ECOLOGY, BEHAVIOR AND BIONOMICS

Galling Arthropod Diversity in Adjacent Swamp Forests and Restinga Vegetation in Rio Grande do Sul, Brazil

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ABSTRACT - Galling arthropods create plant structures inside which they find shelter. Factors acting on galler diversity are still being discussed, with this fauna considered more diverse in xeric than mesic environments (higrothermic stress hypothesis, HSH), and also in more plant diverse sites. Here we compare galler abundance (*N*), equitability (*E*), species richness (*S*) and composition between adjacent restinga (xeric) and swamp forests (mesic) in Parque Estadual de Itapeva (29°21' S, 49°45' W), Rio Grande do Sul, southern Brazil. Five trails, two in swamp forest and three in restingas, were sampled four times each (January/December 2005). After an effort of 60h/person, 621 galled plant individuals belonging to 104 gall morphotypes were recorded. This suggests a high galler diversity for the Park, comparable to the richest places known. No differences were found for *N*, *E* or *S* between restingas and swamp forests. However, faunal composition differs significantly between the vegetation types. The dominant (most abundant) species are different in either vegetation type, and are rare or absent on the other vegetation type. Such species composition analysis is still largely ignored for gallers, and stresses the fact that the HSH cannot explain this pattern, since the latter is based on preferences by the ovipositing galler for xeric sites instead of mesic ones. The two habitats differ in microclimate, but species richness, as would be predicted by the HSH, does not differ. This small scale pattern can perhaps be attributed to biogeographic processes on larger scales, as suggested by the resource synchronisation hypothesis.

KEY WORDS: Hygrothermic stress, gall, species composition, species richness

There have been increasing efforts towards identifying galling arthropod geographical diversity patterns, and a few hypotheses are proposed to explain the data at hand. So far there are positive evidences for all hypotheses and a wider range of studies is needed to reach plausible scenarios. One of the most discussed hypotheses predicts that galling species richness is higher in xeric than in mesic environments due to higrothermal stress being gentle on endophytes such as gallers, but strong towards exophytic galler natural enemies as predators and parasitoids (Fernandes & Price 1988, Fernandes & Price 1992, Lara & Fernandes 1996, Price *et al* 1998, Blanche 2000). Other studies show that galler diversity is correlated to vegetation diversity, since the presence of a higher number of plant species in a given environment represents more potential niches (Wright & Samways 1998, Cuevas-Reyes *et al* 2004, Dalbem & Mendonça 2006), although some failed to find such correlation (Fernandes & Price 1988, Blanche 2000, Cuevas-Reyes *et al* 2003). Furthermore, in some cases it appears that the relationship could be more complex, with the presence of certain groups of plants having stronger effects on galler richness as compared to others (Blanche & Westoby 1995, Mendonça 2007). Mendonça (2001) also proposed an alternative explanation for both patterns (xeric/mesic and plant richness), suggesting galler richness is actually higher where plant growth (meristematic tissue production) is synchronised, facilitating host shifts and consequently galler speciation; it represents therefore an explicit evolutionary rather than an ecological hypothesis.

Other environmental factors have also been considered to affect galler diversity: host plant structural complexity (Fernandes & Price 1988), latitudinal/altitudinal variation (Fernandes & Price 1988, Fernandes & Lara 1993, Price *et al* 1998) and soil fertility (Blanche & Westoby 1995, Cuevas-Reyes *et al* 2003). Evidence is still scant, although increasing, and more tests of these factors are needed for different regions and vegetation types.

The literature on galler diversity usually deals with galler species richness evaluated at a local scale, with sampling sites visited only once and galler identity not recorded. Although such approach is important for mapping vast areas and leading to geographical considerations (as in Price *et al* 1998), galler seasonality, sampling site area coverage (and thus vegetation representation), and perhaps more importantly faunal spatial variation (beta diversity) need to be taken into consideration. Different methods, such as repeated visits to sampling sites with gall/galler/host plant identification (morphotyping, as in Dalbem & Mendonça 2006) may provide a different view of galler diversity to complement existent data. Here we employ this method to compare adjacent vegetation types differing in the degree of environmental water availability: xeric restinga vegetation and mesic swamp forest. Due to galler identification, a range of diversity analyses are provided: galling species richness is compared under two contrasting statistical frameworks (sample-based rarefaction and analysis of variance), and other diversity variables not usually considered, as galler abundance and community equitability, are also included. Beta diversity is explicitly compared in terms of species composition variation among vegetation types.

Material and Methods

Study area. Parque Estadual Itapeva (PEI) (29°21' S, 49°45' W) is located in a narrow strip between RS-389 road and Itapeva beach, in the outskirts of Torres town, in the extreme north of the coastal plain of Rio Grande do Sul state (Fig 1a). It has approximately 1,000 ha, and although it is relatively small for a conservation unit, it represents one of the only remnants of an environmental gradient between sand dunes by the Atlantic Ocean and swamp forests covering the coastal sandy plains. Large mobile and fixed dunes compose the park, including different phytophysiognomies of the Atlantic forest (latu sensu, see Silva 2000), such as: psamophyll vegetation, peats, dry and wet fields, parkland (savanna), sandy forests and swamp forests (Kindel 2002, Dobrovolski *et al* 2004).

Atlantic Coast restingas form an endangered WWF ecoregion associated with the Atlantic forest biome, spanning from northeastern to southern Brazil (Silva 2001). Restingas range from shrubland (average 2-2.5 m) to tall forests (up to 10 m, Colombo *et al* 2008) and represent a xeric environment, developing on low water and nutrient availability, high insolation and/or salinity (due to coastal position) and over well-drained soils. Besides, plants show morphological adaptations to such conditions as spines, microphylly and contorted stems (Rambo 1956, Dillenburg *et al* 1992).

Swamp forests are a more mesic environment, occurring on wet climates, plain and low reliefs and over poorly-drained soils, favouring hydric saturation and organic matter accumulation on the surface (Waechter & Jarenkow 1998). Salt is blown from the sea over the fixed dunes separating Itapeva swamp forests from the beach, so a degree of soil salinity is expected; however, plants do not seem to suffer severely from this or show schleromorphic traits (Kindel 2002). Such forests in the park reach on average 15 m tall (Colombo *et al* 2008).

Sampling. Five trails were sampled for galls (Fig 1b): two on swamp forests (hereafter SN and SS) and three on restingas. The first are in the northern part of PEI and the latter on Itapeva hill, in the southern part of PEI, with two trails on the hill slopes (hereafter RL and RS) and one at the hilltop (hereafter RM). Although the closest trails are not further away than 1 km, proximity among trails is dictated by logistic reasons: as stated above the park is relatively small and representative, whilst around it few comparable preserved areas remain. Furthermore, a previous detailed assessment of gallers among close trails (Dalbem & Mendonça 2006) revealed large differences in galling species composition, indicating an unexpected degree of heterogeneity even at a small scale.

Four samples were taken from each trail along one year (January, May, October and December 2005), but without

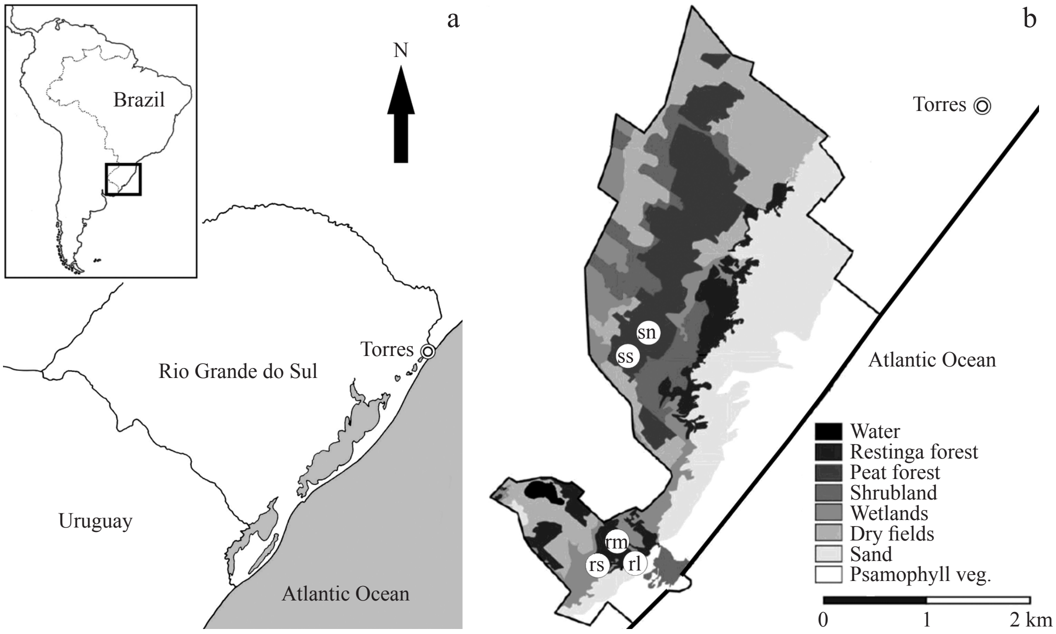

Fig 1 Maps of Parque Estadual de Itapeva, Torres, Rio Grande do Sul state, Brazil. a) geographic position of Rio Grande do Sul in South America and Torres in Rio Grande do Sul; b) vegetation map of Parque Estadual Itapeva with sampling points indicated as small circles with letters (for trail codes see text); swamp forest sites are to the north and restingas to the south of the park.

contemplating winter due to logistics (a typically rainy season in southern Brazil). Sampling was standardised by time: two persons moved along each trail during 1h 30 min at a low pace attentively scanning the vegetation for galls up to 3 m high (see Mendonça 2007). Most samples covered 200-250 m distance along a trail. Gall abundance was measured for each galling species as the number of galled plants (as in Dalbem & Mendonça 2006).

Galls and host plants were collected and taken to the lab; approximately half of all galls seen were collected, either occupied or not, so as not to deplete the trails. At least one gall-free representative plant shoot was collected per host plant species, as well as reproductive material, whenever available. Plants and galls were photographed and the latter dissected under a stereomicroscope. Morphological characters of the galls [organ(s) galled; gall shape, size and colour; chamber number, size and shape], galler identification (at least to order level), along with host plant identification lead to morphotyping of the galls, heretofore referred as galling species (Dalbem & Mendonça 2006). It is necessary to stress that the method employed records abundance as number of host individuals galled, and not number of individual galls; furthermore, it is possible for the same plant to be recorded as galled on different sampling dates since we did not remove all galls. It thus may lead to an inflation of abundance values; however, removing each and every gall would be a logistically and ethically difficult methodological option.

Data analysis. Sample-based rarefaction was employed to compare overall species richness and diversity (Fisher's alpha) between restinga and swamp forests, calculated with EstimateS 8.0 (Colwell 2005). Average galling species richness, abundance and equitability were also compared among vegetation types with transects as replicates, with a non-parametric (NP)MANOVA (10,000 permutations, run with PASt 1.80 software, Hammer *et al* 2001) employed to test the three variables simultaneously. These different analyses with different sampling units were employed so to compare their responses to the pattern: rarefaction pools samples losing power but accumulates species richness increasing the probability of detecting a statistical difference in absolute numbers.

Species composition (beta diversity) was compared among vegetation types with samples as replicates using cluster analysis (UPGMA algorithm, Jaccard and Morisita indexes, qualitative and quantitative, respectively). The observed patterns were tested with ANOSIM (analysis of similarity, 10,000 permutations, Clarke & Green 1998) followed by a SIMPER (similarity percentage) analysis to point out the galling species responsible for any differences in composition (both also run with PASt).

Results

After 20 samples representing 60h/person of effort, 621 galled plant individuals were recorded, on which 104 arthropod gall morphotypes occurred. The latter were induced on at least 75 host plant species. Among the morphotypes, 92 occurred on 27 plant families and 12 have undetermined host plants. Asteraceae, Myrtaceae and Sapindaceae were the most representative host families.

Overall richness for the three restinga trails was 66 morphotypes and for the two swamp forest trails, 48 morphotypes. The sample-based accumulation comparison shows no differences in richness among the two vegetation types (Fig 2a), as well as no differences in terms of diversity, measured as Fisher's alpha (Fig 2b).

There were no statistical differences for diversity when comparing trail averages between vegetation types (Fig 3; NPMANOVA, total SS = 4288; within-group SS = 4192; F = 0.068; P = 0.899). None of these variables was significant on its own under separate ANOVA tests. Visually, restingas appeared to harbour more equitable galler communities (Fig 3c), although not statistically different. Indeed, in the swamp forest, the most abundant galling species was *Guarephila albida* Tavares (Diptera: Cecidomyiidae) found on *Guarea macrophylla* (Meliaceae), corresponding to 40% of the total galled plant individuals in that vegetation type. In restingas, the most abundant galler was *Bruggmannia elongata* Maia & Couri (Diptera: Cecidomyiidae), on *Guapira opposita* (Nyctaginaceae), which did not exceed 15% of the overall abundance.

Restinga vegetation had 56 exclusive morphotypes (26 of them "singletons", that is, found on only one individual plant, but not necessarily a single gall) and swamp forest

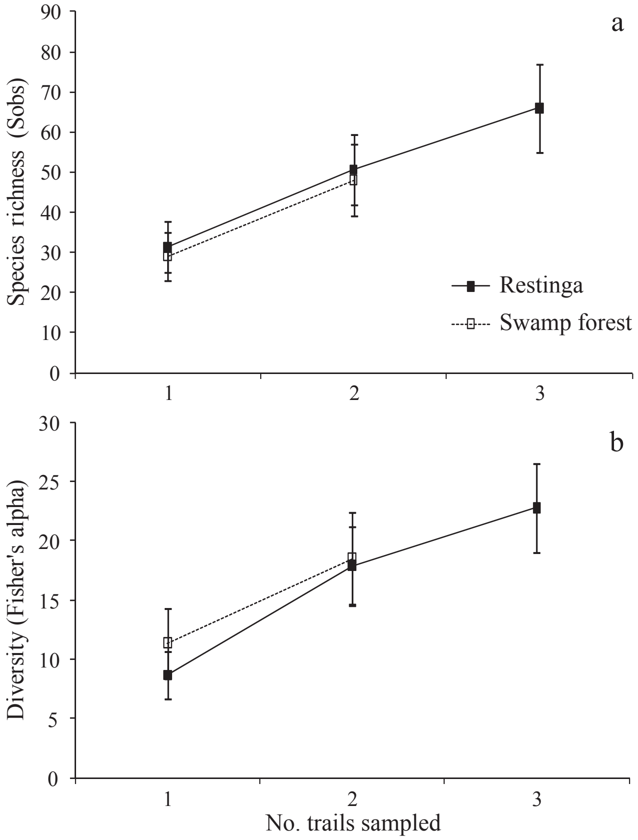

Fig 2 Sample-based rarefaction curves for the galling arthropod fauna of Parque Estadual de Itapeva in restingas (closed squares, full line) and swamp forests (open squares, dotted line). a) species richness (Sobs); b) diversity (Fisher's alpha).

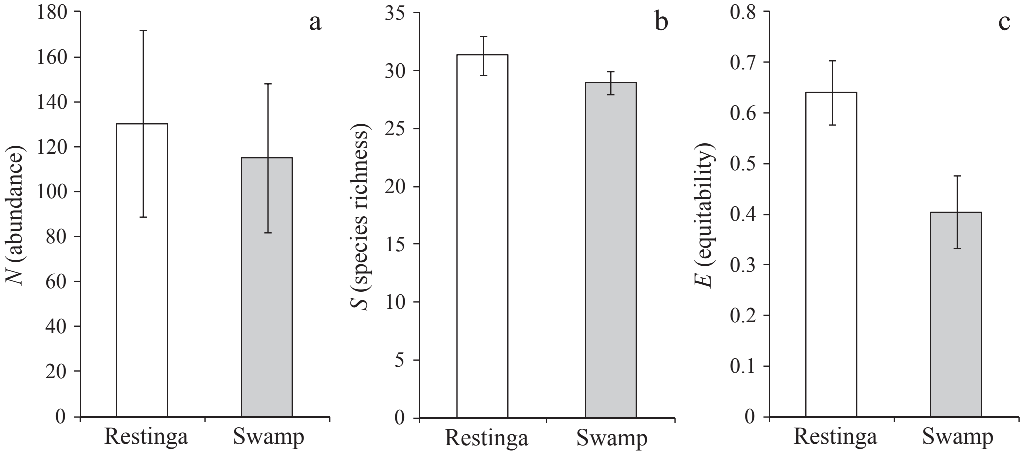

Fig 3 Diversity of galling arthropods in restingas (open bars) and swamp forests (grey bars) in Parque Estadual de Itapeva (averages per sample, bars indicate standard errors). a) gall abundance (no. plants galled); b) galling species richness; c) galling species equitability.

38 (19 "singletons"), with only 10 morphotypes found on both environments. The cluster analysis based on individual samples (repeated visits to different trails) shows a separation among vegetation types, although no clear clustering of trails is visible (Fig 4). The ANOSIM reflects this being highly significant for vegetation types under both similarity indexes: Jaccard (rank within = 55.3; rank between = 134.9; R = 0.838; P < 0.001) and Morisita (rank within = 51.1; rank between = 139; R = 0.925; P < 0.001). The exclusion of singletons did not alter these results: Jaccard (rank within = 55.8; rank between = 134.4; R = 0.828; P < 0.001) and Morisita (rank within = 51.07; rank between = 139; R = 0.926; P < 0.001). SIMPER reveals the morphotypes driving this difference quantitatively were the most abundant ones, *G. albida*, exclusive to swamp forest (contributing 19.3% to the compositional difference between vegetation types), *B. elongata*, much more common on restinga (contributing 5.3%) and a *Pisasphondylia* sp. rosette gall also on *G. opposita*, exclusive to restinga (contributing 5.1%).

Discussion

The arthropod galling richness found in Itapeva can

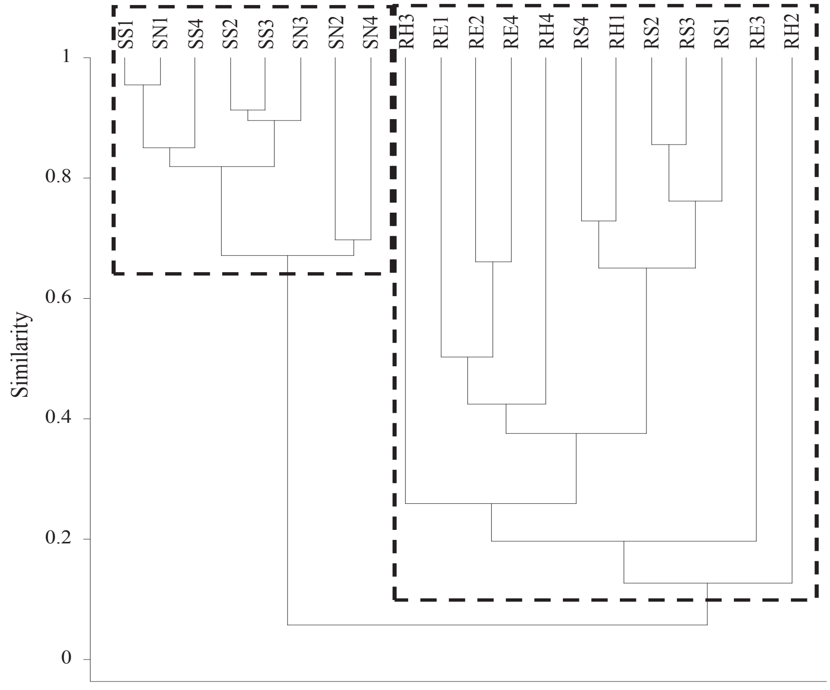

Fig 4 Cluster diagram (UPGMA) for galling species composition similarity (quantitative Morisita index) among samples (for trail codes see text). Dotted lines indicate the two main clusters, each with samples from a single vegetation type (S for swamp forests, R for restingas)

be considered similar to other localities in the Neotropical region given the sampling effort employed (*e.g*. Gonçalves-Alvim & Fernandes 2001, Yukawa *et al* 2001, Dalbem & Mendonça 2006). This is remarkable especially because of the small size of the park and its relative isolation, reiterating its value for conservation (see also Colombo *et al* 2008). Gonçalves-Alvim & Fernandes (2001) obtained 125 gall morphotypes on 81 host plant species in different cerrado phytophysiognomies in Minas Gerais, Brazil, employing distinct methods and intense sampling effort, which are similar to the numbers reported here. These results suggest that certain environments within the Atlantic Forest biome, as the coastal restinga and swamp forests, may harbour galler species richness comparable to regions considered highly diverse for this guild, as the Brazilian cerrado (Lara & Fernandes 1996, Price *et al* 1998, Gonçalves-Alvim & Fernandes 2001).

The absence of differences for either galler richness or diversity cannot be attributed to sampling unbalance (three restinga trails and two swamp forest) since sample-based rarefaction explicitly considers this. Further conjunct testing of galler abundance, richness and equitability (under the usual analysis of variance statistic framework) also failed to reveal differences between xeric restinga and mesic swamp forests. The value and appropriateness of either approach to testing species richness and other diversity variables are still an open question. Sample-based rarefaction curves require species identity to be recognised (even if only as morphotypes, as in here), and thus denote higher sampling effort, but also permits comparisons based on cumulative species richness, perhaps leading to more easily detected statistical differences.

A higher galling richness in xeric environments (perhaps more properly on scleromorphic vegetation, as pointed out by Mendonça 2001) influences the latitudinal gradient in local diversity for these organisms on a global scale (Fernandes & Price 1988, 1991, Price *et al* 1998). According to the hygrothermic stress hypothesis (HSH) proposed by the latter authors, we expected at least a higher richness on the xeric environment. A higher abundance could also be conceived as an expectation of the HSH given that its mechanistic basis relies on higher galler survival on xeric environments, as well as female preference for this kind of habitat (Fernandes & Price 1992). Both diversity measures failed to conform to the HSH; this hypothesis does not have clear predictions for equitability, but the variable represents a different aspect of diversity (abundance distribution among species) not usually considered in galling studies that is worth pursuing.

The dominant galler was the same for both swamp forest trails (*G. albida*), a species already recorded for Santana Hill by Dalbem & Mendonça (pers obs.). For restinga, dominant morphotypes (found on *G. opposita*) were sampled both from Santana Hill and Parque Estadual de Itapuã (Dalbem & Mendonça, pers obs.). These host plants are thus not restricted to a single environment, but rather occur on different types of forest and shrubland on the southern region of the Atlantic forest biome. However, the dominant galling species on each vegetation type did not occur, or occurred in much lower numbers, on the other vegetation type studied here, although sites were close by (about 1 km). Thus there is no superposition of dominant morphotypes between vegetation types. The HSH predicts higher abundances for most gallers on xeric rather than mesic vegetation types, but what we found for PEI is that some species are more abundant on one rather than the other vegetation type, irrespective of environment.

Plant species composition was also different between the two vegetation types, due to the distinct environmental conditions (mainly soil and microclimatic factors, but not macroclimatic ones as rainfall, Dobrovolski *et al* 2004). Various papers have emphasized the importance of host plant diversity for galling diversity (Wright & Samways 1998, Yukawa *et al* 2001, Oyama *et al* 2003, Dalbem & Mendonça 2006), however here the identity of host plants determined the occurrence of gallers and ultimately galler community richness in restingas and swamp forests. This is revealed by the beta diversity analysis, which finds distinct galling faunas for the adjacent vegetations with distinct floras.

Comparing faunas with different species compositions for alpha diversity variables such as species richness actually represents a stern test of the HSH: the species are not the same but the pattern should nevertheless hold. Sites in PEI being nearby add strength to our conclusions since macroenvironmental conditions are the same across sites, although microenvironmental conditions differ. The argument is that since Fernandes & Price (1992, see also Price *et al* 1998) suggested ovipositing galling female habitat preference (allied to differential galling survivorship) driving the mechanism, small scale ecological phenomena were to be at play (dispersal), a comparison fit for nearby sites on a gradient of vegetation structure but with little compositional change. Gallers are usually small, frail insects with restricted active dispersal capabilities (*e.g*. Cecidomyiidae, Gagné 1994). Thus, for either larger scale comparisons or for comparisons among vegetations differing in plant composition (as in PEI) we would suggest the HSH mechanistic explanation not to be feasible: even though gallers may disperse between our sites in PEI, they will not find their host plant in the other vegetation type in most cases. Thus, we suggest larger scale biogeographical processes, including speciation (Mendonça 2001) and species range expansion, as more likely processes explaining significant differences in galling composition and absence of difference in galling species richness between these two vegetation formations.

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