

Geographic distribution patterns of galling insects in a protected area of Atlantic forest (southeast, Brazil)

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Abstract. The present study aimed to increase knowledge about the diversity and factors that determine the distribution of galling insects in the Parque Nacional do Itatiaia (PNI), Southeast, Brazil. For this, collections were performed in April, August and November 2015 and March 2016. Seventy gall morphotypes were found in 12 families, 32 genera and 61 species of host plants. The richness of galls did not vary with altitude, but increased with the richness of plants. The families and genera of plants with greater species richness harbored a greater number of galling insects. The number of gall morphotypes was higher in the autumn than in the other seasons. The spatial distribution of galling insects was better explained by factors such as floristic richness and species composition than by ecological effects, represented here by altitude. Regarding seasonality, the results indicate that the way resources are temporarily distributed to galling insects depends on factors such as the active growth of host plants, making some periods of the year more conducive to the development of galls.

Keywords. Galling insects; Altitudinal gradients; Plant richness; Cecidomyiidae; Neotropical region.

INTRODUCTION

Distribution patterns of gall-inducing insects and their host plants have been tested on several continents (Fernandes & Price, 1988; Fernandes & Lara, 1993). However, there is no consensus regarding the factors that best correlate with the richness of this herbivore guild (Carneiro *et al.*, 2014).

Altitudinal gradients have been frequently used in ecological studies to test the influence of climatic variation associated with increased elevation and its effects on animal and plants communities. Fernandes & Price (1991) observed that the negative relationship between altitude and species richness of gall-inducing insects was dependent on the type of habitat. The richness of insect species is related to altitude in xeric habitats, but not in mesic habitats of the same altitude, suggesting that the relationship between altitude and species richness is questionable (Carneiro *et al.*, 2014).

In addition to environmental factors, host plant richness and taxonomic composition may

play a key role in galling insect richness (Araújo, 2013). The hypothesis of plant richness, proposed on the basis of results obtained by Southwood (1960, 1961), predicts that galling insect richness increases with plant richness. Taxon size has been proposed as another hypothesis, which holds that galling insect diversity can be explained by plant taxon size. This hypothesis predicts a positive correlation between galling insect richness and plant taxon (families or genera) size (Fernandes, 1992). Thus, it is expected that plant family or genera with more species will accumulate a greater number of galling insect species (Lawton & Price, 1979).

Factors related to seasonality may be as important as space regarding the entomofauna distribution. Studies on the influence of seasonality related to the distribution of galling insects are scarce (Dalbem & Mendonça, 2006). Fernandes *et al.* (1995) pointed out that seasonal fluctuations do not interfere with the distribution of galling insects. However, other studies suggest that climatic season may be a determining factor in the richness of these insects (Dalbem & Mendonça, 2006;

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Araújo & Santos, 2009). The occurrence of the host plant, the density of individuals, and the quality of resources offered can be fundamental in determining these patterns for the insects. Thus, seasonal variation in the distribution of galling insects may actually reflect the seasonality of the hosts (Araújo & Santos, 2009).

In this context, we characterized the gall-inducing insects and their host plants in the Parque Nacional do Itatiaia. We also investigated the factors that determine the distribution of galling insects by testing the following hypotheses: H1) elevation gradient (Fernandes & Price, 1988); H2) local plant richness (Southwood, 1960, 1961); H3) seasonality; and H4) plant taxon size (Fernandes, 1992).

MATERIAL AND METHODS

Study area

The study was performed in Parque Nacional do Itatiaia (PNI) (22.4151°S, 44.6301°W), located at the Serra da Mantiqueira near the border between the states of Minas Gerais, São Paulo and Rio de Janeiro (Fig. 1a). The park compasses 28,084 ha and is located on the Atlantic plateau of Mares de Morros (ICMBio, 2013).

According to the classification of Köppen (1931), the climate of the PNI region is temperate with a dry season (Cwa). Segadas-Vianna (1965) identified two seasons: dry

and cold from May to September, and rainy and hot from November to March.

Vegetation

According to the classification of IBGE (1991), the predominant local vegetation is Dense Ombrophilous Forest, with three recognized formations: submontane, montane and high montane or nebular (cloud) forest. Associated with the forest, and above 2,100 m in the plateau region, is the Altitudinal Fields, where herbs and shrubs prevail, and some isolated trees occurs.

Sampling

Gall sampling followed the methodology described by Fernandes & Price (1988), which has been widely used multiple times (Lara *et al.*, 2002; Carneiro *et al.*, 2014; Coelho *et al.*, 2013, 2017). Since galling insect species richness may vary among different types of plant architectures (Price *et al.*, 1997), collections were standardized by sampling galls only on woody plant species varying from 0.3 to 2.5 m in height (Carneiro *et al.*, 2014).

Four two-days collections were carried out, one in each season of the year: April (autumn), August (winter) and November (spring) of 2015, and March (summer) of 2016. Samplings were accomplished at every 200 m

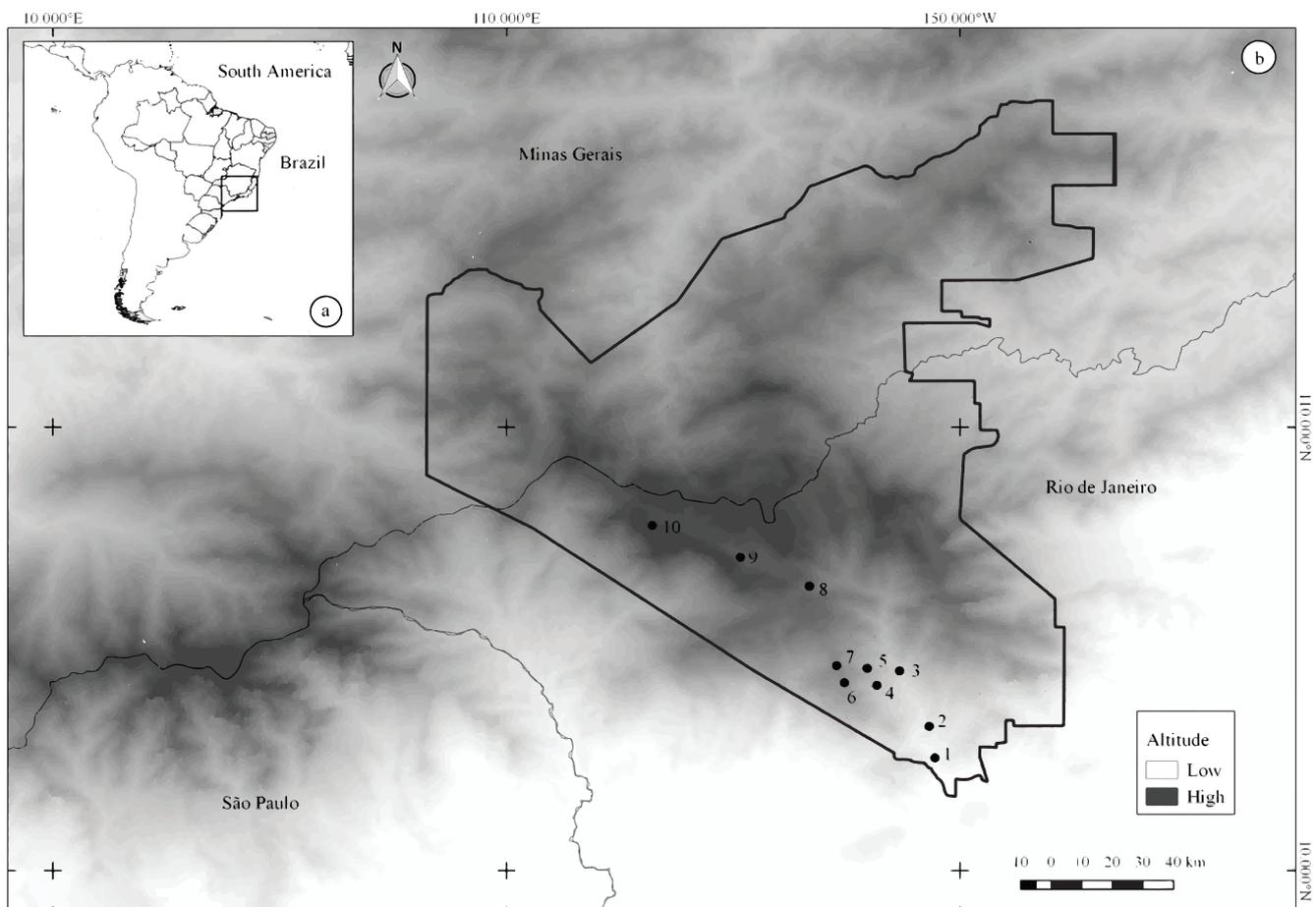


Figure 1. (A) Location of Parque Nacional do Itatiaia (Southeast, Brazil). (B) Sampling points in Parque Nacional do Itatiaia.

Table 1. Geographic coordinates, altitude, climate type and location of the ten collection points in Parque Nacional do Itatiaia (Southeast, Brazil).

Points	Altitudes	Climate type	Coordinates	Location
P1	700 m	Cwa	22°27'25.14"S/44°36'31.43"W	Trilha Barbosa Rodrigues
P2	900 m	Cfb	22°26'48.25"S/44°36'38.49"W	Entrada Lago Azul
P3	1,100 m	Cfb	22°25'43.25"S/44°37'12.80"W	Cachoeira Maromba
P4	1,300 m	Cfb	22°26'00.20"S/44°37'38.20"W	Trilha Ruy Braga
P5	1,500 m	Cfb	22°25'40.85"S/44°37'49.29"W	Trilha Ruy Braga
P6	1,700 m	Cfb	22°25'57.90"S/44°38'15.95"W	Água Branca
P7	1,900 m	Cfb	22°25'37.12"S/44°38'24.83"W	Macieiras
P8	2,100 m	Cwb	22°24'04.84"S/44°38'55.71"W	Trilha Ruy Braga
P9	2,300 m	Cwb	22°23'30.60"S/44°40'14.60"W	Trilha Ruy Braga + Prateleira
P10	2,500 m	Cwb	22°22'53.06"S/44°41'55.01"W	Base do Morro do Couto

along an elevation gradient from 700 to 2,500 m, with a total of 10 samplings equidistant for at least 1 km (Fig. 1b – Table 1). In the lower part of PNI (sampling points 1 to 7), sampling was performed in sub-forest areas of the Dense Ombrophilous Forest. In the upper part (points 8, 9, and 10), sampling was performed in Campos de Altitude.

At each sampling point, three equidistant (10 m) plots were marked with 100 plants each, totaling 300 plants at each sampling point, and 3,000 plants for the entire study. All individuals with or without galls were marked. In each plot, the aerial parts of all plants were inspected for galls. At each season, only new branches were sampled, so, in the following season, these previously sampled galls were not sampled, since the host branches were not new. With this, we avoided the issue of double analyzing the galls from the previous season. Exsiccates of branches preferably with flowers and/or fruits were made according to standard techniques with the aim of identifying plants.

Characterization of galls

All galls were photographed in the field and characterized as to form, color, plant organ of occurrence, indumentum and number of internal chambers (Isaias *et al.*, 2013). Part of the sample of each gall was dissected under a stereomicroscope for the observation of the number of internal chambers and for obtaining immature insects. The remainder was devoted to raising insects. For this, each gall morphotype was conditioned separately in labeled closed plastic pots lined with moistened paper, and inspected daily for documenting adult emergence. All insects thus obtained were preserved in 70% alcohol. The cecidomyiids were mounted on microscope slides following the methodology of Gagné (1994). All the specimens were deposited in the Diptera collection of the MNRJ. The other insects were identified by specialists and were deposited in the collection of the same institution.

The exsiccates were sent to specialists of the Jardim Botânico, Rio de Janeiro, for identification of the plants to the lowest taxonomic level possible, according to APG (2009), and were deposited in the herbarium of the same institution (RB).

Statistical analyses

Since the gall richness of each individual plant consists of temporally repeated measurements (*i.e.*, a clearly longitudinal experimental design), mixed models with negative binomial errors were fitted using the 'glmer.nb' routine in the "lme4" package (Bates *et al.*, 2015). To test the effects of the explanatory variables, the number of gall morphospecies was considered the y variable, and host plant richness, elevation and season (autumn, winter, spring and summer) were fixed factors. As random factors, plot and elevation were used as categorical variables, with plots nested within elevations. In this sense, we consider that the plots nested within elevations were representative of the entire population of plots with the same habitat condition. For validation of the assumptions of the model, we analyzed diagnostic charts of "Pearson" residuals versus the predicted values and the covariables of elevation and season. The likelihood ratio test and AIC were used to compare the goodness of fit of the models and for model simplification (Zuur *et al.*, 2013).

To test the host plant taxon size hypothesis (Fernandes, 1992), the total number of plant species sampled was used as the estimator of taxon size for plant families and/or genera (Carneiro *et al.*, 2014). In this way, the relationship between host plant taxon size, either plant family or genus (variable x), and the number of galling insect species (variable y) found on that taxon was tested using generalized linear models with Poisson errors. Since this model was over-dispersed (when the variance is greater than the average), as was the binomial model as well, a negative binomial GLM was used instead, a commonly used distribution in such cases (Hilbe, 2011). The probable source of over-dispersion of the above models was the excessive number of zeros in the response variable. Because of the low frequency of occurrence of galling species on their host plants, many individual plants and/or plots possessed counts of zero. The excess number of zeros in the y variable (> 25% *sensu* Zuur *et al.*, 2012) is a frequent problem in analysis of count data (*e.g.*, number of species).

We used the "Hurdle" model and the zero-inflated models' ZIP (with Poisson errors) and ZINB (with binomial errors) to deal with this problem using the 'pscl' package (Zeileis *et al.*, 2008). For the relationship between the number of species of galling insects and the number of species in plant families, the most suitable model was the generalized linear model ZIP, while for the relationship between the number of species of galling insects and the number of species in plant genera, the most appropriate model was the "hurdle" model. For model validation we analyzed diagnostic graphs of the Pearson residuals versus the predicted values and the covariable plant richness (Zeileis *et al.*, 2008). The likelihood ratio test was used to compare goodness of fit of the models. The models were also compared using the "Vuong" test (Hilbe, 2011). The analyses were performed using the software R (R Core Team, 2016).

RESULTS

Descriptive data

Seventy gall morphotypes were found in 12 plant families, 32 genera and 61 species (Supplementary Material 1-6). The families and botanical genera with the greatest richness of galls were Melastomataceae, Asteraceae, Sapindaceae and Rubiaceae (n = 16, 15, 9 and 7, respectively – Table 2) and *Serjania* Mill. (Sapindaceae), *Miconia* Ruiz & Pav. and *Tibouchina* Aubl. (Melastomataceae) (n = 7, 5 and 5, respectively – Table 3).

Galls occurred mainly in stems (n = 42) and leaves (n = 21). Stem galls were more frequent in three seasons of the year (autumn: n = 28, summer: n = 9, and winter: n = 5). The majority were fusiform (n = 42), glabrous (n = 57) and with one larval chamber (n = 65). Brown (n = 37) and green (n = 29) were the most frequent colors.

About 28% of the galling insects (n = 19) were identified to at least the order level, and included Diptera – Cecidomyiidae and Tephritidae, Thysanoptera – Phlaeothripidae, Coleoptera and Hemiptera. Diptera were the most frequent inducers (79%) with cecidomyiids representing 68%. The others together accounted for about 21% of the gall morphotypes. The associated fauna comprised Chalcidoidea and Eulophidae (Hymenoptera) as parasitoids; aphids (Hemiptera), Phlaeothripinae (Thysanoptera) and Lepidoptera asinquilines; Formicidae (Hymenoptera) and mites as successors; and Reduviidae (Hemiptera) as predators.

Hypothesis testing

The number of gall-inducing species did not vary with elevation, contrary to expectations. However, the number of gall species increased with the number of plant species in the plots (Table 4). This number was also higher for autumn than the other seasons, which did not differ from each other (Fig. 2 – Table 4). The number of galling insect species increased with plant family size (equation: gall richness = $e^{0.82872 + 0.09332 * \text{richness of the family}}$; vuong test = -2.213; p = 0.014, n = 26) (Fig. 3). When genus data were evaluated, the same pattern was found, showing that the number of galling insect species increased with plant genus size (equation: gall richness = $e^{0.32796 + 0.21727 * \text{richness of the genus}}$; vuong test = -2.712; p = 0.003, n = 57) (Fig. 4).

DISCUSSION

Gall-inducing richness

Galling insect species and their host plants are very diverse. Some host plant taxa are known to have low galling insect species richness even if intensively sampled, while other taxa have high species richness even if poorly sampled (Hawkins & Compton, 1992). Melastomataceae

Table 2. Plant richness, host plants and galls richness by families sampled in Parque Nacional do Itatiaia (Southeast, Brazil).

Plant families	Overall plants		Host plants		Galls	
	Richness	%	Richness	%	Richness	%
Anacardiaceae	1	1	1	1.6	1	1.4
Asteraceae	17	16.8	14	23.0	15	21.4
Euphorbiaceae	5	5	2	3.3	2	2.9
Fabaceae	7	6.9	2	3.3	2	2.9
Melastomataceae	23	22.8	15	24.6	16	22.9
Meliaceae	1	1	1	1.6	1	1.4
Myrtaceae	4	4	4	6.6	5	7.1
Primulaceae	4	4	2	3.3	3	4.3
Proteaceae	1	1	1	1.6	2	2.9
Rubiaceae	7	6.9	7	11.5	7	10
Sapindaceae	7	6.9	7	11.5	9	12.9
Solanaceae	3	3	1	1.6	3	4.3
Other families	17	16.8	0	0.0	0	0
Not determined	4	4	4	6.6	4	5.7
Total	101	100	61	100	70	100

Table 3. Plant richness, host plants and galls richness by genera sampled in Parque Nacional do Itatiaia (Southeast, Brazil).

Plant Genera	Overall plants		Host plants		Galls	
	Richness	%	Richness	%	Richness	%
<i>Tapirira</i>	1	1.0	1	1.6	1	1.4
<i>Baccharis</i>	5	5.0	4	6.6	4	5.7
<i>Barrosoa</i>	1	1.0	1	1.6	1	1.4
<i>Chionolaena</i>	1	1.0	1	1.6	2	2.9
<i>Critonia</i>	1	1.0	1	1.6	1	1.4
<i>Eupatorium</i>	2	2.0	2	3.3	2	2.9
<i>Mikania</i>	2	2.0	2	3.3	2	2.9
<i>Pitocarpa</i>	1	1.0	1	1.6	1	1.4
<i>Symphopappus</i>	1	1.0	1	1.6	1	1.4
<i>Vernonia</i>	1	1.0	1	1.6	1	1.4
<i>Acalypha</i>	1	1.0	1	1.6	1	1.4
<i>Croton</i>	2	2.0	1	1.6	1	1.4
<i>Dalbergia</i>	1	1.0	1	1.6	1	1.4
<i>Inga</i>	5	5.0	1	1.6	1	1.4
<i>Clidemia</i>	3	3.0	3	4.9	3	4.3
<i>Leandra</i>	1	1.0	1	1.6	1	1.4
<i>Maieta</i>	1	1.0	1	1.6	1	1.4
<i>Miconia</i>	11	10.9	5	8.2	5	7.1
<i>Tibouchina</i>	6	5.9	4	6.6	5	7.1
<i>Guarea</i>	1	1.0	1	1.6	1	1.4
<i>Eugenia</i>	2	2.0	2	3.3	3	4.3
<i>Myrcia</i>	2	2.0	2	3.3	2	2.9
<i>Myrsine</i>	3	3.0	2	3.3	3	4.3
<i>Roupala</i>	1	1.0	1	1.6	2	2.9
<i>Borreria</i>	1	1.0	1	1.6	1	1.4
<i>Gallium</i>	1	1.0	1	1.6	1	1.4
<i>Psychotria</i>	4	4.0	4	6.6	4	5.7
<i>Sipanea</i>	1	1.0	1	1.6	1	1.4
<i>Cupania</i>	1	1.0	1	1.6	1	1.4
<i>Matayba</i>	1	1.0	1	1.6	1	1.4
<i>Serjania</i>	5	5.0	5	8.2	7	10.0
<i>Solanum</i>	2	2.0	1	1.6	3	4.3
Other genera	24	23.8	0	0	0	0
Not determined	5	5.0	5	8.2	5	7
Total	101	100	61	100	70	100

Table 4. Relationship between galling insect richness and the studied variables in Parque Nacional do Itatiaia, Southeast, Brazil.

Variables	Estimate	Std. Error	z value	Pr(> z)
Fixed Effects				
Intercept	-4.162	1.023	-4.070	< 0.001
Elevation	0.0005	0.0004	1.412	0.16
Plant richness	0.240	0.05	4.209	< 0.001
Season (autumn)	1.365	0.315	4.329	< 0.001
Season (spring)	0.000007	0.3981	0.000	1.00
Season (summer)	0.6061	0.3492	1.736	0.80

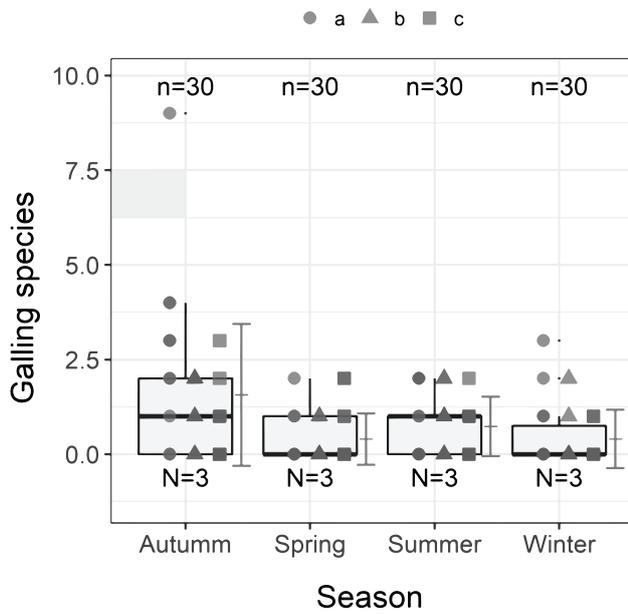


Figure 2. Boxplots with jittered illustrating the galling species richness between year season, with jittered raw values strung vertical corresponding to plots (a, b, c), numbers the plots (N) and sites (n), and mean \pm SD bars.

were the botanical family with the greatest richness of galls in this study, followed by Asteraceae, Sapindaceae and Rubiaceae, respectively. Studies in other Brazilian ecosystems have shown similar patterns, such as Cerrado (Gonçalves-Alvim & Fernandes, 2001), Atlantic Forests (Fernandes *et al.*, 2001), and Tropical Dry Forests (Coelho *et al.*, 2009). *Serjania* (Sapindaceae), *Miconia* (Melastomataceae) and *Tibouchina* (Melastomataceae) were the genera with greatest richness of galls in this study. These genera were already been reported in other inventories as rich in galling insects (Coelho *et al.*, 2009; Maia & Carvalho-Fernandes, 2016).

The greater richness of leaf galls was recognized as a global pattern by Felt (1940). In PNI, Maia & Mascarenhas (2017) confirmed this pattern. However, in the present study, we found a different result since there was greater richness of branch galls. Coelho *et al.* (2013), also at PNI and Veldtman & McGeoch (2003) in African savannas, found greater richness of stem galls. In these three studies, the authors used the plot method, while Maia & Mascarenhas (2017) adopted the walking methodology, fully traversing all trails of PNI, which resulted in a larger sampling effort. This methodological difference may explain the different results obtained by these studies.

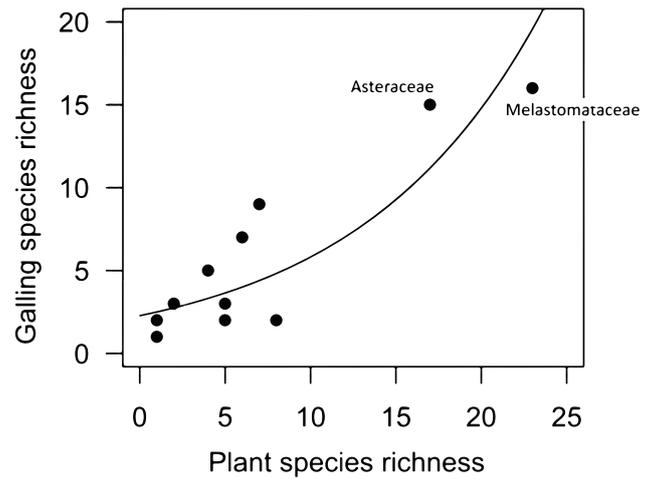


Figure 3. The fit of the count part of the ZIP model to the relationship between galling species richness and plant family species richness.

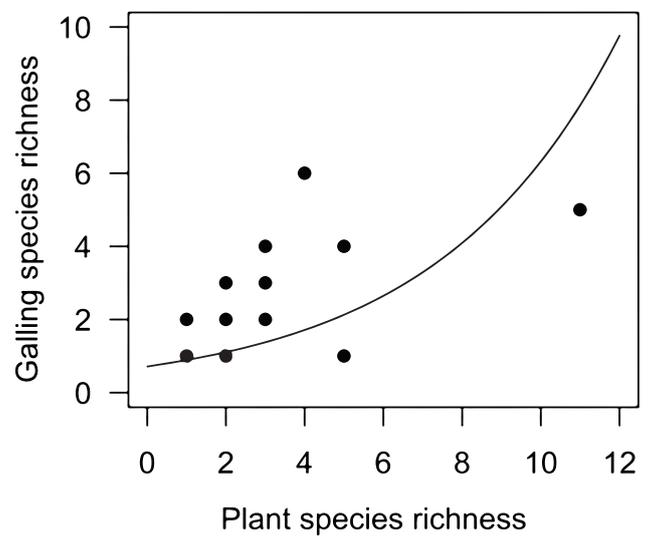


Figure 4. The fit of the count part of the "hurdle" model to the relationship between galling species richness and plant genus species richness.

Cecidomyiidae is, in fact, the main galling taxon in the world (Felt, 1940). The associated fauna comprised four different guilds. Hymenoptera are considered the most important natural enemies of species of Cecidomyiidae (Diptera) (Maia & Azevedo, 2009). They are often found on galls induced by these midges, and act primarily as parasitoids and, in some cases, as phytophagous species capable of modifying the structure and morphology of the gall (Maia & Azevedo, 2009).

Factors that determine the distribution of galling insects

Elevation did not influence the number of galling insect species in the present study, which does not corroborate other studies that points to elevation as a determinant factor for the distribution of these insects (Blanche & Ludwig, 2001; Carneiro *et al.*, 2005; Coelho *et al.*, 2017). Our results corroborate the plant richness and the plant taxon size hypotheses (Fernandes, 1992), since the num-

ber of galls species increased with the number of plant species. Finally, galling insect richness varies among the seasons, and insect gall richness was highest in autumn.

Species richness of galling insects has been reported to decrease with increasing altitude in various biogeographical regions of the world (Coelho *et al.*, 2017). Fernandes & Lara (1993) demonstrated this relationship for galling insects along an altitudinal gradient of 3,400 m. With data from Arizona and southeastern Brazil extracted from paired samplings conducted in mesic and xeric environments, altitude was identified as the variable that best explained galling insects' richness in xeric environments (Fernandes & Price, 1988; Lara *et al.*, 2002). The authors argued that high species richness of galling insects is more associated with sclerophyllic vegetation, which is characteristic of plants in xeric environments, than altitude per se. Sclerophyllic vegetation, which is common in extreme environments, has long-lived leaves and elevated dry weight, and is rich in defense compounds, protecting the guild of galling insects against predators (Fernandes & Price, 1988).

An important factor that may obscure elevation patterns of galling insect richness is the presence of families and/or genera with great number of species (Veldtman & McGeoch, 2003). This statement was supported by the present study, which found genera such as *Serjania* (Sapindaceae), *Miconia*, *Tibouchina* (Melastomataceae) and *Baccharis* (Asteraceae) with a high number of galling insect species along the elevation gradient. The occurrence of super-hosts (*sensu* Veldtman & McGeoch, 2003) along the altitudinal gradient, and especially the mountain tops, can increase species richness, thereby obscuring the effect of hygothermal stress (Carneiro *et al.*, 2014, Coelho *et al.*, 2017).

In this study, the insect gall distribution was influenced by plant families and genera that are important for both the composition of the regional flora and the local number of galling insect species (Veldtman & McGeoch, 2003; Mendonça, 2007). The Melastomataceae and Asteraceae families are the most frequent when it comes to species richness in altitudinal grasslands and rupestrian fields of Brazil (Martinelli, 2007). In this work, the Melastomataceae family was also the most frequent, accounting for 22.8% of the total richness of plants sampled, followed by the Asteraceae family (16.8%). These results corroborate the floristic composition data from Safford (1999) for two altitudinal field regions, Itatiaia and Serra dos Órgãos.

Galling insect richness increased with plant richness. Considering the fact that galling insects are species-specific (Carneiro *et al.*, 2009), increasing the number of plant species in a local habitat leads to a potential increase in the number of host plant species, that is, the number of possible niches for these insects to colonize (Strong *et al.*, 1984). A study employing extensive standardized sampling in the Serra do Espinhaço found host plant richness to be the factor that best explained the increase of galling insects independently of the altitude effect (Carneiro *et al.*, 2014). In fact, various studies have provided evidence in favor of this hypothesis (Gonçalves-Alvim &

Fernandes, 2001; Cuevas-Reyes *et al.*, 2004; Araújo *et al.*, 2013).

Our results corroborated the plant taxon size hypotheses since the number of galling insect species increased with the size of plant family and genus. According to Mendonça (2007), the process that leads to this pattern, is a result of plant taxa being natural groups with chemical, structural and ecological similarities. Galling insect usually have univoltine cycles and are highly synchronized with their host plants (Araújo & Santos, 2009; Yukawa, 2000). This synchrony could lead to speciation via host change being more common among plants within the same family (Mendonça, 2001). Thus, the greater the number of species within a taxon, the more likely they have synchronous development, involve the greater the chances of speciation and, consequently, the greater the diversity of galling insects (Araújo, 2011). Many studies in different ecosystems in Brazil, such as Cerrado (Gonçalves-Alvim & Fernandes, 2001; Araújo *et al.*, 2013), Rupestrian fields (Coelho *et al.*, 2013), Atlantic Forest (Fernandes *et al.*, 2001), seasonally dry forest (Coelho *et al.*, 2009), and subtropical forest (Mendonça, 2007), presented data corroborating this hypothesis.

The number of gall-inducing species was higher in the beginning of the dry season (autumn). Water scarcity in this season causes several changes in plant physiology (Larcher, 2000). Through water stress, plants initiate a complex of responses, starting with the perception of stress itself, triggering a cascade of molecular events, which ends in various levels of physiological and developmental responses, highlighting the increased susceptibility to attack of herbivores (Fernandes *et al.*, 1995; Nepomuceno *et al.*, 2001). The high infestation found during the dry season would be explained by the diversion of metabolites from the host plant to maintain their physiological activities at the expense of responses aimed at defending against herbivory (Ferreira *et al.*, 2007). Thus, in the dry period, the plants would be more susceptible to attack by the gallers and, consequently, the richness of gall morphotypes would be greater compared to the rainy season (Araújo & Santos, 2008).

CONCLUSION

This work shows that both the floristic richness and the specific composition of the vegetation influence the distribution of galling insects more significantly than the altitude. Regarding seasonality, the results indicate that the way resources are temporarily distributed to galling insects depends on factors such as the active growth of host plants, making some periods of the year more conducive to the development of galls. However, research on this topic is still scarce in Brazil. New studies are crucial to investigate the importance of seasonality on the distribution of gallers and to determine the response patterns of these insects to these variations.

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inal draft, Visualization, Investigation; **VCM, MAAC:** Supervision; **ICF, MAAC:** Formal analysis; **ICF, VCM, MAAC:** Writing – review & editing. All authors actively participated in the discussion of the results; they reviewed and approved the final version of the paper.

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SUPPLEMENTARY MATERIAL 1

Characterization of insect galls recorded in Parque Nacional do Itatiaia (Southeast, Brazil) (SM – Supplementary Material).

Family	Host Plant	Gall morphotype	Altitude	Galler	Associated fauna	Figures
Anacardiaceae	<i>Tapirira guianensis</i> Aubl.	Stem, fusiform and brown	1,900 m	Curculionidae (Coleoptera)	Not found	SM 2 (a)
Asteraceae	<i>Baccharis dentata</i> (Vell.) G.M. Barroso	Leaf, conical and green	2,300 m	Cecidomyiidae (Diptera)	Not found	SM 2 (b)
	<i>Baccharis stylosa</i> Gardner	Stem, fusiform, green and multi-chambered	1,700 m	Not determined	Not found	SM 2 (c)
	<i>Baccharis</i> sp.1	Leaf, globose and green	1,900 m	Not determined	Not found	SM 2 (d)
	<i>Baccharis</i> sp.2	Leaf, globose, white and hairy	1,500 m	Not determined	Not found	SM 2 (e)
	<i>Barrosoa organensis</i> (Gardner) R.M. King & H. Rob.	Stem, fusiform and brown	2,100/2,300 m	Not determined	Not found	SM 2 (f)
	<i>Chionolaena lychnophorioides</i> Sch. Bip.	Stem, fusiform and brown	2,300 m	Not determined	Not found	SM 2 (g)
		Stem, fusiform and brown	2,500 m	Not determined	Not found	SM 2 (h)
	<i>Critonia morifolia</i> (Mill.) R.M. King & H. Rob.	Bud, ovoid, green and multi-chambered	2,300 m	Tephritidae (Diptera)	Chalcidoidea (Hymenoptera) – parasitoid	SM 2 (i)
	<i>Eupatorium</i> sp.1	Leaf, discoid and green/pink	1,700 m	Not determined	Not found	SM 2 (j)
	<i>Eupatorium</i> sp.2	Leaf/stem, fusiform and brown	1,700 m	Cecidomyiidae (Diptera)	Not found	SM 2 (k)
	<i>Mikania</i> sp.1	Stem, fusiform and green	700 m	Hemiptera	Not found	SM 2 (l)
	<i>Mikania</i> sp.2	Stem, fusiform and green	1,900 m	Cecidomyiidae (Diptera)	Not found	SM 2 (m)
	<i>Piptocarpha axillaris</i> (Less.) Baker	Stem, fusiform and brown	1,900 m	Cecidomyiidae (Diptera)	Not found	SM 2 (n)
	<i>Symphopappus reticulatus</i> Baker	Stem, fusiform and green	1,500 m	Cecidomyiidae (Diptera)	Aphids (Hemiptera) – inquiline	SM 2 (o)
<i>Vernonia</i> sp.	Stem, fusiform, brown and multi-chambered	1,900 m	Not determined	Formicidae (Hymenoptera) – successor	SM 2 (p)	
Euphorbiaceae	<i>Acalypha communis</i> Müll. Arg.	Leaf, conical, green and hairy	1,100 m	Not determined	Not found	SM 3 (a)
	<i>Croton floribundus</i> Spreng.	Leaf/stem, globose, green and hairy	900 m	Not determined	Not found	SM 3 (b)
Fabaceae	<i>Dalbergia brasiliensis</i> Vogel	Stem, fusiform and brown	900 m	Not determined	Not found	SM 3 (c)
	<i>Inga grandiflora</i> Ducke	Stem, fusiform and brown	700 m	Not determined	Not found	SM 3 (d)
Melastomataceae	<i>Clidemia capitellata</i> (Bonpl.) D. Don	Leaf, globose, green and hairy	900 m	Not determined	Not found	SM 3 (e)
	<i>Clidemia</i> sp.1	Stem, fusiform, brown and multi-chambered	1,700 m	Not determined	Not found	SM 3 (f)
	<i>Clidemia</i> sp.2	Leaf, globose and green	1,300 m	Not determined	Chalcidoidea (Hymenoptera) – parasitoid	SM 3 (g)
	<i>Leandra regnellii</i> (Triana) Cogn.	Bud, rosette, green and hairy	1,900 m	Not determined	Not found	SM 3 (h)
	<i>Maieta guianensis</i> Aubl.	Leaf (vein), fusiform and green	1,300 m	Not determined	Not found	SM 3 (i)
	<i>Miconia ceramicarpa</i> (DC.) Cogn.	Stem, fusiform and green	1,900 m	Not determined	Not found	SM 3 (j)
	<i>Miconia urophylla</i> DC.	Stem, fusiform and brown	1,900 m	Cecidomyiidae (Diptera)	Not found	SM 3 (k)
	<i>Miconia</i> sp.1	Stem, fusiform and brown	1,100 m	Not determined	Not found	SM 3 (l)
	<i>Miconia</i> sp.2	Leaf roll (vein), green and hairy	900 m	Not determined	Not found	SM 3 (m)
	<i>Miconia</i> sp.3	Stem, globose and brown	700 m	Not determined	Not found	SM 3 (n)
	<i>Tibouchina hospita</i> Cogn.	Stem, globose and brown	1,700 m	Cecidomyiidae (Diptera)	Not found	SM 4 (a)
		Stem, fusiform and brown	1,700 m	Not determined	Not found	SM 4 (b)
	<i>Tibouchina</i> sp.1	Stem, fusiform and brown	1,700 m	Not determined	Not found	SM 4 (c)
	<i>Tibouchina</i> sp.2	Stem, fusiform and brown	1,700 m	Not determined	Not found	SM 4 (d)
<i>Tibouchina</i> sp.3	Stem, fusiform and brown	1,700 m	Not determined	Not found	SM 4 (e)	
sp.1	Stem, globose and brown	1,900 m	Not determined	Not found	SM 4 (f)	
Meliaceae	<i>Guarea</i> sp.	Marginal leaf roll and brown	900 m	Not determined	Not found	SM 4 (g)
Myrtaceae	<i>Eugenia bunchosifolia</i> Nied.	Bud, fusiform and green	700 m	Cecidomyiidae (Diptera)	Not found	SM 4 (h)
		Leaf, cylindrical and green	900 m	Not determined	Not found	SM 4 (i)
	<i>Eugenia uniflora</i> L.	Leaf, circular and green	700 m	Not determined	Not found	SM 4 (j)
	<i>Myrcia splendens</i> (Sw.) DC.	Stem, globose and yellow	1,700 m	Cecidomyiidae (Diptera)	Not found	SM 4 (k)
	<i>Myrcia</i> sp.	Bud, globose and green	700 m	<i>Holopothrips</i> aff. <i>conducans</i> (Thysanoptera)	Eulophidae (Hymenoptera) – parasitoid	SM 4 (l)
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.	Stem, fusiform and brown	1,700 m	Cecidomyiidae (Diptera)	Not found	SM 4 (m)
		Leaf, parenchymal and pink	2,300 m	Not determined	Not found	SM 5 (a)
	<i>Myrsine</i> sp.1	Stem, fusiform and brown	1,700 m	Not determined	Not found	SM 5 (b)
Proteaceae	<i>Roupala montana</i> Aubl.	Stem, fusiform and brown	2,300 m	Not determined	Not found	SM 5 (c)
		Stem, fusiform and brown	1,700 m	Not determined	Formicidae (Hymenoptera) – successor	SM 5 (d)

Family	Host Plant	Gall morphotype	Altitude	Galler	Associated fauna	Figures
Rubiaceae	<i>Borreria tenera</i> DC.	Stem, fusiform and green	1,500 m	Cecidomyiidae (Diptera)	Reduviidae (Hemiptera) – predator/ Lepidoptera – inquiline	SM 5 (e)
	<i>Gallium</i> sp.	Stem, fusiform and brown	1,500 m	Not determined	Acari – successor/ Hymenoptera – successor	SM 5 (f)
	<i>Psychotria vellosiana</i> Benth.	Leaf, globoid, brown and hairy	900 m	Not determined	Not found	SM 5 (g)
	<i>Psychotria</i> sp.1	Stem, fusiform and green	1,500 m	Not determined	Not found	SM 5 (h)
	<i>Psychotria</i> sp.2	Bud, globoid and brown	1,500 m	Not determined	Not found	SM 5 (i)
	<i>Psychotria</i> sp.3	Leaf, globoid and green	1,500 m	Not determined	Not found	SM 5 (j)
	<i>Sipanea</i> sp.	Leaf, globoid, green and hairy	1,300 m	Not determined	Acari – successor	SM 5 (k)
Sapindaceae	<i>Cupania</i> sp.	Stem, fusiform and brown	900 m	Not determined	Phlaeothripinae (Thysanoptera) – inquiline	SM 5 (l)
	<i>Matayba</i> sp.	Stem, amorphous and brown	1,700 m	Not determined	Not found	SM 5 (m)
	<i>Serjania meridionalis</i> Cambess.	Stem, fusiform and brown	900 m	Not determined	Not found	SM 5 (n)
	<i>Serjania</i> sp.1	Stem, fusiform, brown and hairy	700 m	Not determined	Not found	SM 5 (o)
	<i>Serjania</i> sp.2	Stem, globoid, green and hairy	700 m	Diptera	Not found	SM 5 (p)
		Leaf, globoid and green	900 m	Not determined	Not found	SM 6 (a)
	<i>Serjania</i> sp.3	Stem, fusiform, brown and multi-chambered	900 m	Not determined	Not found	SM 6 (b)
	<i>Serjania</i> sp.4	Stem, fusiform and green	900 m	Not determined	Not found	SM 6 (c)
		Leaf, triangular and green	700 m	Cecidomyiidae (Diptera)	Not found	SM 6 (d)
Solanaceae	<i>Solanum</i> sp.	Leaf (vein), fusiform, green and hairy	1,700 m	Not determined	Not found	SM 6 (e)
		Stem, fusiform and brown	1,700 m	Coleoptera	Not found	SM 6 (f)
		Leaf, fusiform, green and hairy	1,100 m	Not determined	Chalcidoidea (Hymenoptera) – parasitoid	SM 6 (g)
	Not determined sp.1	Stem, fusiform and brown	1,900 m	Not determined	Not found	SM 6 (h)
	Not determined sp.2	Leaf (vein), fusiform, green and hairy	1,300 m	Cecidomyiidae (Diptera)	Acari – successor	SM 6 (i)
	Not determined sp.3	Stem, fusiform and brown	1,700 m	Not determined	Not found	SM 6 (j)
	Not determined sp.4	Stem, fusiform and brown	1,700 m	Not determined	Not found	SM 6 (k)

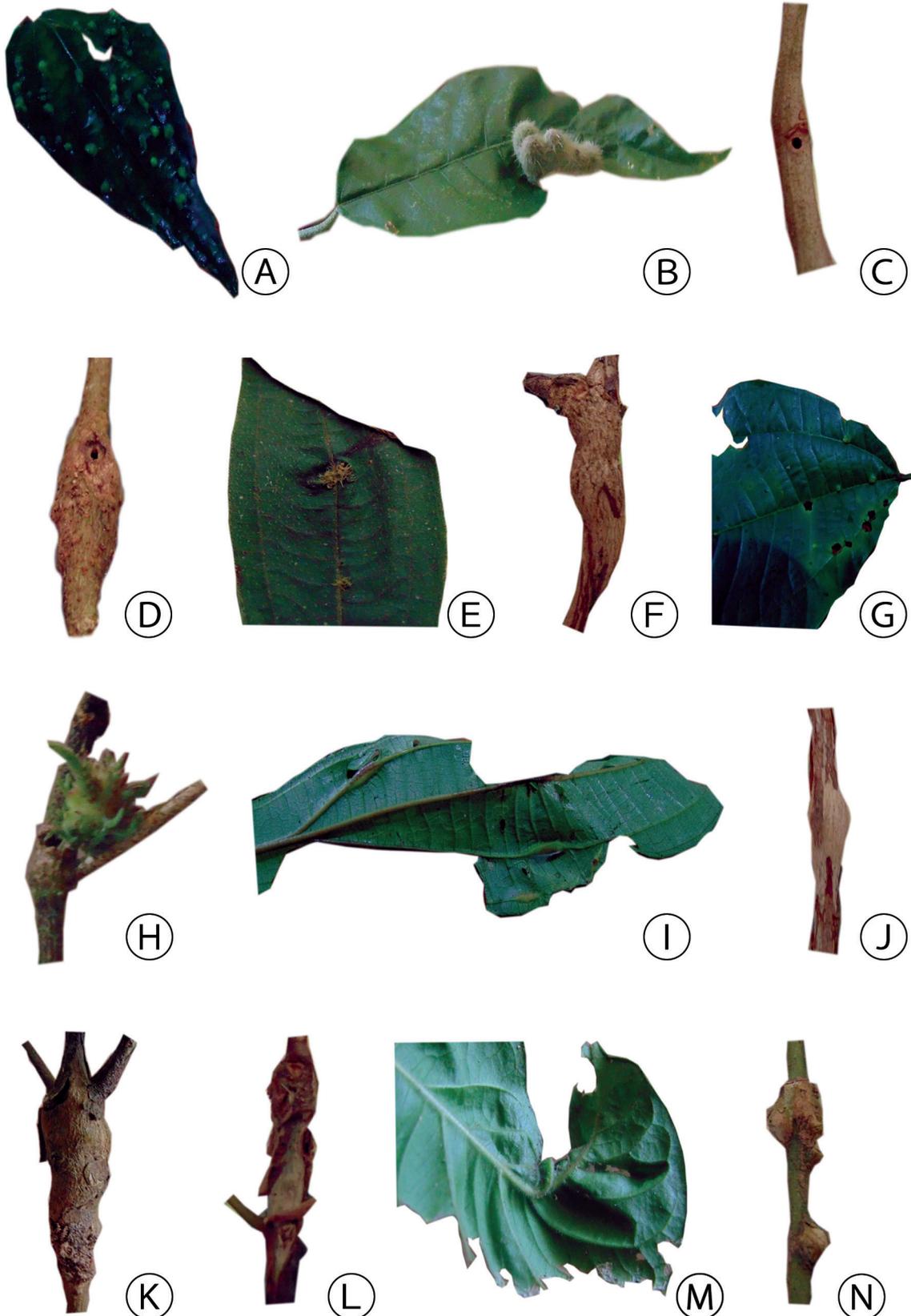
SUPPLEMENTARY MATERIAL 2

Insect galls from Parque Nacional do Itatiaia (Southeast, Brazil). (A) Anacardiaceae: *Tapirira guianensis*, stem gall; (B-P) em Asteraceae: (B) *Baccharis dentate*, leaf gall; (C) *Baccharis stylosa*, stem gall; (D) *Baccharis* sp.1, leaf gall; (E) *Baccharis* sp.2, leaf gall; (F) *Barrosoa organensis*, stem gall, (G-H) *Chionolaena lychnophorioides*, (G) stem gall, (H) stem gall, (I) *Critonia morifolia* apical bud gall, (J) *Eupatorium* sp.1, leaf gall, (K) *Eupatorium* sp.2, leaf gall/stem gall, (L) *Mikania* sp.1, stem gall, (M) *Mikania* sp.2, stem gall, (N) *Pitocarpha axillaris*, stem gall, (O) *Symphypappus reticulatus*, stem gall, (P) *Vernonia* sp., stem gall.



SUPPLEMENTARY MATERIAL 3

Insect galls from Parque Nacional do Itatiaia (Southeast, Brazil). (A-B) Euphorbiaceae: (A) *Acalypha communis*, leaf gall; (B) *Croton floribundos*, leaf gall/stem galls; (C-D) Fabaceae: (C) *Dalbergia brasiliensis*, stem gall, (D) *Inga grandiflora*, stem gall; (E-M) Melastomataceae: (E) *Clidemia capitellata*, leaf gall, (F) *Clidemia* sp.1, stem gall, (G) *Clidemia* sp.2, leaf gall, (H) *Leandra regnellii*, bud gall, (I) *Maieta guianensis*, leaf gall, (J) *Miconia ceramicarpa*, stem gall, (K) *Miconia urophylla*, stem gall, (L) *Miconia* sp.1, stem gall, (M) *Miconia* sp.2, leaf gall; (N) *Miconia* sp.3, stem gall.



SUPPLEMENTARY MATERIAL 4

Insect galls from Parque Nacional do Itatiaia (Southeast, Brazil). (A-F) Melastomataceae: (A-B) *Tibouchina hospita*, stem gall, (C) *Tibouchina* sp.1, stem gall, (D) *Tibouchina* sp.2, stem gall, (E) *Tibouchina* sp.3, stem gall, (F) sp.1, stem gall; (G) Meliaceae: *Guarea* sp., leaf gall; (H-L) Myrtaceae: (H-I) *Eugenia bunchosiifolia*: (H) bud gall, (I) leaf gall, (J) *Eugenia* sp., leaf gall, (K) *Myrcia splendens*, stem gall, (L) *Myrcia* sp., bud gall; (M) Primulaceae: *Myrsine coriacea*, stem gall.



SUPPLEMENTARY MATERIAL 5

Insect galls from Parque Nacional do Itatiaia (Southeast, Brazil). (A-B) Primulaceae: (A) *Myrsine coriacea*, leaf gall, (B) *Myrsine* sp.1, stem gall; (C-D) Proteaceae: *Roupala montana*, stem gall; (E-K) Rubiaceae: (E) *Borreria tenera*, stem gall, (F) *Gallium* sp., stem gall, (G) *Psychotria vellosiana*, leaf gall, (H) *Psychotria* sp.1, stem gall, (I) *Psychotria* sp.2, bud gall, (J) *Psychotria* sp.3, leaf gall, (K) *Sipanea* sp., leaf gall; (L-P) Sapindaceae: (L) *Cupania* sp., stem gall, (M) *Matayba* sp., stem gall, (N) *Serjania meridionalis*, stem gall, (O) *Serjania* sp.1, stem gall, (P) *Serjania* sp.2, stem gall.



SUPPLEMENTARY MATERIAL 6

Insect galls from Parque Nacional do Itatiaia (Southeast, Brazil). (A-D) Sapindaceae: (A) *Serjania* sp.2, leaf gall, (B) *Serjania* sp.3, stem gall; (C-D) *Serjania* sp.4, (C) stem gall, (D) leaf gall; (E-G) Solanaceae: *Solanum* sp., (E) leaf gall, (F) stem gall, (G) leaf gall; (H-K) Not determined: (H) sp.1, stem gall, (I) sp.2, leaf gall, (J) sp.3, stem gall, (K) sp.4, stem gall.

