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Questioning the environmental stress hypothesis for gall diversity of restinga vegetation on dunes

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Abstract: The Atlantic Coast Restinga is a mosaic of plant communities with a distinct floristic and phytophysiology, exposed to luminous, thermal, and saline stresses. Plants of the *restinga* must have special features commonly associated to xeric environments, and are expected to host a high diversity of galling herbivores. We studied gall morphotypes, and recorded the diversity of galls on plants growing in sand dunes in a remnant area of *restinga* (Acarai State Park) in São Francisco do Sul, Santa Catarina State, Brazil. The sampling was done in four plots (250 x 5 m), constituting a total area of 5000 m², during April, May and June. Plant branches (n ≥ 5) with galls were sampled, identified, and the galls were photographed. The galls were classified into eight morphotypes, associated to eight host plants constituting 15 host plants - galling herbivores systems. The identification of the gall - inducers was based on literature, and on the species-specific feature of this kind of host plant-gall inducers interaction. There was a predominance of leaf galls, green in color. The most common morphotypes were the globoid, lenticular, conical, rosette, marginal, and fusiform galls, similarly to the inventories performed on other Brazilian biomes. Despite the environmental stresses, the xeric features of the dunes of the ASP, and the high local plant diversity, the diversity of galling herbivores were low. *Varronia curassavica* (Boraginaceae), *Smilax campestris* (Smilacaceae), and *Guapira opposita* (Nyctaginaceae) were superhosts of galling herbivores in the dunes, with about 70 % of the total associated parasites. The environmental effect seems to be neutral, either for the host plants or for the generation of gall morphotypes. Alternatively, the scarce nutritional resources could be restrictive for the establishment of the galling herbivores inside plant tissues. Rev. Biol. Trop. 63 (4): 959-970. Epub 2015 December 01.

Key words: dunes, environmental stress, insect-plant interaction, restingas, super-hosts.

The Atlantic Coast Restinga is a mosaic of plant communities, a component of the Atlantic Forest, with a distinct floristic and phytophysiology located on plains of Quaternary origin (Scarano, 2002). The major coastal portion of the *restinga* has pioneer vegetation on sand banks, and is highly influenced by the topography, salinity, water shortages, incidence of winds and acidic nutrient-poor soils (Bigarella, 2001; Boeger & Gluzezak, 2006). The halophyte plants, called psammophiles, play a key role in the stabilization of sand and natural

drainage of this environment (Cordazzo, Paiva, & Seeliger, 2006).

A greater diversity of gall-inducing insects is expected to occur in hygrothermally stressed environments (Fernandes & Price, 1988), such as that of the dunes of the *restinga*. Galls are plant structures that protect and nurture the larvae of the gall - inducing insect (Abrahamson & Weis, 1987; Fernandes & Price, 1991; Fernandes & Price, 1992; Raman, Schaefer, & Withers, 2005; Shorthouse, Wool, & Raman, 2005) which consist of a wide and

taxonomically unknown fauna of galling herbivores in species-specific interactions, resulting in closely related morphotypes (Isaias, Carneiro, Oliveira, & Santos, 2013; Isaias, Carneiro, Santos, & Oliveira, 2014). These morphotypes are representative of the diversity of the inducing insects (Floate, Fernandes, & Wilson, 1996; Carneiro et al., 2009), which should also be associated with a diversity of insects at other tropic levels (Dreger-Jauffret & Shorthouse, 1992; Stone & Schonrogge, 2003). Galling insects-host plants relationships are generally species-specific, nevertheless, some taxa are capable of hosting three or more gall morphotypes, which indicated their capability of reacting to the stimuli of more than one inducer. These host plants are named “super-hosts”, and contribute to the increasing of the diversity of gall - inducing insects in a given area (Araújo, Scareli-Santos, Guilherme, & Cuevas-Reyes, 2013).

There is an estimated 21 000-211 000 gall-inducing species of insects (Espírito-Santo & Fernandes, 2007), in addition to an extensive associated guild of parasitoids, inquilines, predators and successors (Maia, 2001). The diversity of galls in the *restingas* has been mainly inventoried in Rio de Janeiro, São Paulo, and Espírito Santo states (Maia, 2001; Oliveira & Maia, 2005; Maia, Magenta, & Martins, 2008; Bregonci, Polycarpo, & Maia, 2010; Maia, 2013). In contrast, the literature on galls and their inducers from the coastal regions of Southern Brazil is restricted to a single inventory in Rio Grande do Sul state (Mendonça Jr., Piccardi, Janhke, & Dalbem, 2010).

As far as we are aware, the current inventory represents the first systematic effort to sample galls on the *restingas* of Santa Catarina state, focusing specifically on the vegetation of the dunes. As Formiga, Silveira, Fernandes and Isaias (2014) proposed, we use the widely accepted concept of gall morphotypes, for it has been widely used in inventories of gall diversity and richness in the Neotropics. Also, each pair of host plant-gall inducer is referred to as a morphospecies, similar to Portugal-Santana and Isaias (2014).

This study presents the inventory of the galls, and their morphology, focusing on future physiological and ecological researches on the plant-insect interactions at the dunes of the Acaraí State Park (ASP) in São Francisco do Sul municipality. The gall morphotypes are herein used to estimate the richness and diversity of galling herbivores, as proposed by Carneiro et al. (2009). Based on Fernandes and Price (1988), these diversity and richness should be higher in xeric environments, as the dunes of the ASP. Our objective is to perform the inventory of the gall morphotypes on the dunes of the ASP, and discuss the data together with the patterns of distribution and adaptive convergences of the galls to the peculiar environment on host species and morphotypes basis.

MATERIAL AND METHODS

The study area comprises a remnant area of *restinga* located in the municipality of São Francisco do Sul, in the coastal plain of Santa Catarina state, Brazil (48°33' W - 26°17' S; Fig. 1). As an area of high priority for biodiversity conservation, it has been recently transformed into a Conservation Unit, the Acaraí State Park (ASP). With a total area of 6 667 ha, the ASP is characterized by the presence of dunes (Fig. 2), *restinga* vegetation and lowland forests, other less repetitive formations also appear, as submontane forests, wetlands and mangroves (Fatma, 2008). The flora of the ASP is constituted of 319 species, belonging to 215 genera and 82 plant families. The most representative families in number of species are the Asteraceae (35), Fabaceae (30), Myrtaceae (20), Rubiaceae (18) and Poaceae (13) (Melo Jr., 2015). The local climate is Cfa of Köppen (subtropical climate, with hot summer), influenced by maritime humidity, with an average annual temperature of 20.3 °C, and an average rainfall of 1 874 mm/year (Knie ed., 2002). The soil is classified as quartzarenic neosol (Melo Jr., 2015). The sampling was done in the herbaceous vegetation of the dunes on April 10th, May 29th, and June 11th and 30th, 2014. The

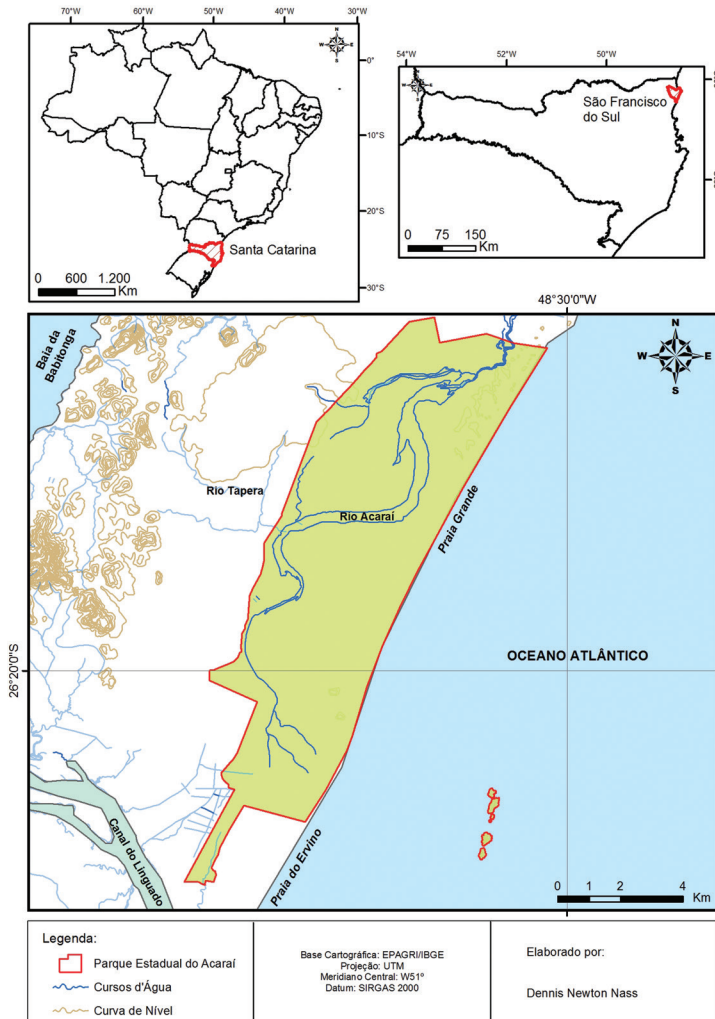


Fig. 1. Localization of Acaraí State Park (São Francisco do Sul, Brazil). Adapted from Melo Jr. 2015.

total sampling area measured 5 000 m², divided in four plots of 1250 m² (250 x 5 m), and the insect galls were investigated during six hours in each plot, in a total of 24 hours.

All plants within the sampling area were inspected for the occurrence of galls. Plant branches ($n \geq 5$) with galls were collected, and stored in labeled plastic bags. The host plants were identified to the lowest possible taxonomic level using the usual techniques for floristic studies (Fidalgo & Bonoini, 1989). Plant material was also compared with the material in MBM Herbarium and with literature.

For confirmation of species names and their respective authors, the List of Species of Brazilian Flora (2014) was used. The vouchers were deposited in the Herbarium of the Universidade de Joinville (JOI). The identification of the galling insects was based on the revision of galls from the Southeastern Brazil (Maia, 2013). The gall morphotypes were classified according to Isaias et al. (2013), and photographed under a desk magnifier (model Toyo TL1020, 5 times magnifying lenses), with the aid of a digital camera, model Samsung ES68.



Fig. 2. Herbaceous vegetation on the dunes of Acaraí State Park (São Francisco do Sul, Brazil).
Credits: João Carlos F. Melo Jr. (Personal archive).

RESULTS

The current inventory recorded 15 gall morphospecies on eight plant species, belonging to eight botanical families (Table 1; Fig. 3A, Fig. 3B, Fig. 3C, Fig. 3D, Fig. 3E, Fig. 3F, Fig. 3G, Fig. 3H, Fig. 3I, Fig. 3J, Fig. 3K, Fig. 3L, Fig. 3M, Fig. 3N, Fig. 3O, Fig. 3P and Fig. 3Q). These morphospecies were classified into six distinct morphotypes including simple isolated symmetric, globoid, lenticular, conical, rosette, marginal, and fusiform galls, and a ninth type, asymmetric, formed by the coalescence of galls. This last morphotype was exclusive of *Guapira opposita* and *Smilax campestris*, and was the most common gall morphotype, with 26.6 % of occurrence, followed by the globoid and the lenticular (20 %), and the fusiform galls (13.3 %). The less frequent was the rosette, the marginal intumescence and the conical gall morphotypes (6.7 %, each).

The marginal intumescence gall in *Scaevola plumieri* Blume (Goodeniaceae) differed from a leaf rolling due to its succulence. *Dalbergia ecastaphyllum* L. (Taub.) (Fabaceae) had a minute lenticular gall. Also, some dry leaves of *Smilax campestris* Griseb. (Smilacaceae)

were observed on the ground with opened galls on midrib veins. Most of the morphotypes occurred on leaves (53.4 %), with others on stems (26.6 %), petioles (13.3 %), and buds (6.7 %). The galls varied in color, with predominance of the green galls (46.6 %), followed by the brown and yellow (20 %), and the black and pink galls (6.7 %).

The host species diagnosed as superhosts of galling herbivores were *Varronia curassavica* Jacq. (Boraginaceae), *Smilax campestris* Griseb. (Smilacaceae) and *Guapira opposita* (Vell.) Reitz (Nyctaginaceae), with three or four gall morphotypes, each.

DISCUSSION

This is the first inventory of arthropod galls from the Acaraí State Park (ASP). It is also the first one whose sampling efforts were concentrated on the vegetation of dunes. The dunes are stressful environments, which constrains plant colonization (Cordazzo et al., 2006). Nevertheless, the botanical diversity of the dunes of ASP is notorious, with 77 plant species, 66 genera, distributed in 33 plant

TABLE 1
 Characterization of the gall morphotypes by color, sites of oviposition, and their respective host plants in the dunes of Acaará State Park, São Francisco do Sul, Brazil

Family	Plant species	Morphotype	Oviposition sites	Color	Possible gall-inducer*	Figure
Araliaceae	<i>Hydrocotyle bonariensis</i> Lam.	Globoid	Leaf lamina	Green	Unknown	3m, 3n
Asteraceae	<i>Ageratum conyzoides</i> L.	Fusifiform	Stem	Brown	Unknown	3l
Boraginaceae	<i>Larromia curassavica</i> Jacq.	Globoid	Leaf lamina	Yellow	<i>Cordiamyia globosa</i> Maia, 1996	3d
		Conical	Leaf lamina	Yellow	Cecidomyiidae	3c
Fabaceae	<i>Dalbergia ecastaphyllum</i> L. (Taub.)	Fusifiform	Petiole/Leaf lamina	Green	<i>Lopexiini</i> sp.	3a, 3b
		Lenticular	Leaf lamina	Green	Unknown	3e
Goodeniaceae	<i>Scaevola plumieri</i> Blume	Marginal intumescence	Leaf lamina	Green	Unknown	3j
Nyctaginaceae	<i>Guapira opposita</i> (Vell.) Reitz	Intralaminar lenticular	Leaf lamina	Green	<i>Bruggmannia elongata</i> Maia & Couri, 1993	3p
		Rosette	Bud	Green	<i>Pisphondylia braziliensis</i> Couri & Maia, 1992	3q
		Coalescent	Stem	Brown	<i>Prosphondylia guapirae</i> Maia & Couri, 1993	3o
Portulacaceae	<i>Portulaca oleraceae</i> L.	Globoid	Leaf lamina	Yellow	Unknown	3k
Smilacaceae	<i>Smilax campestris</i> Griseb.	Lenticular	Leaf lamina	Black	Cecidomyiidae	3h
		Coalescent	Petiole/Leaf lamina	Pink	Unknown	3i
		Coalescent	Stem	Brown/Grey	Unknown	3g
		Coalescent	Stem	Green	Unknown	3f

*Based on Maia (2013).

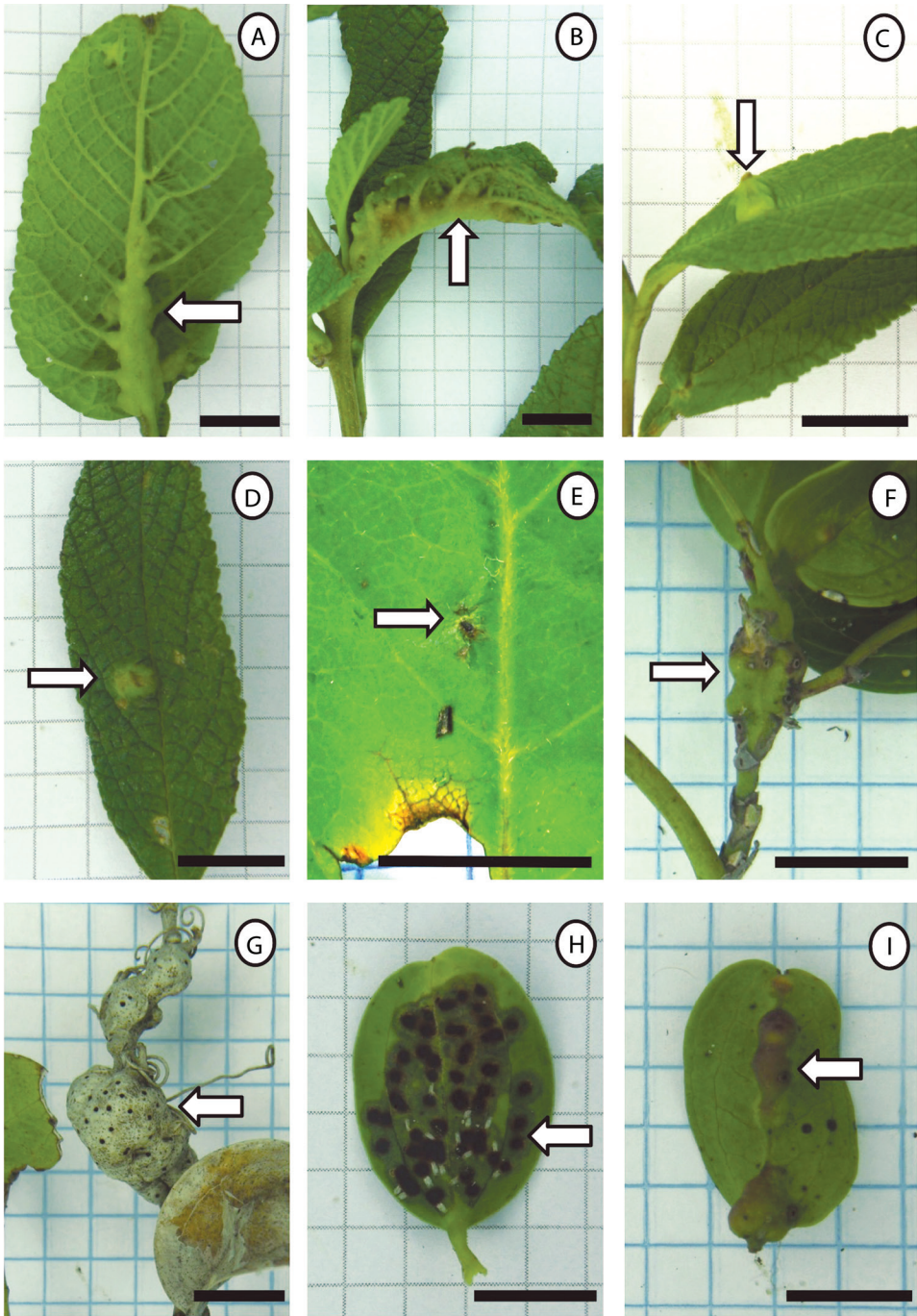


Fig. 3 (A-I). Galls of the dunes of Acaraí State Park (São Francisco do Sul, Brazil). Galls indicated by arrows. Scale bar = 1 cm. A-D) Galls on *Varronia curassavica* (Boraginaceae). (A-B) Fusiform galls on the petiole and mid vein. (C) Conical gall. (D) Globose leaf gall. E) Lenticular open galls on *Dalbergia ecastaphyllum* (Fabaceae). F-I) Galls on *Smilax campestris* (Smilacaceae). F-G) Coalescent stem gall. H) Black lenticular gall with larvae on the opening of the scape channel. I) Pinkish coalescent leaf gall.

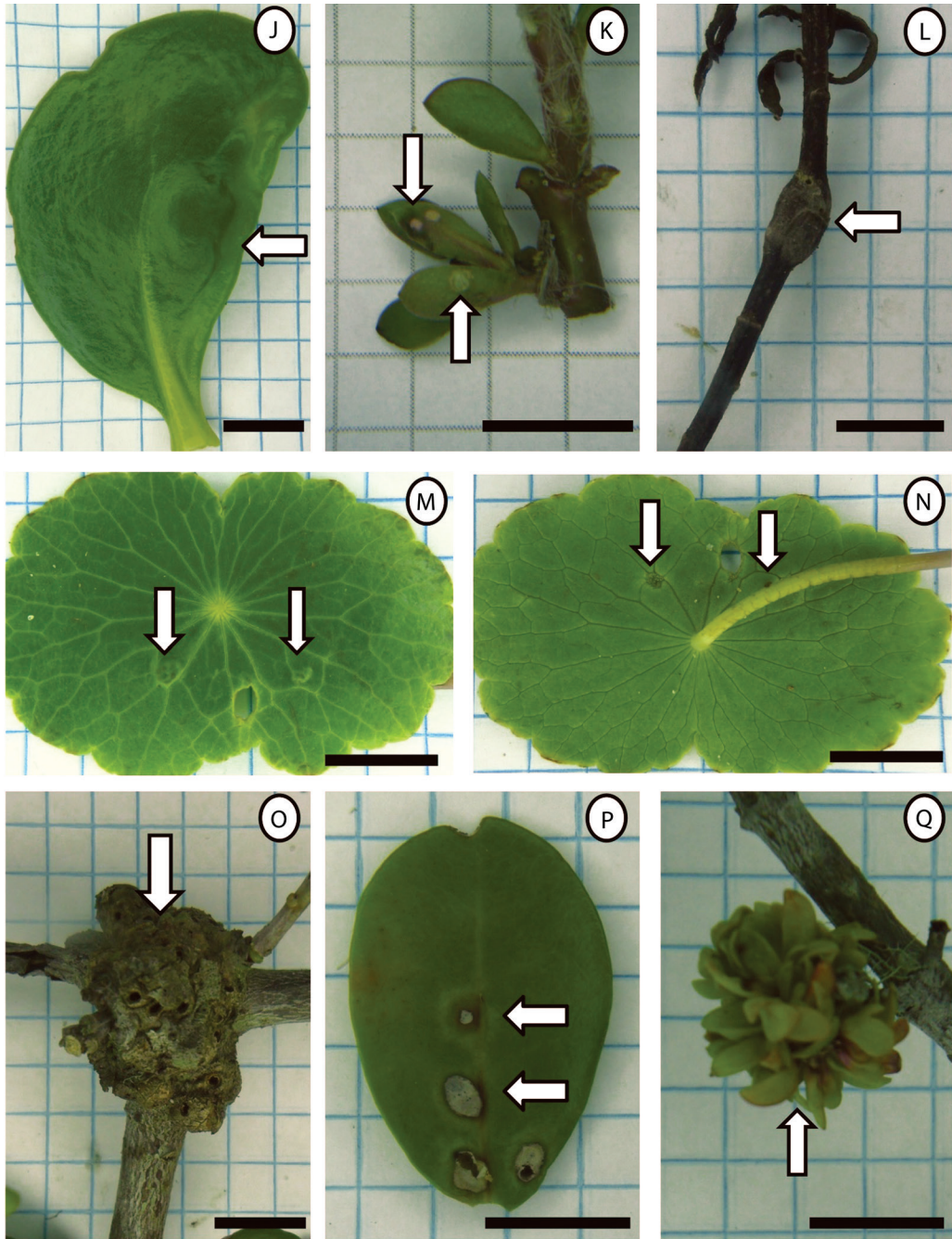


Fig. 3 (J-Q). Galls of the dunes of the Acaraí State Park (São Francisco do Sul, Brazil). Galls indicated by arrows. Scale bar = 1 cm. J) Marginal leaf intumescence on *Scaevola plumieri* (Goodeniaceae). K) Globoid leaf gall on *Portulaca oleraceae* (Portulacaceae). L) Fusiform stem gall on *Ageratum conyzoides* (Asteraceae). M-N) Globoid galls. View from the adaxial (M) and the abaxial surface (N) on *Hydrocotyle bonariensis* (Apiaceae). O-Q) Galls on *Guapira opposita* (Nyctaginaceae). (O) Coalescent stem gall. (P) Intralaminar lenticular gall. (Q) Rosette gall.

families (Melo Jr., 2015). The low number of interactions inventoried in the dunes (15 morphotypes in 8 plant species) cannot be related either to the low diversity of potential host plants, as proposed by Araújo (2011), or by the water stress, as predicted by Fernandes and Price (1992) for an increment on the diversity of galling herbivores on xeric habitats.

Considering the diversity of morphospecies as indicative of the insects's diversity (Floate et al., 1996; Carneiro et al., 2009), the highest the plant diversity, the highest should the galling herbivores distribution be, as proposed by Mendonça Jr. (2007). This author reported the Asteraceae and Myrtaceae as the host plant families with the highest diversity of galls in the *restingas* of Rio Grande do Sul. Unexpectedly, even though at the herbaceous vegetation of the *restinga* of the ASP, the Asteraceae was the most diverse plant family, with 13 of the 77 described species (Melo Jr., 2015), only one species of Asteraceae hosted galls at the ASP.

The presence of important superhosts, such as the *G. opposita*, *V. curassavica* and *Smilax campestris* influenced on the diversity of galling herbivores in the ASP, for these plants hosted almost 70 % of the sampled morphotypes. *Guapira opposita* is a superhost of galling herbivores, which had already appeared in inventories of the *restingas* in the Southeastern region of Brazil, with up to ten different morphotypes (Maia, 2001; Maia et al., 2008; Maia & Oliveira, 2010; Maia, 2013). These plant species hosts a galling Diptera: Cecidomyiidae, one of the most specialized group of galling herbivores (Maia et al., 2008; Maia, 2013). This plant species is also an important structuring species of the post-dune formations (shrub *restinga*), occurring less frequently in the herbaceous dunes (Melo Jr., 2015). In the dunes of the ASP, *G. opposita* hosts three gall morphotypes, corroborating its superhost feature. Current results reinforce the argument that the diversity of galls is related to the presence of superhosts in a given area (Mendonça Jr., 2007). In the dune vegetation, the superhost plants constitute just 4 % of the vegetation,

with inconspicuous phytosociological status (Melo Jr., 2015). The richness of the galling herbivores in the dunes seems to be closely related to the presence of the superhosts, and less to the environmental stresses. Anyhow, local diversity is in accordance to the expected for Neotropical systems (Araújo et al., 2013), with leaves being the preferential site of oviposition, for instance.

In the dunes of ASP, the preferential sites of oviposition is corroborated, with leaves hosting 66.7 % of the recorded morphotypes, both in the petioles and in the leaf lamina. As the sites of the highest photosynthetic rates (Evert, 2013), the leaves have an optimum source of nutrients. Among the leaf gall morphotypes, the lenticular and the globoid are the most abundant. The globoid is, indeed, one of the most common gall morphotype in Brazilian flora, quoting for about 27 % of the total galls listed by Isaias et al. (2014). Nevertheless, the lenticular morphotype quotes for about 2 % of the galls recorded in the inventories checked by Isaias et al. (2013; 2014). In the ASP, together with the marginal intumescence and the conical morphotypes, the lenticular and globoid galls depict for the high morphogenetic potential of the host plants to respond to distinct galling stimuli. This capacity is neither linked to the host plant species nor to the environmental stresses; for these four geometrical final shapes also common on other host species were inventoried in other Brazilian biomes (i.e. Isaias et al., 2013).

The stem galls have a less variety of shapes, which demonstrated the less plastic potential of this host organ (Formiga et al., 2014) to alter its morphogenesis under external stimuli, such as that of the galling herbivores. The fusiform morphotype develops along the longest axis of the host stems with the increment in volume attributed to cell hypertrophy and tissue hyperplasia, as described by Ferreira and Isaias (2013) for stem galls on *Marcetia taxifolia* (Melastomataceae). The coalescent galls constitute more than 25 % of the total gall morphotypes of the ASP. This relative high percentage of occurrence is a peculiarity of the

galls on the vegetation of the ASP as well as in the checklist of Brazilian gall morphotypes (Isaias et al., 2013). The oviposition in near sites leading to the fusion of plant tissues does not appear as a main strategy of galling herbivores. Also, this gall shape had been referred as amorphous galls, and its coalescent nature was firstly reported by Isaias et al. (2013) for less than 0.5 % of galls documented in the inventories. Alternatively, such confronting data may be result of underestimating field sampling or lack of standardization of nomenclature (i.e. Isaias et al., 2014).

The midrib gall on *Smilax campestris* seems to affect the stomatal conductance on its host plants, for dry leaves with galls were observed on the ground. The leaf falling may be consequence of a wound to the major vascular bundles, which should prejudice the hydraulic conductivity, affecting the stomatal conductance, resulting in precocious death of the leaves. This supposition is based on Sack, Dietrich, Streeter, Sánchez-Gómez and Holbrook (2008), who reported the loss of photosynthetic productivity, chlorophyll *a* and *b* contents, and stomatal conductance after the damage to the main vascular bundle. Also, galled portions of live branches, still attached to the host plants, had senescence features. When compared to similar stem galls on the same host plant, the galls had a higher proportion of survivorship with no indicatives of early senescence. In most of the host plants-galling herbivores systems, the life cycles are not synchronous, with the host leaves, living longer after gall eclosion, as reported for *Psidium myrtoides*-*Nothotrioza myrtoidis* (Carneiro, Oliveira, & Isaias, 2014), for instance. However, some cases of synchrony should also occur as reported for *Rollinia laurifolia*-*Pseudotectococcus rollinae* (Gonçalves, Isaias, Vale, & Fernandes, 2005; Gonçalves, Moreira, & Isaias, 2009), for *Pseudobombax gradiflorum*-*Eriogalococcus isaias* (Magalhães, Oliveira, & Isaias, 2014). In cases of the host stems, when the galls do not affect the apical meristem, shoot axis may keep developing after gall senescence.

Taking for granted that the morphological aspects of the galls together with their species-specific association with their host plants are indicative of the taxonomical uniqueness of each gall morphotype, the inventory of galls of the ASP indicated that the presence of superhost plants is the most important factor affecting the relative richness of galling herbivores in the dunes, similarly to the observation for neotropical savannas (Araújo et al., 2013). The predominance of the globoid and fusiform galls is similar to the inventories in other Brazilian ecosystems, such as the *restingas* (Maia & Oliveira, 2010; Maia & Souza, 2013; Rodrigues, Maia, & Couri, 2014), the Cerrado *strictu sensu*, and the rupestrian fields (Maia & Fernandes, 2004; Carneiro et al., 2009; Malves & Frieiro-Costa, 2012), the Amazon forest (Maia, 2011), the rain forest (Santos, Almeida-Cortez, & Fernandes, 2011a; Santos, Almeida-Cortez, & Fernandes, 2012), and the caatinga (Santos, Almeida-Cortez, & Fernandes, 2011b), which demonstrates an adaptive convergence induced by the galling herbivores over the morphogenetic potential of distinct host plants. This first inventory on the vegetation of dunes indicates the neutral influence of this environment either on host species or generated morphotypes basis. An alternative interpretation deals with a convergent ecological strategy of the host plants in the peculiar environment of the dunes. The lack of nutritional resources for the plants should be restrictive for the galling herbivores to establish in plant tissues.

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RESUMEN

Cuestionando la hipótesis de estrés ambiental para la diversidad de agallas en la vegetación restinga de las dunas. La Costa Atlántica Restinga es un mosaico de comunidades de plantas con una florística distinta y

fitofisionomía, expuestas al estrés lumínico, térmico y salino. Las plantas de la *restinga* deben tener características especiales comúnmente asociadas con ambientes xerófilos, y se espera que alberguen una gran diversidad de herbívoros de agallas. Estudiamos morfotipos de agallas, y registramos la diversidad de agallas en las plantas que crecen en las dunas de arena en un área remanente de *restinga* (State Park Acarai) en São Francisco do Sul, estado de Santa Catarina, Brasil. El muestreo se realizó en cuatro parcelas (250 x 5 m), lo que constituye una superficie total de 5 000 m², durante abril, mayo y junio. Las ramas de la planta (n ≥ 5) con agallas se muestrearon, identificaron y las agallas se fotografiaron. Las agallas se clasificaron en ocho morfotipos, asociados a ocho plantas hospederas que constituyen 15 sistemas planta hospera-herbívoro de agallas. La identificación de los inductores de agallas se basó en la literatura y en la característica específica de la especie de este tipo de interacción planta-inductor de agallas. Hubo un predominio de agallas en las hojas, de color verde. Los morfotipos más comunes fueron: globoides, lenticular, cónico, roseta, marginal y fusiforme, de manera similar a los inventarios realizados en otros biomas brasileños. A pesar de las presiones ambientales, las características xerófitas de las dunas de la ASP, y la alta diversidad de plantas locales, la diversidad de herbívoros de agallas era baja. *Varronia curassavica* (Boraginaceae), *Smilax campestris* (Smilacaceae) y *Guapira opposita* (Nyctaginaceae) fueron super-hospederas de herbívoros de agallas en las dunas, con alrededor del 70 % del total de parásitos asociados. El efecto del ambiente parece ser neutral, ya sea para las plantas hospederas o para la generación de morfotipos de agallas. Por otra parte, los recursos nutricionales escasos podrían ser restrictivos para el establecimiento de los herbívoros parasíticos dentro de los tejidos vegetales.

Palabras clave: dunas, estrés ambiental, interacción insecto-planta, *restingas*, súper - hospedero.

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