

# Altitudinal patterns in a tropical ant assemblage and variation in species richness between habitats

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## Abstract

The distribution of ants along an altitudinal gradient from 800 m to 1500 m was studied in southeastern Brazil. Two hypotheses were tested: a) "the altitudinal gradient hypothesis", which predicts that ant species richness decreases with increasing altitude; and b) "the habitat favourability hypothesis", which predicts that ant species richness is higher in mesic habitats than in xeric habitats, independent of altitude. Pairs of mesic and xeric habitats were randomly established and replicated three times at each 100 m of elevation. Mesic habitats were those along washes, creeks and rivers while xeric habitats were those away from water resources. Ants were collected utilizing sardine baits distributed along transects on both vegetation and on soil. The species richness of ants collected on vegetation and soil increased with decreasing elevation. This pattern was found for ants collected on the ground in both mesic and xeric habitats. Also, we found more ant species in mesic habitats ( $0.64 \pm 0.05$  ants/sample set) than in xeric habitats ( $0.45 \pm 0.05$  ants/sample set) ( $t = 3.51$ ,  $p < 0.001$ ). The decreased number of ant species at higher elevations as well as in xeric habitats may be caused by a decrease in habitat complexity that limits the success of ants. Furthermore, at high altitudes harsher habitat conditions and lower temperatures prevail, further limiting the success and establishment of ants.

**Keywords:** Altitudinal Gradients, Ants, Cerrado, Diversity, Habitat Complexity

## Introduction

In the Brazilian cerrado the variations in the patterns of distribution of insects along altitudinal gradients have been described for only a few areas (Fernandes & Price, 1988, 1991; Carneiro et al., 1995; Araújo, 1996). These studies have either corroborated the pattern of diminishing species richness with increasing elevation (Fernandes & Price, 1988; Fernandes et al., 1997), detected no pattern (Carneiro et al., 1995), or pointed to an increase in species richness in relation to altitude (Ribeiro et al., 1994) (for review see Fernandes et al., 1997).

The cerrado (savanna) is a xeromorphic formation that covers about 23% of Brazil (Eiten, 1979; Furley & Ratter, 1988; Ratter et al., 1997). Its flora displays a high level of endemism (Ab'Saber, 1971; Ratter et al., 1997) and harbors a rich diversity of insect species (Silveira & Campos, 1995). Serra do Cipó is a high altitudinal area in the southeastern central Brazilian plateau. It is covered by a cerrado formation with a predominance of xeric habitats. The landscape is composed of various vegetation physiognomies that change gradually from cerrado to altitudinal grassland. Nevertheless, sclerophylly predominates across all altitudes (Giullietti & Pirani, 1988).

Although ants play a fundamental ecological role in cerrado ecosystems (Lévieux, 1982, 1984), little is known about the structure of their communities in the cerrado (but see Moraes, 1980). For the first time, we test two hypotheses on the distribution of ants along an altitudinal gradient and their differential distribution between mesic and xeric habitats in Brazil. Data were collected in the various physiognomic formation of the cerrado in Serra do Cipó. The "altitudinal gradient hypothesis" predicts a negative correlation between ant species richness and altitude. Several studies have shown that decreased availability of nesting sites and increased habitat harshness at higher altitudes limit ants distribution and richness (Brown, 1973; Janzen, 1973). The "habitat favourability hypothesis" predicts a greater richness of ant species in mesic habitats compared to xeric habitats (Andersen, 1986; Levieux, 1982; Benson & Harada, 1988). We believe that in the Serra do Cipó the larger woody plants encountered in mesic habitats, result in increased habitat complexity and availability of resources, therefore providing more diverse nesting sites and better foraging conditions (Carroll, 1974; Young, 1982, 1986).

## Methods

This study was conducted in the southeastern portion of the Espinhaço Mountains in the Serra do Cipó region (19° 10' - 19° 40' S and 43° 30' - 43° 55' W). This region presents a diversified vegetation, varying with altitudinal and soil type,

and is dominated by sclerophyllous species (Giulietti & Pirani, 1988; Giulietti et al., 1997, Fernandes, unpublished).

Ants were collected at eight different altitudes between 800 m and 1500 m above sea level. At each altitude, six sampling sites were defined and paired: three in mesic and three in xeric habitats. Mesic habitats were defined as those near washes, canyons and rivers, while xeric habitats were defined as those habitats away from water sources (see Fernandes & Price, 1988 for details). Hence, the vegetation of mesic habitats was primarily riparian. Xeric vegetation varied from cerrado at lower elevations (800 m) to altitudinal grassland at the highest sites (1500 m). Sampling sites were separated from each other by a least 1 km in an attempt to avoid pseudoreplication.

To evaluate the species richness of ants, we used baits of canned sardines in vegetable oil. Baits comprised of animal protein have been used frequently in ant surveys (Leving, 1983; Caldas & Moutinho, 1993; Roth & Perfecto, 1994) and sardine baits are especially effective in capturing ants in cerrado vegetation (Morais, 1980). All ant collections were conducted during the dry season, from April to August, in order to reduce environmental variations associated with the increased humidity during the wet season. A transect of 100 m was established at each sample site. Baits were placed on 8x 8 cm squares of paper towel and set out 10 m apart along the transect line. Baits were placed in pairs: one on ground and one on adjacent vegetation at a height of 1.5 m above the ground. Hence, 120 baits were distributed at each altitude between 800 m and 1300m: 60 baits on the ground and 60 baits on vegetation. Only one hundred baits were used at 1400 m because we only found two mesic habitats at this altitude. No mesic habitat was found at 1500 m. Since the vegetation at this altitude was of low stature (lower than 1,5m), only 50 grounds samples from 5 xeric sites were taken.

Sampling was done between 09:00 and 16:30h, enabling us to capture only diurnal ants. Baits were exposed for 45 minutes. This exposure time was tested through a saturation curve elaborated from data sampled in the area (Araújo, 1996). Each bait, with its associated ants, was then sprayed with ethyl acetate and placed in a marked plastic bag. When ant identification was not possible, the specimens were separated into morphospecies and preserved in 70% alcohol. Samples of species collected were deposited at the Departamento de Biologia Geral, ICB/Universidade Federal de Minas Gerais and the Museum of the Instituto de Zoologia Agrícola MIZA (Agricultural Zoology Institute) Venezuela.

To complement the bait captures and to further compare the species richness in mesic and xeric habitats, we also sampled ants directly from the vegetation. At each transect, three branches (about 1.0 m long) were cut from each of 20 randomly select trees and/or large shrubs. Branches were immediately placed in marked plastic bags and sprayed with ethyl acetate to kill ants. We measured the diameter at breast height (DBH) for each sampled plant. These measurements of plant size were then correlated with ant species number to obtain an indirect indication of resource availability. The index for the basal area (BA) of trees and shrubs sampled in this study was adapted from Müller-Dambois (1977) and then transformed into  $\log_{10}(BA + 1)$  (Zar, 1984). In the laboratory, we recorded the ant species found, and the presence or absence of immature stages (eggs, larvae and pupae) in an attempt to

estimate colony size (see Young, 1986). Each occupied branch was considered as an ant nest. Since only ants residing in stems were included, this study does not provide information about the size of the entire arboreal nesting ant fauna. Those ants that nest in myrmecophytes, trunk epiphytes, and bound leaves were excluded. To test the altitudinal gradient hypothesis we used simple linear regressions, while to compare ant species richness between mesic and xeric habitats we used the Wilcoxon signed rank test. Differences in ant species richness on branches of plants in mesic and xeric habitats was compared by the t-test (Zar, 1984).

## Results

A total of 42 morphospecies of ants from 18 genera were recorded from 870 baits and 820 trees in Serra do Cipó. Of these, 17 morphospecies were obtained from the vegetation within xeric and mesic habitats (Tab. 1). Thirty morphospecies were widely distributed along the ground of both adjacent and contiguous habitats (Tab. 2). The richness of ants obtained was lower than that reported by Morais (1980) for the cerrado vegetation and Samson et al. (1997) along an altitudinal gradient in the Philippines.

The richness of ant species obtained utilizing baits on vegetation and on the ground was negatively associated with altitude in mesic habitats. Most of the variation in the number of species of arboreal ants in mesic habitats was explained by the altitude ( $r^2 = 0.87$ ,  $F = 32.82$ ,  $y = 13.32 - 0.007x$ ,  $p < 0.002$ , Fig. 1). The richness of ants sampled on the ground was negatively correlated with altitude both in mesic and xeric habitats (mesic:  $r^2 = 0.57$ ,  $F = 6.56$ ,  $y = 25.75 - 0.014x$ ,  $p < 0.05$ ; xeric:  $r^2 = 0.81$ ,  $F = 29.14$ ,  $y = 27.3 - 0.017x$ ,  $p < 0.001$ , Fig. 2). However, this relationship was not statistically significant for arboreal ants in xeric habitats ( $r^2 = 0.26$ ,  $F = 1.76$ ,  $y = 6.25 - 0.179x$ ,  $p > 0.05$ , Fig. 1).

The richness of ant species obtained by directly cutting branches from vegetation at the same altitude yielded more species of arboreal ants in mesic than in xeric habitats. Each plant in mesic habitats supported on average 50% more species of ants than plants in xeric habitats (Tab. 3). Plants in mesic habitats also supported larger colonies (measured by the presence or absence of ant eggs, larvae and pupa) than plants in xeric habitats (Tab. 3). Plants in mesic habitats were larger (Tab. 3). The richness of ant species collected on the ground did not differ statistically between mesic and xeric habitats (mesic =  $2.55 \pm 0.25$  ants per bait; xeric =  $3.04 \pm 0.27$  ants per bait, Wilcoxon = 0.326,  $p > 0.05$ ).

## Discussion

The 42 morphospecies of ants which were recorded in the Serra do Cipó was low compared to other studies in tropical habitats. We argue that this difference may be due to sampling effects. Baiting is an effective technique for recording ant species but it usually recruits aggressive foraging ant species disproportionately (Andersen, 1997). Furthermore, the presence of aggressive ant species also negatively influences species richness, by excluding the presence of other less aggressive species. As the sampling was purposefully done in the dry season, in order to reduce environmental variation associated

**Table 1** – Distribution of ants found on the vegetation (collected in branches) of xeric (black) and mesic (gray) habitats in Serra do Cipó, MG, Brazil.

SPECIES	ALTITUDE (m)						
	800	900	1000	1100	1200	1300	1400
<i>Azteca</i> sp.							
<i>Camponotus crassus</i>	■		■		■		■
<i>C. sericeiventris</i>							
<i>Camponotus</i> sp.3						■	■
<i>Cephalotes atratus</i>		■					
<i>Cephalotes pusillus</i>	■	■	■	■	■	■	■
<i>Cephalotes</i> sp.1	■						
<i>Crematogaster</i> sp.1	■	■	■	■			
<i>Ectatomma muticum</i>							
<i>Leptothorax</i> sp.1					■		
<i>Leptothorax</i> sp.2			■	■	■		
<i>Linepithema</i> sp.3							■
<i>Myrmelachista</i> sp.1							
<i>Pachycondyla</i> sp.1							
<i>Pseudomyrmex</i> sp.1					■		
<i>Pseudomyrmex</i> sp.2		■	■	■	■	■	

with the increased humidity of the wet season. The aggressive component may further increase its negative effect due to the paucity of resources, given that winners of competitive interactions with other species become dominant (Andersen, 1986; Hölldobler & Wilson, 1990).

Another likely important effect on the richness pattern found is the sampling regime. Wolda (1987) suggested that continuous sampling over long periods of time may provide different results than sampling over short periods. Therefore, future studies should focus on separating sampling effects to ant species composition and richness as well as be performed for longer periods of time.

In order to explain the low occurrence of arboreal ants species encountered in the branches of trees and shrubs

sampled it is important to note the behavior of the species which were recorded. Some species such as *Cephalotes pusillus* are quite effective colonizers in the cerrado (Morais, 1980). In the Serra do Cipó, *C. pusillus* is the most abundant species encountered in trees and shrubs (Araújo, 1996). This rapid colonizing ability could be the reason for the relatively low species richness. Because this rapid and efficient occupation of stems may confer an advantage to *C. pusillus* in interspecific competition. The dynamics of competitive interactions indicate that a type of dominance order can exist among interspecific neighboring colonies (Hölldobler & Wilson, 1990).

The distribution of ant species along altitudinal gradients in the tropics has only been studied in rare instances (e.g., Jaffe

**Table 2** – Distribution of ants found on the ground in xeric (black) and mesic (gray) habitats in serra do Cipó, MG, Brazil

SPECIES	ALTITUDE (m)								
	800	900	1000	1100	1200	1300	1400	1500	
<i>Brachymyrmex</i> sp.	■				■				
<i>Camponotus crassus</i>	■					■			
<i>Camponotus sericeiventris</i>	■								
<i>Camponotus rufipes</i>	■				■				
<i>Camponotus</i> sp.3				■		■			
<i>Camponotus</i> sp.4	■					■			
<i>Camponotus</i> sp.5	■				■				
<i>Camponotus</i> sp.8						■			
<i>Ectatomma</i> sp.1	■								
<i>Ectatomma</i> sp.2	■			■		■			
<i>Linepithema</i> sp.1		■							
<i>Linepithema</i> sp.2		■							
<i>Linepithema</i> sp.3	■		■		■				
<i>Linepithema</i> sp.4	■					■			
<i>Odontomachus chelifer</i>	■		■						
<i>Pachycondila</i> sp.1	■		■						
<i>Pheidole oxyops</i>	■								
<i>Pheidole</i> sp.1	■		■		■				
<i>Pheidole</i> sp.2	■		■			■			
<i>Pheidole</i> sp.3	■				■				
<i>Pheidole</i> sp.4	■		■		■				
<i>Pheidole</i> sp.5	■		■			■			
<i>Pheidole</i> sp.6	■		■						
<i>Pheidole</i> sp.10	■						■		
<i>Pogonomyrmex</i> sp.1			■						
<i>Ponera</i> sp.1			■						
<i>Pseudomyrmex</i> sp.1			■						
<i>Solenopsis bondari</i>	■		■		■		■		
<i>Solenopsis (Diplorhoptrum)</i> sp						■			
<i>Solenopsis saevissima</i>	■		■			■		■	

**Table 3** – Comparison between arboreal ants in mesic and xeric habitats, taking into consideration species richness (number of ants species per habitat), number of ants species per tree, presence of eggs, larvae, and pupae of ants per branch, and the basal area of trees and shrubs in Serra do Cipó, Brazil

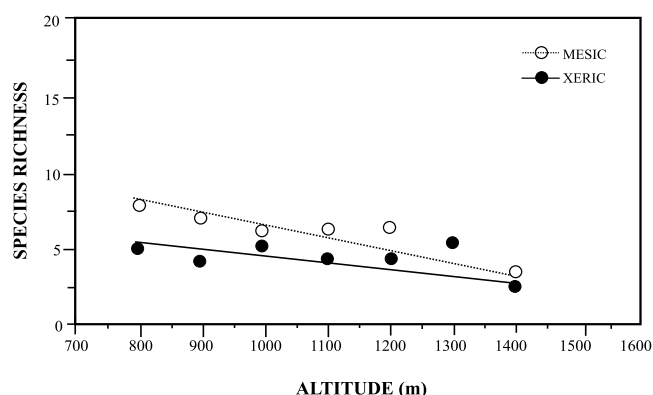
	AVERAGE NUMBER (± 1SE)		T	P
	MESIC	XERIC		
SPECIES RICHNESS	0.64 ± 0.05	0.45 ± 0.03	3.51	< 0.001
SPECIES/TREE	0.84 ± 0.04	0.45 ± 0.03	2.81	< 0.05
EGGS/LARVAE/PUPAE	0.37 ± 0.24	0.29 ± 0.23	2.35	< 0.05
“BASAL AREA”	10.6 ± 0.04	9.78 ± 0.004	15.21	< 0.001

et al., 1993; Samson et al., 1997), despite their enormous diversity and importance in that biogeographical region. The differential distribution of ants along the altitudinal gradient studied supports the general pattern of negative correlation of species richness with altitude, already reported for many other plant and animal taxa in several geographical regions (e.g., Cook, 1974; Terborgh, 1977; Young, 1982; Krisan et al., 1984; Wolda, 1987; Fernandes & Price, 1988, 1991; Fernandes & Lara, 1993). The inverse relationship between the number of ant species and altitude may be caused by a diverse array of factors, such as diminished complexity of the vegetation structure, reduction in habitat area and increasing habitat harshness. Mountain tops in Serra do Cipó display a strong reduction in area and at the highest altitudes shrubs and trees are sparsely distributed (Giulietti & Pirani, 1988; Meguro et al., 1996 a, b). Reduction in the availability of resources at high altitudes has been commonly reported as the cause for low species diversity (see MacArthur & Wilson, 1967). According to MacArthur & Wilson’s (1967) theory of biogeography of islands smaller areas also support fewer species due to higher extinction rates and lower colonization rates.

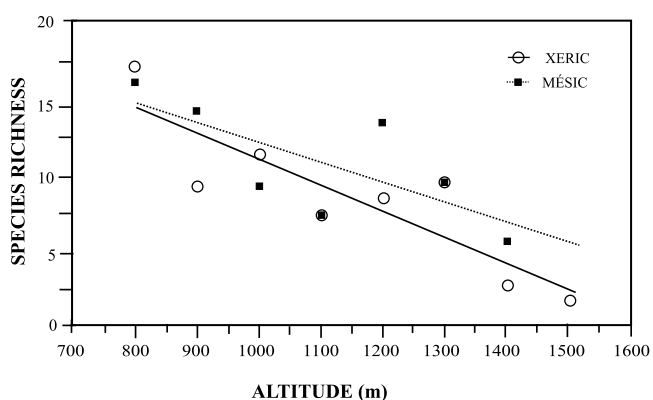
At high altitudes, air humidity is higher resulting in high soil humidity, but no permanent mesic habitat exists due to

the lack of a constant water course and corresponding vegetation. The existence of a constant water course, typically promotes the formation and subsistence of traditional mesic habitat vegetation (Fernandes & Price, 1988). This vegetation defines mesic habitats and influences comparisons with other habitats. Also lower temperatures, at these higher altitudes, prolong larval development and reduce survival; thereby further decreasing colonization and increasing extinction rates (Brown, 1973; Torres, 1984; Lawton et al., 1987), which affects ant species richness. In other regions, both low temperature and high humidity were shown to adversely affect the development of ant colonies (e.g. Torres, 1984; Young, 1986). The soil at high elevations in Serra do Cipó is shallow and humid throughout the year (Meguro et al., 1996 a, b). This soil characteristic may limit establishment of colonies (Wilson, 1971; Brown, 1973). Controlled studies on the impact of environmental factors on ant physiology and reproduction are needed, mainly for species in tropical areas.

The differential distribution of arboreal ants between mesic and xeric habitats supports the habitat favourability hypothesis. The gallery forests in Serra do Cipó are more structurally complex than the surrounding vegetation (Giulietti & Pirani,



**Figure 1** – Species richness of arboreal ants in mesic and xeric habitats in an altitudinal gradient in Serra do Cipó. Mesic habitat:  $r^2 = 0.87$ ,  $F = 32.82$ ,  $y = 13.32 - 0.007x$ ,  $p < 0.002$ ; Xeric habitat:  $r^2 = 0.26$ ,  $F = 1.76$ ,  $y = 6.25 - 0.179x$ ,  $p > 0.05$ .



**Figure 2** – Species richness of soil ants in mesic and xeric habitats in an altitudinal gradient in Serra do Cipó, MG. Mesic habitat:  $r^2 = 0.57$ ,  $F = 6.56$ ,  $y = 25.75 - 0.014x$ ,  $p < 0.05$ ; Xeric habitat:  $r^2 = 0.81$ ,  $F = 29.14 - 0.017x$ ,  $p < 0.001$ .

1988; Meguro et al., 1996a,b), and may support more species of opportunistic ants. We postulate that the larger number of ants species found in mesic habitats throughout the altitudinal gradient is positively influenced by a greater number of microhabitats in comparison to adjacent xeric habitats which probably furnished more resources to ant fauna (Carroll, 1974).

Nevertheless, the association between habitat complexity and ant species richness needs further study. Despite the generalized sclerophylly in mesic and xeric habitats in Serra do Cipó, the plant species found in xeric habitats are characteristically bushy and thin. This phenomenon is generally associated with evolutionary and developmental histories of plants which may have important consequences for development and protection of ant colonies. Morais (1980) found a low average number of ants per plant in cerrado areas where the vegetation had an average height of 2.0 m, while Carroll (1974, 1979) found higher numbers of ants per plant on larger plants in forest habitats.

In conclusion our results corroborate two long standing hypothesis concerning species richness along altitudinal gradients and distribution between habitats. However, we argue that the negative correlation between altitude species richness must be further investigated to better understand the factors that drive species distribution at global and regional levels (see Erlich et al., 1972; Murphy et al., 1990; Boggs & Murphy, 1972). Future studies should concentrate on the mechanisms that influence ant success between habitat types along the elevational gradients in Serra do Cipó in an attempt to provide the fuel to better understand species richness patterns in the cerrado.

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