

ECOLOGY, BEHAVIOR AND BIONOMICS

Convergence in the Variation of Local and Regional Gallling Species Richness

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Convergência na Variação Local e Regional da Riqueza de Espécies de Insetos Galhadores

RESUMO - Foram investigados os determinantes locais e regionais da riqueza de insetos indutores de galhas sobre o arbusto dióico *Baccharis concinna* Barroso (Asteraceae) na porção sudeste da Cadeia do Espinhaço, MG. O número total de espécies de insetos indutores de galhas e a riqueza de Cecidomyiidae (Diptera) foram influenciados pelo sexo da planta. Plantas masculinas apresentaram maior riqueza de insetos indutores de galhas do que plantas femininas, corroborando a hipótese da herbivoria mediada pelo sexo na comunidade. O número total de espécies de insetos galhadores e a riqueza de Cecidomyiidae mostraram um pico em altitudes intermediárias. A riqueza de todas as espécies de insetos galhadores e de cecidomyiídeos foi fortemente influenciada pelo habitat. Plantas no habitat xérico apresentaram mais espécies de insetos galhadores do que plantas no habitat méxico, corroborando a hipótese do estresse higrotérmico/nutricional. Os resultados indicam que os fatores locais podem ser importantes estruturadores da comunidade de insetos galhadores em *B. concinna*.

PALAVRAS-CHAVE: *Baccharis concinna*, comunidade ecológica, diversidade, gradiente altitudinal, herbívoro

ABSTRACT - We investigate the local and regional determinants of galling insect richness on the dioecious shrub *Baccharis concinna* Barroso (Asteraceae) in the southeastern portion of the Espinhaço Mountains in Brazil. The total number of galling species and the richness of galling Cecidomyiidae (Diptera) were influenced by plant gender. Male plants supported a higher richness of galling insects than female plants, supporting the hypothesis of sex-biased herbivory at the community level. The total number of galling species and the richness of galling cecidomyiids showed a peak at intermediate altitudes. The richness of all galling species and galling cecidomyiids were strongly influenced by habitat. Plants in xeric habitats supported more galling species than plants in mesic habitats, corroborating the hypothesis of hygrothermal/nutritional stress. Our results indicate that local factors may be the most important factors structuring the galling insect community on *B. concinna*.

KEY WORDS: Altitudinal gradient, *Baccharis concinna*, diversity, ecological community, herbivore

How many species exist on earth? For arthropods alone, estimates vary from 10 to 30 million species (Gaston 1991). Such a discrepancy denotes the amount of uncertainty still involved in the problem. Patterns in the distribution and abundance of organisms are easily recognizable and more informative than the number of species. In this sense, ecology should profit best from identifying repeated patterns and formulating broad generalizations (MacArthur 1972; Lawton 1996).

At the global scale, the clearest pattern of diversity is the decrease of species number with increasing latitude (Pianka 1966, Price 1991, Rohde 1992, Willig *et al.* 2003). Several hypotheses have been proposed to explain such a gradient, but they are circular or weakly supported by empirical data (Rhode 1992, Willig *et al.* 2003). As far as it is known, galling insects are one of the exceptions to this pattern, presenting a peak of diversity at intermediate latitudes (Price *et al.* 1998). At the regional scale, such differences between gallers and

other species are remarkably parallel: insect species diversity is, again, negatively correlated with altitude (Fernandes & Price 1988, 1991; McCoy 1990 and papers cited in; Fernandes & Lara 1993; Skuhrová 1994; Skuhrová & Skuhrová 1994), whereas in some cases galling insect diversity peaks at intermediate altitudes (Waring & Price 1990).

Such a convergence of latitudinal and altitudinal patterns in species diversity of gallers has led authors to speculate about the mechanisms involved (Fernandes *et al.* 2005). Fernandes & Price (1991) observed that the negative relationship between altitude at regional scale and galling species richness was heavily dependent on xeric habitat than mesic habitat, suggesting that altitude is a spurious correlate, and environmental harshness is the key factor determining galling species richness. Such a conclusion is supported by the latitudinal pattern, which galling species richness is higher at intermediate latitudes on warm habitats and sclerophyllous vegetation under water and nutrient stress (e.g., Cerrado or 'Brazilian savannas', Chaparral, and other Mediterranean-type vegetation, Price *et al.* 1998). At the local scale, species richness does not correlate either with host plant architecture (Fernandes & Price 1988) and is only weakly correlated with plant species richness (Fernandes & Price 1988, Blanche & Westoby 1995, but see Wright & Samways 1996).

The pattern of higher richness of galling species in xeric habitat could arise from a few coupled mechanisms. Firstly, the gall itself may be an effective protection against the direct action of climate (Price *et al.* 1987, Stone & Schönrogge 2003). Secondly, given that plant nutrients become toxic to gallers at high levels, gallers would succeed better in harsh environments where plants tend to have low nutrient status (Fernandes & Price 1991). Galling species are able to circumvent the excess of chemical defense, typical of stressed plants (Müller *et al.* 1987, Stone *et al.* 2002), by inducing a phenol-free plant tissue when producing their galls (see Stone & Schönrogge 2003). Thirdly, the differential selective pressures inflicted by natural enemies and plant resistance between xeric and mesic habitats on gallmakers (Fernandes & Price 1988, 1992; Fernandes 1990, 1998).

Nevertheless, most of the above patterns have been observed by gathering data from several environments and host plant species. Those analyses are, therefore, obscured by a variety of correlates, which may confound the results. Here we investigate local determinants of galling insect richness, in a unique system nearly void of confounding variables. We use the system composed by the dioecious shrub *Baccharis concinna* Barroso (Asteraceae) and its associated galling insect community, in a local altitudinal gradient within the same latitude. Using such a system, effects of latitude, plant species richness, and plant architecture need not be considered, reducing the number of confounding variables. Moreover, because we use altitudinal data on a local scale, regional contributions to altitudinal patterns need not to be considered. Our aim is to check the validity of some patterns already reported for galling species, namely, that altitude, plant gender and plant habitat influence the richness of this group of organisms.

Material and Methods

Plant and Galling Insects. *Baccharis* spp. (Asteraceae) are native to the New World and present the highest diversity of galling insects in the Neotropics (Fernandes *et al.* 1996). *B. concinna* is dioecious, and endemic to the Espinhaço range, Minas Gerais southeastern Brazil (Barroso 1976). This plant hosts nine species of galls induced by Cecidomyiidae (Diptera), two by Lepidoptera, two by Curculionidae (Coleoptera), one by Psyllidae (Homoptera), one induced by a fungus, and another by a parasitic plant (Loranthaceae) (Fernandes *et al.* 1996). The present study considered only galls induced by insects.

Study Sites. Collections were taken at Serra do Cipó, in the southern portion of the Espinhaço range, (19°15' e 19°30' S e 43°30' e 43°55' W) at 900, 1000, 1100, and 1300 m above sea level. One site was studied at each altitude. Habitats were typically xeric, with rocky soils, dominated by cerrado and rupestrian field vegetation (see Eiten 1978, Giuliatti *et al.* 1987). At 1300 m additional collections were taken in a mesic habitat, in a site bordering a stream. At all sites, *B. concinna* occurred in patches. Since no obvious barrier was observed, so as to impair interpopulational exchanges, patterns and processes are considered "local", as opposed to "regional".

Sampling and Analyses. Fifty plants of similar size, belonging to each sex, were randomly chosen in each of the four xeric sites along the altitudinal gradient, except at 900 m where we only found 30 males and 20 females. The mesic site at 1300 m held 38 female and 37 male plants. A total of 425 plants were sampled. Gall richness was counted directly on the plants, in the rainy season of 1993. The terms "diversity" and "richness" are used here interchangeably to refer to the number of species. Gall richness refers to (i) the total number of galling insect species or (ii) the number of Cecidomyiidae species, each of these being used as y-variables in separate analyses. They are referred to below as "total richness" and "richness of Cecidomyiidae", respectively.

Statistical analyses were conducted in two stages. Firstly, data from xeric sites were used in a multiple regression to check for the effects of plant gender and local altitude on the number of galling species per plant. In the second stage, data from xeric and mesic sites were used in an analysis of variance to check for the effects of plant habitat and plant gender on the number of galling species per plant. All analyses were followed by inspection of residuals.

Multiple regressions followed the backward stepwise procedure, in which significance is assessed by removing terms from an initial (full) model and observing the F statistic associated to such a change. Terms making up the full model included: plant gender, local altitude, local altitude squared, and their respective interactions. The minimum adequate model achieved by deletion of insignificant terms was used to plot graphs of the relationships studied.

Data used in ANOVAs refer to gallers counted on plants inhabiting xeric and mesic sites at the same altitude (1300 m). Because galls were counted on female as well as on male

plants, plant gender has also been included in these analyses. Thus, factors for the ANOVAs included plant habitat, plant gender, and their interactions.

After performing analyses on the total number of galling insect species, similar statistical procedures were applied to the number of galling Cecidomyiidae species per plant as a separate y variate. The reasoning behind such analyses is that Cecidomyiidae are the most common galling insect taxon (Gagné 1989). Therefore, most patterns might depend heavily on the responses of this one taxon (see Fernandes *et al.* 1994).

Results

Plant Gender and Altitude. The total number of galling species was influenced by plant gender, with male plants supporting higher richness of gallers than female plants (Table 1, Fig. 1). Total richness peaked at intermediate altitudes (Fig. 1), independently of plant gender, as denoted by the absence of a significant interaction term in Table 1. The amount of variance in total richness explained by altitude alone was nearly ten times higher than the variance explained by plant gender (Table 1).

Similar patterns were found for the richness of Cecidomyiidae (Table 2, Fig. 2). The richness of Cecidomyiidae species was influenced by plant gender, with male plants supporting higher richness than female plants. A peak in richness was also observed at intermediate altitudes. Plant gender and altitude did not interact to influence Cecidomyiidae richness. The amount of variance explained by altitude was only 1.5 times higher than the variance explained by plant gender.

Plant Habitat. Galling species richness was strongly influenced by habitat (Table 3). Plants in xeric habitats

supported more galling species than plants in mesic habitats (Fig. 3). In both habitat types, male and female plants did not differ in the richness of galling species (ANOVA $F = 0.028$; $P = 0.867$ xeric habitat; $F = 2.916$; $P = 0.092$ mesic habitat; Fig. 3).

Richness of Cecidomyiidae was also affected by habitat (Table 3). Plants in xeric habitats supported more Cecidomyiidae species than plants in mesic habitats (Table 3, Fig. 4). Within both habitat types, male and female plants did not differ in the richness of galling Cecidomyiidae (ANOVA $F = 2.323$; $P = 0.131$ xeric habitat; $F = 2.765$; $P = 0.121$ mesic habitat; Fig. 3). However at 1300 m altitude, male plants supported more Cecidomyiidae species than female plants (Table 3, Fig. 4).

Discussion

Patterns of galling insects diversity are currently well documented (e.g. Fernandes *et al.* 1994, Price *et al.* 1998), in spite of a poor understanding of the mechanisms generating them (see Fernandes 1990, 1998; Fernandes *et al.* 2005). Hypotheses so far proposed generally rely on local determinants, such as plant gender (Boecklen & Hoffman 1993), plant sclerophylly (Fernandes & Price 1988, 1991), plant water stress (Fernandes & Price 1988, Waring & Price 1990), and environmental-dependent mortality (Taper & Case 1987, Fernandes & Price 1992). A common difficulty faced by researchers in such area of knowledge is to distinguish the actual determinant of the patterns, among a variety of possible interdependent variables. This is a vital step when proposing hypotheses regarding underlying mechanisms for such patterns.

Our data present a unique situation that helps to clearly define the importance of some local determinants of galling species richness. Effects of latitude, plant architecture, plant

Table 1. Effects of plant gender and local altitude of plant location on insect galling species richness attacking *B. concinna*, in Serra do Cipó, Brazil. General model for minimum adequate model is $nsp = alt + alt^2 + intercept$; where nsp = number of galling insect species per plant, and alt = local altitude. The minimum adequate model is presented graphically in Fig. 1.

Multiple regression	df	Deviance	F	P
Plant gender	1	9.740	6.23	0.013
Altitude	1	8.851	5.66	0.018
Altitude ²	1	87.010	55.67	0.001
Plant gender*altitude	1	3.905	2.50	0.115
Plant gender*altitude ²	1	0.001	0.00	0.980
Error	344	537.703		
Total	349	647.210		
Minimum adequate model	n	r ²	F	P
Female plants				
$nsp = 0.069 alt - 0.00003 alt^2 - 35.04$	171	0.18	18.41	< 0.001
Male plants				
$nsp = 0.069 alt - 0.0000306 alt^2 - 33.80$	179	0.14	14.14	< 0.001

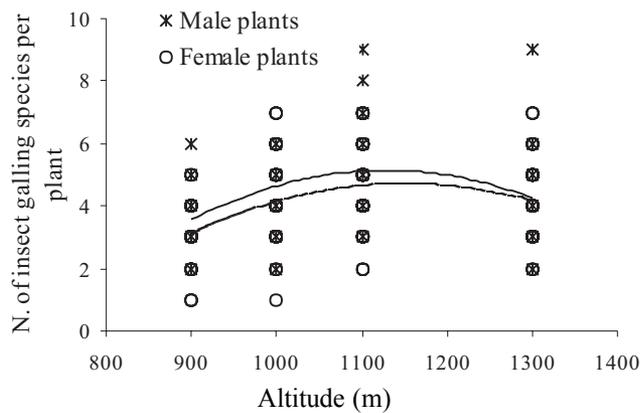


Figure 1. Galling species richness on male and female *B. concinna* along altitudinal gradient in Serra do Cipó, Brazil.

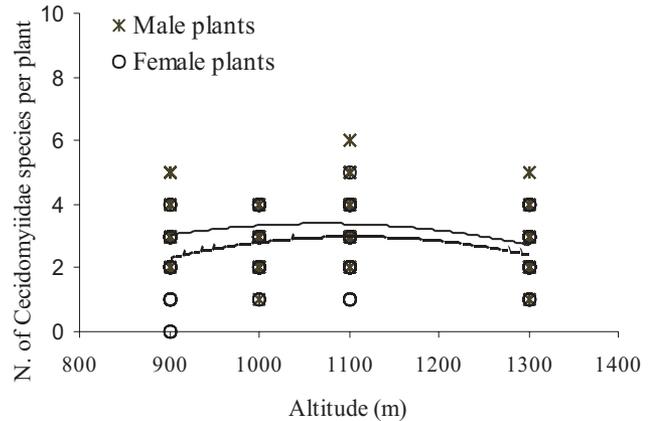


Figure 2. Cecidomyiidae species richness on male and female *B. concinna* along altitudinal gradient in Serra do Cipó, Brazil.

richness, and regional geographical variation needed not be considered, since our system comprises by the entire galling insect community inhabiting a single plant species in closely neighboring sites. Therefore, by using a restricted set of variables, causal factors are more apparent, so that new light could be shed on previous hypotheses.

The first pattern we could clearly define is the effect of altitude on total number of galling species (Fig. 1). Our data revealed a peak of richness at intermediate altitudes (= 1100 m), independent of plant gender. A similar peak has been reported for *Asphondylia* spp. (Cecidomyiidae) on *Larrea tridentata* (DC) Coville by Waring & Price (1990), but with elevation studied over a regional scale, spanning 400 km, and the richest sites located around 700 m. These authors did not analyze explicitly the peak of richness. Rather, they analyzed the reasons why lower elevations would

support fewer galling species. Because their lower elevation sites were located in a desert, they hypothesized that the actual causal factor was plant water stress. Whether or not our results reveal some effect of plant stress mediated by altitude, remains to be explicitly tested in future study. The most important novelty here is that the peak of richness at intermediate altitudes, already reported for cecidomyiid species in a single genus at a regional scale (*Asphondylia* spp, Waring & Price 1990), is also valid for the community of insect gallers on *B. concinna* at a local scale, and is independent of plant gender.

Our data also confirm that male plants support more galling species than female plants. Female plants have been shown to support lower herbivore abundance for a variety of organisms, from fungi to mammals (Herms & Mattson 1992, Boecklen & Hoffman 1993, and references therein).

Table 2. Effects of plant gender and local altitude of plant location, on Cecidomyiidae galling species richness attacking *B. concinna*, in Serra do Cipó, Brazil. General model for minimum adequate model is $nsp = alt + alt^2 + intercept$; where nsp = number of galling Cecidomyiidae species per plant, and alt = local altitude. The minimum adequate model is presented graphically in Fig. 2.

Multiple regression	df	Deviance	F	P
Plant gender	1	15.064	9.64	0.002
Altitude	1	6.745	4.32	0.039
Altitude ²	1	15.800	10.11	0.002
Plant gender*altitude	1	0.826	0.53	0.468
Plant gender*altitude ²	1	0.021	0.01	0.909
Error	344	335.615		
Total	349	374.070		
Minimum adequate model	n	r ²	F	P
Female plants				
$nsp = 0.00295 alt - 0.0000134 alt^2 - 13.21$	171	0.07	5.91	0.003
Male plants				
$nsp = 0.00267 alt - 0.0000125 alt^2 - 10.89$	179	0.07	6.09	0.003

Table 3. Effects of plant gender and plant habitat (xeric or mesic), on galling species richness attacking *B. concinna* in Serra do Cipó, Brazil. Histograms for these analyses are presented in Figs. 3 and 4.

Analysis of variance	df	SS	F	P
Richness of insect gallers (y)				
Plant gender	1	1.512	1.24	0.266
Plant habitat	1	32.900	27.11	< 0.001
Pl.gender*Pl.habitat	3	1.420	0.39	0.760
Error	171	207.460		
Total	176	243.900		
Richness of Cecidomyiidae (y)				
Plant gender	1	2.810	4.76	0.030
Plant habitat	1	4.858	8.23	0.005
Pl.gender*Pl.habitat	3	0.003	0.00	0.999
Error	171	100.920		
Total	176	108.590		

The simplest consequence of this would be that female plants, by supporting fewer galling individuals, would 'miss' rare species, thereby generating lower galler richness, as revealed by our data. An in depth analysis of galler abundance will be presented elsewhere.

Another pattern, which has been already reported for gallers on a variety of host plant species, is the increased richness in xeric environments (Fernandes & Price 1992). Our data, again, confirmed such a pattern, but more clearly than previous studies, since these data refer to a single plant species, in closely neighboring sites, at the local scale.

All but one of the above patterns were closely followed by the Cecidomyiidae alone: richness presented a peak at intermediate altitudes (Fig. 2), plant gender did not interact with altitude (Table 2), male plants presented higher galling species richness than female plants (Fig. 2), and xeric habitats present higher galling species richness than mesic habitats.

However, Cecidomyiidae did not show any inter-sex bias in plant attack (Table 3, Fig. 4). Considering that Cecidomyiidae is the most common galling taxon (Gagné 1989, 1994), we tend to believe that this will be the general pattern for gallers elsewhere. In other words, plant habitat seems to be more important than plant gender in determining local galling richness.

In conclusion, local patterns observed here confirm general trends presented by galling species richness elsewhere, even when such trends are apparent at regional scales. This seems to suggest that whatever the mechanisms, underlying such patterns, the key factor may be operating at the local level. Also, a striking resemblance exists between patterns observed elsewhere for abundance of gallers and the patterns described here, despite the fact that our data refer only to species richness. When richness mirrors abundance, it means that losses in individuals represent

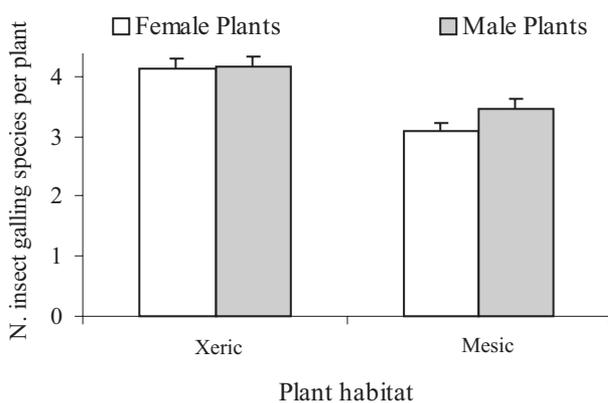


Figure 3. Galling species richness on male and female *B. concinna* on xeric and mesic habitats in Serra do Cipó, Brazil.

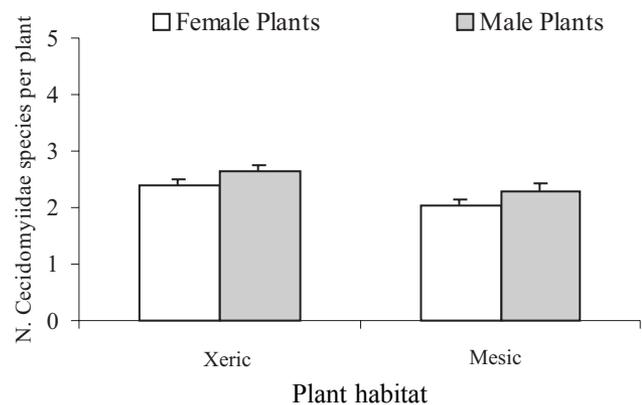


Figure 4. Cecidomyiidae species richness on male and female *B. concinna* on xeric and mesic habitats in Serra do Cipó, Brazil.

proportional losses in species numbers. In other words, species rank abundances remain unchanged when population densities change, which suggests that community organization, should be more dependable on environmental conditions than on species interactions. We conclude that galling insect species on *B. concinna* seems to be regulated by local determinants unrelated to species interactions. Nevertheless studies should be extended to other populations along distribution at gradients of other suitable test this conclusion.

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