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ECOLOGY

Positive relationship between soil fertility, plant diversity, and gall richness

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ABSTRACT. The complexity of nutrient distribution patterns in soils is a determinant environmental component of the structure of plant communities. Numerous insect species that interact with plants are associated with these communities, and some of these interactions result in the formation of unusual structures called galls. In this study, we investigated the relationship of galls, soil fertility and plant communities in three vegetation types, herbaceous *restinga* (HR), shrub *restinga* (SR) and shrub-tree *restinga* (STR), in an area of *restinga* in southern Brazil. We identified 217 species belonging to 159 genera and 82 families. The plant diversity recorded in the STR was 42.8% higher than the diversity in the other vegetation types. Gall richness increased significantly with increased plant richness. The edaphic gradient was correlated with the floristic diversity in the vegetation types. Our data suggest that an increment in soil fertility (organic matter and litter thickness), associated with climatic conditions, should increase the number of plants that can potentially host galls and, consequently, the richness of galling insects. Gall richness may also be influenced by a higher occurrence of woody plants, due to an increase in leaf surface area available in the tree canopy, especially in STR.

Keywords: environmental filter; herbivory; plant-insect interaction; sandbank; specialist herbivore.

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Introduction

Environmental conditions vary spatially and exhibit complex patterns in nature that influence plant establishment and development. Among these conditions, soil fertility is considered one of the most important for vegetation (Rossatto, Hoffmann, & Franco, 2009). Nutrient supply in soil proportionally increases the diversity of plant species in a given ecosystem and influences the structural complexity of the communities (Melo Júnior & Boeger, 2015). Fertile soils favor the allocation of nutrients by plants, which results in higher amounts of leaf nitrogen, an essential resource for herbivorous species (White, 1984). Foliar herbivory is a critical ecological interaction in tropical environments due to the high diversity of herbivorous insects (Coley & Barone, 1996).

Among the families with herbivorous insects, Cecidomyiidae (Diptera) is the world's most diverse group with galling herbivores (Espírito-Santo & Fernandes, 2007). The family has 6,203 described species in 736 genera (Gagné & Jaschhof, 2017) and a global distribution. Moreover, other insect groups, such as Coleoptera, Hemiptera, Hymenoptera, Lepidoptera and Thysanoptera, have several families with gall-inducer species (Price, 2005). There are approximately 21,000 – 211,000 gall-inducing species of insects (Espírito-Santo & Fernandes, 2007), in addition to an extensively associated guild of parasitoids, inquilines, predators, and successors (Maia, 2001).

Plant galls are structures that may form in any host-plant organ in response to the activity of a parasite (Isaias, Carneiro, Oliveira, & Santos, 2013) that is capable of inducing the dedifferentiation of specialized plant tissues (Oliveira & Isaias, 2010), mainly by hyperplasia and/or cell hypertrophy (Mani, 1964). Environmental restrictions, such as water and light stress, besides predation, competition and parasitoidism, have probably driven the evolution of galling insects (Fernandes & Price, 1992). The dedifferentiated tissues altogether constitute the galls, which are abnormal structures that guarantee nutrition and a safe site for the development of galling insects and their offspring (Shorthouse, Wool, & Raman, 2005). The interaction between a host plant and the gall inducer usually ends up in a gall morphotype with a peculiar shape, size, color and indumentum (Isaias et al., 2013), which reflects the extended phenotype of the gall-inducing species (Stone & Schönrogge 2003). Galls are believed to be intimate representations of the diversity of galling species (Carneiro, Branco, Braga, Almada, Costa, Maia, & Fernandes, 2009).

However, studies that establish patterns of insect-plant interaction in response to soil nutrient dynamics are scarce. Some environments, under limiting soil fertility conditions, have a greater diversity of galling insects (Cuevas-Reyes, Siebe, Martínez-Ramos, & Oyama, 2003, Cuevas-Reyes, Quesada, Siebe, & Oyama, 2004, Cuevas-Reyes, Oliveira-Ker, Fernandes, & Bustamante, 2011) and some studies have shown that the greater diversity of galls is directly associated with the greater diversity of plant communities (Mendonça Júnior, Piccardi, Jahnke, & Dalbem, 2010, Araújo, Scareli-Santos, Guilherme, & Cuevas-Reyes, 2013, Rodrigues, Maia, & Couri, 2014, Arriola, Melo Júnior, & Isaias, 2015, Arriola & Melo Júnior, 2016). In another case, soil fertility was associated with gall diversity; however, through its direct effects on the structure and composition of a super-host taxon (Blanche & Westoby, 1995).

In xeric environments with low soil fertility, greater richness of galling insects is related to longer leaf longevity and greater investment in leaf chemical defenses that protect the galling insects against parasitoids and fungi (Cuevas-Reyes et al., 2004, 2011). However, the production of defenses by plants represents a high cost and stems from the quality of the light and soil in the environment (Gianoli, Molina-Montenegro, & Becerra, 2007; McGuire & Agrawal, 2005).

In general, studies of the effects of soil fertility on the richness of galling insects are based only on P and N concentrations as indicators of soil nutrient quality (Cuevas-Reyes et al. 2011, 2014). Nevertheless, soil fertility is also related to other essential soil attributes, such as cation exchange capacity and organic matter content (Melo Júnior & Boeger, 2015).

Based on these ideas, our study aims to evaluate the relationship of soil x plant (richness and structure) x diversity of galls in a tropical environment, in southern Brazil, using an edaphic fertility gradient as a model. Our questions are: i) is there a pattern of gall richness as a function of soil fertility?; and ii) does the variation in gall richness reflect the variation in the richness and structure of the plant communities as a function of soil fertility?

Material and methods

Study area

The study was conducted in *restinga* vegetation within the 6,667 ha Acaraí State Park (ASP) in the municipality of São Francisco do Sul, on the northeastern coast of the state of Santa Catarina, in southern Brazil (26° 17 'S and 48° 33' W, Figure 1).

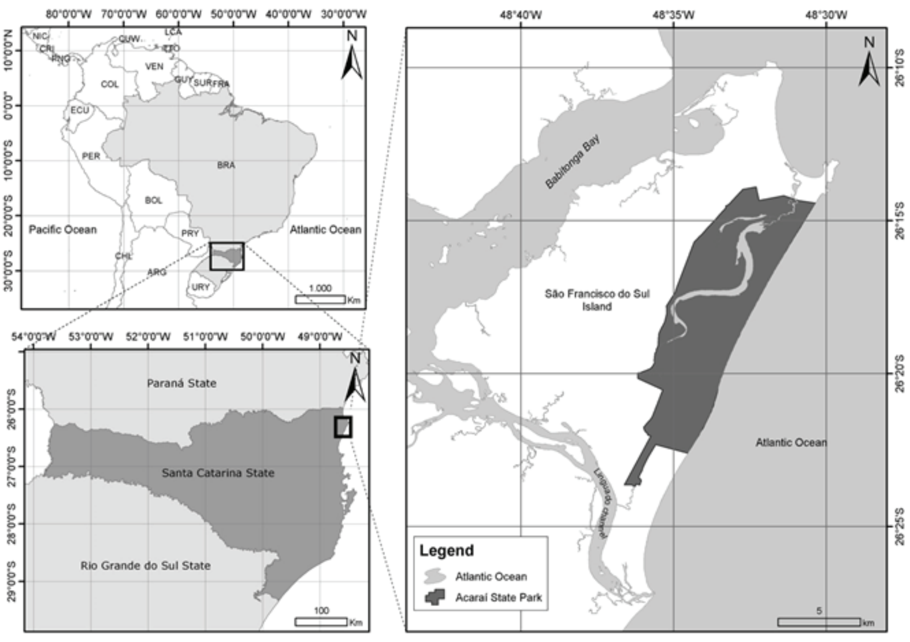


Figure 1. Location of the study area on São Francisco do Sul Island.

The climate is classified as mesothermic and Cfa, based Köppen's classification (McKnight & Hess, 2011), and strongly influenced by maritime moisture, with hot summers and no defined dry season. Average annual rainfall is 2,372 mm and the average annual temperature is 21.3°C (Empresa de Pesquisa Agropecuária e Extensão Rural [Epagri], 2014). The geology of the study area is formed by marine deposits covered by eolic deposits that constitute the Holocene barrier known as São Francisco do Sul Island (Possamai, Vieira, Oliveira, & Horn-Filho, 2010).

This area has different vegetation types and soils, such as herbaceous *restinga* (HR) with quartzipsamment soil of eolic and marine origin, and shrub *restinga* (SR) and shrub-tree *restinga* (STR) with ferrihumiluvic spodosol soil of eolic origin (Empresa de Pesquisa Agropecuária e Extensão Rural [Epagri], 2002).

Soil fertility

Soil characterization included evaluating the nutritional status and salinity based on five homogenized samples from each physiognomy, collected 15 cm deep, according to the methodology recommended by Santos et al. (2013). Soil chemical analyses for pH, phosphorus (P), potassium (K), sodium (Na - salinity), magnesium (Mg), potential acidity (H + Al, H^+ and Al^{3+} ions), sum of bases (SB), cation exchange capacity (CTC), base saturation (V), and organic matter (OM) were performed by the *Instituto Agronômico de Campinas* / SP-Brazil. Soil water availability in each vegetation type was estimated based on the gravimetric moisture content of 60 soil samples (Santos et al., 2013). Litter thickness was evaluated in the field using a centimeter ruler; 25 measurements were made in each vegetation type.

Plant assemblage inventory

Plant species richness was verified by wide patrolling (Ratter, Bridgewater, & Ribeiro, 2003). The botanical material, sampled over two years, was herborized according IBGE (2012) and classified based on the APG IV system (Chase et al., 2016). The specimens were deposited in the JOI herbarium (Joinville, SC) and the associated collector numbers are listed in the text. Species names and their authors were confirmed using the Species List of Brazil´s Flora (Reflora, 2016). The Shannon (H ') diversity index, based on the natural logarithm, and Jaccard's similarity (Magurran, 2013) index were calculated for each of the sandbank formations studied, using the software Past (Hammer, Harper, & Ryan, 2001).

Gall inventory

The samples were collected in four plots of 1,250 m² (250 x 5 m), in each vegetation type, totaling a sample area of 15,000 m². All plants within the sampling area were inspected for the occurrence of galls. The plants of each plot were inspected for 8 hours, totaling 96 sample hours (Maia, Magenta, & Martins, 2008). Plant branches ($n \geqslant 5$) with galls were collected and stored in plastic bags. Host plants were identified during the plant inventory. The galls were described according to the standardization of nomenclature for neotropical galls proposed by Isaias et al. (2013) and photographed with a Samsung ES68 digital camera. Identification of the gallers was based on the review of *restinga* galls of the Southeast Region of Brazil (Maia & Souza, 2013) and on the world catalog of Cecidomyiidae (Diptera) (Gagné & Jaschhof, 2017).

Data Analysis

The Mantel test (Clarke & Ainsworth, 1993) was used to explain the floristic diversity among vegetation types as a function of edaphic factors, using matrices of species abundance and soil variables. A principal component analysis (PCA) (Clarke & Warwick, 1994) was performed to verify the relationships between biological variables and soil fertility trait parameters for each vegetation type. The Chi-square test (Gotelli & Ellison, 2004) was carried out to test differences in the significances in plant richness, plants with galls, and the presence and absence of galls in the vegetation types.

Results

Soil fertility

The chemical analysis of *restinga* soils showed that the soil acidity increased gradually from the HR to the STR. The K and Na values showed little variation. Phosphorus, Ca and Mg concentrations decreased from the HR to the STR. Soil water availability (gravimetric moisture), litter thickness, and OM were higher in the STR and, consequently, CTC was higher in this vegetation type (Table 1).

The Mantel test ($r = 0.6$, $p < 0.001$) indicated that there is an edaphic gradient correlated with the floristic diversity of the vegetation types. The soil variables that explained the observed variations were OM, potential acidity (H + Al), and litter thickness. The first two components of the PCA explained 100% of the total variance of the analyzed data and allowed the separation of the vegetation types (Table 1, Figure 2). PC1 (95.2 %) represented the highest values of gravimetric moisture, litter, K and H + Al for the STR and the highest values of salinity, Mg and V for the SR and HR.

Table 1. Chemical characteristics (n = 3), salt content (n = 3), litter accumulation (n = 25) and gravimetric moisture (n = 15) of the soil types, and correlation among soil variables represented by components 1 and 2 obtained from the PCA, from *restinga* in Acaraí State Park (ASP), São Francisco do Sul, SC, Brazil. Legend: Herb *restinga* (HR), Shrub *restinga* (SR), Shrub-tree *restinga* (STR), PC1 (Principal Component 1), PC2 (Principal Component 2), phosphorus (P), potassium (K), sodium (Na), magnesium (Mg), potential acidity (H + Al), sum of bases (SB), ion exchange capacity (CTC), base saturation (V), and organic matter (MO).

Variables	Soil class (Vegetation types)			PCA (*Eigenvectors*)	
	Quartzipsamments soil	ferrihumiluvic spodosol soil	ferrihumiluvic spodosol soil	PC1	PC2
	(HR)	(SR)	(STR)		
pH	5.47	4.73	3.53	0.053	0.004
P (mg dm^{-3})	2.67	2.00	1.00	0.045	0.008
K (mmolc dm^{-3})	1.13	1.33	1.30	- 0.004	- 0.019
Na (mmolc dm^{-3})	0.93	1.10	0.83	0.004	- 0.028
Ca (mmolc dm^{-3})	9.33	10.33	5.67	0.110	- 0.318
Mg (mmolc dm^{-3})	2.67	2.33	1.00	0.047	- 0.037
H + Al (mmolc dm^{-3})	9.00	15.00	21.67	- 0.338	- 0.184
SB (mmolc dm^{-3})	14.07	15.10	8.80	0.157	- 0.403
CEC (mmolc dm^{-3})	23.07	30.10	30.47	- 0.181	- 0.587
BS (%)	59.67	50.00	29.00	0.840	- 0.214
OM (g dm^{-3})	7.33	14.00	14.67	- 0.181	- 0.541
Litter (cm)	0.1	2.4	3.7	- 0.093	- 0.133
Soil water availability (%)	4.9	8.3	14.1	- 0.250	- 0.004

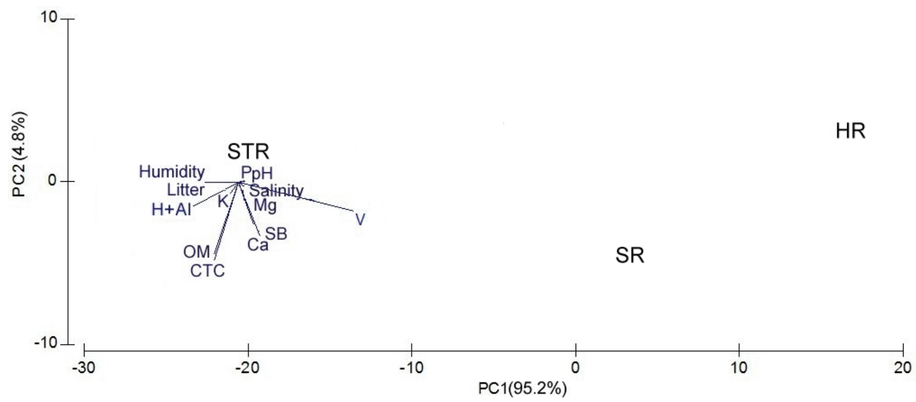


Figure 2. Principal component analysis of soil variables from the vegetation types. Legend: Herb *restinga* (HR), Shrub *restinga* (SR), Shrub-tree *restinga* (STR), PC1 (Principal Component 1), PC2 (Principal Component 2), phosphorus (P), potassium (K), salinity (sodium [Na]), magnesium (Mg), potential acidity (HAl), sum of bases (SB), Cation exchange capacity (CEC), base saturation (BS), and organic matter (OM).

Plant assemblage and gall inventory

In the three vegetation types, we identified 217 species belonging to 159 genera and 82 families (Table 2, Figure 3). The most representative families, in number of species, were Asteraceae (35), Fabaceae (30), Myrtaceae (20), Rubiaceae (18), and Poaceae (13). Of this total, 141 species occurred exclusively in one vegetation type: 63 species in HR, 32 in SR and 46 in STR. The other species were shared between two or more vegetation types. Greater co-occurrence of species was recorded between the SR and STR, with 15 shared species. Only three species occurred in all vegetation types. Plant diversity in the STR was 42.8% higher than the diversity in the other vegetation types. The HR and SR presented similar H' values while the STR had a lower value for this index.

A total of 86 gall morphotypes were recorded on 43 plant species from 27 botanical families in the three vegetation types (Tables 2 and 3, Figure 3). The number of gall morphotypes increased from HR to STR: HR had 14 gall morphotypes, SR had 30 and STR had 56. Of these, only two gall morphotypes occurred in all three vegetation types. Some gall morphotypes were common between vegetation types: HR and SR (5) and HR and STR (7) (4).

Table 2. Comparison of different soil types related to plant species richness, more representative families and Shannon diversity index (H ') of the vegetation types in Acaraí State Park (ASP), São Francisco do Sul, SC, Brazil.

Vegetation	Soil class	FN	GN	SN	H'P	GMN	HP	SHP	H'G
HR	quartzipsamments soil	31	65	77	4.34	14	8	3	2.64
SR	ferrihumiluvic spodosol soil	32	62	76	4.33	30	16	3	3.40
STR	ferrihumiluvic spodosol soil	47	81	110	4.77	56	31	9	4.02

Legend: Herb *restinga* (HR), Shrub *restinga* (SR), Shrub-tree *restinga* (STR), family number (FN), genus number (GN), species number (SN), Shannon diversity index (H'P), gall morphotype number (GMN), host plant number (HP), super-host plant number (SHP), and Shannon diversity index of galls (H'G).

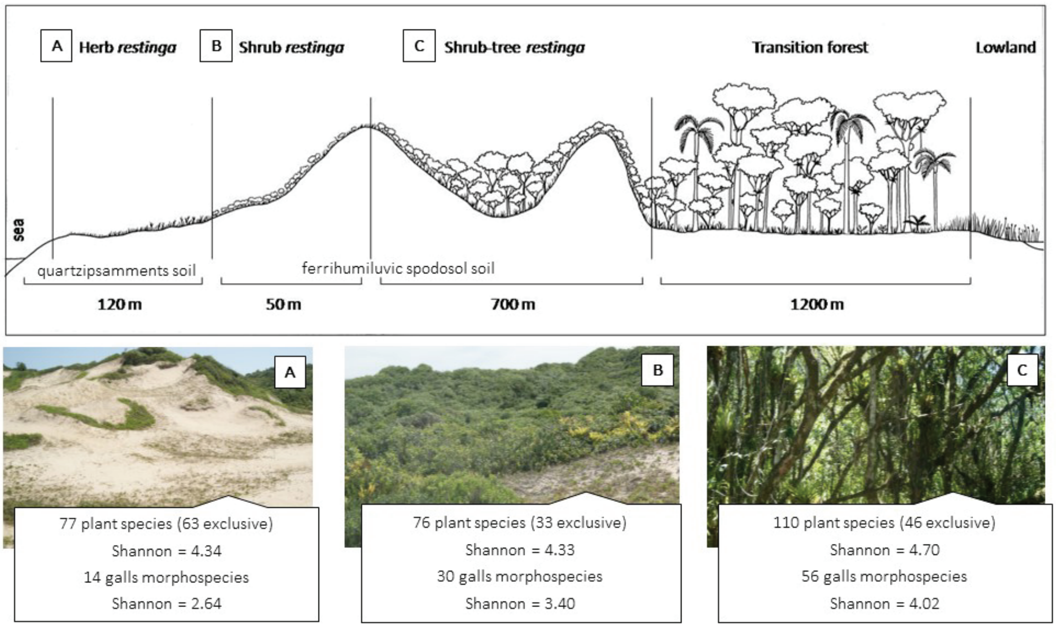


Figure 3. Vegetation types of edaphic gradient, and respective plant and gall richness values, in Acaraí State Park (ASP), São Francisco do Sul, SC, Brazil. Legend: Herb *restinga* (A), Shrub *restinga* (B), and Shrub-tree *restinga* (C).

Table 3. Gall morphotypes associated with the *restinga* flora of Acaraí State Park, São Francisco do Sul, Brazil.

Plant family/species	Collector number	Morphotype traits	Galler
Anacardiaceae			
Schinus terebinthifolius	1055	Leaf, lenticular extra laminar, green	*Calophya terebinthifolii* (Psylloidae, Hemiptera)
Annonaceae			
Guatteria australis	1156	Stem, fusiform, pubescent brown	undetermined
		Leaf, globoid, green	undetermined
		Leaf, lenticular, green	undetermined
Araceae			
Philodendron surinamense	1370	Root, fusiform, green	undetermined
		Root, fusiform, main coalescent, green	Cecidomyiidae (Diptera)
		Leaf, lenticular extra-laminar, green	undetermined
Araliaceae			
Hydrocotyle bonariensis	1011	Leaf, lenticular intra-laminar, green	undetermined
Asteraceae			
Ageratum conyzoides	1213	Stem fusiform, brown	undetermined
Baccharis longiattenuatta	1035	Stem fusiform, green	undetermined
		Leaf globoid, green	Eryophidae (Acarina)
Mikania trinervis	1243	Leaf cylindrical, green	*Liodiplosis cylindrica* (Cecidomyiidae, Diptera)
		Leaf, globoid, green	*Liodiplosis* sp. (Cecidomyiidae, Diptera)
		Stem globoid, main coalescent, green/red	*Mikaniadiplosis* sp. (Cecidomyiidae, Diptera)
Boraginaceae			
Varronia curassavica	1013	Leaf, conical, yellow	Cecidomyiidae (Diptera)
		Stem, fusiform, brown	Lepidoptera
		Flower, fusiform, green	*Asphondylia* cfr. *cordiae* (Cecidomyiidae, Diptera)
		Leaf fusiform, isolated or coalescent, green	*Lopesiini* sp. (Cecidomyiidae, Diptera)
		Leaf globoid, yellow pubescent	*Cordiamyia globosa* (Cecidomyiidae, Diptera)
		Leaf, lenticular intra laminar, yellow	undetermined

Calophyllaceae			
Calophyllum brasiliense	1072	Winding leaf, green	Cecidomyiidae (Diptera)
		Leaf, fusiform, green	*Lopesia linearis* (Cecidomyiidae, Diptera)
		Stem globoid, brown	*Lopesia caulinaris* (Cecidomyiidae, Diptera)
		Lenticular intra laminar, green	*Lopesia ellipitica* (Cecidomyiidae, Diptera)
Celastraceae			
Maytenus glazioviana	1128	Leaf, lenticular, green	*Mayteniella robusta* (Cecidomyiidae, Diptera)
Clusiaceae			
Clusia criuva	1078	Leaf, fusiform intra laminar, green	Lepidoptera
Convolvulaceae			
Jacquemontia sp.	1371	Stem fusiform, green	undetermined
Fabaceae			
Andira fraxinifolia	1126	Leaf, fusiform, pubescent green	*Lopesia* sp. (Cecidomyiidae, Diptera)
		Leaf globoid, yellow	*Asphondyliina* sp. (Cecidomyiidae, Diptera)
Dalbergia ecastaphyllum	1048	Leaf, lenticular intra laminar, green	*Lopesia sp.* (Cecidomyiidae, Diptera)
Dalbergia frutescens	1049	Leaf, nailed, pubescent green	*Lopesia grandis* (Cecidomyiidae, Diptera)
Goodeniaceae			
Scaevola plumieri	1101	Intra laminar lenticular, green	undetermined
Lauraceae			
Aiouea saligna	1253	Leaf lenticular, green	undetermined
Endlicheria paniculata	1355	Stem fusiform, isolated or coalescent, brown	undetermined
Nectandra grandiflora	1373	Leaf, globoid, pubescent red	undetermined
Nectandra membanacea	1374	Leaf, conical, pubescent green	undetermined
		Leaf, green	undetermined
		Lenticular foliar, green	undetermined
Ocotea catharinensis	1375	Leaf, globoid, red	*Neolasioptera* sp. (Cecidomyiidae, Diptera)
Ocotea pulchella	1085	Lenticular intra laminar, green	Coccidae (Hemiptera)
		Stem, rosette, green	*Clinodiplosis* sp. (Cecidomyiidae, Diptera)
Malvaceae			
Pavonia sp.	1102	Leaf, globoid, pubescent green	undetermined
Sida sp.	1068	Winding leaf, green	undetermined
		Stem globoid, brown	undetermined
Melastomataceae			
Miconia pussiliflora	1071	Stem fusiform, brown	undetermined
		Leaf fusiform, green	undetermined
Tibouchina pulchra	1027	Leaf fusiform, pubescent green	Curculionidae (Coleoptera)
		Stem globoid, main coalescent, brown	Lepidoptera
Meliaceae			
Guarea macrophylla	1255	Stem fusiform, brown	Cecidomyiidae (Diptera)
		Leaf fusiform, green	*Neolasioptera* sp. (Cecidomyiidae, Diptera)
		Leaf globoid, pubescent brown	*Sphaeromyia flava* (Cecidomyiidae, Diptera)
		Leaf lenticular, green	undetermined
Myrtaceae			
Myrcia brasiliensis	1113	Leaf globoid, main coalescent, green	undetermined
Myrcia pulchra	1060	Stem globoid, brown	undetermined
		Leaf lenticular, green	undetermined
		Leaf lenticular, pubescent yellow	undetermined
		Leaf lenticular, white	undetermined
Psidium cattleianum	1076	Leaf cylindrical, green	*Lasiopteridi* sp.
		Leaf globoid extra laminar, yellow	*Nothotrioza cattleiani* (Psylloidae, Hemiptera)
		Leaf globoid extra laminar, green	Cecidomyiidae (Diptera)
		Leaf globoid intra laminar, with apical projection, green	*Tectococcus ovatus* (Eriococcidae, Heteroptera)
		Leaf lenticular, green	Cecidomyiidae (Diptera)
		Stem, rosette, green	*Dasineura gigantea* (Cecidomyiidae, Diptera)
Myrtaceae sp.	1376	Leaf lenticular, green	undetermined
Nyctaginaceae			
Guapira opposita	1098	Stem fusiform, brown	*Proasphondylia formosa* (Cecidomyiidae, Diptera)
		Stem globoid, main coalescent, brown	*Proasphondylia guapirae* (Cecidomyiidae, Diptera)
		Leaf lenticular, green	*Bruggmannia elongata* (Cecidomyiidae, Diptera)
		Leaf lenticular, yellow	undetermined
		Stem, rosette, green	*Pisphondylia brasiliensis* (Cecidomyiidae, Diptera)
Orchidaceae			
Vanilla chamissonis	1193	Leaf globoid, green	undetermined
Pentaphylacaceae			
Ternstroemia brasiliensis	1074	Leaf lenticular, black/gray	undetermined

		Stem, rosette, green/purple	undetermined
Piperaceae			
Peperomia sp.	1044	Stem fusiform, green	undetermined
		Lenticular intra laminar, green	Cecidomyiidae (Diptera)
Piper solmsianum	1341	Leaf globoid, pubescent green	Cecidomyiidae (Diptera)
Portulacaceae			
Portulaca oleraceae	1031	Leaf globoid, yellow	Coleoptera
Rubiaceae			
Chiococca alba	1062	Leaf lenticular, green	undetermined
Psychotria carthagenensis	1136	Leaf conical, green	undetermined
Sapindaceae			
Paullinia trigonia	1266	Leaf globoid, green	Cecidomyiidae (Diptera)
Sapotaceae			
Pouteria beaurepairei	1114	Stem globoid, brown	undetermined
Smilacaceae			
Smilax campestris	1018	Leaf globoid, isolated or coalescent, green	Cecidomyiidae (Diptera)
		Stem globoid, main Coalescent, green	undetermined
		Leaf lenticular, green/black	*Smilasioptera* sp. (Cecidomyiidae, Diptera)
Solanaceae			
Solanum pseudoquina	1138	Stem globoid, brown	undetermined
		Stem globoid, coalescent, brown	undetermined
		Leaf lenticular, green	undetermined

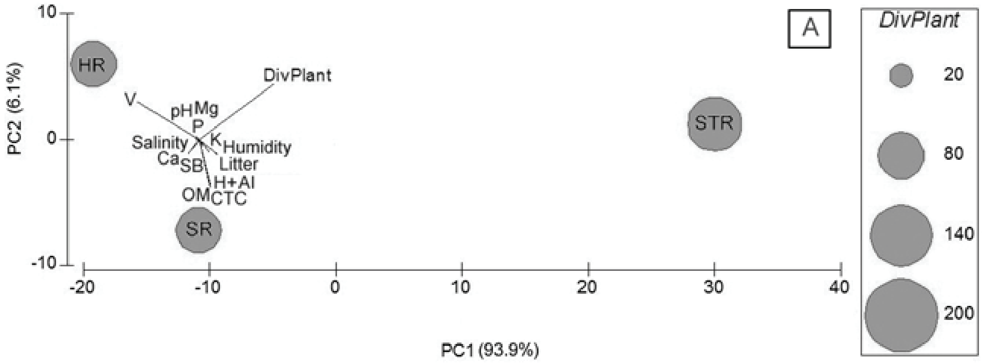
The highest number of galls occurred on Myrtaceae (12), Lauraceae (9), Asteraceae (6), and Boraginaceae (6). The number of super-host plants was similar between the HR and SR and three times greater in the STR. Seven of these species were found in all vegetation types. The H' values for the galls increased from the HR to the STR. The diversity of the number of interactions between plant species and gallers, as well as gall richness by vegetations type, increased significantly with increased plant richness ($\chi 2$ = 20.82, gl = 6, p = 0.001) and along the edaphic gradient of the studied *restinga* (Table 4).

Table 4. Contingency test between total plant richness and galls from an edaphic gradient in Acaraí State Park (ASP), São Francisco do Sul, SC, Brazil. Legend: observed frequency (expected frequency), Herb *resting* (HR), Shrub *restinga* (SR), and Shrub-tree *restinga* (STR). χ^2 = 20.82, gl = 6, p = 0.001.

	Total plant richness	Number of plants with galls	Number of plants without galls	Total gall richness
HR	77 (70.58)	8 (13.95)	69 (56.62)	14 (26.83)
SR	76 (76.46)	13 (15.11)	63 (61.34)	30 (29.07)
STR	110 (115.95)	31 (22.92)	79 (93.02)	56 (44.08)

Soil fertility and biologic relationships

PC1 explained more than 90% of the variance of the edaphic gradient among vegetation types (Figure 4A). Plant diversity, the number of plants with galls (Figure 4B) and gall richness (Figure 4C) increased from the HR to the STR and were related to the increase of soil moisture and litter thickness and the reduction of BS and soil salinity. On the other hand, the absence of galls, which increased from the STR to the HR (Figure 4D), was related to the increase in BS and salinity and the decrease in soilmoisture and litter thickness.



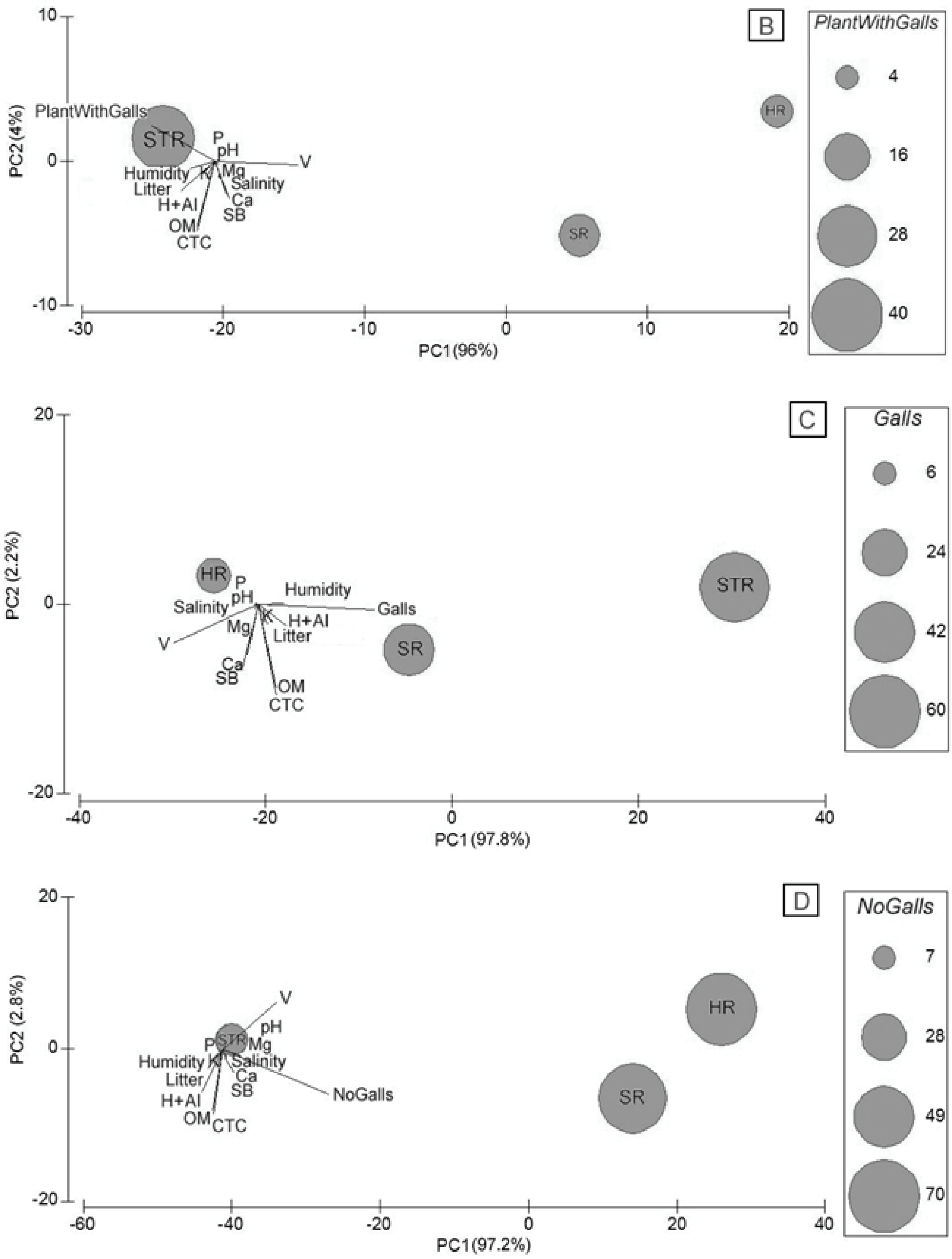


Figure 4. Principal Component Analysis of: A) soil variables of vegetation types related to plant richness (*DivPlant*) (richness values represented by circles); B) soil variables of vegetation types related to plants and galls (*PlanWithGalls*) (plants with galls represented by circles); C) soil variables of vegetation types related to gall presence (*Galls*) (gall presence values represented by circles); and D) soil variables of vegetation types related to gall absence (*No Galls*) (gall absence values represented by circles). Legend: Herb *restinga* (HR), Shrub *restinga* (SR), Shrub-tree *restinga* (STR), PC1 (Principal Component 1), PC2 (Principal Component 2), phosphorus (P), potassium (K), salinity (sodium [Na]), magnesium (Mg), potential acidity (HAl), sum of bases (SB), ion exchange capacity (CEC), base saturation (BS), and organic matter.

Discussion

Edaphic nutrition and plant assemblages

The chemical analysis showed the oligotrophic status of the soil, something very common in Brazilian *restinga* soils (Araujo & Lacerda, 1987). However, the nutritional variations in *restinga* soils seem to be sufficient to establish significant differences among vegetation types. Edaphic conditions appear to be a key factor in the increasing richness of plant species in the sea-continent direction in the studied site. The acidic soil pH in the study area can affect the establishment of plant communities (Santos-Filho, Almeida Júnior, & Zickel, 2013) and reduce soil decomposition rates. These features can explain the gradual increase of organic matter (OM) along the edaphic gradient.

In *restinga* environments, organic matter content is responsible for increasing the cation exchange capacity (CEC), which contributes to soil nutrient retention (Ruivo, Amaral, Faro, Ribeiro, Guedes, & Santos, 2005, Guedes, Barbosa, & Martins, 2006). Thus, CEC represents the nutrient release capacity, promoting the maintenance of soil fertility for an extended period (Ronquim, 2010). Environments with higher organic matter content are more prone to having woody plants, because soil fertility, associated with water availability, influences differences in species richness (Silva & Somner, 1984, Sztutman & Rodrigues, 2002, Cestaro & Soares, 2004, Almeida Júnior, Olivo, Araujo, & Zickel, 2009). Additionally, a progressive increase in litter thickness along the *restinga* gradient represents a source of organic matter that will decompose and, consequently, release nutrients into the soil. Similar results also indicate that organic matter is an important contribution in the differentiation of species composition in plant communities of *restinga* (Magnano, Martins, Schaefer, & Neri, 2010, Almeida Júnior, Santos-Filho, Araújo, & Zickel, 2011, Santos-Filho et al. 2013).

Diversity, nutrition, and galls

According to the harsh environment hypothesis (Fernandes & Price, 1988), galling species richness should be higher in dry and hygrothermically stressed environments. Consequently, high gall richness should be expected in the ASP *restinga*. In the three vegetation types studied herein, gall diversity increased from the sea toward the continent, like plant diversity and abundance. Vegetation complexity can positively influence the increment of gall richness, as reported in several Brazilian inventories (Mendonça Júnior et al., 2010, Araújo et al., 2013, Rodrigues et al., 2014, Arriola & Melo Júnior, 2016), as well as soil quality. The proposal that soil fertility influences gall diversity has been controversial. In the Lacandona tropical rainforest region (Mexico), the higher fertility of alluvial soil is inverse to the number of plants associated to galling insects as well as the range of galling insects (Cuevas-Reyes et al., 2003). This is because the P concentration decreases from the sea toward the continent, decreasing soil fertility, plant diversity, and gall richness (Blanche & Ludwig, 2001).

The low levels of P in the oligotrophic soil of the ASP seem to be compensated by litter thickness, CTC, and organic matter levels, V reduction, and soil salinity. These compensatory parameters of soil composition, associated with the stressful conditions imposed by the hygrothermic features, should favor the establishment of associated galling fauna, as proposed in the harsh environment hypothesis. Infertile soils should support scleromorphic vegetation, which tends to maintain a higher richness of associated galling organisms (Fernandes & Price, 1991). The association of low soil fertility and high gall richness is also influenced by an increment in plant diversity (Melo Júnior & Boeger 2015).

The *restinga* flora can colonize a harsh environment when soil nutrients are not a limiting factor. In this situation, the flora and, consequently, the gall richness can be more diverse. Soil properties exercise a direct effect on the occurrence of super-hosts species (Araújo et al., 2013, Arriola, Melo Júnior, Isaias, Mouga, & Costa, 2016) and an indirect effect on gall abundance (Blanche & Westoby, 1995). However, the nutrient pool can be modified by litter thickness and soil moisture; although, the effect of these soil traits was not estimated.

The edaphic conditions of the *restinga* influenced the development of xeromorphic vegetation with plant diversity increasing from the coast toward the continent. The plant diversity was highest in the STR (42.8% richer than the other vegetation types). Moreover, the number of super-host plants in the STR was threefold higher compared to the HR and SR. The positive effect of soil fertility favors plants to host galling herbivores and greater gall richness in a vegetation type with woody and large plants, such as STR.

Conclusion

Our data suggest that an increment in soil fertility, associated with climatic conditions (high temperature and humidity) of *restinga*, should increase the number of plants with the potential to host galls and, consequently, the richness of galling insects (Fernandes & Price, 1988, Blanche & Ludwig, 2001). Gall richness may also be influenced by a higher occurrence of woody plants, as reported for southeastern Brazil (Lara, Fernandes, & Gonçalves-Alvim, 2002). Greater leaf surface area available for gall induction in the tree canopy can explain the highest occurrence of galls. This scenario favors the STR for higher gall richness.

The richness of the species of gall-inducing insects in the vegetation types in the ASP *restinga* seems to be related to two main factors. First, the low soil nutrition of the ASP *restinga* has increased the sclerophylly and favored gall induction and establishment. Second, the increasing nutritional status of the soils in a sea-continent direction contributed positively to an increase in plant diversity and interactions with galling organisms, which is evidence of the interrelation between the soil-plant continuum and the observed galling insect-plant systems in this study.

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