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# Effects of Hygrothermal Stress, Plant Richness, and Architecture on Mining Insect Diversity<sup>1</sup>

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## ABSTRACT

We investigated the distribution patterns of leaf mining insects along an elevational gradient in cerrado vegetation of southeastern Brazil. We tested four hypotheses related to the distribution of mining insects: (1) the “altitudinal gradient hypothesis,” which predicts that mining insect species richness will decrease with altitude or elevation; (2) the “habitat-mediated richness hypothesis,” which predicts that mining insect species richness will be higher in mesic habitats than in xeric habitats; (3) the “plant species richness hypothesis,” which predicts that mining insect species richness will be positively correlated with plant species richness; and (4) the “plant architecture hypothesis,” which predicts a positive correlation between mining insect species richness and plant structural complexity. A total of 33,000 herbs, 3520 shrubs, and 1760 trees were sampled at 44 sites across an elevational gradient of 700 m. Mining insect species richness and plant species richness showed a negative correlation with elevation in xeric habitats, while in mesic habitats mining insect species and plant species richness did not show any statistically significant relationship with elevation. The differential distribution of mining insect species between xeric and mesic habitats supported the habitat-mediated richness hypothesis, which states that miners would be more speciose in mesic, more favorable habitats. Mining species richness also increased with increasing plant structural complexity. The results suggest that the mining habit may not represent a strong adaptive strategy in protecting mining insects against desiccation.

## RESUMO

Nós investigamos os padrões de distribuição de insetos minadores ao longo de um gradiente altitudinal no cerrado, no sudeste do Brasil. Testamos quatro hipóteses relacionadas à distribuição de insetos minadores: (1) a “hipótese do gradiente altitudinal” que prediz que a riqueza de espécies de minadores aumenta com o decréscimo da altitude; (2) a “hipótese da riqueza mediada pelo habitat” que prediz que a riqueza de espécies de minadores deve ser maior em habitats mésicos que em habitats xéricos; (3) a “hipótese da riqueza de espécies de plantas” que prediz que a riqueza de espécies de minas deve ser positivamente correlacionada com a riqueza de espécies de plantas; e (4) a “hipótese da arquitetura da planta” que prediz uma correlação positiva entre riqueza de espécies de minas e complexidade estrutural das plantas. Foram amostradas 33,000 ervas, 3520 arbustos, e 1760 árvores, em 44 sítios ao longo de um gradiente de 700 m: A riqueza de espécies de minadores e de plantas apresentou uma correlação negativa com a altitude em habitats xéricos. Entretanto, em habitats mésicos as espécies de minadores e a riqueza de espécies de plantas não apresentaram nenhuma relação estatisticamente significativa com a altitude. A distribuição diferencial de espécies de minadores entre habitats xéricos e mésicos corroborou a hipótese da riqueza mediada pelo habitat, segundo a qual a riqueza de minas deve ser maior em habitats mésicos, que são mais favoráveis. A riqueza de espécies de minadores aumentou com o aumento da complexidade estrutural da planta. Estes resultados sugerem que o hábito minador não deve representar uma forte estratégia adaptativa para fornecer aos minadores proteção contra dessecação.

*Key words:* altitudinal gradients; habitat-mediated richness hypothesis; insect herbivory; mining insects; rupestrian fields.

THE DECREASE IN INSECT SPECIES RICHNESS WITH INCREASING ELEVATION appears to be a global phenomenon (Randall 1982, Wolda 1987, Fernandes & Price 1988, Price 1991) although some exceptions have been described (Janzen 1973, Janzen *et al.* 1976, Gagné 1979, McCoy 1990, Olson 1993, Samson *et al.* 1997). For example, the decrease in

species richness of galling herbivores with increasing elevation is a consistent pattern observed along elevational gradients in different parts of the globe (Waring & Price 1990, Fernandes & Price 1991, Fernandes & Lara 1993, Price *et al.* 1998). Free-feeding insects, on the other hand, show no consistent distribution patterns along elevational gradients. Free-feeding insect species richness can decrease with increasing elevation (Herbert 1980, Wolda 1987), show mid-elevation peaks in species richness (Janzen 1973, Janzen *et al.* 1976, Gagné

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1979, McCoy 1990, Olson 1993, Samson *et al.* 1997), or show no clear patterns (Carneiro *et al.* 1995, Ribeiro *et al.* 1998, Marques & Price 1999).

Despite the importance in describing patterns of insect species distributions, few studies have tried to test them in the field. Even fewer studies have attempted to identify the mechanisms that explain why species richness changes along elevational or latitudinal gradients (Rohde 1992; *cf.* Fernandes & Price 1992); however, a successful attempt in testing hypotheses regarding the distribution of gall-forming insects has been achieved. The increase in gall-forming species richness with decreasing elevation has been attributed to the increasing environmental harshness at lower elevations (xeric habitats), where gall-forming insect species suffer lower mortality rates due to lower parasitism and plant resistance (Fernandes & Price 1992). Therefore, gallers achieved higher abundances and, ultimately, speciation rates in harsher habitats in which gallers suffered lower pressures caused by natural enemies and plant resistance (Price *et al.* 1987, Fernandes *et al.* 2004).

In an attempt to understand the patterns and driving mechanisms of insect distributions, we studied the distribution of several insect guilds along an elevational gradient in southeastern Brazil. In this elevational range, free-feeding herbivorous insects showed a different pattern than that of galling insects, being more speciose in mesic habitats than in xeric habitats (Fernandes & Price 1988, Carneiro *et al.* 1995, Ribeiro *et al.* 1998). Although parasitism may be greater in mesic habitats, free-feeding insects are more likely to suffer from the harsh environmental conditions imposed by xeric habitats (Fernandes & Price 1992). Ant distributions also showed a similar pattern as that of free-feeding insects, being more species-rich in more humid habitats and at lower elevations. Moreover, habitat structural complexity was the most important factor correlated with ant species diversity along the elevational gradient (Araújo & Fernandes 2003).

In this study, we report the richness of leaf mining insects along an elevational gradient in an attempt to understand if the forces that shape the insect distribution patterns already reported also impact mining insects in the same way. We are unaware of any other study specifically reporting the distribution of mining species along elevational gradients, as well as between habitat types, in the Neotropics. Leaf miners present several spatial distribution patterns (Needham *et al.* 1928, Condras-hoff 1964, Miller 1973, Faeth *et al.* 1981,

MacGarvin *et al.* 1986, Cumbreira 1998) and are of particular interest because they are often abundant and can affect growth and reproduction of both native and cultivated host plants (Hering 1951, Louda 1984). The adults are generally host-specific and females are very selective in their oviposition sites (Hering 1951, Miller 1973, Whitfield *et al.* 1985). Larval occurrence and damage should reflect qualitative and quantitative differences in plant quality detectable by the ovipositing female (Chew 1977, Rausher 1979, Faeth *et al.* 1981, Pritchard & James 1984, Connor *et al.* 1994). Furthermore, leaf miners have an intermediate form of host use between gallers and free-feeders (*i.e.*, their larvae are internal tissue feeders but do not develop galls). Therefore, we predicted that we would find strong habitat preference by mining insects (Fernandes & Price 1988, Price *et al.* 1998).

We tested four hypotheses in this study: (1) the "altitudinal gradient hypothesis," which predicts that species richness will decrease with altitude or elevation (Pianka 1966). Several positive factors would act synergistically and contribute to higher species abundance and richness at low elevations, such as larger area and habitats provided for colonization; (2) the "habitat-mediated richness hypothesis," which predicts that mining insect species richness will be higher in mesic habitats due to their better environmental conditions compared to the harsh conditions of xeric habitats and the low protection the mine would offer in more arid habitats. Leaf miners excavate the leaves leaving only a thin layer of cells to cover them, which does not provide an effective protection against desiccation and predation (Connor & Taverner 1997). Such feeding habit would represent a poor adaptation to xeric habitats where stressful conditions are greater (Fernandes & Price 1991); (3) the "plant richness hypothesis," which predicts a positive correlation between mining species richness and plant species richness. More plant species would represent more diverse resources and niches to be explored and occupied by mining insect herbivores (see Southwood 1960, 1961); and (4) the "plant architecture hypothesis," which predicts that structurally complex plants will have more niches, and hence support more species than architecturally less complex plants. Thus, more mine species would be found on trees than on shrubs and herbs (Lawton & Schröder 1987).

## METHODS

**STUDY SITE.**—The study was performed between Lagoa Santa and Serra do Cipó in Minas Gerais,

southeastern Brazil (19°10'–19°40'S, 43°30'–43°55'W). The study area was located between 800 and 1500 m elevation. The region has a dry period of four to five months in winter (April–August) and a rainy period of four to five months in summer (December–March) with a mean annual rainfall of 1400 mm. January is the month with most rainfall while August is the driest month. Mean annual temperature varies from 18 to 20°C (Nimer 1977). At the highest elevations, the climate is moderated by moisture-laden clouds, which provide humidity throughout most of the year (Giulietti & Pirani 1988). Temperature and habitat dryness, hereafter called hygrothermal stress, increase with decreasing elevation in xeric gradients (Fernandes & Price 1988). Throughout the gradient, narrow gallery forest occurs in riparian habitats along rivers, washes, and creeks. These forests allow for milder environmental conditions since the taller vegetation reduces wind and evapotranspiration, thereby promoting lower temperature variation. Such extreme environmental conditions occurring at the same elevation were ideal to field test these hypotheses.

Several vegetation types were distributed along the elevational gradient. Cerrado vegetation (savanna) occurred from 700 to 900 m; from 900 to 1100 m, there was an ecotone between cerrado and rupestrian fields; and rupestrian fields dominated from 1100 to 1300 m. Above 1300 m, the area was dominated by altitudinal grassland. Sclerophyllous plants are the main component of cerrado and rupestrian field vegetation. These sites are characterized by high solar radiation, low water retention in the soil, low nutrient availability, high aluminum content, and frequent fires in the dry season (Goodland & Ferri 1979, Ribeiro & Fernandes 2000).

**SAMPLING METHODOLOGY.**—Samples were taken in 1991 along an elevational gradient that varied from 800 to 1500 m divided into 100 m intervals. At each elevation, six sample sites were defined, three in xeric habitats (away from water sources) and three in mesic habitats (along water sources). Sites were at least 1 km apart to avoid pseudo-replication. Mines and plants were sampled at eight elevations and comprised 44 sample sites (24 sites in xeric habitats and 20 sites in mesic habitats). There were no water courses at 1500 m and only two at 1400 m; thus we had no mesic sites at 1500 m and only two at 1400 m. For a detailed site description, see Ribeiro and Fernandes (2004).

A transect 10 m wide was set up within each

site, within which 750 herbaceous plants, 80 shrubs, and 40 trees were sampled. These numbers were defined through species–area curves described by Fernandes and Price (1988), which were estimated to obtain an asymptotic accumulation of species. Categories of plant architecture analyzed were herbs, shrubs, trees, and all plants (herbs + shrubs + trees). To test the hypotheses, we required a gradient of niche availability from trees, to shrubs, and then herbs. The length of the transect varied according to the density of herbs, shrubs, and trees in the habitat. Mines were surveyed on a total of 33,000 herbs, 3520 shrubs, and 1750 trees ( $N = 38,270$  plants). All plants and mining species were recorded as morphospecies because most of the species are still undescribed. The methodology used for sampling galling insects should be appropriate for sampling mining species because of the conspicuousness and persistence of mined leaves on the plants. Most plants in the area have sclerophyllous leaves, which are mostly persistent on the plant (Fernandes & Price 1991). A survey was conducted during the growth period of plants, diminishing the probability of leaf abscission. Furthermore, because of their diverse morphology, mines formed by different species generally can be distinguished by their architectural patterns and used to accurately estimate the abundance and richness of mining species in an area (Hering 1951, Basset 1991, Esposito 1994).

**STATISTICAL ANALYSES.**—Simple linear regression analyses were used for testing the distribution patterns of mining species richness with elevation in both mesic and xeric habitats. The number of mining species ( $S$ ) was log transformed. Differences in species richness in xeric and mesic habitats were analyzed by using a paired Student  $t$ -test (Zar 1996). To test the effects of plant species richness, on mining species richness, we also used simple linear regression analysis. Mining species richness on plant architectural types was analyzed by a one-way analysis of variance (ANOVA), and mean differences were compared through a Tukey HSD multiple comparisons test.

## RESULTS

**THE ALTITUDINAL GRADIENT HYPOTHESIS.**—Mining insect species richness was negatively correlated with elevation in harsh habitats (Fig. 1). In the more arid xeric habitats of Serra do Cipó, elevation accounted for 76 percent of the variation in mine richness on all plants ( $R^2 = 0.76$ ;  $y = 6.02 - 0.004x$ ;

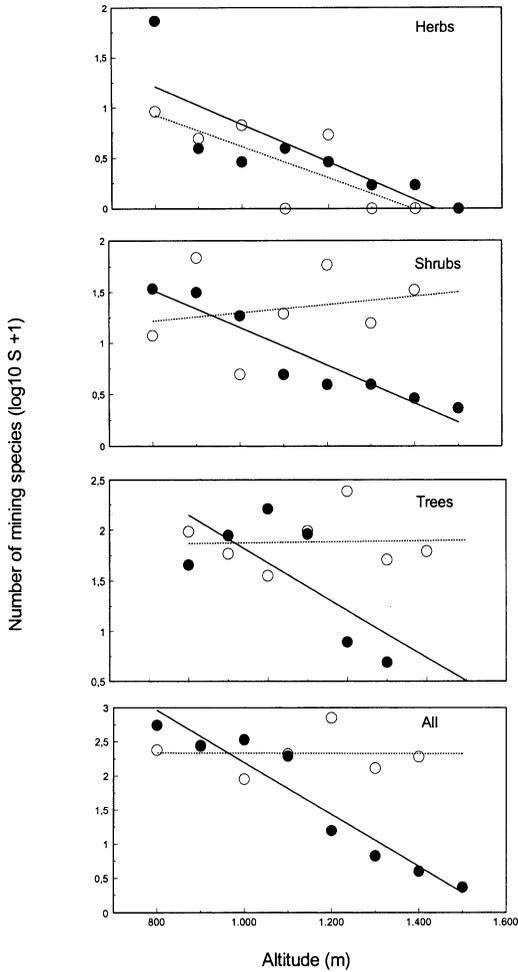


FIGURE 1. Regression of mining species richness on herbs, shrubs, trees, woody plants (shrubs + trees), and all plants (trees + shrubs + herbs) with elevation (800 m–1500 m) in xeric (solid lines, closed circles) and mesic (dotted lines, open circles) habitats of Serra do Cipó. The “y”-axes are on logarithmic scales. See text for details.

$F = 76.83, P < 0.001$ ), 44 percent of the variation on shrubs ( $R^2 = 0.44, y = 2.99 - 0.002x; F = 16.90, P < 0.001$ ), and 42 percent of the variation on herbs ( $R^2 = 0.42; y = 2.71 - 0.002x; F = 16.14, P < 0.005$ ). Despite the trend of decreasing numbers of mining insect species on trees with elevation in xeric habitats, the relationship was not statistically significant.

In mesic habitats, mining insect species richness showed a statistically significant relationship with elevation only for herbs ( $R^2 = 0.46; y = 2.28 - 0.002x; F = 12.03, P < 0.005$ ; Fig. 1).

**THE HABITAT-MEDIATED HYPOTHESIS.**—The mean number of mine species per host plant was only  $1.11 \pm 0.02$ . Comparisons of mine species richness between xeric and mesic habitats for shrubs, trees, and all architectural plant categories showed higher richness of miners in mesic habitats compared to xeric habitats. Only herbs showed an inverse pattern (Table 1).

**THE PLANT RICHNESS HYPOTHESIS.**—Elevation negatively influenced plant species richness in xeric habitats (Fig. 2). In these habitats, elevation influenced 69 percent of the variation in the number of plant species on all plants ( $R^2 = 0.69; \log y + 1 = 6.31 - 0.002x; F = 48.53, P < 0.001$ ), 48 percent of the variation on shrubs ( $R^2 = 0.62; \log y + 1 = 5.53 - 0.003x; F = 35.65, P < 0.001$ ), and 55 percent of the variation on herbs ( $R^2 = 0.55; \log y + 1 = 4.76 - 0.001x; F = 27.10, P < 0.001$ ). No relationship was found for trees.

On the other hand, in mesic habitats, plant species richness did not show any statistically significant relationship with elevation (Fig. 2). No relationship was found between plant richness and elevation for herbs, shrubs, trees, and for all plants ( $P < 0.05$ , all).

Plant species richness positively influenced mining species richness in xeric habitats. In these habitats, plant species richness influenced 76 percent of the variation in the number of leaf mining

TABLE 1. Results of Wilcoxon signed rank test performed for mining species richness on plants of different structural complexities in xeric and mesic habitats.

Plant category	Mean mine number ( $\pm 1$ SE)		Wilcoxon test	P-value
	Xeric	Mesic		
Herbs	1.25 $\pm$ 0.40	0.82 $\pm$ 0.21	2.34	<0.05
Shrubs	1.96 $\pm$ 0.43	3.35 $\pm$ 0.47	4.94	<0.05
Trees	5.53 $\pm$ 0.85	6.15 $\pm$ 0.68	5.17	<0.05
All	6.63 $\pm$ 1.25	10.20 $\pm$ 1.03	5.51	<0.05

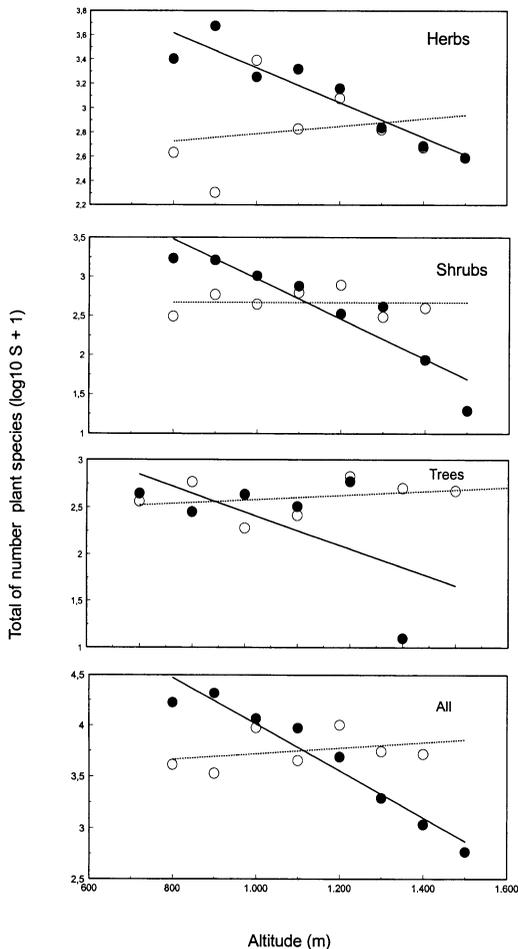


FIGURE 2. Regression of the total number of plant species on herbs, shrubs, trees, woody plants (shrubs + trees), and all plants (trees + shrubs + herbs) with elevation (800–1500 m) in xeric (solid lines, closed circles) and mesic (dotted lines, open circles) habitats of Serra do Cipó. The “y”-axes are on logarithmic scales. See text for details.

species on all plants ( $R^2 = 0.76$ ;  $\log y + 1 = -3.38 + 1.36 \log x + 1$ ;  $F = 68.68$ ,  $P < 0.001$ ), 42 percent of the variation on shrubs ( $R^2 = 0.42$ ,  $\log y + 1 = -0.56 + 0.56 \log x + 1$ ;  $F = 15.74$ ,  $P < 0.005$ ), and 31 percent of the variation on herbs ( $R^2 = 0.31$ ;  $\log y + 1 = -2.05 + 0.84 \log x + 1$ ;  $F = 10.01$ ,  $P < 0.005$ ), and 33 percent of the variation on trees ( $R^2 = 0.33$ ;  $\log y + 1 = -0.04 + 0.74 \log x + 1$ ;  $F = 5.85$ ,  $P < 0.05$ ).

In mesic habitats, only shrubs showed a positive relationship between plant species richness and mining species. In this plant growth form, plant richness explained 24 percent of the variation of mining insect richness ( $R^2 = 0.24$ ;  $\log y + 1 =$

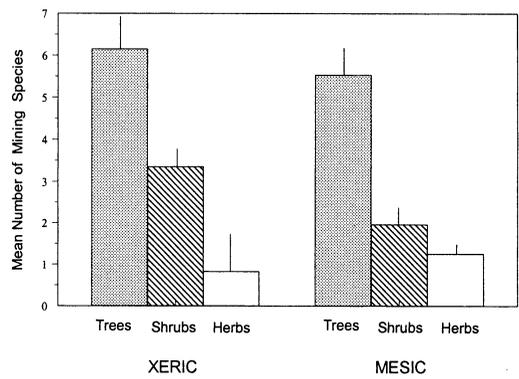


FIGURE 3. Mean number ( $\pm 1$  SE) of mining species on plants of different structural complexity in xeric and mesic habitats. (Tukey HSD multiple comparison,  $N = 20$ ,  $P < 0.0001$ ).

$-1.35 + 1.00 \log x + 1$ ;  $F = 5.70$ ,  $P < 0.05$ ). No relationship was found in the other categories.

**THE PLANT ARCHITECTURE HYPOTHESIS.**—Plant architecture influenced mine species richness in xeric (one-way ANOVA,  $F_{4, 80} = 5.48$ ,  $P < 0.05$ ), as well as in mesic (one-way ANOVA,  $F_{4, 83} = 128.44$ ,  $P < 0.05$ ) habitats. Mining species richness increased with increasing plant structural complexity. In mesic habitats, the mean number of mining species was higher on trees ( $\bar{x} = 6.15 \pm 0.68$ ) than on shrubs ( $\bar{x} = 3.35 \pm 0.47$ ) and herbs ( $\bar{x} = 0.82 \pm 0.21$ ). Similarly, in xeric habitats the mean number of mining species was higher on trees ( $\bar{x} = 5.53 \pm 0.85$ ) than on shrubs ( $\bar{x} = 1.96 \pm 0.43$ ) and on herbs ( $\bar{x} = 1.25 \pm 0.405$ ). All means were significantly different according to Tukey HSD multiple comparisons test ( $N = 24$ ,  $P < 0.05$ ; Fig. 3).

## DISCUSSION

Overall, along the harsh conditions offered by the xeric habitats of Serra do Cipó, leaf mining species richness decreased with increasing elevation as predicted by the altitudinal gradient hypothesis (Fernandes & Price 1991); along the most favorable conditions provided by the mesic habitats, the altitudinal gradient hypothesis was not corroborated. These findings indicate that the mining habit is more favorable at lower elevations and in mesic habitats.

The differential distribution of leaf mining species between xeric and mesic habitats supports the habitat-mediated richness hypothesis, which states that miners would be more speciose in mesic, more

favorable habitats. This pattern is similar to that found for sucking and chewing insect herbivores (Ribeiro *et al.* 1998) and ants (Araújo & Fernandes 2003) at the same sites and elevational gradients. Nevertheless, the pattern is opposite to that found for gall-forming insects (Fernandes & Price 1988, Lara *et al.* 2002), all sampled at the same sites and times of the year. Otherwise, the pattern differs from that reported for three tropical forests in Panama, where leaf miners were more speciose on tree canopies compared to the understory (Cumbreira 1998). The canopy should naturally simulate harsher conditions compared to the more humid and shaded understory, thereby presenting a paradox that can only be resolved with more studies.

The mechanisms that drive the pattern we found are still unknown for leaf mining insects. Plant species richness, however, may play a part. The association between mining insects and host plants is very specific (Hering 1951) and can drive the richness pattern. The positive correlation between mine richness and elevation may be explained by the positive correlation between plant species richness and altitude at lower elevations. Within xeric habitats, sites at lower elevations had more plant species than habitats at higher elevations.

Another important factor that may account for the lower diversity of miners in xeric habitats is the high degree of sclerophylly in cerrado host plants, which would reduce larval establishment and success. The cerrado vegetation has a high index of sclerophyllous plants (Goodland & Ferri 1979, Allain *et al.* 1998). Furthermore, sclerophylly is said to be strongly correlated with high levels of chemical defenses, particularly tannins (Janzen 1974, Coley 1983, Coley *et al.* 1985, Ribeiro & Fernandes 2004). In contrast to gall-forming insects that are able to circumvent and manipulate host defenses in these more stressful habitats (Fernandes & Price 1991), miners may not be as successful. These traits may hinder the colonization and use by free-feeding insect herbivores as well as mining insects (Feeny 1970, Coley 1983, Raupp 1985, Coley & Aide 1991, Fernandes & Price 1991). Toughness and sclerophylly may act syn-

ergistically with the high concentration of immobile defenses to diminish the success of mine colonization in xeric habitats. Hence, mining insect communities may be strongly influenced by the quality of their hosts and climatic factors, such as high temperature and solar radiation in arid habitats (Connor & Taverner 1997). Interestingly, Cumbreira (1998) has made use of almost the same factors we mentioned to explain the higher richness of miners on the more stressed conditions found in canopy habitats relative to understory habitats of tropical forests in Panama. We suggest that studies on life table and population dynamics that consider host plant quality under different habitat conditions must be urgently performed to better understand the differential distribution of miners in dry versus humid and light-exposed (canopy) versus shaded (understory) habitats.

The plant architecture hypothesis was corroborated in this study. Architecturally more complex host plants have a greater number and variety of ecological niches available for insects, enabling these plants to support more insect species (Lawton & Schröder 1987). These results, however, differ from those obtained for gallers in which more species were found on shrubs than on trees or when no statistical differences were found between them (Fernandes & Price 1988, Lara *et al.* 2002).

The mine is believed to be an adaptive strategy of mining organisms to avoid the harsh conditions of the environment that lead to desiccation, but very little evidence exists to support this conclusion (Connor & Taverner 1997). The greater species richness of miners in mesic habitats provides evidence to support the hypothesis that the mining habit may not represent a strong adaptive strategy for protection against desiccation (*cf.* Cumbreira 1998).

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