

ARTÍCULO INVITADO

PLANT DIVERSITY AND GALLING ARTHROPOD DIVERSITY SEARCHING FOR TAXONOMIC PATTERNS IN AN ANIMAL-PLANT INTERACTION IN THE NEOTROPICS

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Summary: Gall-inducers are a special guild of endophytic herbivores generating distinct structures known as galls. Gallers are species-specific, as the galls they induce: each gall morphotype is unique. The relationship between plants and gallers is close, and some of the hypotheses to explain galling diversity consider plants directly; others do not. Here I review current diversity hypotheses on galls and their hosts, adding ideas on the interpretation of galler host plant data. The example comes from an ongoing standardised inventory of galls and hosts in Rio Grande do Sul (RS) state, southern Brazil. The questions addressed here are whether: a) galls occur consistently on some plant taxa in different areas, b) these taxa are important for vegetation composition, and c) taxon size influences galling richness. Families harbouring more gallers are usually the same throughout the Neotropics (Fabaceae, Myrtaceae, and in RS, Asteraceae), which is not unexpected as these are important components of vegetation. Larger plant families have more galls, a pattern driven by Asteraceae. At lower taxonomic levels, the dominance of a few taxa in galler richness («super-hosts») is higher. *Mikania* and *Eugenia*, for example, hold much more galls than others in the RS survey.

Key words: gall, species richness, plant taxon size hypothesis, Fabaceae, Myrtaceae, Asteraceae.

Resumo: Diversidade de plantas e diversidade de artrópodes galhadores. procurando padrões taxonômicos numa interação animal-planta nos Neotrópicos. Os galhadores são uma guilda especial de herbívoros endofíticos geradores de estruturas distintas, as galhas. Galhadores são espécie-específicos, como as galhas que induzem: cada morfotipo de galha é único. A relação entre plantas e galhadores é estreita; algumas das hipóteses para explicar a diversidade de galhadores consideram as plantas diretamente; outras não. Aqui são revistas as correntes hipóteses sobre a diversidade de galhadores e suas hospedeiras, adicionando idéias sobre a interpretação de dados dos hospedeiros. Os exemplos advêm de um inventário de galhas no Estado do Rio Grande do Sul (RS), sul do Brasil. As questões aqui são: a) as galhas ocorrem consistentemente em alguns táxons de planta em diferentes áreas?, b) esses táxons são importantes para a composição da vegetação?, e c) o tamanho do táxon influencia a riqueza de seus galhadores? Famílias apresentando mais galhadores são usualmente as mesmas nos Neotrópicos (Fabaceae, Myrtaceae, e, no RS, Asteraceae), o que é esperado uma vez que são importantes componentes da vegetação. Famílias de planta maiores possuem mais galhas, padrão influenciado por Asteraceae. Em níveis taxonômicos baixos a dominância de poucos táxons em riqueza de galhadores («super-hosts») é maior. *Mikania* e *Eugenia*, por exemplo, têm mais galhas que outros gêneros no inventário do RS.

Palavras-chave: galha, riqueza de espécies, hipótese do tamanho do táxon de planta, Fabaceae, Myrtaceae, Asteraceae.

INTRODUCTION

Gallers compose a separate and unique guild of herbivores, exploring the host plant parasitically from

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the inside (endophytically, Fig. 1), inducing host tissue changes including mainly hyperplasia (cell multiplication) and hypertrophy (cell size increase)(Rohfritsch, 1992). Although the mechanism behind gall induction is not known in detail for any single system (Stone & Schönrogge, 2003), chemical substances secreted by the female ovipositor and/or by the salivating larva (depending on the arthropod taxonomic group) are probably involved (for a recent

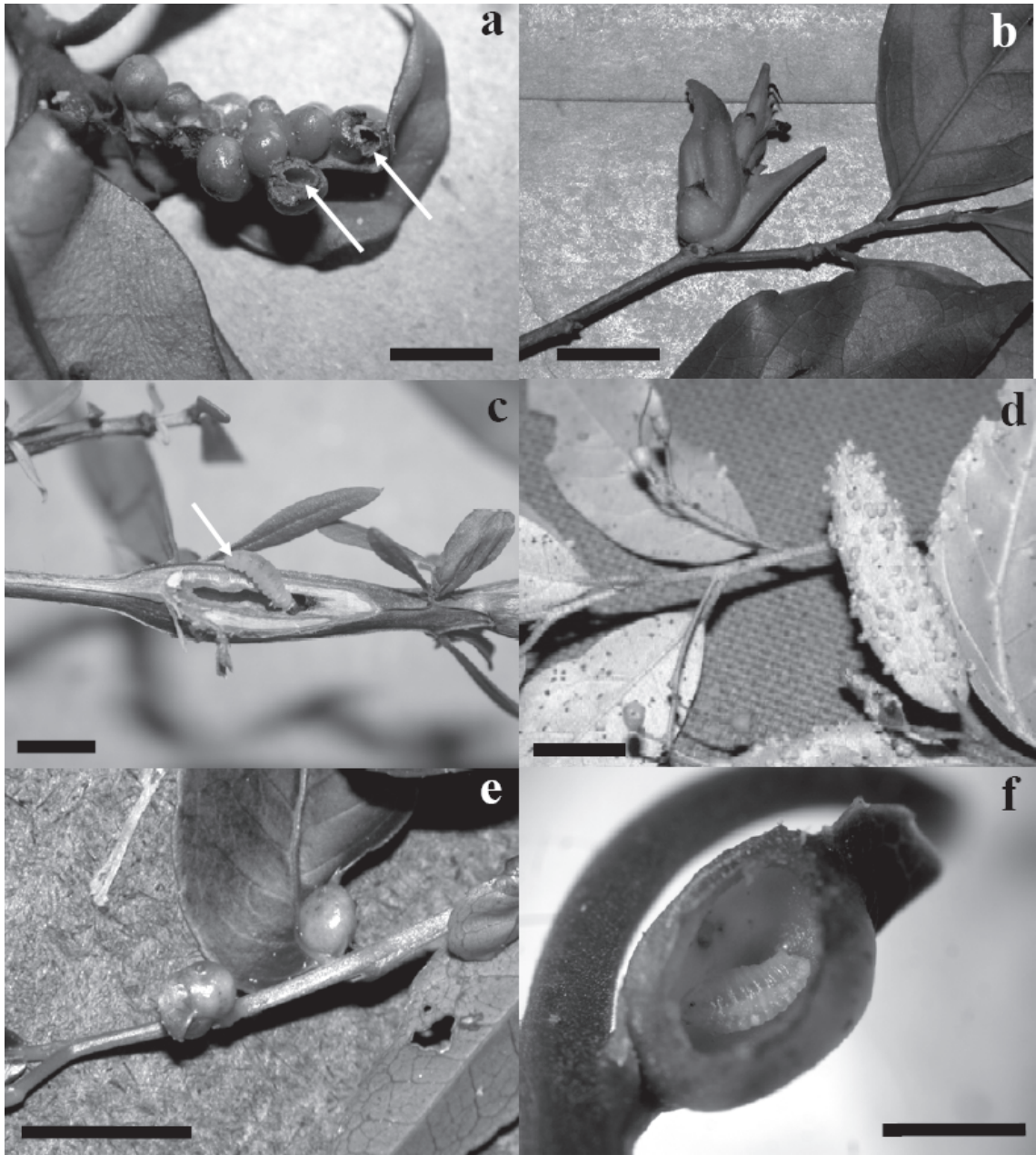


Fig. 1. Examples of galls from Rio Grande do Sul state, southern Brazil. **a)** spherical insect (Cecidomyiidae) leaf gall on *Guapira opposita* (Nyctaginaceae), two galls are cut to show chamber (arrows); **b)** rosette insect (Diptera) stem gall on *Casearia decandra* (Salicaceae); **c)** fusiform insect (Lepidoptera) stem gall on an unidentified herbaceous plant, cut to reveal chamber and larva (arrow); **d)** small blister-shaped mite (Eriophyiidae) leaf gall on *Styrox leprosum* (Styracaceae); **e)** spherical insect (Cecidomyiidae) leaf-shoot gall on *Sebastiania commersoniana* (Euphorbiaceae); **f)** the same gall, cut to show the larva inside the chamber. Scale: 5 mm (1 mm in f).

example see Lillo & Monfreda, 2004).

A first question as yet unresolved, as mentioned above, is how can arthropods gall plants. There is a high degree of detail shown by at least some of the

galler groups in inducing galls: in Cecidomyiidae (Diptera) and Cynipidae (Hymenoptera), for example, gall structure can be complex: layers of harder and softer tissue may be evident, along with a nutritive

tissue on which the inducer feeds (Rohfritsch, 1992). The specialisation on very young tissue for starting gall morphogenesis seen on almost every gall-inducing group reveals that undifferentiated tissue is needed to begin galls (Weis *et al.*, 1988), and that arthropods tightly control plant tissue differentiation. Gall structure is also consistent and repeatable among plant organs, parts and even individuals, representing effectively an extended phenotype of the insect (Dawkins, 1982). Even knowing chemical and mechanical factors are involved in changing plant tissue, how can such detail result is not understood: inducing galls is a very precise process. Earlier suggestions even proposed to look for viruses and plasmids associated to gallers as candidates for indirect mechanisms of gall induction (Cornell, 1983).

But a second perhaps more interesting question is why would arthropods gall plants, that is, what is the advantage of being a galler, compared to other forms of herbivory as mining, boring and chewing. After a lengthy debate in which ideas on how gallers could be mutualistic towards plants or even defences of plants to contain herbivores abounded, a seminal paper (Price *et al.*, 1987) reviewed the then current hypotheses on the adaptive nature of galls. The authors found that the hypotheses on nutrition, microenvironment and natural enemies held the best evidence: a) galls provide differential nutrition to gallers through specialised tissues; b) galls being closed or nearly so, provide an adequate environment reducing the hygrothermal stress suffered by the (very small) gallers; and c) hard or large galls, and tannin rich galls may also provide a defense against natural enemies as predators and parasitoids, and perhaps even other herbivores, as chewers.

Galls are a scattered phenomenon in taxonomic terms at different scales. At a large scale a) almost all groups of terrestrial plants bear them, but most are on dicots, a few on monocots and 'Gymnosperms', and very few on Pteridophyta and other more basal groups; b) among arthropods only a few families of Acari have gallers, but many insect orders (namely Thysanoptera, Hemiptera, Lepidoptera and Coleoptera, Dreger-Jauffret & Shorthouse, 1992) have at least some, and a few orders (Diptera and Hymenoptera) have a plethora of galling families. The most important galling families on the latter two orders are Cecidomyiidae and Cynipidae, the first dominating galling faunas worldwide but the latter being very species rich on a few plant groups (Rosidae and Fagaceae) and subject to many important studies in

the history of cecidology (the branch of ecology studying galls). At a smaller scale a) many Angiosperm plant families have galls, but some families are «evolutionarily preferred», usually the largest (Raman *et al.*, 2005) in terms of species ; b) acquiring the galling habit has been pointed as a decisive evolutionary force leading to diversification among different galler groups, but in some cases the habit appeared repeatedly even within a single arthropod family (e.g. Gagné, 1986, Stone & Schönrogge, 2003), indicating certain insects to be «pre-adapted» for galling.

This taxonomic pattern alone raises questions on how host plants influence the evolution of galling arthropods. Such wide questions can only be tackled on different grounds. An important way of addressing questions at the evolutionary level is to link present-day ecological patterns to biogeographical patterns. Analysing such distributions (environmental distributions as well as taxonomic ones) of gallers and host plants in space provides a proper ground to test how plant species richness and species composition affect galling arthropod species richness and species composition. Inventories of arthropod (and usually insect) galls are becoming more common in Brazil and in the Neotropics generally, with data on host plants increasing in quantity and quality. However, inventories can be limited in geographical (small areas), temporal (short periods) or environmental scope (a few different vegetation types, for example). Furthermore, comparing results from work employing different sampling efforts and even methods can be problematic (Magurran 2004). This paper aims at unveiling some taxonomic patterns found for gallers and host plants in the Neotropics, by adding new data on gallers sampled in Rio Grande do Sul state, southern Brazil.

A brief review: diversity hypotheses associating gall-inducing arthropods to host plants.

Some of the current hypotheses on how host plants affect gallers derive from basic ecological processes, often proposed for other parasitic groups as well. For example, Lawton (1983) and later Strong, Lawton & Southwood (1984) explore the structural hypothesis, stating that herbivorous insects would be richer on structurally complex plants, and thus trees would host richer faunas than shrubs and herbs. This idea stems from the niche concept: trees are plants with a richness of cell, tissue and organ types,

each a potential niche for herbivores to specialise in. Price & Fernandes (1988, 1991) considered this question directly by using a structural sampling regime (differentiating number of herbs, shrubs and trees searched for galls) to evaluate local galling species richness. They found this relationship to hold, but shrubs also have more galls than expected. This may have to do with sampling Mediterranean-like vegetation types (Chaparral and Cerrado), which are rich in shrub species.

The plant richness hypothesis argues that the higher the number of plant species present in a given place/vegetation type, the higher the number of galling species should be (Fernandes & Price, 1988; Wright & Samways, 1996). Considering that arthropod gallers are usually very specific (Raman *et al.*, 2005), then each plant species represents a potential niche for gallers. This can perhaps be deemed a null hypothesis – a homogeneous evolutionary process may be at work, although leading to environmental heterogeneity due to differences in vegetation diversity. Hanson & Gómez-Laurito (2005) used a similar approach and restated this hypothesis in terms of the species-area relationship: the number of gallers (especially Cecidomyiidae) per host species would be more or less invariable, but the number of plants per area is larger in the tropics, which thus have more galling species as well. Some sources find this pattern in the field (Wright & Samways, 1996; Wright & Samways, 1998; Blanche, 2001; Cuevas-Reyes *et al.*, 2004; Dalbem & Mendonça, 2006), whilst others do not (Fernandes & Price, 1988; Blanche, 2000; Cuevas-Reyes *et al.*, 2003).

However, gall-inducers compose a guild, not an assemblage, and each galling taxonomic group can show distinct evolutionary and ecological relationships with plant taxonomic groups on a given geographical scale (as in the Cynipidae, above). Thus, different plant groups can influence galler richness distinctly. Cuevas-Reyes *et al.* (2003) are the latest to argue that the correlation between plant and galling richness is more complex than admitted by the plant richness hypothesis: the presence of certain plant groups leads to different effects on galling species richness than others. This was seen in Australia, where Myrtaceae in general and *Eucalyptus* in particular are unusually species-rich taxa (Blanche & Westoby, 1995; Blanche, 2000). Another example are «superhosts» (Veldtman & McGeoch, 2003), plant species hosting a large number of galling species; their local and regional distribution have a decisive

influence on the local and regional galling diversity.

The plant taxon size hypothesis develops from a analogous perspective, and proposes that gallers would be richer in species on plants from taxa also richer in species, usually at the family or genus level (Cornell, 1985; Fernandes, 1992). The process behind this pattern depends on plant taxa being natural groups in which chemical, structural and ecological characteristics are similar, and thus galler speciation through host shifts (see below) would tend to be between plants of the same family, at least more commonly than between plants of different families. This hypothesis has rarely been tested, although the few papers attempting it have given credence to the idea (Gonçalves-Alvim & Fernandes, 2001; Veldtman & McGeoch, 2003). On a similar tone, the plant geological age hypothesis predicts that geologically older taxa would offer more (longer) opportunity for galler host shifts and would thus accumulate galling species over time (Fernandes, 1992). There is room for more detailed consideration of this hypothesis in the literature, the only source for gallers (this is an old idea for herbivores in general, Southwood, 1960) appearing to be Fernandes (1992), who found no effect of plant family age on gallers (actually some of the more recent families sported the higher numbers of gallers).

Finally, the resource synchrony hypothesis aims to explain galling richness explicitly considering ecological processes and their evolutionary consequences (Mendonça, 2001). The central proposition is that vegetation types in which plants have a higher degree of synchrony in the production of vegetative (or reproductive) organs could provide gallers with higher chances for host shifts (for example through «oviposition mistakes»), leading to the new species in a scenario of sympatric speciation. Certainly both plant species richness and plant phylogenetic affinity determine the probability that host shifts result in «successful» speciation. Thus, this hypothesis qualifies and deepens the plant richness, plant taxon richness and the super-host hypotheses, exposing the need to explore the botanical side of the galling arthropod diversity.

MATERIALS AND METHODS

Rio Grande do Sul state (RS) sits in the southernmost part of Brazil (Fig. 2), being thus subtropical in climate (in the Köppen classification, mostly Cfa but Cfb in the northern Highlands). Two

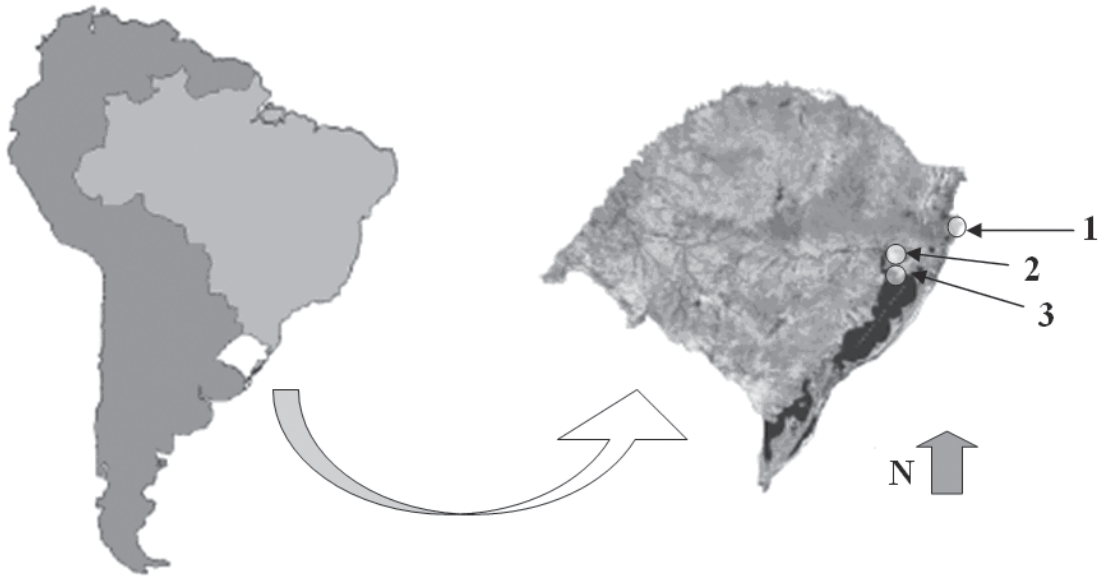


Fig. 2. Position of Rio Grande do Sul (RS) state in South America and Brazil (left) and geographic situation of the sampling areas in northeastern RS (circles and arrows): 1) Itapeva State Park, municipality of Torres; 2) Morro Santana, municipality of Porto Alegre; 3) Itapuã State Park, municipality of Viamão.

biomes are represented in this region, the Atlantic forest and the Pampas. The former is a global diversity hotspot (Myers *et al.*, 2000), highly at risk through historical human intervention. A few conservation units remain, representative of the varied ecosystems formerly present. The latter biome, the Pampas, is a grassland dominated system shared with Uruguay and the northern parts of Argentina. High plant diversity is also present, although not necessarily in forested formations, which nevertheless exist along rivers (riparian forests) and represent an important ecosystem.

A series of field inventories of gallers and their hosts was undertaken in RS, however not all of them with enough botanical detail to allow for more complete analyses. Here, only three more completely sampled sites in the Atlantic forest are considered: a) Itapuã State Park, in Viamão (30°27' S, 51°05' W), b) Itapeva State Park, in Torres (29°21' S, 49°45' W) and c) Santana Hill, in Porto Alegre (30°04' S, 51°07' W). Vegetation types include, respectively (number of transects between brackets): a) hillslope humid forest (2), restinga shrubland (2) and a rocky field/forest mosaic (2); b) swamp forest (2) and restinga shrubland (3); and c) hillslope humid forests at two different stages of succession (better preserved sites: 3; less preserved site: 1).

Fixed homogeneous trails cutting through these

vegetation types were chosen as transects. Sampling involved following the trails for 1h30min, attentively searching for galls in the vegetation. Repeated samples along at least a year were employed (5 trimonthly samples for Itapuã and 4 for Itapeva, 8 biseasonal samples for Morro Santana). All galls found were recorded, photographed and hosts identified whenever possible with the help of botanists. Galls were assigned to morphotypes based on host plant, organ galled, gall structure (shape, size, colour, presence of hairs or spines, number of chambers, chamber shape and size) and gall occupants (for illustrative examples, see Fig. 1).

Simple statistical analyses involved a) linear regressions run on SPSS software; b) Simpson dominance index and bootstrap confidence intervals calculated with PAST statistical package (Hammer *et al.*, 2001). Data on species numbers for plant orders and families were taken from the APG site (Stevens, 2007).

RESULTS AND DISCUSSION

For the whole RS state, the current number of different gall morphotypes so far is at about 429 (Mendonça, unpublished). This includes eight different micro regions with differing numbers of sampled transects each (from 3 to 7) and varied

vegetation types (from grasslands to humid forests). This is by no means a complete assessment of the galling fauna and associated flora in RS – on the contrary, it is probably the tip of a biological iceberg. I will not attempt a comparison of such regional richness values with other places or biomes, since sampling methods and both geographical and temporal extent are quite different from other work. Perhaps one brief example would suffice to demonstrate this: Costa Rica is probably the better surveyed tropical country in terms of galls, and being a fifth of RS in area, harbours more than twice the number of arthropod galling species (AGS), at a current 967 (Hanson & Gómez-Laurito, 2005) – but it is a well preserved country and has been surveyed for 10 years, although sporadically, with no standard ecologically based sampling methods.

For the three microregions included here, a total of 282 gall morphotypes were sampled from the 15 sampling transects: 110 from Itapuã State Park (Mendonça, submitted), 104 from Itapeva State Park (Piccardi *et al.*, in prep.) and 130 from Santana Hill (Dalbem & Mendonça, 2006). Thirty-nine plant families belonging to 20 plant orders (APG II system was used, Stevens 2007) were identified hosting galls in the three sampled areas of RS state. An important point is that not all host plants were identified thus far (71 undetermined species) since it is difficult both to find reproductive material for many host plants and to recollect rare galls; however some of these plants were identified to family level (44 undetermined to family level).

As usual (Gagné, 1994; Hanson & Gómez-Laurito, 2005), most galls were on eudicots (35 families, 229 AGS) than on magnoliids (4 families, 21 AGS) and monocots (4 families, 8 AGS) with galls on Pteridophyta very rare (1 family, 1 AGS). Galls on Gymnoperms were absent from our survey in this part of RS; it is expected since this group is rare in the sampled vegetation types, and galls on these plants are also rare in general. Sapindales and Lamiales are the richest orders in galled plant families (4 each), but Asterales and Myrtales have more AGS (more than thirty each), followed by Sapindales (Fig. 3a). Some orders «dominate» over others, with many more galling species, but the curve is smooth enough so as to be difficult to assign a threshold: Asterales and Myrtales are very rich, but not clearly richer than Sapindales and Malpighiales. Plant orders are not usually considered in galling inventories, but I would propose they can be useful: a higher taxonomic level

would better group up plant species, genera and families when comparing widely different regions or floras.

Plant families with more galling species in RS (Fig. 3b) are among those usually found rich in galls for the Neotropical region as well, either in taxonomic compilations (Gagné, 1994; Maia, 2005) or field inventories (Hanson & Gómez-Laurito, 2005; Gonçalves-Alvim & Fernandes, 2001; Fernandes *et al.*, 2002; Julião *et al.*, 2002), as Fabaceae, Asteraceae and Myrtaceae. However, Asteraceae appears as the «preferred» family for galling arthropods in RS, in contrast with what is found for other sites in the Neotropical region. This family appears in all other taxonomic compilations and inventories at least as the fifth richest and the most comprehensive work actually record Asteraceae as the second richest family, losing only to Fabaceae (Gagné, 1994; Hanson & Gómez-Laurito, 2005; Gonçalves-Alvim & Fernandes, 2001).

A further question is whether these groups are the richest in the vegetation at large, not only as hosts for gallers. Indeed, Fabaceae and Myrtaceae are the richest families in many surveys of the Atlantic forest biome (Peixoto *et al.*, 2004). Myrtaceae are very rich in coastal restinga vegetation throughout Brazil, so much so that some of these schlerophyllous forests on sandy soils are called «Myrtaceae woods» (Assis *et al.*, 2004). Although it may appear that Fabaceae is underrepresented in our work, actually the Atlantic, *Araucaria* and ombrophyll forests of northern and northeastern RS lack legumes relative to other formations, as the subtropical seasonal forests of central RS (Jarenkow & Waechter, 2001). Thus, this difference in galling host plant flora is derived from the biogeographical situation of RS, not from a change in galling arthropod evolutionary «preferences». Another case of such evolutionary «preferences» in the galling fauna is Asteraceae. It is a very rich family overall (Stevens, 2007), however not in developed Atlantic forests. It is distinct for harbouring pioneer shrub species (even Brazilian environmental legislation recognises this, CONAMA, 1994). Many Asteraceae species, especially in the genus *Baccharis*, are known for a very rich galling fauna (Fernandes *et al.*, 1996) – it may be that these plants being abundant, widespread and schlerophyllous, they would represent very apparent targets for galler evolution.

As treated above for plant orders, some taxa have many more galls than most others: at the family level,

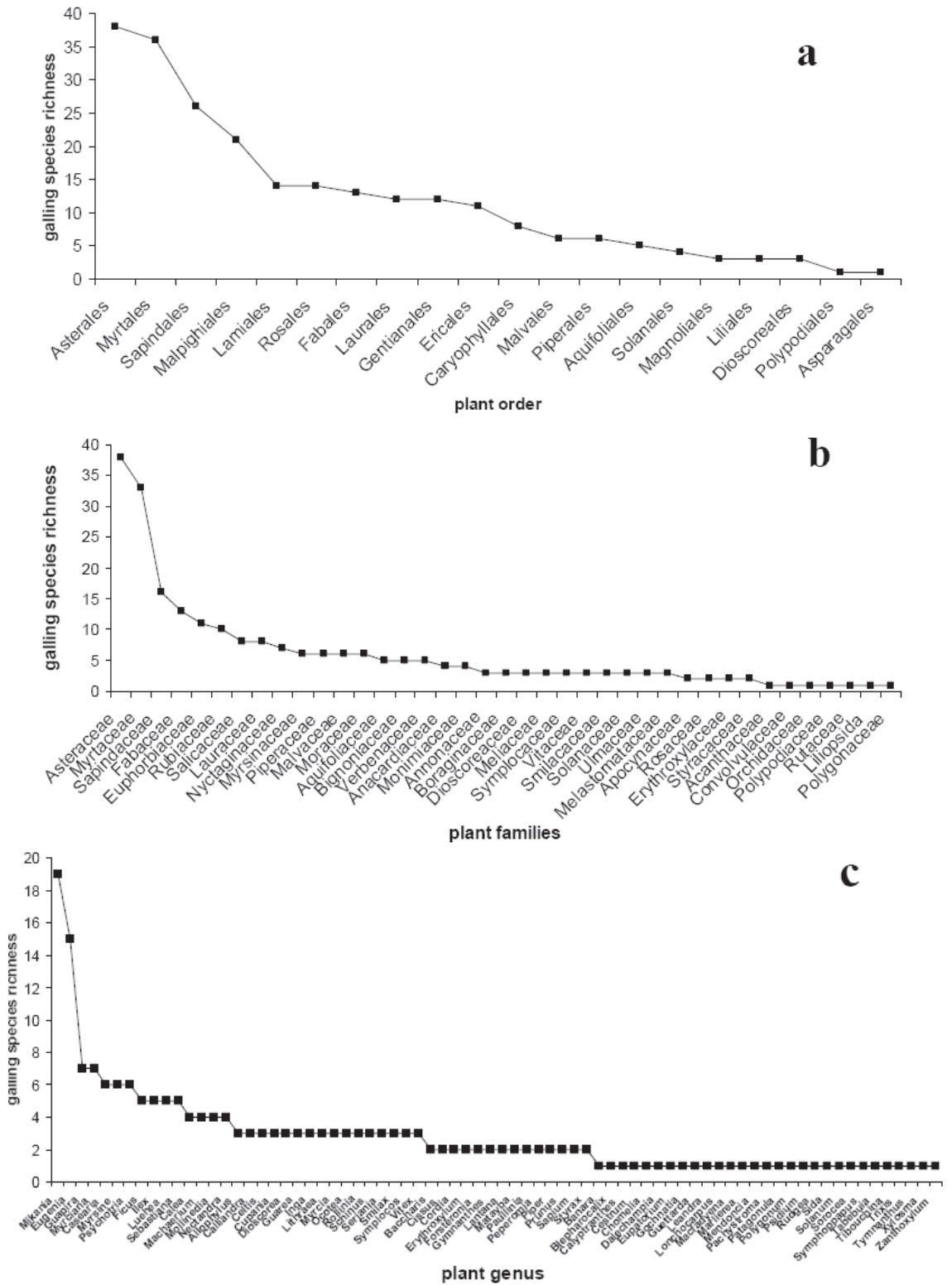


Fig. 3. Galling species richness ranked distributions for plant taxa (number of galling species per host taxon) at different levels in the sampled areas of northeastern RS: **a)** plant orders; **b)** plant families; **c)** plant genera.

Asteraceae and Myrtaceae (Fig. 3b, and see above), at the genus level, *Mikania* and *Eugenia* (from the two abovementioned families, respectively, Fig. 3c) and at the species level, *Guapira opposita* and *Myrciaria cuspidata*. Also visible is that the lower the taxonomic level, the clearer the patterns of dominance become. Figure 4 illustrates this, showing Simpson dominance value significantly increasing from class down to genus. Since there are only four groups at the class level, dominance is low even though eudicots are much richer than the other classes. At the genus and species levels the highest dominance occurs. The conclusion is that especially at lower taxonomic levels there are stronger concentrations of galls on certain taxa, this being the first time a quantitative way is found to express the well-known phenomenon of «super-hosts» (Veldtman & McGeoch, 2003). It can be also argued that not only there are «super-host» species but also «super-host» genera, as shown here.

Attempting to test the plant taxon richness hypothesis with the RS gall database, order, family and genera of plants were compared in terms of global plant species richness and local galling species richness. This is not the ideal situation but the appropriate spatial scale to test this relationship has still not been defined: at what scale galling arthropod evolution occur? For the data at hand, a) regressing AGS richness in a plant order against order species richness is not significant (regression: $y = 186.5x +$

7791.8 ; $F_{1,18} = 1.06$; $P = 0.315$; Fig. 4a); b) regressing AGS richness in a plant family against family species richness is significant (regression: $y = 0.000691x + 3.703$; $F_{1,36} = 12.72$; $P = 0.001$; Fig. 4b); regressing AGS richness in a plant genus against genus species richness is not significant (data on genus size missing for 18 genera; regression: $y = 0.0013x + 2.67$; $F_{1,54} = 1.67$; $P = 0.201$; Fig. 4c). Actually, the significance of the family level regression is dependent on the statistical leverage exerted by Asteraceae (large family with many gallers); excluding this family returns a non-significant result ($P = 0.233$). Thus, support for the plant taxon richness hypothesis is scant in this database, although it remains to be seen whether data on local plant taxon size (that is, the size of the plant taxa in the specific area sampled, northeastern RS) would change this conclusion. This would imply that local processes may have stronger effects on galler-host plant diversity than regional processes, an unexpected finding in itself.

I presented what I believe are interesting but very initial developments toward using gall inventory data to test hypothesis regarding the role of plants in shaping galling arthropod diversity. The taxonomic data on plants alone can bring fruitful insights into the importance of vegetation richness and composition allowing galls to occur in any area of any vegetation type. Much more can be done in this direction, and future inventories should take special notice of plants in order to optimise data gathering

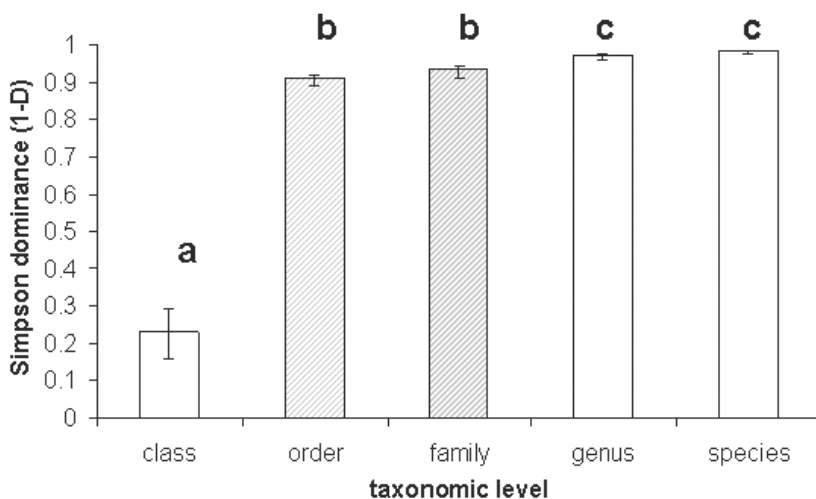


Fig. 4. Dominance (Simpson's dominance index) of plant taxa in terms of number of galling species, at different plant taxonomic levels in the sampled areas of northeastern RS. Different letters indicate significantly different groups under a bootstrap calculation of confidence intervals (indicated as bars).

and especially analysis.

Although much has been done to document the galls of some of the Neotropical biomes, as the cerrado (Fernandes *et al.*, 2005), and some regions, as Costa Rica (Hanson & Gómez-Laurito, 2005), inventorying the gall-inducing arthropod fauna is still in its infancy in Brazil and specially in Latin America.

There is much to describe and discover both in terms of species and ecological patterns. The plant aspect is capital in helping understand such patterns and further on the processes generating them, ecologic and evolutionarily. Without taking the plants into full consideration, we will not understand the ‘reasons’ of the gallers.

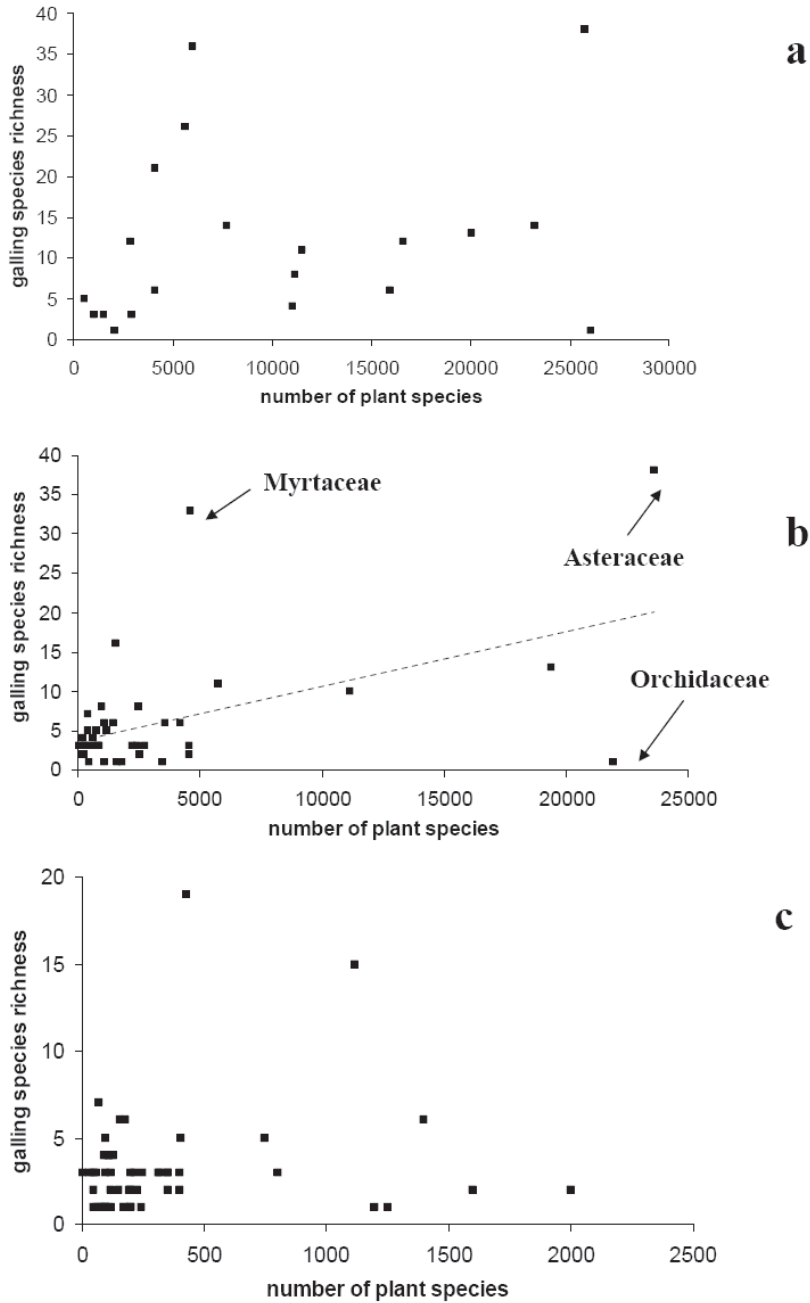


Fig. 5. Regressions of galling species richness per plant taxon (in the sampled areas of northeastern RS) against taxon size in number of plant species: **a)** plant orders; **b)** plant families; **c)** plant genera.

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