

ECOLOGY, BEHAVIOR AND BIONOMICS

The Importance of Beta Diversity in Local Gall-Inducing Arthropod Distribution

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ABSTRACT - Many studies over the past twenty years have documented the richness of arthropod galling species around the world, and some have proposed hypotheses to explain local and global patterns of galling species richness. However, few studies have been directed toward understanding how the gall-inducing species are locally distributed. The aim of this study was to determine the distribution of gall-inducing arthropods species at Coiba National Park, a tropical habitat on the Pacific coast of Panama. Our results suggest that more gall-inducing species had an aggregated distribution, and gall-inducing arthropod diversity shows a strong beta diversity component. Geographic distance was not correlated with similarity in gall-inducing species composition between the studied sites. This fact has important implications when trying to estimate gall-inducing arthropod richness and general patterns, and could cause contradictory results for hypotheses that attempt to explain the local and global patterns of galling species richness.

KEY WORDS: Coiba Island, geographic distribution, Panama, plant community

The induction of plant gall is the result of a complex association between insects and plants (Shorthouse *et al* 2005). Galls represent a complex series of interactions between the tissues of a plant and another living organism, more frequently an insect. The understanding of these interactions involves studies in many scientific fields, from systematics to ecology, but also morphology, physiology, biological control, evolutionary biology or agricultural and forest entomology (Mani 1964, Raman *et al* 2005). Gall-inducing species are excellent models for ecological studies due to their abundance, diversity and sessile habit, which make them easier to census than free-feeding herbivores and thus allowing species diversity comparisons among different habitats (Fernandes & Price 1988).

During the past twenty years, many studies have documented galling insect lists and galling species richness around the world (see Veldtman & McGeoch 2003, Raman *et al* 2005). There are also data regarding factors that affect local and regional gall richness and thus infer global patterns in local number of insect galling species (Raman *et al* 2005). However, few studies have been directed toward understanding how the gall-inducing species are locally distributed. Understanding spatial patterns of species distribution is a crucial topic in ecology and conservation biology; for instance, when predicting species richness from local to regional scales (Gering & Crist 2002).

The main proposed hypotheses explaining factors that affect local gall-inducing species richness involve hydrothermal stress, low soil fertility, host plant richness, structural complexity of host plants, host plant families and genus size and their range of distribution (for a complete discussion of each hypothesis see Veldtman & McGeoch 2003). However, most of the above hypotheses have caused controversy because many recent studies provide evidence against a given hypothesis while others support it (Wright & Samways 1998, Blanche 2000, Yukawa *et al* 2001, Veldtman & McGeoch 2003, Hanson & Gómez-Laurito 2005, Nieves-Aldrey *et al* 2008).

An important problem when comparing studies of gall-inducing arthropods richness is the use of different sampling methods (Dalbem & Mendonça 2006). But, independent of sampling methods, one result that remains consistent across all studies is that local distribution of gall-inducing arthropods shows low similarity between the sampled sites (see Blanche & Westoby 1996, Gonçalves-Alvin & Fernandes 2001, Cuevas-Reyes *et al* 2003, Medianero *et al* 2003). This low similarity between the sampled sites has important implications when trying to estimate gall-inducing arthropod richness and general patterns, and could cause contradictory results for hypotheses that attempt to explain the local and global patterns of galling species richness. Low similarity between sampled sites suggests that Beta

diversity (the variation in species composition among sites in a geographic region) might have an important role in the regional diversity of species pools from large geographic areas (Gamma diversity).

Beta diversity is an important property of ecosystems because it provides information about the partitioning of habitats by species and constitutes an empirical and theoretical link between Alpha (the local diversity of a community) and Gamma diversity (Cornell & Lawton 1992). It captures a fundamental aspect of the spatial pattern of diversity, and its study is fundamental to understanding the geographic patterns of species richness (Whittaker 1972, Koleff 2005). Factors influencing species turnover among local fauna are usually a combination of environmental and geographical variables (i.e. geographic distance) (Borcard *et al* 1992), and determining their relative weighting is crucial for understanding the shaping of biogeographic patterns (Duivenvoorden *et al* 2002).

The aim of our study was to determine the distribution of gall-inducing arthropods species at Coiba National Park, a tropical island off the Pacific coast of Panama. Secondly, we aimed to investigate the effect of geographic distance on species similarity between communities. In particular, the study addresses the following question: Is the beta component an important factor in gall-inducing species diversity?

Material and Methods

Study area. The research was performed at Coiba National Park (World Heritage Site), as part of the Joint Hispanic-Panamanian Program for National Parks. Coiba National Park comprises several islands in the Panamanian Pacific Ocean (7° 39' -7° 18' N & 81° 53' -81° 35' W), 22 km from the mainland, and includes an area of 270,125 ha (53 582 ha are insular and 216,543 are marine). The insular area is composed of Coiba (50,314 ha), the largest island in tropical Pacific America, eight other minor islands and 30 islets. The maximum altitude in the Park is 420 m, found on Coiba Island, and the annual rainfall is 3,483 mm. The annual

average humidity is 80% with annual average temperature of 25°C. The area is characterized by an intense dry season (December to April) and a rainy season (May to November). The original vegetation is well conserved, with about 80% forest coverage. An untouched tropical, moist and wet forest occupies 60% of the Park (Castroviejo 1997).

Sampling protocol. Field data were obtained from samplings between August 1997 and September 1999, during one study of seven plots (1 ha each one) of the vegetation of Coiba island (see Ibañez 2001), with three more intensive samplings (two-week long = 21 sampling) in August 1997, July 1998 and August 1999, with part of a preliminary census of fauna and flora of Coiba island (Castroviejo 1997). Seven sites representing the main terrestrial habitats and vegetation types on Coiba Island were surveyed: Cerro de la Equis, Estación Biológica, Isla Ranchería, Manglar de Santa Cruz, Manila, Playa Hermosa-Cerro de la Torre and Playa Blanca-Cativales (Table 1).

The sampling method used – 60 min census –, is one of the two methods used in the literature to estimate the local number of insect galling species in the world (see Price *et al* 1998). At each site, during no less than 1h, census was taken by carefully examining all plants while moving slowly through an area. Trails were commonly used as census routes because foliage was lower in the canopy at their edges, and they provided access through dense vegetation. Disturbance of vegetation, including trimming, increases the chances of finding galls because many species attack rapidly growing shoots (Price *et al* 1998). Therefore, use of trails no doubt increased the rate of discovery of galling species, although the total species richness in a locale would be little affected because all species should be usually discovered well within the 1h sample time (Price *et al* 1998). According to Price *et al* (1998), this method is similar to sample a 10m-wide transect, wherein all plants are examined for gall above ground until 1,000 herbs, 100 shrubs, and 45 trees. Plants with galls were collected and photographed. Specimens of galled plants were dried and put into a herbarium collection, where plants were identified at species level. Samples of the galls

Table 1 Geographic characteristics and habitat type of sampling sites at Coiba Nacional Park.

Sites	Latitude (deg. N)	Longitude (deg. W)	Altitude (m)	Habitat	Gall richness (morphotype number)
Cerro de la Equis	7° 37' 14.27"	81° 44' 27.91"	100-200	Mature forest	19
Playa Hermosa-Cerro de la Torre	7° 31' 59.88"	81° 47' 59.99"	0-400	Mature forest	12
Manglar de Santa Cruz	7° 37' 07.36"	81° 45' 29.04"	0	Mature and secondary forest	12
Manila	7° 22' 08.96"	81° 45' 01.44"	0	Mature forest and coastal vegetation	9
Isla Ranchería	7° 38' 18.56"	81° 42' 10.89"	0-100	Mature, secondary forest and coastal vegetation	5
Playa Blanca-Cativales	7° 22' 09.85"	81° 40' 02.33"	0	Secondary forest	4
Estación Biológica	7° 37' 34.18"	81° 43' 43.50"	40	Secondary forest and degraded vegetation	3

were also stored in 70% ethanol to allow further dissection and identification. Altitude and geographic position were measured in the field (Table 1). The galls were dissected in the laboratory for adult and larval identification at the family level. The gall inducer species were sorted to morphotype based on external morphology of the galls, the larvae and the host plant. In accordance with Fernandes & Price (1988), we assumed that each morphotype of gall is unique for each gall-inducing species.

Data analysis. To verify sampling efficiency, we built rarefaction curves and a species distribution test was made with BioDiversity Professional Ver. 2 (McAleece 1997). In order to determine differences in gall-inducing arthropod species number for the seven sites and the distribution of each species, a Chi-square test for Goodness of fit was made. The expected frequencies are those that we would hope to find if the null hypothesis ($H_0 = 0$) is true, given the total number of observations (Zar 1999).

The level of similarity between the seven sites sampled, based on presence of galls, was calculated using a multiple-site similarity measure (range = 0-1), according with Diserud & Ødegaard (2007):

$$C_S^T = \frac{T}{T-1} \left(1 - \frac{S_T}{\sum_i a_i} \right)$$

Where a_i is the number of species in site A_i , $i = 1, \dots, T$; a_{ij} is the number of species shared by sites A_i and A_j and a_{ijk} is the number of species shared by the sites A_i , A_j and A_k , etc. Multiple-site similarity measures provide a more relevant index for a species' spatial distribution. Instead of calculating the average over a set of dependent pairwise similarities, we use the information on the identity of species shared across more than two sites. For a given number of sites T , C_S^T decreases with increasing number of "rare" species (i.e., species observed in only one or a few sites). Conversely, C_S^T

increases with the increasing number of species observed in several sites (Diserud & Ødegaard 2007).

The Jaccard's index was used in a cluster analysis to illustrate similarity patterns at the seven sites. We used a single link procedure, because in the algorithm, single linkage selects the shortest distance between sites.

A Mantel test was used to determine the correlation between the matrix of dissimilarity of the sites based on gall-inducing species presence and a matrix of geographic distance between the sites (10000 permutations). The Mantel test can be considered a "distance approach" because the input data are in the form of distance matrices, based on the raw data, and it has been extensively used throughout the ecological literature (Tuomisto & Ruokolainen 2006). We used the software XL-STAT (Addinsoft 2007) for this test.

Results

A total of 3,046 galls of 48 morphotypes (39 insects and nine mites), associated with 39 species of plants from 29 genera and 24 botanical families were collected at the seven sites. Most of the galls (62%) were induced by species of the family Cecidomyiidae (Diptera) and by Eriophyidae (Acari) (19%). The plant species with the greatest diversity of galls was *Calophyllum longifolium* (Clusiaceae) with three, seven species were found with two galls (Online Supplementary Material). Detailed information on the faunistic components of the gall-inducing arthropods of Coiba Island is given in Nieves-Aldrey *et al* (2008). Gall species richness per collecting site varied between three (at Estación Biológica) and 19 (at Cerro Equis; Table 1). Rarefaction curves suggest that all species were collected in five out of the seven sites sampled (Fig 1). The distribution of the gall-inducing species was mainly (90%) aggregated at Coiba National Park (Online Supplementary Material). Estimates of gall-inducing arthropod species richness (Table 1), was significantly different among sites ($\chi^2 = 21, 87, df = 6, P < 0.05$).

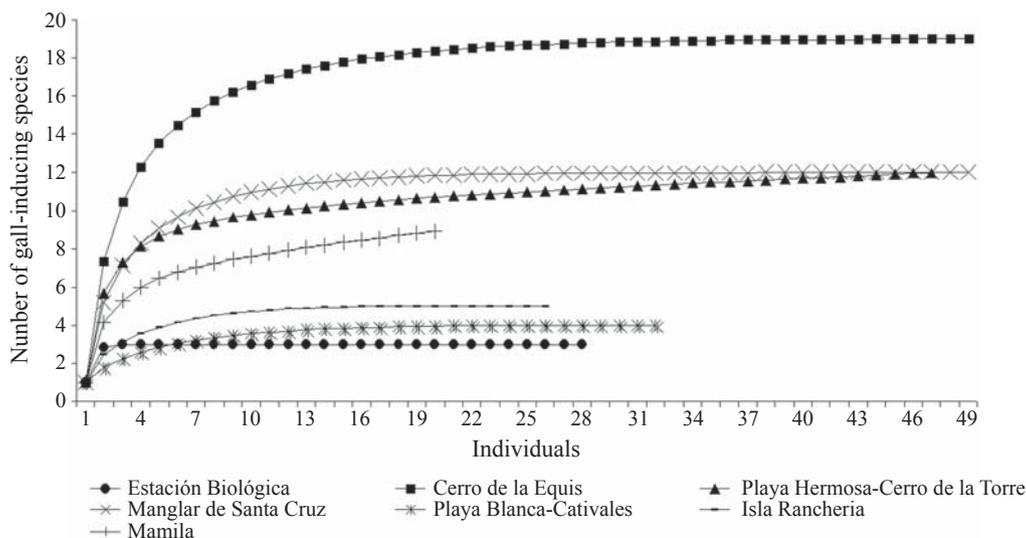


Fig 1 Comparison of gall-inducing species richness (individual-based rarefaction curves) of the seven sampled sites. Curves suggest that in five out of the seven sites sampled all gall-inducing arthropods were collected.

The multiple-similarity measures indicated that similarity in gall composition and community between collecting sites was generally low (0.292), even among proximate sites. The higher percentage of similarity (about 18%, Jaccard's index), was found between the sites of Manglar de Santa Cruz, Cerro de la Equis, and Estación Biológica. The Playa Blanca-Catívaes community is the most different from all other localities (Fig 2).

Mantel tests indicated that there are no correlations between the matrix of community dissimilarity and geographic distance (Pearson's product-moment correlation $r = -0.15$, $P > 0.05$) (Fig 3).

Discussion

Patterns of the distribution of species diversity are the result of ecological, physical and historical factors across time and space (Hill & Hill 2001). In this study, the gall-inducing arthropod richness is the result of the complementarity among sites, which is reflected in the low similarity values of the multiple-similarity index measures (0.292). This pattern is similar to patterns found in other neotropical areas. At four neotropical savannas (12 sampling sites) in Brazil, the highest similarity in gall-inducing insect communities was 0.117, (Gonçalves- Alvin & Fernandes 2001). At seven sampled sites in a tropical rain forest in Mexico, Cuevas-Reyes *et al* (2003) reported that 62% of the gall-inducing species found had restricted distributions. In mainland Panama, the gall-inducing insect community in two rain forest areas separated by 90 km shared two species (Medianero *et al* 2003). Turnover of gall-inducing species is also reported for vertical distribution; in a dry forest in Panama, of 50 gall-inducing insects collected, the canopy community shared just three species with the understorey community (separated by 40 m; Medianero *et al* 2003).

Our results suggest that beta diversity is a very important factor in local gall-inducing arthropod community

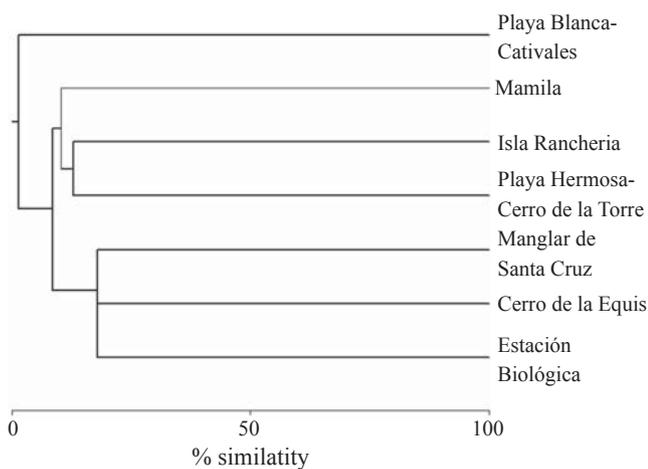


Fig 2 Cluster similitude (single linkage) of sampling sites for gall community distances. The higher percentage of similarity was found between the sites of Manglar de Santa Cruz, Cerro de la Equis, and Estación Biológica.

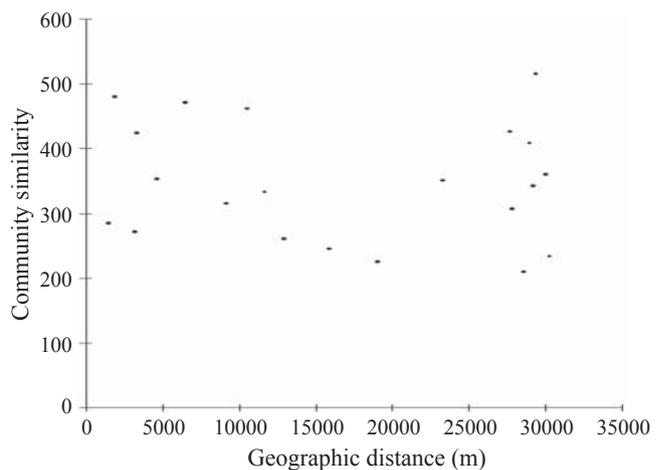


Fig 3 Scatter plot of pairwise Jaccard index (vertical axis) plotted against geographic between-site distances. Mantel tests indicate that there are no correlations between the matrix of community dissimilarity and geographic distance.

composition and that geographic distance is not correlated with similarity in gall-inducing species composition between the studied sites. According to Weis *et al* (1988), due to the fact that gall-inducing species are highly specialized (even at the level of plant organs) its presence in a site is determined by the presence, abundance, physiological and phenological status of its host plant. In tropical forests the plants species show a strong spatial and temporal pattern in the production of plant organs attacked by the gall-inducing arthropods, varying within the seasons and presenting frequent asynchronies in the phenological state of two individuals of the same plant species, which can be separated by a short distance (van Schaik *et al* 1993). Plant communities in tropical forests, particularly in Panamanian forests, show high beta diversity (Condit *et al* 2002, Duivenvoorden *et al* 2002) and as gall inducers are predominantly monophagous, it is very likely that the same effect will be observed for them. Additionally, the presence of "super hosts" (i.e., plant species that support a high richness of gall-inducing insects) is relatively common (Espírito-Santo & Fernandes 2007, Medianero *et al* 2007), and this can increase the gall-inducing species richness of a given locality independent of distance between sites.

Our results suggest that gall-inducing arthropod species distribution shows a strong influence of the component of beta diversity, so any estimate of gall-inducing species richness of a region should be made by means of intensive samplings, taking into account the spatial distribution of the vegetation and inducers, because geographical distance at the local level is not a determinant factor in their distribution.

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Online Supplementary Material

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Distribution type and host plant species of each gall-inducing species found in seven sites at Coiba National Park (d. f. = 6).

Gall-inducing	Host plant species	Chi-square	Probability	Distribution
Cecidomyiidae sp. 1	<i>Amphitecna latifolia</i>	66.00	0.00	Aggregated
Cecidomyiidae sp. 2	<i>Licania hypoleuca</i>	456.00	0.00	Aggregated
Cecidomyiidae sp. 3	<i>Terminalia amazonia</i>	450.00	0.00	Aggregated
Cecidomyiidae sp. 4	<i>Croton schiedeanus</i>	204.00	0.00	Aggregated
Cecidomyiidae sp. 5	<i>Manihot esculenta</i>	108.00	0.00	Aggregated
Cecidomyiidae sp. 6	<i>Casearia commersoniana</i>	48.00	0.00	Aggregated
Cecidomyiidae sp. 7	<i>Casearia commersoniana</i>	12.00	0.06	Random
Cecidomyiidae sp. 8	<i>Calophyllum longifolium</i>	313.67	0.00	Aggregated
Cecidomyiidae sp. 9	<i>Calophyllum longifolium</i>	786.00	0.00	Aggregated
Cecidomyiidae sp. 10	<i>Lacistema aggregatum</i>	168.00	0.00	Aggregated
Cecidomyiidae sp. 11	<i>Lacistema aggregatum</i>	24.00	0.00	Aggregated
Cecidomyiidae sp. 12	<i>Inga multijuga</i>	540.00	0.00	Aggregated
Cecidomyiidae sp. 13	<i>Prioria copaifera</i>	1758.00	0.00	Aggregated
Cecidomyiidae sp. 14	<i>Cydista aequinoctialis</i>	211.41	0.00	Aggregated
Cecidomyiidae sp. 15	<i>Ficus popenoei</i>	234.00	0.00	Aggregated
Cecidomyiidae sp. 16	<i>Virola</i> sp.	708.00	0.00	Aggregated
Cecidomyiidae sp. 17	<i>Ardisia</i> sp.	102.00	0.00	Aggregated
Cecidomyiidae sp. 18	Myrtaceae sp. 1	126.00	0.00	Aggregated
Cecidomyiidae sp. 19	<i>Mansoa</i> sp.	60.00	0.00	Aggregated
Cecidomyiidae sp. 20	Myrtaceae sp. 2	6.00	0.42	Random
Cecidomyiidae sp. 21	Myrtaceae sp. 3	6.00	0.42	Random
Cecidomyiidae sp. 22	<i>Neea</i> sp.	152.10	0.00	Aggregated
Cecidomyiidae sp. 23	<i>Ouratea lucens</i>	69.33	0.00	Aggregated
Cecidomyiidae sp. 24	<i>Cassipourea elliptica</i>	78.00	0.00	Aggregated
Cecidomyiidae sp. 25	<i>Mansoa</i> sp.	42.00	0.00	Aggregated
Cecidomyiidae sp. 26	<i>Faramea occidentalis</i>	42.71	0.00	Aggregated
Cecidomyiidae sp. 27	<i>Psychotria horizontalis</i>	293.50	0.00	Aggregated
Cecidomyiidae sp. 28	<i>Pouteria cf. foveolata</i>	396.07	0.00	Aggregated
Cecidomyiidae sp. 29	<i>Pouteria cf. foveolata</i>	181.75	0.00	Aggregated
Cecidomyiidae sp. 30	<i>Maytenus schippi</i>	120.00	0.00	Aggregated
Coccidae sp. 1	<i>Amphitecna latifolia</i>	60.00	0.00	Aggregated
Coccidae sp. 2	Myrtaceae sp. 4	486.00	0.00	Aggregated
Coccidae sp. 3	<i>Pelliciera rhizophorae</i>	2310.00	0.00	Aggregated
Coccidae sp. 4	<i>Cassipourea elliptica</i>	138.00	0.00	Aggregated
Eriophyidae sp. 1	<i>Acalypha diversifolia</i>	6.00	0.42	Random
Eriophyidae sp. 2	<i>Acalypha diversifolia</i>	461.45	0.00	Aggregated
Eriophyidae sp. 3	<i>Calophyllum longifolium</i>	216.00	0.00	Aggregated
Eriophyidae sp. 4	<i>Clidemia discolor</i>	120.00	0.00	Aggregated
Eriophyidae sp. 5	<i>Miconia nervosa</i>	52.67	0.00	Aggregated

Continue

Continuation

Gall-inducing	Host plant species	Chi-square	Probability	Distribution
Eriophyidae sp. 6	<i>Miconia lacera</i>	132.00	0.00	Aggregated
Eriophyidae sp. 7	<i>Miconia minutiflora</i>	500.00	0.00	Aggregated
Eriophyidae sp. 8	Myrtaceae sp. 5	804.00	0.00	Aggregated
Eriophyidae sp. 9	<i>Cissus microcarpa</i>	144.00	0.00	Aggregated
Phlaeotripidae sp. 1	Asteraceae sp. 1	114.00	0.00	Aggregated
Phlaeotripidae sp. 2	Myrtaceae sp. 6	6.00	0.42	Random
Psyllidae sp. 1	<i>Cinnamomum triplinerve</i>	845.49	0.00	Aggregated
Psyllidae sp. 2	<i>Tetragastris panamensis</i>	186.00	0.00	Aggregated
Psyllidae sp. 3	<i>Protium confusum</i>	976.72	0.00	Aggregated