Insect herbivores associated with *Baccharis dracunculifolia* (Asteraceae): responses of gall-forming and free-feeding insects to latitudinal variation

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Abstract: The spatial heterogeneity hypothesis has been invoked to explain the increase in species diversity from the poles to the tropics: the tropics may be more diverse because they contain more habitats and micro-habitats. In this paper, the spatial heterogeneity hypothesis prediction was tested by evaluating the variation in richness of two guilds of insect herbivores (gall-formers and free-feeders) associated with *Baccharis dracunculifolia* (Asteraceae) along a latitudinal variation in Brazil. The seventeen populations of *B. dracunculifolia* selected for insect herbivores sampling were within structurally similar habitats, along the N-S distributional limit of the host plant, near the Brazilian sea coast. Thirty shrubs were surveyed in each host plant population. A total of 8 201 galls and 864 free-feeding insect herbivores belonging to 28 families and 88 species were sampled. The majority of the insects found on *B. dracunculifolia* were restricted to a specific site rather than having a geographic distribution mirroring that of the host plant. Species richness of free-feeding insects was not affected by latitudinal variation corroborating the spatial heterogeneity hypothesis. Species richness of gall-forming insects was positively correlated with latitude, probably because galling insect associated with *Baccharris* genus radiated in Southern Brazil. Other diversity indices and evenness estimated for both gall-forming and free feeding insect herbivores, did not change with latitude, suggesting a general structure for different assemblages of herbivores associated with the host plant *B. dracunculifolia*. Thus it is probable that, insect fauna sample in each site resulted of large scale events, as speciation, migration and coevolution, while at local level, the population of these insects is regulated by ecological forces which operate in the system. Rev. Biol. Trop. 59 (3): 1419-1432. Epub 2011 September 01.

Key words: community organization, latitudinal diversity gradient, spatial heterogeneity hypothesis, species diversity.

Latitudinal variations in species diversity are among the most conspicuous and universal patterns in community ecology (Pianka 1966). According Willig *et al*. (2003), just with notable exceptions, the pattern of higher diversity at low latitudes holds true regardless of the biota's taxonomic affiliation (e.g., mammals, fishes, arthropods and plants), geographic context (e.g., all continents and oceans) or time domain (recent and 70 Mya). Explanations for higher species diversity in tropical regions include greater predation and competitive pressures, greater climatic stability, larger area extent, higher energy input and greater habitat heterogeneity in tropical regions than elsewhere (Shepherd 1998, Rohde 1998, Hillebrand 2004). Still, there is an astonishing lack of consensus about the mechanisms leading to this spatial variation in diversity (Hillebrand 2004) and recent study has invoked niche conservatism

(Buckley *et al*. 2010) or habitat heterogeneity (Whitehouse *et al*. 2009) to explain the increase of diversity towards the tropics.

In this paper the focus is on the spatial heterogeneity hypothesis, and the study objects are different insect herbivore guilds associated with a single host plant. On the local scale, the spatial heterogeneity hypothesis suggests that the tropics are more diverse because they contain more microhabitats (Pianka 1966). On a regional scale, this hypothesis has been proposed to explain the increase of species diversity from the poles to the tropics: the tropics are more diverse because they contain more habitats and microhabitats (Dawidowitz & Rosenzweigh 1998). This greater number of habitats and microhabitats allows taxa to partition the environment more finely, and more species to co-exist in the tropics (Pianka 1966). A positive relationship between habitat complexity and species diversity has been shown in a variety of environments and for a large number of taxa (Otte 1976, Terborgh 1992, Gaston & Williams 1996, Ribeiro *et al*. 1998, Thomaz *et al*. 2008). On the other hand, as a corollary, the spatial heterogeneity hypothesis also implies that, within structurally uniform environments, species diversity should not change along a latitudinal gradient.

The most species alive are tropical arthropods associated with plants (Price *et al*. 1995). Herbivorous arthropods maintain many important ecosystem processes and form sizeable parts of terrestrial food webs (Lewinsohn & Roslin 2008). In fact, in terms of biomass, insects in tropical forests constitute several tons per hectare compared to a few kilograms per hectare for birds and mammals. Moreover, insects in the tropics munch through an estimated 680 kg/ha.y of leaves compared to 100 to 300 kg/ha.y of leaves by vertebrates (Dajoz 2000). Herbivorous insects are composed of various feeding guilds (e.g. free-feeding and galling insects), with different specialization levels on their host plant and habitat (Koricheva *et. al*. 1998, Novotny & Basset 2005). In fact, comparatively to free-feeding insects, galling insects generally are considered more specialized herbivores (Frenzel & Brandl 1998). Thus, it is probable that, when the insect fauna associated with single host plant is analyzed, free-feeding insects (generally with more oligophagous feeding habit) are more dependent on habitat characteristics, while galling insects respond more finely to specific host plant attributes (Koricheva *et al*. 1998, Golden & Crist 1999).

Despite the high diversity of insect herbivores in the tropics, few studies have adequately addressed the influence of historical and biogeographical processes on species richness patterns of tropical insect herbivores (Price *et al*. 1995, Ribeiro *et al*. 1998, Majer *et al*. 2001). Moreover, many insect taxa as aphids (Dixon *et al*. 1987), Ichneumonidae (Sime & Brower 1998) and gall-forming insects (Fernandes & Price 1988) do not fit the general pattern of increasing species richness with decreasing latitude. Evolutionary explanations to these latitudinal diversity anomalies have focused on either variation in rates of diversification or the amount of time available for speciation within a region (Buckley *et al*. 2010). While some studies include herbivores from several insect orders, studies of more than one guild on the same hosts are lacking from tropical regions (Novotny & Basset 2005). In this study the prediction of spatial heterogeneity hypothesis was tested by evaluating the variation in diversity of two guilds of insect herbivores (galling and free-feeding) along the distributional limits of the host plant, near the Brazilian sea coast. The data were collected within homogeneous habitat and the arthropod sampled was associated with the host plant *Baccharis dracunculifolia*.

MATERIALS AND METHODS

Study system: The Asteraceae comprises approximately 1 110 genera and 25 000 species. The genus *Baccharis* belongs to the subtribe Baccharidinae, which is restricted to the American Continent (Barroso 1976). The Baccharidinae probably appeared during Middle Miocene (Boldt 1989) when South

American and African continents were totally separated by the Atlantic Ocean (Cox & Moore 1993), justifying its natural occurrence just in the American continent. *Baccharis* is the largest genus of Baccharidinae (approximately 400 species) and most species are found in the South and Southeast regions of Brazil, suggesting that this region represent the center of the genus origin (Jarvis *et al*. 1991). *B. dracunculifolia* (alecrim vassourinha) is a widespread, perennial and woody dioecious shrub, 2-3m high, which occurs in Southern and Southeastern Brazil, Argentina, Uruguay, Paraguay and Bolivia (Espírito-Santo *et al*. 2003, Fagundes *et al*. 2005). It grows in open and disturbed habitats, especially along highways and in abandoned pastures. Because it is an evergreen plant, its leaves and branches are important food resources for a variety of insect herbivores, especially coleopterans, heteropterans, hemipterans and orthopterans (Fagundes *et al*. 2005). Furthermore, the shrub *B. dracunculifolia* also supports the largest known fauna of galling insects (17 species) in the Neotropics (Fernandes *et al*. 1996). The degree of habitat disturbance did not influence the richness of galls associated with the host plant *B. dracunculifolia* (Julião *et al*. 2005).

Study areas: The *B. dracunculifolia* shrubs selected for insect samples belonged to seventeen populations located along the Brazilian sea coast, from the Southern to the Northern distributional limit of the host plant inside Brazil. All plant populations occurred in disturbed environments along highways, within 500m of the seashore and were similar in phenology, size and density. The climate of all the seventeen sample points is broadly influenced by Atlantic Ocean air mass. However, from Northern São Paulo State through Rio de Janeiro, Espírito Santo and Bahia States the climate is moist tropical (Af according Köppen classification). In contrast, from Southern São Paulo State through Parana, Santa Catarina e Rio Grande do Sul States the climate is classified as subtropical (Cfa according Köppen classification). All selected host plant populations were located at similar altitude (06-130m) and were grown on typical seashore sand soil with high levels of moisture and salinity (Table 1, Fig. 1). The surrounding vegetation ranged from

TABLE 1
Description of seventeen sample sites of the insect herbivores associated with *Baccharis dracunculifolia* along the distributional limits of host plant in Brazilian seacoast

Sample sites	District (State)	Sample date	Latitude	Longitude	Altitude
S1	Arraial D’ajuda (BA)	4/10/2001	16º22’ S	39 º 18’ W	130 m
S2	Prado (BA)	5/10/2001	17 º11’ S	39 º 13’ W	26 m
S3	Aracruz (ES)	17/1/2002	19º50’ S	40 º 22’ W	32 m
S4	Anchieta (ES)	16/1/2002	20 º 49’ S	40 º 37’ W	20 m
S5	Piúma (ES)	15/1/2002	20 º 52’ S	40 º 46’ W	33 m
S6	Carapebus (RJ)	13/1/2002	22 º 11’ S	41 º 43’ W	57 m
S7	Rio das Ostras (RJ)	12/1/2002	22 º 28’ S	41 º 53’ W	28 m
S8	Mangaratiba (RJ)	11/1/2002	22 º 59’ S	44 º 03’ W	21 m
S9	Caraguatatuba (SP)	28/10/2001	23 º 35’ S	45 º 21’ W	24 m
S10	Bertioga (SP)	27/10/2001	23 º 46’ S	45 º 57’ W	10 m
S11	Iguape (SP)	26/10/2001	24 º 39’ S	47 º 24’ S	06 m
S12	Juréia (SP)	25/10/2001	24 º 42’ S	47 º 32’ S	18 m
S13	Itajai (SC)	13/11/2001	26 º 56’ S	48 º 38’ S	42 m
S14	Camburiu (SC)	12/11/2001	27 º 00’ S	48 º 39’ S	12 m
S15	Laguna (SC)	11/11/2001	28 º 27’ S	48 º 48’ S	26 m
S16	Torres (RS)	10/11/2001	29 º 21’ S	49 º 46’ S	49 m
S17	Tramandai (RS)	9/11/2001	29 º 59’ S	50 º 13’ S	10 m

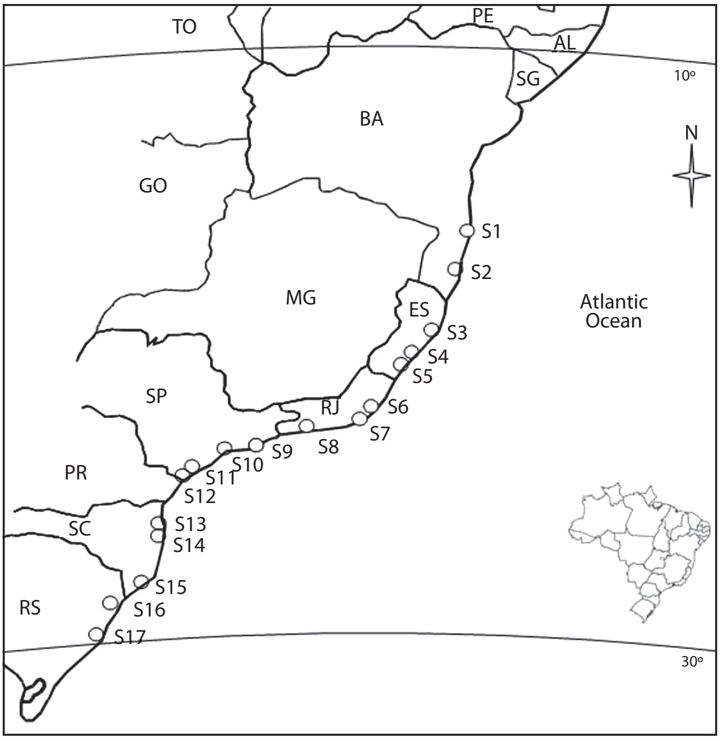

Fig. 1. Sampling sites location along the N-S distributional limits of the host plant *B. dracunculifolia* near the Brazilian sea coast (see also Table 1).

0.3 to 2.0m height and was comprised by grasses and other invasive species belonging principally to the Asteraceae, Convolvulaceae, Malvaceae, Melastomataceae and Solanaceae botanical families. At each host plant population, thirty *B. dracunculifolia* shrubs were selected to take herbivores samples. The shrubs selected for this were young, non-flowering or fruiting plants with 1.5-2.0m high and stem diameters <15cm.

Herbivore samples: Herbivore insects associated with *B. dracunculifolia* were censused by direct sampling on the host plant. Thus, each shrub was inspected during ten minutes and all free-feeding herbivore insects and galls observed were handling collected. The herbivores were sampled during the summer season (October of 2001 through January of 2002) in order to minimize the possible effects of climate variation in insect population dynamics. All galling and free feeding herbivore insect samples were taken to the Laboratório de Biologia da conservação at Universidade Estadual de Montes Claros (Unimontes) where they were assigned into morphospecies and identified. We fail to test the insect ability to feed on *B. dracunculifolia*. Therefore, potentially transient insect herbivores could have been included in data collection and analysis.

The effects of latitudinal variation on the two guilds of insect herbivores were tested using simple linear regressions. For each guild, linear regression analyses were performed using latitudinal variation as the independent variable and the Hill's number of diversity (N0, N1 and N2) or evenness as dependent variable.

The Hill's number of diversity N0, N1 and N2 represent, respectively, the total number of species (richness), number of abundant species, and number of very abundant species within a species assemblage. Thus, the unity of Hill's numbers is species, making easy data interpretation and comparisons with other results. The number of abundant species (N1) represent the exponential function of Shannon's index ($N1=e^{H'}$), while the number of very abundant species (N2) is the inverse of Simpson's index ($N2=1/S$). In addition, evenness was determined by the ratio of very abundant species (N2) to abundant species (N1), known as the modified Hill's ratio. See Ludwig & Reynolds (1998) for a detailed description of this diversity index and evenness.

RESULTS

General patterns: A total of 8 201 galls and 864 free-feeding insect herbivores were collected from *B. dracunculifolia* at the seventeen sample points. The fauna of herbivorous insects associated with *B. dracunculifolia* was composed by 88 species from 28 families. The insect families with more species were Chrysomelidae (12 species), Curculionidae (12 species), Acrididae (7 species) and Cecidomyiidae (7 species). In general, free-feeding herbivore abundance and frequency were low, but an unidentified species of Scolytidae deserve further studies due to their high abundance and frequency in the samples. This species was commonly observed feeding on meristems and new leaves of host plant (Appendix).

The guild of free-feeding insects represented 90.99% of total insect herbivore species associated with *B. dracunculifolia*, while gall-forming contributed with 9.01% of the sampled species. On the other hand, gall-forming insects represented the most abundant feeding guild (90.48%), whereas free-feeding insects represented just 9.52% of total herbivore insect abundance. In general, the richness of insects per sample site (local richness) was low (mean=14.47, range: 09-23) when compared to total richness (regional richness=88), indicating high species substitution among sample sites. This observed pattern was due mainly to free-feeding, rather than gall-forming insects (Appendix).

Latitudinal gradient hypothesis: The number of gall-inducing insect species associated with *B. dracunculifolia* decreased significantly towards the North, low latitude, limit of the host plant distribution ($F=31.563$, $p=0.007$, $r^2=67.78$). However, the number of abundant species ($F=1.469$, $p=0.245$, $r^2=9.49$), very abundant species ($F=2.289$, $p=0.152$, $r^2=14.05$) and evenness ($F=0.234$, $p=0.636$, $r^2=1.642$) did not vary significantly along the latitudinal gradient (Fig. 2). When free-feeding insect herbivores were analyzed, none of the measures of species diversity (specie richness: $F=1.988$, $p=0.179$, $r^2=11.70$; number of abundant species: $F=0.372$, $p=0.551$, $r^2=2.42$; number of very abundant species: $F=0.005$, $p=0.944$, $r^2=0.34$ and evenness: $F=0.234$, $p=0.636$, $r^2=1.64$) were significantly related to variations in latitude (Fig. 3).

DISCUSSION

The number of gall-inducing insect species associated with *Baccharis dracunculifolia* decreased towards the equator. The observed result did not fit the more common pattern of increasing species diversity as latitude decreases (Willig *et al*. 2003, Lewinsohn & Roslin 2008). Factors such as geographic distribution, center of origin, taxonomic isolation and local diversity of the host plants have been used to justify the absence of correlation between species diversity of other insect herbivores and latitudinal variations (Cornell 1985, Leather 1986, Lewinsohn & Roslin 2008). We argue that our results are related to the evolutionary history of the host plant and the highly specialized feeding habit of gall-inducing insects. The genus *Baccharis* is more species-rich in the Southern region of Brazil, that probably corresponds to the genus origin center (Jarvis *et al*. 1991). Moreover, given the narrow host plant requirements of gall-inducing insects, it would

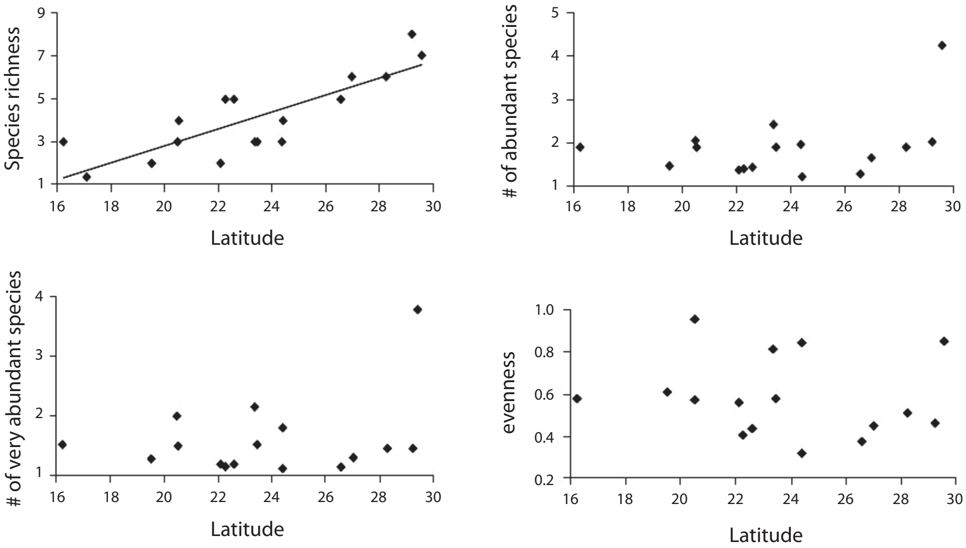

Fig. 2. Hill's diversity indices (species richness, number of abundant and very abundant species) and evenness of gall-forming insects associated with *B. dracunculifolia* along the latitudinal gradient in Brazilian sea coast.

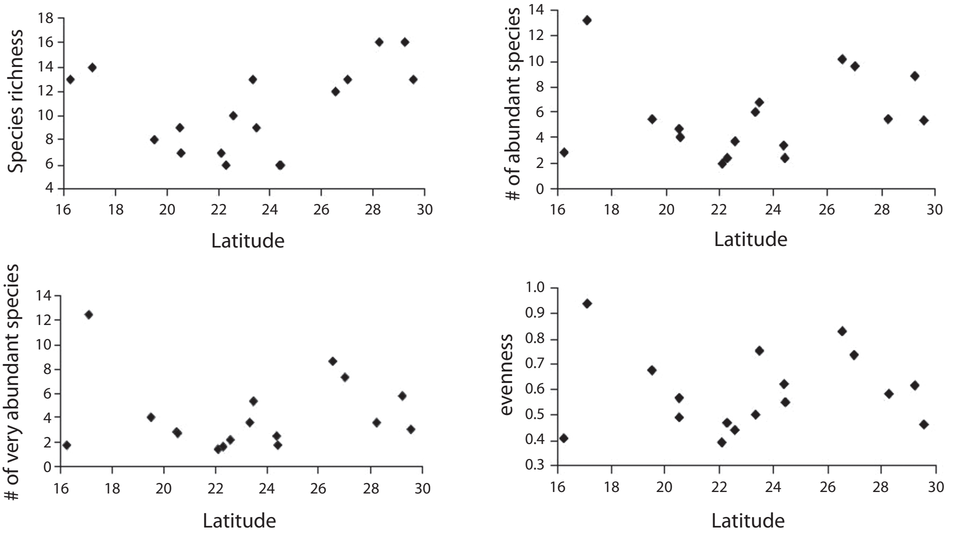

Fig. 3. Hill's diversity indices (species richness, number of abundant and very abundant species) and evenness of free-feeding herbivore insects associated with *B. dracunculifolia* along the latitudinal gradient in Brazilian sea coast.

be expected that exchange of gall-inducing insect species between closely related plant species would be easier than exchange between more distantly related plant species (Lawton & Schroder 1977, Leather 1986). Thus, it is possible that the galling insect associated with *Baccharis* genus radiated into the Southern region of Brazil, justifying the decrease of galling insect richness towards the North, limit of host plant observed in this study.

Species' ranges may be constrained by both climatic tolerances and barriers to dispersal (e.g. mountains and rivers). In the former case, species can disperse to a new habitat but fail to become established, whereas in the latter case species might never have opportunity to reach the new habitat even though they have attributes needed to persist there (Buckley *et al.* 2010). In this study, physical barriers are uncommon among the sample sites, but the temperature results higher in Northern regions. Thereby, climatic intolerances should represent a constraint to some galling species establishment in the extreme Northern limit of host plant which would generate the observed pattern of high gall richness in the Southern region. In fact, recent studies indicate that climatic specialization and retention of climatic tolerances over time (niche conservatism hypothesis) might drive species distributions in space (Buckley *et al.* 2010, Kozak & Wiens 2010). However, adequate experimental design is need to test the effectiveness of niche conservatism to determine the regional distribution of galling species associated with *B. dracunculifolia*.

The variation in latitude did not influence the richness of free-feeding insect herbivores associated with *B. dracunculifolia*. This result supports the spatial heterogeneity hypothesis prediction because species richness should not change within structurally similar habitats along a latitudinal gradient. However, Dawidowitz & Rosenzweigh (1998) present four examples (ants, grasshopper, scorpions and mammals) where diversity trends within single biome types change along the latitudinal variation. In contrast, no significant correlations were found between the proportion of mining species and latitude (Sinclair & Hughes 2008). The authors argument that leaf mining is a widespread type of insect herbivory whose distribution patterns are more likely to be influenced by biotic than abiotic factors. Similarly, Andrew & Hughes (2005) found no consistent North to South (tropical to temperate) change in arthropod community structure associated with *Acacia* trees in Eastern Australia. The findings suggest that different mechanisms operate for different taxa and that it is not wise to generalize the effects of latitude on species diversity across taxa.

Despite of different patterns of species richness observed for gall-inducing and free feeding insects, neither the diversity indices represented by Hill's number N1 and N2 or evenness of these two guilds were related to latitudinal variation. These patterns suggest that even though species composition and richness can vary among habitats, there is a general structure to the herbivore community associated with *B. dracunculifolia* (Fagundes *et al.* 1996, Andrew & Hughes 2005). In fact, there are strong evidences that bottom-up (Faria & Fernandes 2001, Espírito-Santo & Fernandes 2002) and top-down (Fagundes *et al.* 2005) forces operating in the system can influence the relative abundance of insect herbivores on *B. dracunculifolia* and regulate diversity at the local level.

The majority of tropical insect herbivores are relatively rare (Price *et al.* 1995). Generally, just a few groups of insect herbivores with specialized feeding habits, such as some macrolepidoptera (Price *et al.* 1995), Homoptera (Dansa & Rocha 1992) and galling insects (Fernandes *et al.* 1996), can be found predictably and at high densities on specific host plants in tropical regions. However, the composition of herbivorous families observed in this study corroborates the general insect composition patterns described in other tropical areas. Usually, Chrysomelidae and Curculionidae are folivores recurrently important components of free-feeding insect communities (Kitching *et al.* 1997, Basset 2001, Neves *et al.* 2010), while Cecidomyiidae is dominant among the galling insects (Carneiro *et al.* 2009).

The general pattern of low density and frequency, specially observed in free-feeding insect guild, probably may be related to high plant diversity and the more polyphagous feeding habits of these insects in the tropics (Strong *et al.* 1984, Lawton 1991, Lewinsohn & Roslin 2008). The majority of insect herbivores, especially free-feeding insects found associated with *B. dracunculifolia*, showed low population density and frequency. Low density could be associated with generalist habits of herbivores permitting migration to a variety of host plants, while low species frequency indicates high variation in insect fauna between sample sites. In fact, the majority of the insects found on *B. dracunculifolia* were restricted to a specific site rather than having a geographic distribution mirroring that of the host plant.

The variation in insect fauna among habitats is determined by their host specificity, interactions with natural enemies and their ability to follow host plant species in space and time and across different environments (Novotny 2009). Thus, it is probable that local events, such as biological interactions, regulate the population dynamics of herbivores associated with *B. dracunculifolia*. In contrast, the insect fauna collected at each sample site represent just a portion of the local *pool* of insect herbivores capable of colonizing *B. dracunculifolia*. Thereby, the insect fauna sample from each site, resulted of large scale events, as speciation, migration and coevolution, while at local level, the population of these insects is regulated by ecological forces which operate in the system. Understanding the core of the relative role of ecological and evolutionary processes will be essential to predict general community structure, and advance in new strategies for insect conservation (Perry *et al*. 1998, Lawes *et al*. 2000).

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RESUMEN

La hipótesis de heterogeneidad espacial se ha utilizado para explicar el aumento en la diversidad de especies desde los polos a los trópicos: los trópicos pueden ser más diversos ya que están conformados por una mayor cantidad de hábitats y micro-hábitats. En este estudio, la hipótesis de heterogeneidad espacial se puso a prueba evaluando la variación en la riqueza de dos gremios de insectos herbívoros (formadores de agallas y de alimentación libre) asociados con *B. dracunculifolia* (Asteracea) a lo largo de un gradiente latitudinal en Brasil. Las diecisiete poblaciones de *B. dracunculifolia* seleccionadas para el muestreo de insectos herbívoros estaban en hábitats con una estructura similar, a lo largo del límite Norte-Sur de distribución de la planta hospedera, cerca de la costa brasileña. De cada población de planta hospedera, se muestrearon treinta arbustos y se obtuvo un total de 8 201 agallas y 864 insectos de alimentación libre pertenecientes a 28 familias y 88 especies. La mayoría de los insectos que se encontraron en *B. dracunculifolia* estaban restringidos a un sitio específico en lugar de tener una distribución geográfica similar a la de la planta hospedera. La riqueza de especies de insectos de alimentación libre no se vió afectada por el gradiente latitudinal, por lo que se corroboró la hipótesis de heterogeneidad espacial. Mientras que la riqueza de especies de insectos formadores de agallas se correlacionó positivamente con la latitud, probablemente debido a que los insectos asociados al género *Baccharis* se extendieron hacia el sur de Brasil. Otros índices de diversidad y equidad estimados no variaron con la latitud para ninguno de los dos grupos de insectos herbívoros evaluados, lo que sugirie una estructura general para diferentes conjuntos de herbívoros asociados con la planta hospedera *B. dracunculifolia*. Por lo tanto, es probable que, la muestra de insectos en cada sitio sea resultado de eventos a gran escala, como la especiación, migración y coevolución; mientras que a nivel local la población de estos insectos está regulada por fuerzas ecológicas que operan dentro del sistema.

Palabras clave: organización de comunidades, gradiente latitudinal de diversidad, hipótesis de heterogeneidad espacial, diversidad de especies.

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APPENDIX

Composition, abundance and richness of insect herbivores associated with *Baccharis dracunculifolia* at the seventeen sampling sites, along the N-S distributional limits of the host plant, in the Brazilian sea coast (F=free-feeding and G=galling insects)

Taxonomic group	Feed guild	Sample points																	Total
		S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	
Diptera																			
Cecidomyiidae																			
Cecidomyiidae sp. 1	G	8		78	201	10		19	62	135		158	405	37	18	109	154	6	1400
Cecidomyiidae sp. 2	G	1			2	71	43	36	1			2	2	10	4	24	178	2	376
Cecidomyiidae sp. 3	G							6	11								8	7	32
Cecidomyiidae sp. 4	G			11				1					7		2	5	4	6	36
Aspondila sp.	G	1	6			9					9							2	27
Geraldesia sp.	G									19	71		8	15	27	16	9	71	236
Rhoasphondylia friburguensis	G								11	72	9			4	3	1	64	27	191
Heteroptera																			
Alydidae																			
Alydidae sp. 1	F								1										1
Coreidae																			
Coreidae sp. 1	F	1																	1
Coreidae sp. 2	F		1																1
Leptoglossus sp.	F																	1	1
Lygaeidae																			
Lygaeidae sp. 1	F									1									1
Lygaeidae sp. 2	F				1														1
Myridae																			
Myridae sp. 1	F		1																1
Myridae sp. 2	F				1														1
Myridae sp. 3	F									3	2							2	7
Myridae sp. 4	F													1					1
Pentatomidae																			
Pentatomidae sp. 1	F								1	1									2
Pentatomidae sp. 2	F																11		11
Homoptera																			
Acanalonidae																			

Taxonomic group	Feed guild	Sample points																	Total
		S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	
Acanalonidae sp. 1	F																1		1
Cercopidae																			
Cercopidae sp. 1	F	5			12														17
Cercopidae sp. 2	F															5			5
Cercopidae sp. 3	F																	2	2
Cicadellidae																			
Cicadellidae sp. 1	F			1									1						2
Cicadellidae sp. 2	F						4												4
Cicadellidae sp. 3	F															1			1
Cicadellidae sp. 4	F									2					2				4
Cicadellidae sp. 5	F	1					2		3	3	7	18		2					36
Cicadellidae sp. 6	F													3					3
Cicadidae																			
Cicadidae sp. 1	F	16																	16
Cixiidae																			
Cixiidae sp. 1	F										5		1						6
Membracidae																			
Membracidae sp. 1	F	115	2	8										2	1	1			129
Membracidae sp. 2	F	7								1						1			9
Endrenopa sp.	F									1				1					2
Psyllidae																			
Neopelma bacccharidis	G				247	357	416	797	917			76		1238	391	707	214	543	5903
Coleoptera																			
Alleculidae																			
Alleculidae sp. 1	F		1	4			1												6
Alleculidae sp. 2	F																	1	1
Bruchidae																			
Bruchidae sp. 1	F							1											1
Bruchidae sp. 2	F												1						1
Bruchidae sp. 3	F															2			2
Buprestidae																			
Buprestidae sp. 1	F							1											1
Buprestidae sp. 2	F			1			1					2					2		6

Taxonomic group	Feed guild	Sample points																	Total
		S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	
Cantharidae																			
Cantharidae sp. 1	F								1										1
Cerambicydae																			
Cerambicydae sp. 1	F														1		2	3	6
Cerambicydae sp. 2	F															1			1
Cerambicydae sp. 3	F																1		1
Crysomelidae																			
Crysomelidae sp. 1	F	3							1	5									9
Crysomelidae sp. 2	F										1					1			2
Crysomelidae sp. 3	F	1																	1
Crysomelidae sp. 4	F	1	1																2
Crysomelidae sp. 5	F		1							2					1				4
Crysomelidae sp. 6	F		1																1
Crysomelidae sp. 7	F				1														1
Crysomelidae sp. 8	F				1														1
Crysomelidae sp. 9	F								4	2									6
Crysomelidae sp. 10	F											1							1
Crysomelidae sp. 11	F															1			1
Crysomelidae sp. 12	F																	1	1
Curculiionidae																			
Curculionidae sp. 1	F	1																	1
Curculionidae sp. 2	F		2																2
Curculionidae sp. 3	F	1	2																3
Curculionidae sp. 4	F				2														2
Curculionidae sp. 5	F					1										3			4
Curculionidae sp. 6	F								1	1							2		4
Curculionidae sp. 7	F										2							2	4
Curculionidae sp. 8	F										1				3	22	2	7	35
Curculionidae sp. 9	F												1						1
Curculionidae sp. 10	F														3				3
Curculionidae sp. 11	F													1	5		3	2	11
Curculionidae sp. 12	F														1				1
Elateridae																			

Taxonomic group	Feed guild	Sample points																	Total
		S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	
Elateridae sp. 1	F											2							2
Lagriidae																			
Lagriidae sp. 1	F					1													1
Lampyridae																			
Lampyridae sp. 1	F		1		1	1		1											4
Lampyridae sp. 2	F								4					1	1				6
Mordelidae																			
Mordelidae sp. 1	F													2		1	1	1	5
Scarabaeidae																			
Scarabaeidae sp. 1	F		1																1
Scarabaeidae sp. 2	F														1				1
Scarabaeidae sp. 3	F																	1	1
Scolytidae																			
Scolytidae sp. 1	F	1	2	2		12	61	30	33	25	2	7	9	6	8	25	38	19	280
Orthoptera																			
Acrididae																			
Acrididae sp. 1	F		1	1							1			2					5
Acrididae sp. 2	F			1		1		4	1							1	2		10
Acrididae sp. 3	F				1	3	2	2						2	2	2		2	16
Acrididae sp. 4	F					2										62	2	15	81
Acrididae sp. 5	F						1									4		3	8
Acrididae sp. 6	F									1			34		1		3		39
Acrididae sp. 7	F													3					3
Tettigoniidae																			
Tettigoniidae sp. 1	F	1	1																2
Tettigoniidae sp. 2	F			1	1						1	1						1	5
Total		164	24	108	471	468	531	898	1052	274	111	267	469	1330	475	995	701	727	9065