuses (Price *et al.*, 1998), or are large-scale bio-inventories, both old and new (Docters van Leeuwen-Reijnvaan & Docters van Leeuwen, 1926; Hanson & Gomez-Laurito, 2005). These methods provide snapshots in time, but do not necessarily resample localities

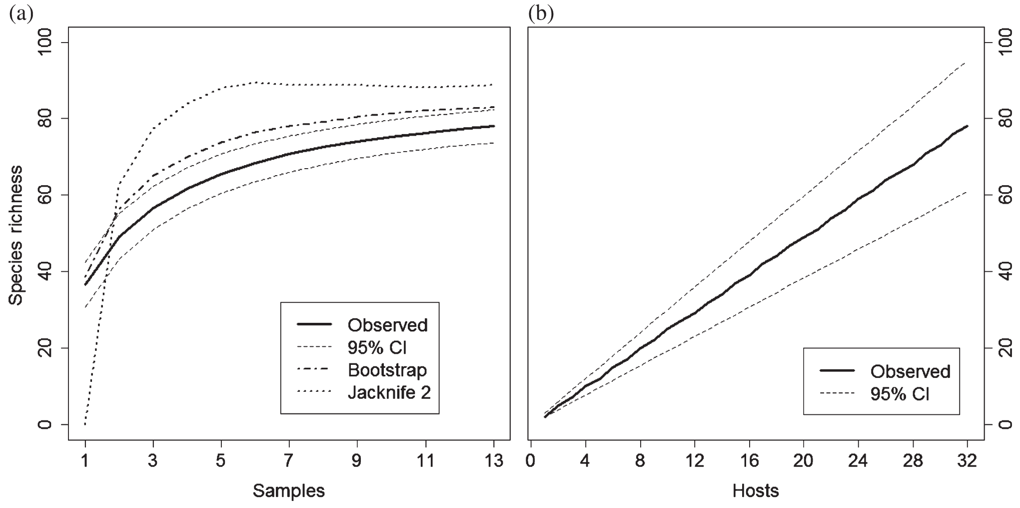

Fig. 2. Randomised species accumulation curves with 95% confidence intervals are shown for (a) increasing sampling effort on the same set of plant species, with Bootstrap and Jacknife 2 species estimators shown, and (b) increasing number of plant species sampled. Thirteen samples from each of the 32 plant species studied (416 individual samples in total) are separated into 13 sets, each comprising one sample from each plant species.

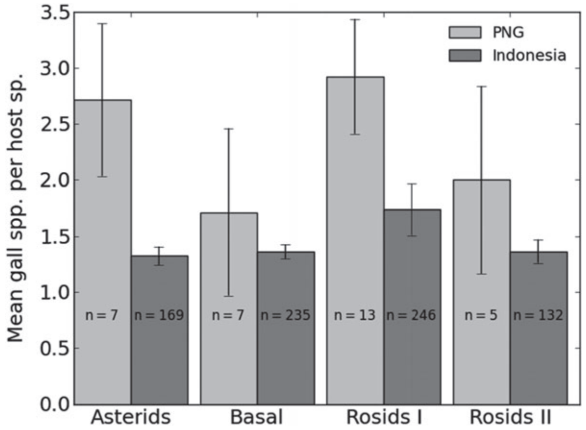

Fig. 3. The mean (± SE) gall species richness per host plant among angiosperm clades for Papua New Guinea (PNG) and Indonesia, with the number of host plants per clade (*n*). The basal clade includes all species basal to the rosid-asterid clade (i.e. basal Eudicots, Monocots, Magnoliids, and Gymnosperms). All clades follow the APG classification (APG III, 2009). Indonesian data from Docters van Leeuwen-Reijnvaan and Docters van Leeuwen (1926).

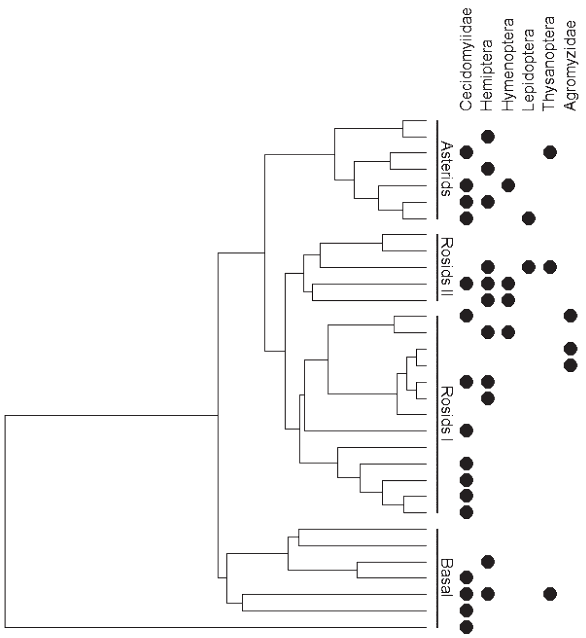

Fig. 4. Dispersion of the main gall-forming taxa based on presence/absence across an ultrametric phylogeny of host plants (see Fig. 1 for host plant codes). Only agromyzidae were significantly clustered, and most others were randomly dispersed. Annotated plant clades follow the APG classification (APG III, 2009). The basal clade includes all species basal to the rosid-asterid clade (i.e. Eudicots, Monocots, Magnoliids, and Gymnosperms).

and host plants over longer periods. It took seven repeated samples to accumulate 90% of the galling species observed in this study. Even in the datasets that include Brazilian cerrado, where gallers can be locally very rich (Lara & Fernandes, 1996; Price *et al.*, 1998), the mean number of gall species per galled host plant species does not exceed two (Fernandes *et al.*, 1997; Goncalves-Alvim & Fernandes, 2001; Maia & Fernandes, 2004; Coelho *et al.*, 2009; Carneiro *et al.*, 2009b). Although a relatively small comparison of datasets, the indication is that the number of galling insect species per galled host plant species is remarkably stable across tropical and subtropical latitudes, in spite of differences in the spatial scale, sampled habitat, and host plant sample size. Therefore, we find no evidence to suggest that galling insects in tropical rainforests are less speciose than in any other tropical or subtropical habitat, at least per galled host plant species, and therefore contend that galler richness in the wet tropics could be greater than currently thought. However,

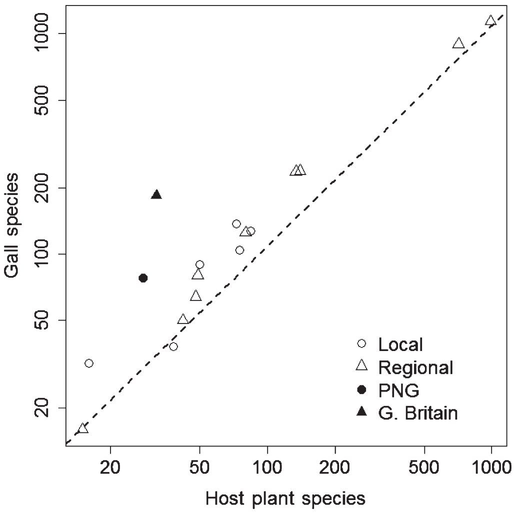

Fig. 5. The number of gall species against the number of plant species hosting them for 16 local and regional tropical studies (primarily Neotropical), including the present study [Papua New Guinea (PNG)]. Both axes are log transformed. Mean galls per host is 1.56 (2.79 for PNG). Plants sampled but not colonised by any galls were not included. The regression line was forced through the origin ($r^2 = 0.996$, $F_{1,15} = 3932$, $P \ll 0.001$). The Great Britain point is shown for reference and is not included in the regression.

in order to make meaningful comparisons between different habitats and/or latitudes, the number of not-galled (null) host species needs to be known and very few data provide this (Espirito-Santo & Fernandes, 2007).

Why do common British tree species appear to host two or three times more species of insect gall (Cornell & Kahn, 1989) than do plant species at southern latitudes? Perhaps the main reason is simply how comprehensively the British gall fauna is known, having been sampled by scientific researchers and amateur entomologists alike for over a century. Although the datasets we categorised as 'regional' might be similar in their spatial extent, the spatial grain – the number and proximity of sampled sites within the extent – of these studies vary greatly. The jigsaw of Great Britain is almost complete whereas we have barely assembled the edge pieces of most tropical regions. However, other factors, such as the presence of so-called 'superhosts' and resource synchronisation, may also be influential. Superhosts, such as *Quercus petraea* & *Q. robur* in Britain, which host around 60 species of gall between them, obviously influence gall species richness, but there are also examples at southern latitudes that host more than ten gall species, for example, *Baccharis* spp. (Asteraceae) in Brazillian cerrado (Lara & Fernandes, 1996). There were no superhosts in our sampling, but plant species with large host ranges may support a regional fauna worthy of a superhost (Cornell, 1985) that might not be obvious at the local scale. Or perhaps tropical forests do not provide the necessary ecological conditions for a superhost to exist due to, for example, species being less dominant and more dispersed in the ecosystem than their temperate cousins. Finally, the synchronised phenology of temperate vegetation may provide greater opportunity for speciation through host shifting by multiple resources becoming available to short-lived female gallers at the same time (Mendonca, 2001).

Conclusion

Our results reveal, for the first time in New Guinea, that highly specialised galling insects may be ubiquitous among the angiosperms of tropical rainforests, but in species-poor assemblages. According to niche theory, species-poor assemblages of specialised herbivores are paradoxical because the compartmentalisation of plant resources should facilitate the coexistence of many species (Lewinsohn & Roslin, 2008; Novotny *et al.*, 2012). Alternatively, such assemblages might be best explained by the diversity of the regional species pool for each guild (Novotny *et al.*, 2012), which are largely or, in the case of gallers, completely unknown. Further sampling effort will be required in order to expand on some of the results highlighted in this study: the relative richness of galling insects in tropical forests compared with other habitats, the role of plant successional preference as a potential determinant of galler assemblages, and whether or not such extreme specialisation is maintained across a wider range of host plants.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:
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Document S1. Appendix S1–Measurement of host plant characteristics; Table S1–Plant species with taxonomy and traits; Appendix S2–Host plant topology in Newick format;

Table S2–Internal node ages used; Figure S1–Frequency distribution of galling insect species; Figure S2–Effect of host plant latex presence on gall species colonisation; Figure S3–Barcode gap analysis; Figure S4–Lineplot of barcode gap analysis for dipteran gall-forming species; Table S3–Morphotyping of gall-forming taxa; Table S4–Species richness estimates based on morphotyping.

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