ECOLOGY, BEHAVIOR AND BIONOMICS

Diversity of Galling Arthropods and Host Plants in a Subtropical Forest of Porto Alegre, Southern Brazil

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Diversidade de Artrópodos Galhadores e Plantas Hospedeiras em uma Floresta Subtropical em Porto Alegre, Sul do Brasil

RESUMO - Muitas hipóteses têm sido propostas para explicar os padrões de diversidade de insetos galhadores, porém existem evidências contraditórias quanto aos principais processos ecológicos e evolutivos responsáveis por esses padrões. Adicionalmente, questões como sazonalidade dos artrópodos, suficiência amostral e aprendizado dos amostradores têm sido praticamente ignoradas. Este estudo registra artrópodos galhadores e avalia essas questões. Amostragens sazonais de artrópodos galhadores e suas plantas hospedeiras foram realizadas numa floresta subtropical úmida. Quatro transectos foram amostrados duas vezes por estação, por duas pessoas, procurando galhas na vegetação durante 1h30min. Após 96h.pessoa de amostragem, 130 morfotipos de galhas foram encontrados em 84 espécies de plantas hospedeiras. A análise do número de galhas e morfotipos encontrados por transecto demonstrou que a experiência dos amostradores influencia os resultados sobre riqueza de galhadores e os dados relativos a sazonalidade. Diferentes espécies apresentaram distintos padrões sazonais. A riqueza de artrópodos galhadores demonstrou estar ligada à riqueza de plantas. Os resultados sugerem que a experiência dos amostradores é um fator essencial, bem como os padrões de sazonalidade das diferentes espécies, pelo menos em áreas tropicais/subtropicais. Apesar de a suficiência amostral não ter sido atingida, a heterogeneidade da fauna em escalas espaciais pequenas mostrou-se considerável: mesmo com a proximidade entre os locais amostrados (trilhas não distavam mais que 500 m entre si), estes mostraram possuir faunas específicas. Este trabalho adiciona à literatura registros sugerindo que tanto a riqueza florística quanto a composição específica da vegetação têm forte influência sobre a riqueza de galhadores, pelo menos em escalas locais.

PALAVRAS-CHAVE: Morfotipo, amostrador, heterogeneidade ambiental, sazonalidade

ABSTRACT - Many hypotheses have been proposed to explain diversity patterns of galling insects. However, there are contradictory evidences on the evolutionary and ecological factors responsible for the trends. Furthermore, questions such as arthropod seasonality, sampling sufficiency and sampling team experience have been almost ignored. This study records galling arthropod diversity while paying attention to these questions. Seasonal sampling of galling arthropods and host plants were conducted in a humid subtropical forest of southern Brazil. Four transects were sampled twice per season, with two persons searching the vegetation for galls during 1h30min. After 96h.persons of sampling, 130 gall morphotypes on 84 species of host plants were recorded. An analysis of the numbers of galls and gall morphotypes found per transect along time showed that sampling team experience influences galler richness results and the interpretation of galler seasonality patterns. Different species had distinct seasonal patterns. Galling arthropod richness was bound to plant richness. Our results suggest that sampling team experience is an important factor that must be explicitly considered, as well as seasonality patterns of different galling species, at least for tropical/subtropical areas. Although sampling sufficiency was not reached, fauna heterogeneity at small spatial scales seems substantial: despite the proximity of the sampled transects (500 m), they harboured significantly specific faunas. This work adds to the literature records suggesting that both plant richness and specific composition of the vegetation have a strong influence on galler richness at least for local scales.

KEY WORDS: Morphotype, sampler, environmental heterogeneity, seasonality

Studies on faunal diversity at any spatial level are essential to conservation strategies as well as to detect ecological patterns. Rigorous analyses of such patterns contribute to the identification of ecological mechanisms underlying biodiversity (Ricklefs 1987, Cornell & Lawton 1992, Huston 1999). A large fraction of the world's biodiversity is composed of arthropods, with gall inducers being generally poorly studied and known (Cuevas-Reyes *et al.* 2004). Nevertheless, there are advantages in studying this guild: galling arthropods come from different taxonomic groups, the gall is a long-lasting and conspicuous structure, and galling species can be easily distinguished based on host plant identity, galled organs and the general morphology of the galls (Veldtman & McGeoch 2003).

There have been considerable efforts aiming to identify patterns of galling arthropod diversity, although all proposed hypotheses have evidence for and against them. A range of studies show the diversity of gall inducing insects to be intimately bound to plant diversity, since the presence of a larger number of plants in a given environment would denote more ecological niches to be explored (Wright & Samways 1998, Cuevas-Reyes *et al*. 2004); other studies, however, do not find a link between these variables (Fernandes & Price 1988, Blanche 2000, Cuevas-Reyes *et al*. 2003). The latter authors argue that the correlation is more complex: the presence of certain groups of plants may have stronger effects on galler richness than others. Other hypotheses have been proposed and tested, as the hygrothermal stress (Fernandes & Price 1988, 1992; Lara & Fernandes 1996), host plant structural complexity (Fernandes & Price 1988), altitudinal/latitudinal variation (Fernandes & Price 1988, Price *et al.* 1998, Fernandes & Lara 1993), and soil fertility (Blanche & Westoby 1995, Cuevas-Reyes *et al*. 2003), among others. Mendonça (2001) proposes an evolutionary explicit hypothesis, suggesting that galler richness is larger in areas/vegetations where plant sprout is synchronized, either seasonally or because of fire influence, facilitating galler host shifts, and consequently, speciation.

Besides the controversies on the mechanisms involved in galler diversity, comparisons among different sources are sometimes difficult because of different methodologies. The paradox is that employing different methodologies and thus obtaining diverse data would certainly provide more insight on the subject. The most common method minimises differences in plant density between distinct vegetation types, sampling standard numbers of plants (Fernandes & Price 1988, Price *et al.* 1998, Wright & Samways 1998, Veldtman & McGeoch 2003). Others use fixed areas quadrats (Blanche 2001; Cuevas-Reyes *et al.* 2003, 2004). Repeated transect sampling standardised by time (Mendonça in press a, b) is a newly proposed method aiming to increase the size of the local areas sampled and thus to reduce the interference of factors such as spatial plant heterogeneity. This is important in richer tropical vegetation types and enables finer analysis of sampling sufficiency and faunal seasonality.

Other questions involving sampling have also been raised but almost never considered in depth. For example, studying galler richness at a global scale, Price *et al.* (1998) used standardized samples and investigated a suite of factors influencing the results, as sampling team experience. Even though this effect was present, the authors chose to consider it of lesser importance.

The present study aims to study the galling arthropod (insects and mites) fauna of Santana Hill, a relatively well preserved forest area in the urban perimeter of Porto Alegre city. Data were gathered on galler species richness and diversity, as well as host flora, employing a method of standardised repeated transections always carried out by the same sampling team. The hypothesis of plant species richness determining galling arthropod species richness was tested. Also, we analysed how sampling team experience and experience acquisition influences galler sampling, and the effect this can have in understanding ecological patterns.

Material And Methods

Study area. Sampling was carried out on the southern slope of Santana Hill (30°04' S, 51°07' W), in four tracks on forest areas near the Campus of the Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Rio Grande do Sul state, southern Brazil, between September 2003 and August 2004. Santana Hill represents one of the most preserved remaining environments of Porto Alegre area, being at the crossroads of different vegetation types such as the Atlantic Forest and the Subtropical Seasonal Forest; it is in the way of becoming a Conservation Unit.

Thirty-two samples were taken, from September 2003 to August 2004, being eight per track (2 samples/track/season). The tracks were called low, middle, high1 and high2, and were no more than 500 m far from each other. The vegetation of the first track (low) was a forest in an advanced stage of regeneration, with large tree individuals and many shrubs composing a thick understory. The second track (middle) was near the low track, and presented an intermediate state of recovery from anthropic influence, with shrubs and trees of small and intermediate size, besides the presence of some exotic *Eucalyptus* sp. The high tracks 1 and 2 were tall forests, similar to the low track, classified as hygrophilous forests (Rambo 1956), or subtropical rainforests with tropical influence (P. Brack, UFRGS, unpublished data). The first two tracks were adjacent to University buildings, whilst the latter two were about 500 m far from them.

Sampling. The tracks were traversed by two samplers searching the vegetation for any galls during 1h30min. The number of plants bearing each gall type per track was recorded, as a surrogate for gall abundance (heretofore, abundance and number of galled plants are used as synonyms). Galls and host plants branches were collected for identification, individualized in plastic bags, and then brought to the lab.

Galling species were separated using morphotypes (or morphospecies) according to host plant identity and morphological characters of galls and gallers, a standard practice in galling insect diversity work (*e.g.* Price *et al.* 1998), assuming specificity of gallers to host plants. Collected galls were observed by naked eye and stereomicroscope and had their external and internal morphological characters recorded. Gallers and their parasitoids, when present, were also observed and morphological characteristics of the former were also used in the characterisation of morphotypes. Digital photos taken of galls, gallers and parasitoids constitute a digital data bank used for reference. Galls, larvae, pupae and adults of the gallers were then preserved in ethanol 70º GL and kept in the collection of the Laboratório de Bioecologia de Insetos, UFRGS.

Additionally, the tracks were sampled with the help of botanists who identified vascular plant species and thus quantified plant species richness. Plants not recognized *in situ* were taken to the UFRGS herbarium and identified. Voucher specimens of these and the galled plant species are also kept in the Laboratório de Bioecologia de Insetos, UFRGS.

Data analysis. The faunistic composition of gallers present at Santana Hill was compared to data from other regions of Rio Grande do Sul state to identify the proportion of exclusive species. A collector curve (sample-based species accumulation curve) was built using field data; to access to which extent sampling sufficiency was achieved, the species richness estimator indexes Chao1, 1st order Jackknife, ACE, Bootstrap and Michaelis-Menten were calculated using EstimateS 7.5 (Colwell 2005).

We used a MANOVA test to identify significant differences in richness and abundance between tracks and seasons, using SPSS 10.0 (Norusis 2000); when present, differences were then submitted to Tukey tests. To attest the effect of sampling team experience two correlations were made: one between sample sequence and galler richness and another for galler abundance.

Presence/absence data for the pooled seasonal samples was used to compare species composition among tracks and among seasons. The Jaccard index was used in a cluster analysis to illustrate similarity patterns. These data were submitted to two independent analysis of similarities (ANOSIM) tests, one for each factor, using PASt software (Paleontological Statistics 1.32, Hammer *et al.* 2001), with significance values with Bonferroni correction for multiple tests.

The total richness of galling arthropods per track, the average galler richness per sample and the number of host plants were analysed through regression against the total number of plants encountered per track. The proportion of galling species per host plant and the proportion of plant species attacked by gallers in each track were calculated and for the latter a G test was used to compare tracks.

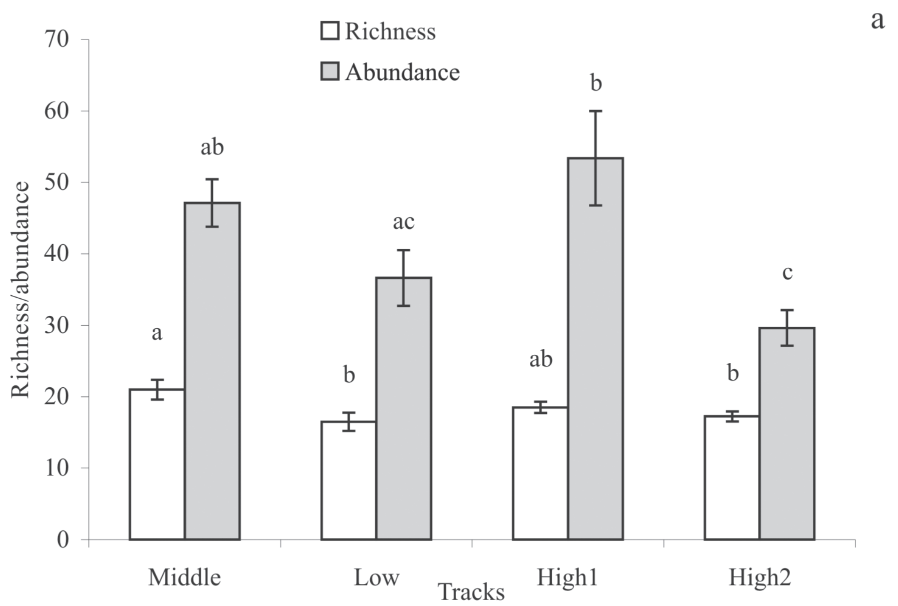
Results

Overall, we found 1334 records of galled plants, with 130 morphotypes of galling arthropods in the four tracks sampled at Santana Hill with an effort of 96h.person. Seventy-two of these morphotypes have not been found in any other areas of the province by our research group after a total of 225h.person of sampling (Mendonça, unpublished data). The gallers used 84 species of host plants, on 34 plant families; thus some host plants had more than one gall morphotype (up to 7 morphotypes per plant). Only three gall morphotypes were induced by Eryophidae mites (2.3%), with most galls being induced by Cecidomyiidae (Diptera); among the other gallers there were Diptera, Lepidoptera and Coleoptera.

The species richness estimators varied between 152 (Bootstrap) and 220 (Chao 1). These indexes suggest that between 59% and 86% of the galling fauna present in the area was effectively sampled. The relative abundance of the morphotypes showed one dominant morphotype (170 galled plants), seven very abundant morphotypes (85-52 galled plants), 18 moderately abundant ones (36-11) and the remaining with low abundances (9 records or less). More than half of the morphotypes were not found on more than two plants (doubletons = 11.5%; singletons = 40%).

The MANOVA showed that both among tracks (Pillai's trace, $F_{6,32} = 7.919$, $P < 0.001$) and among seasons ($F_{6,32} = 3.1$, $P < 0.02$) there were significant differences for richness and abundance considered together. The interaction between tracks and seasons was not significant ($F_{18,32} = 1.835$, $P = 0.065$). The Tukey test comparing tracks for richness showed that the high1 track did not differ from any other, and that the middle track is richer than the other two (Fig. 1a). Abundance values were lower for the high2 track, not differing from that found on the low track, whilst the high1 track showed the highest abundance, along with the middle track. For the season factor the detected differences increased along the sampling period (from spring to winter) for both richness (number of gall morphotypes) and abundance (Fig. 1b). A correlation between the number of samples on each track was significant both for richness ($r^2 = 0.319$; $P < 0.001$) and abundance ($r^2 = 0.330$; $P < 0.001$) of gallers found. The observed tendency is positive: the more samples were done (and the more experienced the sampling team became), the higher was the number of species and individuals of gallers found per sample.

The seasonal abundance patterns of the eight most abundant morphotypes (those with more than 50 abundance records) found at Santana Hill show different apparent seasonal patterns, with abundance peaks occurring at different seasons for each morphotype (Fig. 2). Autumn and winter were the seasons when we found the higher abundance for most of the morphotypes (in conformity with the pattern of increasing abundance and richness stated above), but some of them had peaks in spring and summer.



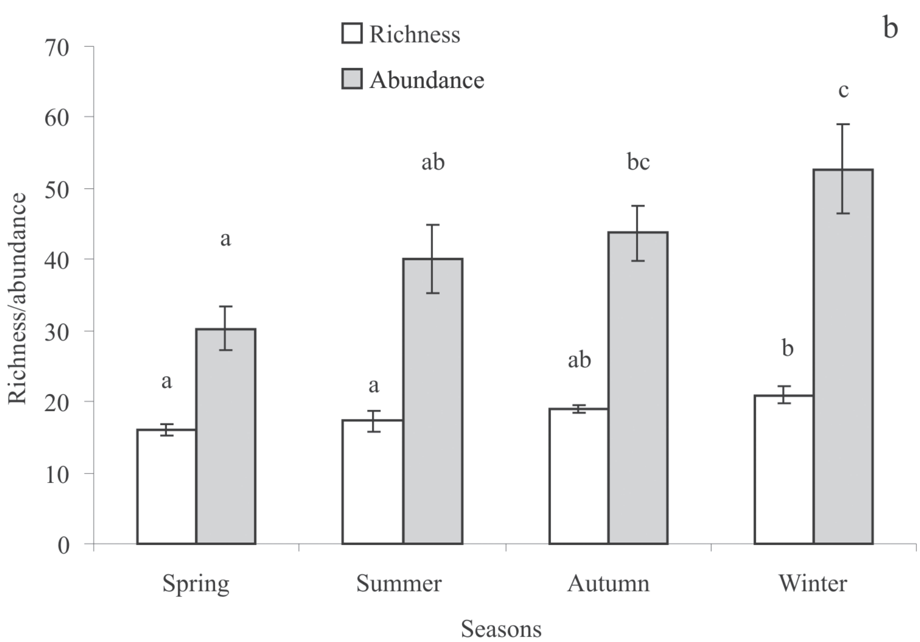


Fig. 1. Average galling arthropod species richness and abundance in four tracks in Santana Hill, Porto Alegre, RS, Brazil. (a) Richness and abundance per track (b) Richness and abundance per season. White bars: species richness; grey bars: abundance; vertical bars are standard errors. Bars with the same letter did not differ significantly after a MANOVA followed by a Tukey test ($\alpha = 0.05$).

Additionally, morphotypes already known from other areas (Mendonça, unpublished data), that is, for which the sampling team had previous knowledge, had peaks in spring and summer (when the study started).

The ANOSIM tests showed that the faunistic composition was significantly distinct among tracks (mean rank within: 16.13; mean rank between: 71.59; $R = 0.9245$; $P < 0.001$), but there were no differences among seasons (mean rank within: 71.08; mean rank between: 57.85; $R = -0.2205$; $P = 0.989$). The cluster analysis illustrates samples of this grouping from the same tracks together, but not samples from the same seasons (Fig. 3). The galling faunas with higher similarities were those of the high1 and high2 tracks, with the middle track having the lowest similarity with the others. Within samples from the same track, the seasons grouped most closely were usually summer and winter, while spring was always the less similar season. Absolute similarity values did not exceed 0.6 (60% of shared species).

An average number of 1.51 gall morphotypes per host plant species was obtained. Among the latter, 65% were

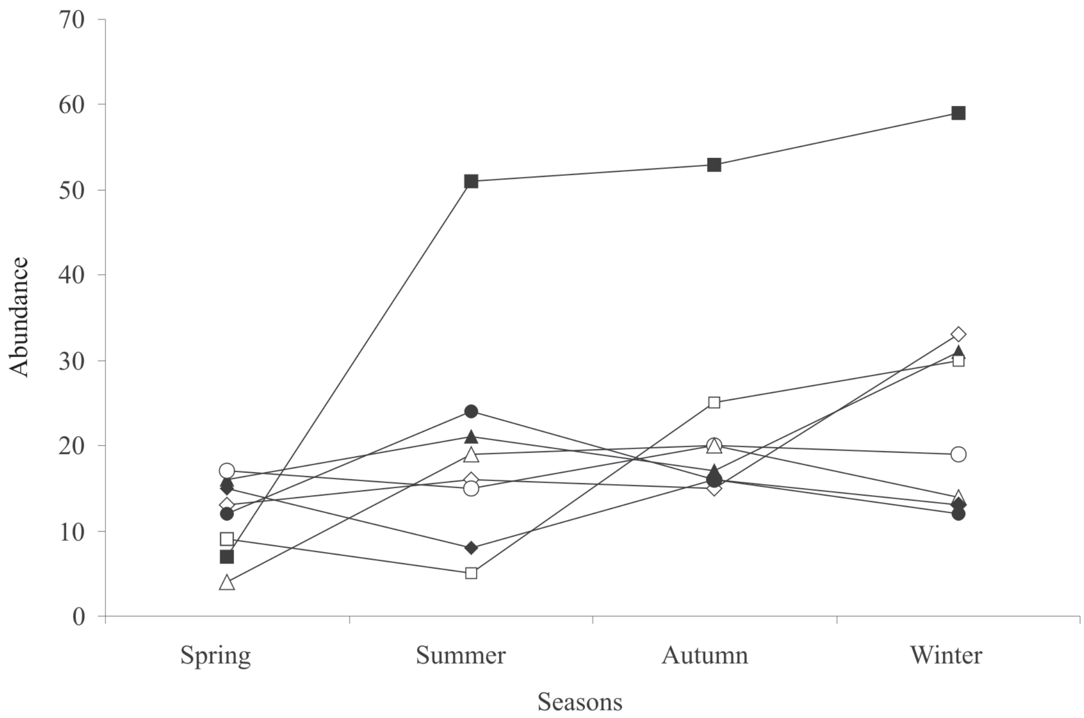


Fig. 2. Seasonal abundance of the eight most abundant gall-inducing arthropod morphotypes (from September 2003 to August 2004) found in Santana Hill, Porto Alegre, RS, Brazil.

host to a single morphotype, 24% had two morphotypes, 8% had three, one plant had four (1.6%) and one plant species to seven morphotypes. On average, 42% of the vascular plant species found at each track had galls. The highest plant richness was found on the middle track (113 spp.) while the poorest was the high1 track (69 spp.). The relationship between plant and galling species richness was positive and significant ($F_{1,3}$ = 35.77; P = 0.027; r^2 = 0.947; y = 0.1477x + 37.62, Fig. 4), despite a small sample size and data range. The regression between average galling species richness found per sample and plant richness was also positive but non-significant ($F_{1,3}$ = 3.165; P = 0.217; r^2 = 0.613). Host plant richness showed no relationship with total plant richness per track ($F_{1,3}$ = 0.073; P = 0.812; r^2 = 0.035). The proportion of host plants per track (relative to total plant richness) was significantly distinct among tracks under a G test (G = 11.08; d.f. = 3; P < 0.02).

Discussion

The galling fauna of Santana Hill is rich and specific: besides the high number of species found, 55% of them were found just in this area of the province until now. Our research group has already sampled seven different places in the province, including many vegetation types as grasslands, savannas, restinga shrublands, swamp forests, hill-slope forests and Atlantic forests (e.g. Mendonça, in press a, b). Since a very small proportion of the galls found on this study are induced by mites, direct comparisons with other studies involving only insects seems reasonable, although other research groups employ different methods. Gonçalves-Alvim & Fernandes (2001), for example, found 125 galling insect species for many sites in the Brazilian cerrado, but their transections were standardised by the number of plant individuals sampled, each track was sampled once and samples were carried out during five months only.

The collector curve is nearing a stabilisation, even though after 96h of sampling on just four tracks we know only about 59-86% of the galling fauna estimated for the area: to carry out a complete inventory of the local galling fauna an even more intense sampling effort is necessary. Methods that explore each location only once may thus represent a partial vision of local galling species richness. Furthermore, repeated sampling coupled to gall morphotyping allows the very estimates that enable us to examine sampling completeness.

The abundance distribution obtained is similar to that encountered in other survey efforts with tropical invertebrates (Novotný & Basset 2000). The high proportion of singletons and doubletons is still intriguing: the above authors conclude that the elevated presence of rare species of free living invertebrates is due to their mobility and low specificity in plant use. Gallers are plant-specific, and the gall is immobile. This, along with the intense sampling effort employed here, suggest that some gallers have low population levels. Our observations are not conclusive, however, since our abundance estimates are in number of galled plants and not galler individuals.

The spatial and temporal patterns found showed that both seasons and tracks differ in respect to species richness

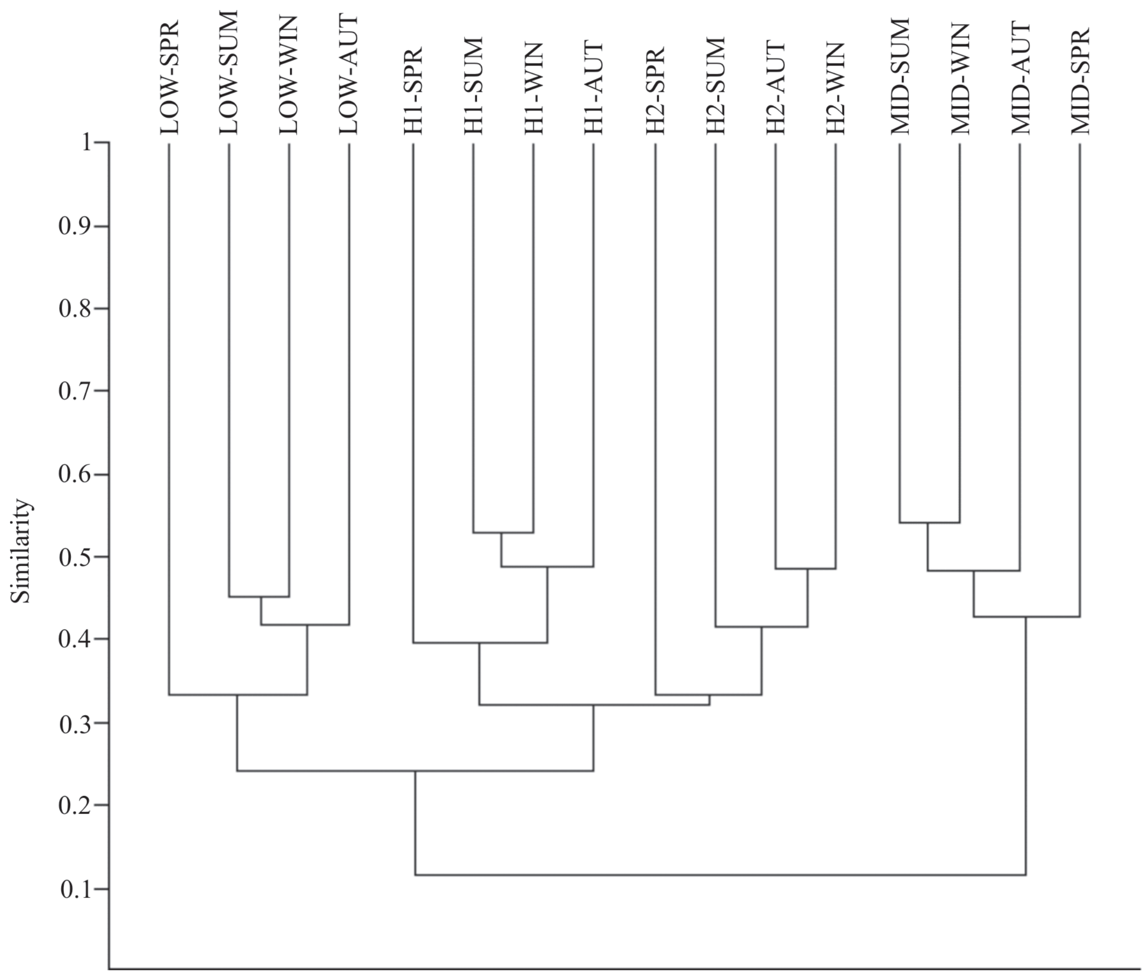


Fig. 3. Similarity of galling arthropod species for pooled season samples for each track and season (Jaccard similarity index, UPGMA clustering), in Santana Hill, Porto Alegre, RS, Brazil. (abbreviations: MID: middle; LOW: low; H1: high1; H2: high2; SPR: spring; SUM: summer; AUT: autumn; WIN: winter).

and abundance of gallers. A certain environmental perturbation appears to have a positive effect on diversity, because the middle track, in an intermediate state of vegetation regeneration, had the highest richness for both galler and plant. Similar cases of increasing diversity after light perturbation, thought to originate from niche diversification, have been documented for other animal groups (Blau 1980, Raguso & Llroente-Bousquets 1990). In relation to temporal variation, winter showed the highest abundance and richness of gallers, however this difference probably results from the interaction with a poorly studied factor: sampling team experience. Price *et al*. (1998) studied the effect of different samplers in gall richness recording for similar areas, perceiving that although being significant, the intensity of the relationship was not too strong. However, when samplers worked in similar, close by sites, a consistent bias was found, in which one sampler could consistently find more species than another. Here we demonstrated an increase in galler species richness and abundance per sampling unit with the gradual increase in sampling team experience; as the fauna turn out to be more familiar it became easier to find in the field. Thus, even comparisons employing the same methodology, but made by different sampling teams, as the one done by Price *et al*. (1998) should be considered with care.

The observed variation in richness and abundance per sample along the development of this study may not be linked to the seasonality of the region, since in winter we found more galling species and in spring less species than in any other season. These findings opposed to our expectation given that the emergence of most zoocecidia is synchronised with the active growth period of the host plant (Rohfritsch 1992) in the subtropical region at spring and summer. Veldtman & McGeoch (2003) sampled between March and May to coincide with the end of the growth and development period of galls (summer) in the southern hemisphere. Price *et al*. (2004) worked with Cynipidae and sampled in fixed periods of the year, at times when early and late galls occur. In those cases aspects of the biology of the local gallers are known, but in the present study distinct seasonality patterns

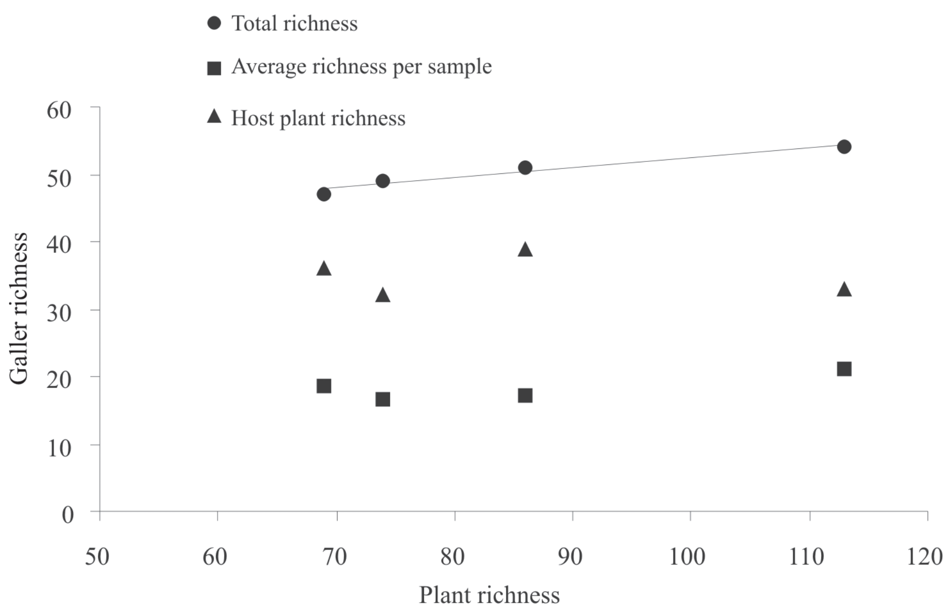


Fig. 4. Regression between plant species richness and total galling arthropod species, average (per sample) galling arthropod species, and number of host plants per track, for four tracks in Santana Hill, Porto Alegre, RS, Brazil. (note: the *x* axis does not start at the origin)

could be tentatively inferred at least for the most abundant species. Galler seasonality is probably more complex in tropical and subtropical areas with no clear wet or dry seasons (as in southern Brazil, e.g. the multivoltine *Eugeniamyia dispar* Maia (Diptera: Cecidomyiidae), present from late winter to early autumn (Mendonça & Romanowski 2002), a factor that must be considered in diversity studies on this guild. Since gallers are protected inside the gall, possibly there is an advantage for gall inducers to stay within the gall during the colder season, as predicted by the microenvironment hypothesis (Stone & Schönrogge 2003). Also, the species seasonal patterns found (Fig. 2) reinforce the sampler experience question, given that morphotypes already know from other areas had abundance peaks at the start of the study.

The low similarity among tracks for galler species composition demonstrates that when the focus is conservation, the optimisation of species richness may come from preserving the highest number of microenvironments (or areas within the same environment), because diverse and specific faunas may be associated even to close by areas (i.e. there is faunal heterogeneity at small scales). Although our estimates show incomplete samples, we believe that similarities would still be low after a complete inventory, because faunal differences among tracks for galling arthropods may in part be attributed to differences in plant composition. Price *et al*. (2004), when analysing the similarity of galling Cynipidae in different areas using an oak species [*Quercus myrtifolia* Willdenow (Fagales: Fagaceae)] conclude that, for conservation purposes, both reserve size and environment heterogeneity are important, since turnover – habitat diversity – for their sampled sites was high. Working with edge and forest patch size effects on galler diversity, many small patches were found to harbour higher galler richness than a few large ones (Julião *et al*. 2004). The small size of these animals and the amount of resources they expend makes this a plausible approach; other animal groups would probably suffer with the choice of conserving smaller but more diverse areas.

Plant richness per track appears to be an important factor determining galling arthropod richness at the studied sites. A small number of sampled points and short data range obtained for galler richness means that the results should be considered with care, although they appear very consistent. The fact that total galler richness was significantly correlated with plant richness while average richness per sample was not so shows that isolated samples may fail in detecting existing patterns. Repeated sampling may also be a way to overcome this problem.

A study in the South African Cape demonstrated that woody plant richness has an important effect in galling insect richness (Wright & Samways 1998), while Cuevas-Reyes (2003) found a negative relationship between galler and host plant richness. However, the latter focused on the plants: they compared the proportion of galled plant species to total plant richness; we believe this measure to be too indirect. With the data obtained in the present study analysed that way, we would not detect any relationship between plant and galler richness. A more plausible view would be to consider both plant composition (Blanche & Westoby 1995, Blanche 2000) and plant richness as influencing galler richness decisively. The intensity of such factors would be accentuated at the local level, since plant richness may vary at small spatial scales (even more among close by areas with different perturbation levels), while at larger scales other variables may be more important. Thus, the presence of a higher number of plants at a given place increases the chances of finding more plant species harbouring galling species, but the occurrence of certain families, genera or species hosting diverse galling faunas is as important, with species composition influencing galler richness.

An interesting possibility would be an ecophysiological focus as the one employed by Price *et al*. (2004), seeking patterns linking diversity and the physiology of the organisms involved. The different proportions of host plant/ plant richness per track demonstrate that vegetation influence galler richness: tracks with the most similar proportions of galled plants also had the highest similarity for the galling fauna. Thus, the flora appears to have a determinant role in the ecology and distribution of gallers, although it may not be the main factor determining its richness and abundance at supralocal levels. Discerning the influence of each variable (plant richness and composition) requires additional studies.

The present study aimed to characterise galling arthropod and host plant diversity giving emphasis to a more complete scanning of the fauna at a given place: the evaluated areas can be considered as having been assessed more completely than usual for galling species. We suggest galling diversity research with focus on repeated sampling could provide more complete faunistic views for a local scale. It corroborated the hypotheses that the preservation of different habitats would be a good strategy for the conservation of species in this guild. Also, we conclude that vegetation composition at the species and higher taxonomic levels has an important role in determining galler diversity at a given site. Finally, this was the first study explicitly analysing the effect of sampling team experience, showing the need to pay more attention to such factors when comparing data from different sources and samplers with different levels of experience in the field.

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