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Species richness of gall-forming insects in a tropical rain forest: correlations with plant diversity and soil fertility

PABLO CUEVAS-REYES, CRISTINA SIEBE, MIGUEL MARTÍNEZ-RAMOS and KEN OYAMA*
Departamento de Ecología de los Recursos Naturales, Instituto de Ecología, UNAM, Antigua Carretera a Pátzcuaro No. 8701, Col. Ex-Hacienda de San José de la Huerta, Morelia, 58190 Michoacán, México;
**Author for correspondence (e-mail: akoyama@ate.oikos.unam.mx; fax: +52-5-623-2719)*

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Abstract. We tested two hypotheses to explain changes in species richness of gall-forming insects. The first hypothesis proposes that gall-forming insect species richness increases as more potential host–plant species are available. The second hypothesis implies that soil fertility affects plant colonization by gall-forming insects. Seven sites, representing strong differences in vegetation and soil were chosen at the Lacandona tropical rain forest region, Chiapas, Mexico. Overall, we found 1522 individual plants belonging to 340 different plant species. From this, we found gall-forming insects on 737 (43.9%) plants and on 74 (22%) of total plant species. We found a significant negative correlation between gall-forming insect species richness and species richness of plants, which does not support the hypothesis that plant species richness is an important factor in generating the radiation of gall-forming insects. Using phosphorus as an indicator of soil fertility, we found the lowest number of plants with gall-forming insects and the smallest gall-forming insect load per individual plant in the more fertile soil (alluvial). In contrast, the highest number of plants with galls and the highest gall-forming insect load per plant were found at a savanna-like vegetation site, where the poorest soil was recorded. These results did not support the soil fertility hypothesis in terms of species richness, but did with respect to abundance of plants with galls.

Introduction

Two hypotheses have been proposed to explain differences in species diversity of gall-forming insects among plant communities. The first is that plant species richness determines gall-forming insect species richness (Fernandes and Price 1988; Wright and Samways 1996, 1998; Goncalves-Alvim and Fernandes 2001), and the second is that soil fertility reduces plant colonization by gall-forming insect species (Fernandes and Price 1991; Price 1991). Assessment of the first hypothesis in different localities had resulted in contrasting results. Fernandes and Price (1988) found that gall-forming insect species diversity was independent of plant species richness, but Wright and Samways (1996, 1998) suggested that plant species richness can act as a driving force of diversification of gall-forming insect species.

Regarding the second hypothesis, it has been proposed that high concentrations of secondary metabolites, such as oils and phenols, are characteristic of plants growing on infertile soils (McKey et al. 1978; Medina et al. 1990; Fernandes and Price 1991). These chemical defenses may benefit gall-forming insects by providing them with protection against natural enemies, such as chewing herbivores, viruses, parasitoids and fungi (Cornell 1983; Hartman 1985; Mattson and Haack 1987; Waring and Price 1990; Fernandes and Price 1992). More recently, Blanche and Westoby (1995) found that gall-forming insect species diversity was not linked directly to soil fertility, but via host–plant taxon establishment.

Altitudinal and latitudinal gradients of gall-forming insect species richness have been reported for several localities in the world (Fernandes and Price 1988; Price 1991; Fernandes and Lara 1993; Price et al. 1998; Blanche 2000; Blanche and Ludwing 2001). However, at a regional scale, few comparative studies on gall-forming species richness exist. Tropical forests have different levels of structural heterogeneity in soil and topographical landscape mosaics (e.g., Denslow 1987). In these forests, the richest site of gall-forming insects has been reported (Lara and Fernandes 1996), but it is unknown how such insect diversity changes across landscape scales.

In this study, we tested current hypotheses on gall-forming insect species richness by using a tropical forest landscape system, taking advantage of the strong vegetation and soil variations present in an area of a few dozen square kilometers in the Lacandona region, Chiapas, Mexico. In particular we addressed the following questions: (1) What is the pattern of gall-forming insect species richness in a heterogeneous tropical forest? (2) Is variation in gall-forming insect species richness related to changes in plant species richness and soil fertility?

Methods

This study was conducted at the Chajul Biological Station (16–17° N; 90°30′ W), which is located within the Montes Azules Biosphere Preserve (340 000 ha), in the Lacandona region, southeastern Mexico. The forest of Lacandona represents the last pristine area of tropical rain forest that remains in Mexico. For more details on the study site, see Orellana (1978) and Martínez et al. (1994).

Seven sites differing in vegetation, soil, and topography were chosen for this study; rainfall was similar among all sites. In each site we established a 20×250 m plot with a grid system of one hundred 5×10 m quadrants. We chose 15 random quadrants from each plot and counted gall insects on all individual plants up to 3.0 m high. Galling insects and their host plants were separated and counted on the basis of host plant and gall morphology. The number of galls per plant species was also recorded. This type of study assumes that each gall morph is unique to a galling species and that gall species are specific to a single plant species (Koach and Wool 1977; Bearsley 1982; Ananthakrishan 1984; Dodson and George 1986; Weis et al. 1988; Mound 1994; Abrahamson et al. 1997; Hartley 1998; Price et al. 1998; Goncalves-Alvim and Fernandes 2001).

Soil traits at each site were analyzed: total soil phosphorus, nitrogen availability,

Table 1. Plant species with and without gall-forming insect species recorded in seven localities of Lacandona reserve, Chiapas.

Localities	Number of plan species with galls	Number of plant species without galls	Total
Flooded	19 (11.1)	64 (71.9)	83
Low hill 1	14 (13.1)	84 (84.9)	98
Low hill 2	13 (13.7)	90 (89.3)	103
Karstified mountain	12 (13.2)	87 (85.8)	99
Savanna	5 (14.4)	103 (93.6)	108
Alluvial 1	15 (12.7)	80 (82.3)	95
Alluvial 2	11 (10.8)	70 (70.2)	81
Total	89	578	667

Expected numbers in parentheses ($\chi^2 = 14.4$; $P < 0.05$; d.f. $= 6$).

organic matter content and exchangeable cations were measured by taking 12 random soil horizon samples of 1 kg in each site having 100 cm of depth and analyzing them by standard methods (Siebe et al. 1995).

The degree of floristic similarity among sites was calculated using the Driver and Kroeber index, calculated as $100C/[(N1)(N2)]^{1/2}$, where C is the number of shared species; $N1$, the species number of the most diverse flora; and $N2$, the species number of the less diverse flora.

Results

In total, we identified 340 different plant species grouped in 29 families. Of these, 74 species (22%) had associated gall-forming insect species. The frequency of species of gall insects differed among sites ($\chi^2 = 14.4$; d.f. $= 6$; $P < 0.05$) (Table 1). The greatest frequency of gall-forming species was present in medium-sized forest (where some trees could reach up to 30 m in height) which is periodically flooded. In contrast, the savanna site recorded the highest richness of plant species, but the lowest gall-insect species richness.

Most plant species (55%) were restricted to one site and only five species were recorded in all sites. Most gall-forming insect species (62.2%) also had a restricted distribution and only few had broad spatial distribution (Figure 1). On average, study sites shared 21% of plant species in common. The savanna site showed the lowest average floristic similarity, while sites in alluvial 1 and 2, and low hill 1 and 2 showed the highest similarity values (Table 2).

In the seven plots (0.53 ha sampled area), we recorded 737 (43.9%) individual plants with gall-forming insects. The savanna site showed the highest abundance of plants with gall-forming insects ($F = 409.07$; $P < 0.0001$) (Figure 2a) and the highest gall density per individual plant ($F = 83.63$; $P < 0.0001$) (Figure 2b). The lowest incidence of galls at the community and individual levels was found in the alluvial sites. Gall-forming insect abundance was significantly greater in plant species with broad distribution ($F = 24.61$; $P < 0.0001$) (Table 3).

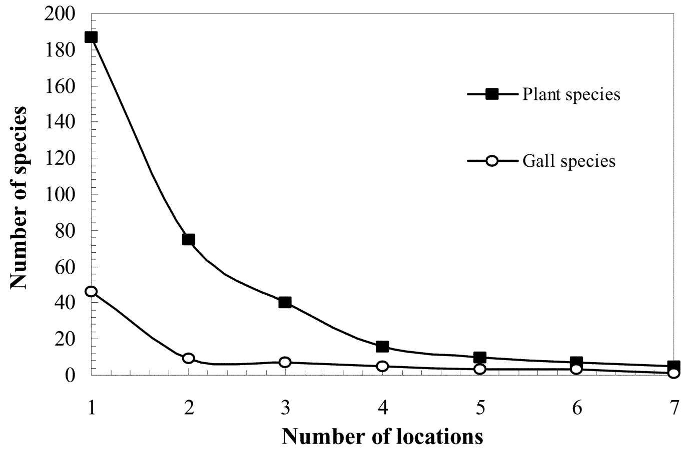


Figure 1. Presence of plant species and gall-forming species in seven localities in the Lacandona reserve, Chiapas. The empty circles indicate the number of locations at which a GFI occurred and the full squares the number of locations at which a plant species occurred.

Table 2. Similarity of plant species composition between locations using the Driver and Kroeber index.

	Flooded	Low hill 1	Low hill 2	Karst. mount.	Savanna	Alluvial 1	Alluvial 2
Flooded	*	17.2	22.5	16.5	12.9	32.0	24.3
Low hill 1		*	**40.3**	28.1	17.2	35.3	21.0
Low hill 2			*	21.5	21.8	24.3	31.6
Karst. mount.				*	12.7	23.1	17.8
Savanna					*	13.8	8.8
Alluvial 1						*	**41.4**
Alluvial 2							*

The bold values indicate the highest plant species overlap between sites.

We found a significant negative correlation between plant species richness and proportion of plant species with gall-forming insects (Figure 3; $y = -0.004x + 0.562$; $R^2 = 77.3\%$; $P < 0.0008$). Using phosphorus availability as an indicator of soil fertility (Table 4), there was no relationship between the proportion of plant species with gall-forming insect species and soil fertility. However, the abundance of gall-forming insects, both at community (Figure 4a; $y = 4.002x^{-0.44}$; $R^2 = 81.1\%$; $P < 0.05$) and at individual plant (Figure 4b; $y = 110.9x^{-0.157}$; $R^2 = 95.2\%$; $P < 0.05$) levels, showed a negative relationship with soil fertility.

Discussion

The number of plant species infected with gall-forming insects at the Chajul rain forest was high. Approximately 22% of recorded plant species were found to be colonized by at least one galling insect, suggesting the successful prevalence of this insect guild in this environment. Although differences in methodology prevent a

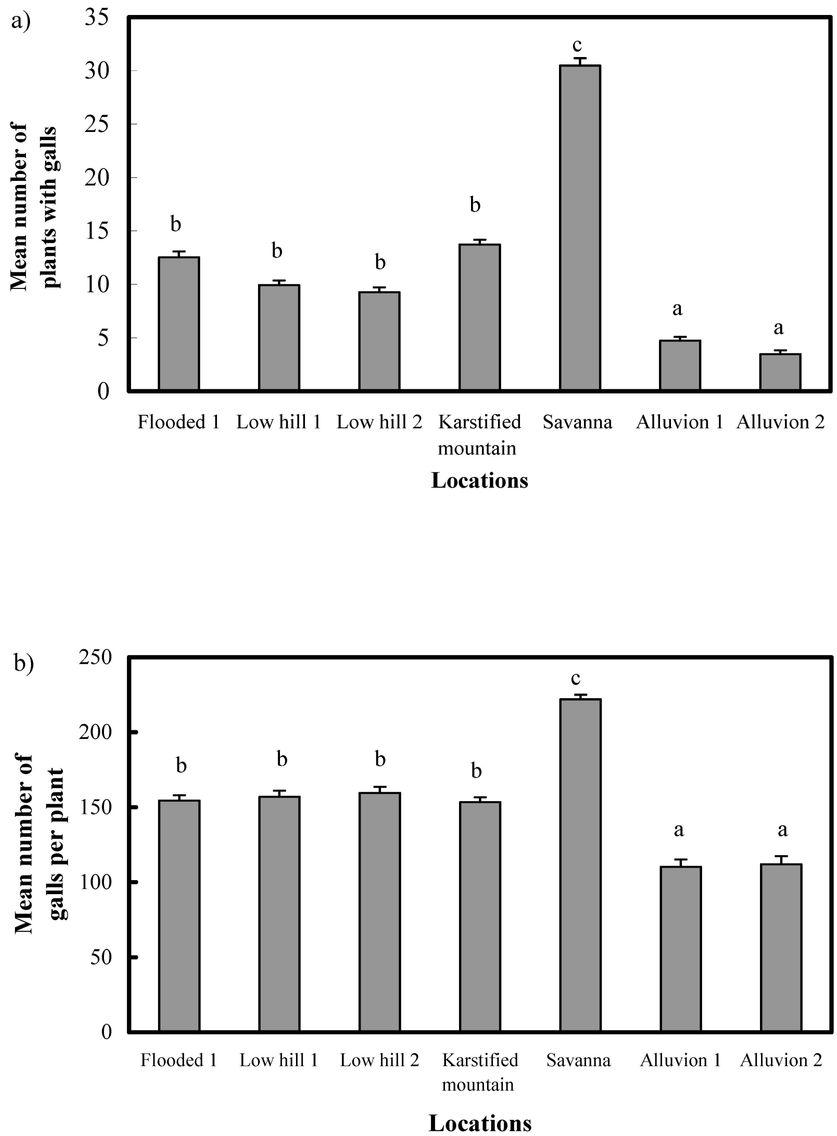


Figure 2. (a) Mean ($\pm$SE) number of plants with galls ($F = 409.07$; $P < 0.0001$), and (b) mean ($\pm$SE) number of galls per plant ($F = 83.63$; $P < 0.0001$), recorded in seven localities in the Lacandona reserve, Chiapas. Means with the same letter did not differ significantly after a multiple comparison test (Tukey's test: $P = 0.05$).

direct comparison of our results with those obtained by others, our study reports higher gall-forming insect species richness at Chajul than in other tropical rain forest localities (Fernandes and Price 1988; Price 1991). Perhaps one reason for this is that our landscape approach allowed us to record more gall-forming insect species, as

Table 3. Mean number of galls (±SD) on plant species with different patterns of distribution in the Lacandona reserve, Chiapas.

Plant species distribution: no. of localities	Number of gall-forming insect species	Mean number of galls
1	45	20.42 ± 14.18[a]
2	9	38.88 ± 16.09[b]
3	7	28.12 ± 13.48[a]
4	5	61.61 ± 20.26[c]
5	3	68.25 ± 23.07[d]
6	3	92.61 ± 14.89[e]
7	2	134.52 ± 37.52[f]

All data were transformed for box-cox transformation, although data are shown without transformation. Means with the same letter did not differ significantly after Tukey test ($P = 0.05$). $F = 24.61$, $P < 0.0001$.

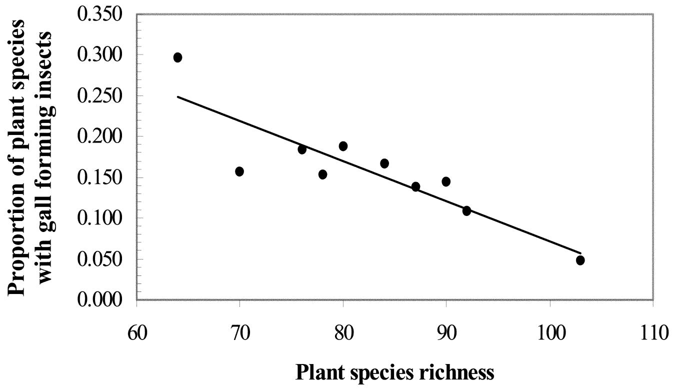
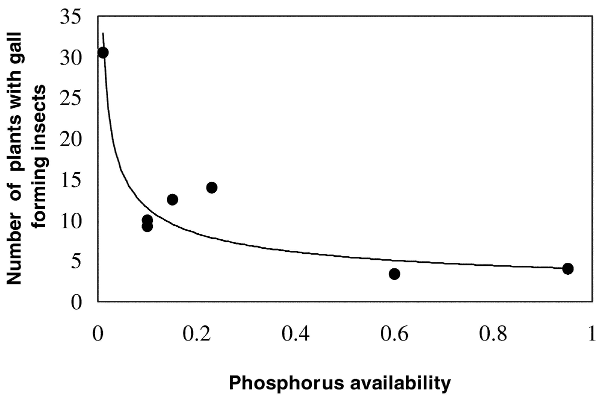


Figure 3. Correlation between the proportion of plant species having gall-forming insects and plant species richness in seven locations at the Lacandona reserve, Chiapas ($y = -0.005x + 0.57$; $R^2 = 78.0$; $P < 0.0008$).

higher β diversity levels for species are considered when environmentally contrasting sites are included in the sampled area. In addition, there was a low similarity of gall-forming insects between sites, demonstrating that site diversity of plant species helps to explain the high richness of gall-forming insects in the Lacandona reserve.

A higher gall-forming insect incidence on plant species with broad distribution indicates that generalist plant species are more susceptible to gall attack than rare, narrowly distributed species. A comparison between congeneric plant species with different geographic ranges also indicated that widespread plant species had a greater number of gall-forming insect species than plants with small ranges (Blanche and Westoby 1996). Whether the chemical defense system of rare species is more effective than that of widely distributed species, or whether widely distributed species are more apparent to attack of gall-forming insects (Opler 1974; Cornell and Washburn 1979; Leather 1986) remains to be investigated.

Our results do not support the view that species richness of gall-forming insects is a)



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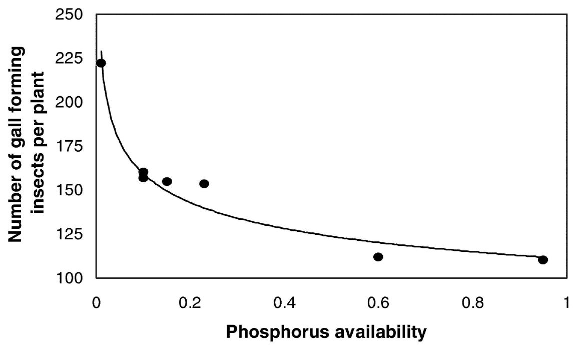

Figure 4. Relationships between (a) abundance of plants with gall-forming insects ($y = 4.07x^{-0.44}$; $R^2 = 70.4$; $P < 0.05$), and (b) density of GFI per plant ($y = 110.9x^{-0.157}$; $R^2 = 95.2$; $P < 0.05$), with soil fertility in seven localities in the Lacandona reserve, Chiapas.

positively related to plant species richness in the tropical rain forest. We found that the least diverse plant community sustained the richest gall-forming insect community and that the most diverse plant community sustained the poorest gall-forming insect community. Plant species richness does not offer an adequate explanation for this trend in gall-forming species richness. The pattern of galling species richness can be associated with life forms of plant species (e.g., woody plants, shrubs, herbs and climbing) (Price 1991) and with some plant families (e.g., Myrtaceae, Leguminosae) (Blanche 1994; Goncalves-Alvim and Fernandes 2001), altering the patterns of gall-forming insect species richness between communities.

Sites with low levels of phosphorus had the highest abundance of individual plants and species associated with the gall-forming species. In contrast, rich-soil locations like alluvial localities had low abundance of individual plants with decreased levels of galls per plant. Some authors have suggested that environmental

Table 4. Selected soil parameters characterizing the nutrient and air balance of the soils in the Lacandona reserve, Chiapas.

Locality	Soil type	1 (cm)	2 ($1/m^2$)	3 ($1/m^2$)	4 (vol %)	5 (kg/m^2)	6 (val/m^2)	7 (mg/kg)	8 C/N	9 (%)	pH
Flooded	Eurtic Planosol	44	79	325	4	24.5	5.6	0.15	10	1.5	4.9
Low hill 1	Stagni-Vertic Cambisol	63	81	461	6	38.3	166.6	<0.1	11	0	5.9
Low hill 2	Humic Acrisol	54	59	231	11	26.4	26	<0.1	12	43	4.6
Karst. mountain	Rendzic Leptosol	12–18	38	98	14	15	61.0	0.23	11	0	7.0
Savanna	Stagni-vertic cambisol	66	89	416	5	22.2	205.8	<0.01	12	7	4.4
Alluvial 1	Eutri-stagnic Cambisol	67	133	413	12	36.5	70	0.95	14.8	0	5.6
Alluvial 2	Haplic Luvisol	100	92	366	12	38	134.3	0.6	11	0	5.9

(1) Soil depth; (2) available water; (3) water retention; (4) aeration; (5) humus; (6) exchangeable bases (Ca, K, Na); (7) available phosphorus; (8) nitrogen content (10–16 indicating good *N* availability); (9) aluminum (%).

factors like soil fertility can affect the abundance, survivorship and richness of many galling species (Price 1991; Blanche 1994; Fernandes et al. 1994; Orians and Fritz 1996; Goncalves-Alvim and Fernandes 2001). In this study, we assess a direct link between soil fertility and gall-forming insects at a regional scale in a tropical forest. The ability of gall-forming insects to manipulate the chemistry of their host plants may be the mechanism explaining the preponderance of galls in plants that grow under nutrient stressed environments (e.g., soil fertility), independently of latitude and altitude (Fernandes and Price 1988; Rohfritsch 1992; Blanche 1994). Our results suggest that soil fertility is an important factor influencing the gall-forming insect abundance in this study.

Plant species richness in the Lacandona reserve was not related to soil fertility. However, gall-forming insect abundance had a negative relationship with the soil fertility, both at the community and plant individual level; this trend might be the result of confounded effects of soil fertility and plant species richness on gall-forming insect species richness. In Australia, the diversity of gall-forming insects is linked to soil fertility via host plant taxon in sites dominated by *Eucalyptus* spp. (Blanche and Westoby 1995).

In tropical rain forests where moisture is not a limiting factor, it was not possible to test the hypothesis that xeric plants promote the richness of gall-forming species (Fernandes and Price 1988; Price 1991; Wright and Samways 1998). However, at Chajul, in sites flooded almost 10 months a year, we recorded the highest gall-forming insect species richness associated with plant species of the Araceae family (12 out of 22 species had galls). This suggests that epiphyte plants may also help to explain the richness of galls in a tropical community. Furthermore, it has been reported that plant species that grow on flooded sites are highly susceptible to the colonization of gall-forming insects (White 1993). This colonization in flooded sites may be enhanced by foliar traits such as larger leaf size and higher leaf growth rate in comparison with plant species of sites where flooding does not occur (Ribeiro et al. 1998). Premature leaf abscission rates are also higher in flooded than in non-flooded plants (Ribeiro et al. 1998), but whether leaf abscission is an induced defense against endogenous insects such as galls and mines or not has been under discussion (Kahn and Cornell 1983, 1989; Williams and Whitham 1986; Stiling and Simberloff 1989).

In this study, we provide the first evidence of the richness of gall-forming insects for a tropical region in Mexico. Our results did not support the patterns obtained by other authors along geographic gradients, probably due to the landscape approach used in this study that confounded the variables associated with richness of gall-forming insects at a regional scale.

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