Austral Ecology (2003) **28**, 305–314

Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness

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Abstract Processes acting on different spatial and temporal scales may influence local species richness. Ant communities are usually described as interactive and therefore determined by local processes. In this paper we tested two hypotheses linked to the question of why there is local variation in arboreal ant species richness in the Brazilian savanna ('cerrado'). The hypotheses are: (i) there is a positive relationship between ant species richness and tree species richness, used as a surrogate of heterogeneity; and (ii) there is a positive relationship between ant species richness and tree density, used as a surrogate of resource availability. Arboreal ants were sampled in two cerrado sites in Brazil using baited pitfall traps and manual sampling, in quadrats of 20 m × 50 m. Ant species richness in each quadrat was used as the response variable in regression tests, using tree species richness and tree density as explanatory variables. Ant species richness responded positively to tree species richness and density. Sampling site also influenced ant species richness, and the relationship between tree density and tree species richness was also positive and significant. Tree species richness may have influenced ant species richness through three processes: (i) increasing the variety of resources and allowing the existence of a higher number of specialist species; (ii) increasing the amount of resources to generalist species; and (iii) some other unmeasured factor may have influenced both ant and tree species richness. Tree density may also have influenced ant species richness through three processes: (i) increasing the amount of resources and allowing a higher ant species richness; (ii) changing habitat conditions and dominance hierarchies in ant communities; and (iii) increasing the area and causing a species–area pattern. Processes acting on larger scales, such as disturbance, altitude and evolutionary histories, as well as sampling effect may have caused the difference between sites.

Key words: Brazil, cerrado, community ecology, Formicidae, local species richness, savanna, spatial scales.

INTRODUCTION

Species richness may be influenced by processes acting on several different spatial and temporal scales (Ricklefs & Schluter 1993; Godfray & Lawton 2001). According to Srivastava (1999), a local area is one where all the species occurring within it are able to encounter and interact in ecological time. The delimitation of a local scale therefore depends on species dispersion and mobility (Soares *et al.* 2001). At the local scale, species interactions, resource availability (Perfecto & Snelling 1995; Alonso 1998) and habitat conditions should be the prominent processes determining species richness. There is also an expected interaction between these factors, because resource availability and its spatial distribution will influence species interactions (Chase 1996; Perfecto & Vandermeer 1996). Similarly, variation in habitat conditions will affect species distribution and interactions (Levins *et al.* 1973; Torres 1984; Nestel & Dickschen 1990; Perfecto & Snelling 1995; Perfecto & Vandermeer 1996).

Other spatial scales are defined according to dispersal rates within and among the areas (Srivastava 1999). On a regional scale, the probability that two individuals belonging to different regions will encounter in ecological time must be smaller than the probability of encounter if they live in the same local area (Srivastava 1999). Processes such as migration, area effects and disturbance may be classified as regional.

On still larger scales, such as the global scale, historical events are more important, and have to be considered when studying species richness patterns (Ricklefs & Schluter 1993; Godfray & Lawton 2001). Processes, which include speciation, large-scale dispersion and global extinction, may influence and confound local species richness patterns.

The relative influence of processes acting on different spatial and temporal scales must vary according to the taxa that are studied. Modular and sessile organisms are most likely to interact with their neighbours (Harper 1981), and therefore the importance of local processes is usually stressed in such

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Accepted for publication December 2002.

organisms (Vuorisalo & Tuomi 1986). Ant assemblages, considered to be made up of modular organisms (Andersen 1991a; López *et al.* 1994), are often structured by interspecific interactions (Savolainen & Vepsäläinen 1988; Andersen & Patel 1994; Acosta *et al.* 1995; Deslippe & Savolainen 1995).

In the specific case of tropical arboreal ants, resources are provided by several different tree species, which directly and indirectly provide various food and nesting resources to the ants. Food resources include extrafloral nectaries, honeydew from coccids and prey foraging on the trees (Davidson 1997; Oliveira & Pie 1998; Blüthgen *et al.* 2000a; Orivel & Dejean 2001; Richard *et al.* 2001), whereas nesting sites are located in both dead and living trees (Black 1987; Rocha & Bergallo 1992; Fonseca 1999; Palmer *et al.* 2000). Ants also scavenge on a variety of food items, especially insect corpses (Vasconcelos & Davidson 2000). Some authors have described specific relationships between some ant and myrmecophyte plant species (Fonseca & Ganade 1996; Yu & Davidson 1997; Fonseca 1999; Vasconcelos & Davidson 2000). Other studies have described ant species that use several plant species as resources (Oliveira & Pie 1998; Blüthgen *et al.* 2000a,b). If there is a strong relationship between ant and plant species, then higher plant species richness may provide a more heterogeneous environment for the ants (Murdoch *et al.* 1972; Roth *et al.* 1994; Perfecto & Snelling 1995; Bragança *et al.* 1998a,b; Zanuncio *et al.* 1998; Rojas & Fragoso 2000). Tilman and Pacala (1993) discuss the implication of increased resource types allowing more species to coexist, and consequently increasing species richness. Even though the definition of heterogeneity is controversial (Bell *et al.* 1993; Li & Reynolds 1995; Cooper *et al.* 1997), some authors have already reported the positive effect of habitat heterogeneity on species richness (Roth 1976; Reed 1978; Bell *et al.* 2000; Bestelmeyer & Wiens 2001; but see Paglia *et al.* 1995).

The present paper aims to test two hypotheses linked to the question of why there is local variation in arboreal ant species richness in the Brazilian savanna ('cerrado'). The hypotheses are: (i) there is a positive relationship between ant species richness and tree species richness, used as a surrogate of environmental heterogeneity; and (ii) there is a positive relationship between ant species richness and tree density, used as a surrogate of resource availability.

METHODS

Study sites

The ants were collected from two sites in the Brazilian savanna ('cerrado'), which is a plant formation composed of several physiognomical types (Coutinho 1978; Ribeiro & Walter 1998), varying from field to forest formations. These physiognomical types have different names, according to tree density: 'campo sujo' (less than 1000 trees per ha), 'campo cerrado' (more than 1400 trees per ha), 'cerrado *sensu stricto*' (more than 2000 trees per ha), and 'cerradão' (more than 3000 trees per ha; Goodland 1971). Cerrado occupies an area of approximately 1800 000 km^2, located mostly in central Brazil (Ratter 1992; Câmara 1993). There is a pronounced wet season generally from late September to April, with an average total precipitation of approximately 1500 mm, and a dry season during the coldest months of the year (May–August) (Goodland 1971).

The first site was located in Distrito Federal (15°55′–15°57′S, 47°55′–47°57′W), in a reserve of approximately 10 000 ha, with an average altitude of 1100 m a.s.l. The second site was located in Paraopeba (19°20′S, 44°20′W), Minas Gerais, in a reserve of approximately 200 ha, with an altitude ranging from 734 to 750 m a.s.l.

Ant and plant sampling

We considered arboreal ants as all those ants foraging or nesting in trees. Sampling was carried out in 20 m × 50 m quadrats in each site. In Distrito Federal (DF) we sampled 30 quadrats, 15 in campo sujo and 15 in campo cerrado physiognomical areas, and in Paraopeba (PP) we sampled seven quadrats, four in campo cerrado, two in cerrado *sensu stricto* and one in cerradão physiognomical areas. Inside each quadrat, at both sites, all woody plants with a trunk diameter of more than 5 cm at 30 cm above soil level were counted and identified. Ten trees were arbitrarily selected in each quadrat and the ants were collected using one baited pitfall trap per tree (radius = 7 cm; height = 9 cm) and by manual collection. The pitfall traps were tied to the trees as close as possible to the crown, and baited with sardine (DF) or sardine and honey (PP). The pitfall traps remained on the trees for 48 h, after which arboreal ants were manually sampled for 5 (PP) or 10 min (DF) in the whole tree.

The ants were sorted to species, identified to genus (Bolton 1994), and sent to Dr Jacques H. C. Delabie (CEPLAC) for confirmation and identification of species.

Statistical analyses

We considered tree species richness within the quadrats as a surrogate of environmental heterogeneity, because each tree species may represent a different set of food and shelter resources. Resource availability was defined as tree density (tree individuals per quadrat) within the quadrats.

We tested the hypothesis that tree species richness and tree density increase ant species richness by using an analysis of covariance (ANCOVA), in which ant species richness within quadrats was the response variable. The explanatory variables were tree species richness, tree density, sampling site and the two interaction terms: tree species richness × site and tree density × site.

Because it is possible that tree species richness and tree density are correlated, we carried out another ANCOVA using tree density, sampling site and the interaction between them as explanatory variables and tree species richness as the response variable.

In all analyses, we fitted a complete model and then removed each term in turn, verifying the change in deviance (step-wise multiple regression backward analysis; Crawley 1993). After the analyses we carried out residual analyses to check the models used.

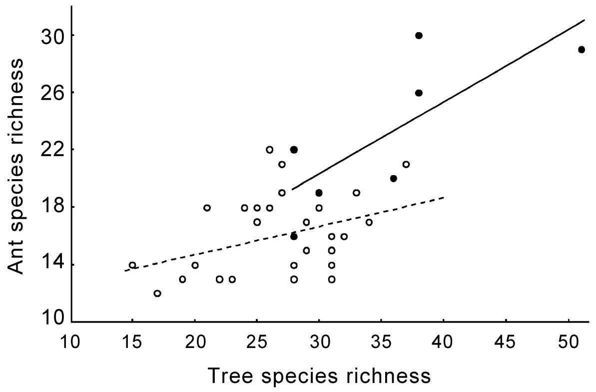

Fig. 1. Influence of tree species richness, used as surrogate of heterogeneity, on ant species richness ($F_{1,31} = 8.34$; $P = 0.007$). Sampling site ($F_{1,31} = 26.11$; $P << 0.0001$) and the interaction between sampling site and tree species richness ($F_{1,31} = 9.94$; $P = 0.004$) also influenced ant species richness. (○), Distrito Federal; (●), Paraopeba.

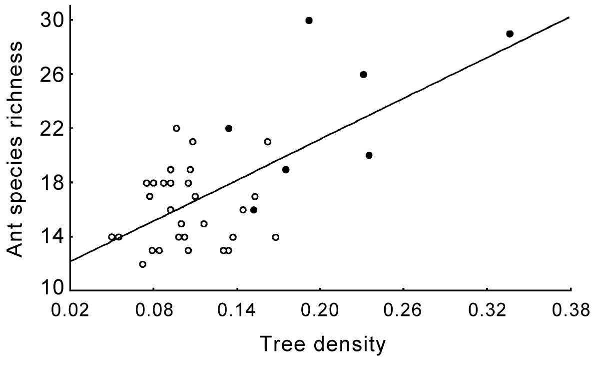

Fig. 2. Influence of tree density, used as surrogate of resource availability, on ant species richness ($F_{1,31} = 4.31$; $P = 0.046$). Sampling site ($F_{1,31} = 26.11$; $P << 0.0001$) also influenced ant species richness, although the interaction between sampling site and tree density was not significant ($F_{1,31} = 2.37$; $P = 0.134$). (○), Distrito Federal; (●), Paraopeba.

RESULTS

We collected 95 ant species in PP and 64 in DF. There were 133 species in all, 26 of which occurred in both sites (Table 1). Table 2 shows the response of ant species richness to tree species richness and tree density variation (ANCOVA). The complete model in this analysis was significant ($F_{5,31} = 15.47$; $P < 0.001$), and ant species richness responded positively to both tree variables. Figures 1 and 2 show the response of ant species richness to tree species richness and to tree density, respectively, in the two sampling sites. Ant species richness responded differently to tree species richness in the two sampling sites (Fig. 1), showed by the interaction term in Table 2. Conversely, the response of ant species richness to tree density was similar in both sampling sites (Fig. 2).

Tree species richness was higher in quadrats where tree density was also higher ($F_{1,33} = 60.7$; $P < 0.001$; $r^2 = 0.46$; Fig. 3). There was also an effect of sampling site ($F_{1,33} = 13.57$; $P = 0.001$), showing that tree species richness in PP was significantly larger than in DF. The interaction between sampling site and tree density was not significant ($F_{1,33} = 0.114$; $P = 0.74$), meaning that tree species richness responded similarly to tree density in both sampling sites.

DISCUSSION

Ant fauna

Ant species richness at our sampling sites is high when compared with that in Australian savannas (Andersen 1991b, 1991c, 1992; Andersen & Patel 1994), and even when compared with that in tropical rainforests (Majer 1990; Majer & Delabie 1994; Soares *et al.* 2001). However, comparisons of data collected

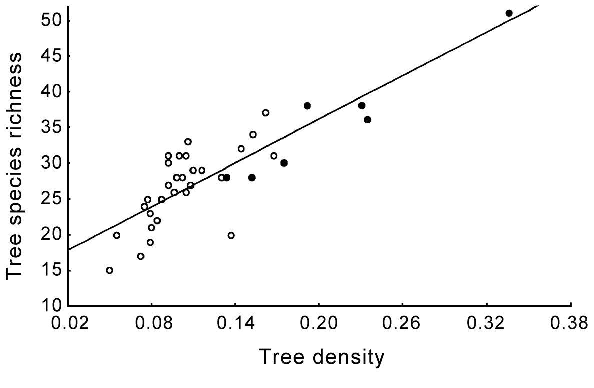

Fig. 3. Relationship between tree species richness and tree density ($F_{1,33} = 60.7$; $P << 0.0001$). There was also an effect of sampling site ($F_{1,33} = 13.57$; $P = 0.001$), although the interaction between sampling site and tree density was not significant ($F_{1,33} = 0.114$; $P = 0.74$). (○), Distrito Federal; (●), Paraopeba.

Table 1. Arboreal ant species sampled in Paraopeba, Minas Gerais (PP) and in Distrito Federal (DF), Brazil

Species	PP	DF
Dolichoderinae		
Azteca instabilis		X
Azteca sp. 1	X	
Dolichoderus lamellosus	X	X
Dolichoderus lutosus	X	
Dorymyrmex jheringi	X	
Forelius sp. 1	X	
Forelius sp. 2	X	
Linepithema humile	X	
Linepithema sp. 1	X	
Linepithema sp. 1M		X
Tapinoma melanocephalum	X	
Tapinoma sp. 1	X	
Ecitoninae		
Labidus praedator		X
Neivamyrmex orthonotus		X
Formicinae		
Brachymyrmex sp. 1	X	X
Brachymyrmex sp. 2	X	
Brachymyrmex sp. 3	X	X
Brachymyrmex sp. 4	X	
Camponotus (Myrmaphaenus) blandus	X	
Camponotus (Myrmaphaenus) genatus		X
Camponotus (Myrmaphaenus) leydigi	X	
Camponotus (Myrmaphaenus) novogranadensis	X	
Camponotus (Myrmaphaenus) sp. 1	X	
Camponotus (Myrmaphaenus) sp. 2	X	
Camponotus (Myrmaphaenus) sp. 3	X	X
Camponotus (Myrmaphaenus) sp. 4	X	
Camponotus (Myrmaphaenus) sp. 5	X	
Camponotus (Myrmaphaenus) sp. 6	X	
Camponotus (Myrmaphaenus) sp. *prox. blandus*		X
Camponotus (Myrmepomis) sericeiventris	X	
Camponotus (Myrmobrachys) arboreus		X
Camponotus (Myrmobrachys) crassus	X	X
Camponotus (Myrmobrachys) godmani		X
Camponotus (Myrmobrachys) sp. 1	X	
Camponotus (Myrmobrachys) sp. 1M		X
Camponotus (Myrmobrachys) sp. 2	X	
Camponotus (Myrmobrachys) sp. 3	X	
Camponotus (Myrmobrachys) trapezoideus	X	
Camponotus (Myrmothrix) atriceps	X	X
Camponotus (Myrmothrix) cingulatus	X	X
Camponotus (Myrmothrix) renggeri	X	
Camponotus (Myrmothrix) rufipes	X	X
Camponotus (Myrmothrix) sp. 1		X
Camponotus (Tanaemyrmex) agra	X	
Camponotus (Tanaemyrmex) balzani		X
Camponotus (Tanaemyrmex) melanoticus	X	X
Camponotus (Tanaemyrmex) sp. 2	X	
Camponotus (Tanaemyrmex) sp. 3	X	
Camponotus (Tanaemyrmex) sp. 4	X	X
Camponotus (Tanaemyrmex) sp. 5	X	
Camponotus (Tanaemyrmex) sp. *punctulatus group*		X
Camponotus (Tanaemyrmex) vitattus	X	X
Myrmelachista sp. 1	X	X
Paratrechina longicornis		X
Paratrechina sp. 1	X	
Myrmicinae		
Acromyrmex subterraneus	X	
Atta rubropilosa	X	X

Table 1. (continued)

Species	PP	DF
Cephalotes adolphi		X
Cephalotes atratus	X	X
Cephalotes betoi		X
Cephalotes borgmeieri	X	
Cephalotes clypeatus	X	
Cephalotes depressus		X
Cephalotes frigidus		X
Cephalotes goeldii	X	
Cephalotes grandinosus	X	X
Cephalotes minutus		X
Cephalotes pallens	X	
Cephalotes pusillus	X	
Cephalotes simillimus		X
Crematogaster sp. 1	X	
Crematogaster sp. 1*quadriformis* group	X	
Crematogaster sp. 1M *quadriformis* group		X
Crematogaster sp. 2	X	
Crematogaster sp. 2 *quadriformis* group	X	X
Crematogaster sp. 3	X	
Leptothorax (Nesomyrmex) sp. *ininodis*		X
Leptothorax asper	X	
Leptothorax sp. 1	X	
Leptothorax sp. 2	X	
Leptothorax sp. 3	X	
Leptothorax tristani	X	
Mycocepurus goeldii	X	
Ochetomyrmex sp. 1	X	
Pheidole fallax	X	X
Pheidole sp. 1	X	X
Pheidole sp. 2	X	X
Pheidole sp. 2M		X
Pheidole sp. 3	X	
Pheidole sp. 4	X	
Pheidole sp. 4M		X
Pheidole sp. 5	X	
Pheidole sp. 6	X	
Pheidole sp. 7	X	
Pheidole sp. 8	X	
Pheidole suzanae		X
Solenopsis sp. 1 *diplorhoptrum* group	X	X
Solenopsis sp. 1 *solenopsis* group	X	
Solenopsis sp. 2 *diplorhoptrum* group	X	
Solenopsis sp. 3 *diplorhoptrum* group	X	
Solenopsis sp. 4 *diplorhoptrum* group	X	
Solenopsis substituta		X
Trachymyrmex sp. 1	X	
Trachymyrmex sp. 1M		X
Wasmannia auropunctata	X	X
Wasmannia sp. 1	X	
Wasmannia sp. *prox. rochai*		X
Xenomyrmex sp. 1	X	
Ponerinae		
Dinoponera australis		X
Ectatomma brunneum	X	
Ectatomma planidens	X	
Ectatomma tuberculatum	X	X
Gnamptogenys sulcata	X	
Odontomachus chelifer		X
Pachycondyla rostrata		X
Pachycondyla villosa	X	X

Table 1. (continued)

Species	PP	DF
Pseudomyrmecinae		
Pseudomyrmex cubaensis		X
Pseudomyrmex elongatus	X	X
Pseudomyrmex filiformis	X	
Pseudomyrmex gracilis	X	X
Pseudomyrmex kuenckeli	X	X
Pseudomyrmex pisinnus	X	
Pseudomyrmex pupa	X	
Pseudomyrmex sp. 1 *palidus* group	X	
Pseudomyrmex sp. 1M *palidus* group		X
Pseudomyrmex sp. 2 *palidus* group	X	
Pseudomyrmex sp. 2M *palidus* group		X
Pseudomyrmex sp. 3M *palidus group*		X
Pseudomyrmex tenuissimus		X
Pseudomyrmex termitarius	X	
Pseudomyrmex unicolor		X
Pseudomyrmex urbanus		X
Not determined		X
Total	95	64

Table 2. Results of the analysis of covariance for the response of ant species richness to tree density, tree species richness and sampling sites

Source	d.f.	*SS*	*MS*	*F*	*P*
Site	1	292.3	292.3	26.11	<0.001
Tree density	1	44.05	44.05	4.31	0.046
Tree species richness	1	70.16	70.16	8.34	0.007
Site × Tree density	1	19.17	19.17	2.37	0.134
Site × Tree species richness	1	62.74	62.74	9.94	0.004
Error	31	195.70	6.31		
Total	36	684.11			

SS are the changes in deviance caused by step-wise removal of each variable.

through different sampling regimes and methods may be misleading. Other ant communities were sampled by using several different methods, including baits, pitfall traps of different diameters, hand collecting, and litter sifting. Furthermore, sampling regimes have varying duration, and there is a positive relationship between sampling effort and species richness (Delabie *et al.* 2000).

The observed high diversity of ants in the present study may have resulted because all ants found in trees were defined as arboreal ants. However, not all the recorded species are truly arboreal ants, that is, species that nest in the trees. For instance, *Labidus*, *Neivamyrmex* and *Solenopsis* may not be truly arboreal. Other species, such as *Azteca*, *Crematogaster*, most *Pseudomyrmex* species, *Cephalotes*, some *Camponotus* species and *Wasmannia* are typically arboreal (Brown 2000). Andersen and Yen (1992) observed that from 44 ant species sampled in tree canopies, only two were truly arboreal. Even considering the above overestimation, the arboreal ant fauna of Brazilian savanna seems to be more diverse than in other regions. *Tetraponera*, that is the Pseudomyrmecinae genus of the Old World, related to *Pseudomyrmex* in the New World, produced only nine species in Borneo (Floren *et al.* 2001), whereas we sampled 16 species of *Pseudomyrmex*.

Heterogeneity and ant species richness

Heterogeneity, estimated by tree species richness, may have influenced ant species richness through three processes. Sites having more resource variety may shelter more species specialized in different resources, in which case we would expect a high proportion of the ant species to be plant specialists, and sites with more tree species would offer more opportunities for such specialist species. Several plant species of the cerrado have extrafloral nectaries and shelter for ant species, indicating some degree of ant-plant specialization, but we are not aware of any studies of specific relationships between ant and plant species in the cerrado.

Secondly, an increase of tree species richness may represent a higher resource availability to generalist ant species, because tree species richness and tree density are related (Fig. 3). However, both tree variables separately influenced ant species richness, shown by the decrease of significance of the explanatory model when each variable was removed (Table 2), thus relationships between both tree variables and ant species richness are not spurious. Therefore, the ants may be responding not only to tree species richness, or heterogeneity, but also to the general increase in resource availability (tree density). In this case, low resource availability may generate interspecific competition and competitive exclusion. Higher resource availability would relax interspecific competition, allowing the coexistence of more ant species. Competition, however, is not necessary to explain the pattern. The increase of resource availability may only affect the number of individuals (or colonies) in a given area, increasing the number of species by chance.

Finally, an indirect relationship between ant and tree species richness may also occur. Both ant and tree species richness may be responding to an independent external factor (Murdoch *et al.* 1972; August 1983; Rosenzweig & Abramsky 1993; Rojas & Fragoso 2000). Cerrado is heterogeneous vegetation, and usually occurs in patches ranging from open fields to forest-like physiognomical types. These variations may be caused by variation in nutrient and moisture availability, or disturbance and fire occurrence and frequency (Goodland 1971; Goodland & Ferri 1979; Eiten 1994), and these factors may affect both plant and ant communities.

Resource availability and ant species richness

Tree density may affect ant species richness through three mechanisms. First, as discussed above, the increase in resource availability may relax interspecific competition, or allow the existence of more colonies, resulting in increased ant species richness. Second, a higher tree density may also result in change of habitat conditions inside the quadrat, such as higher cover, and lower temperature and moisture variation. These condition changes may alter the dominance order and allow the existence of more species in ant communities (Perfecto & Vandermeer 1994, 1996).

Finally, higher tree densities may be related to an area increase for arboreal ants. The species–area relationship is commonly cited (Margules *et al.* 1982; Robinson & Quinn 1988; Turner 1996; Ricklefs & Lovette 1999), even though the mechanisms causing such a relationship are difficult to test (for further discussion see Rosenzweig 1995).

Why is ant species richness different in the two sites?

Figures 1 and 2 show that ant species richness is significantly different in the two sampling sites, and that ants responded differently to tree species richness, with a more pronounced increase in PP than in DF. This difference may be explained by the differences in sampling effort between the two areas, or by factors acting on a larger scale than in the local area.

Ant manual sampling was carried out for 10 min in DF and for 5 min in PP, a sampling difference that would bias estimates toward higher species richness in DF, which is opposite to that observed. The pitfall sampling, however, used two different baits in PP, which may have attracted ant species from different guilds. Several arboreal ants feed on honeydew and extrafloral nectaries and the use of honey in the baited pitfalls may have increased their collection. This is the case, for instance, for *Camponotus crassus*, *C. atriceps*, *C. renggeri*, *C. rufipes*, *Cephalotes atratus*, *Ce. pusillus*, *Ectatomma tuberculatum*, *Solenopsis* sp., *Pseudomyrmex* sp., *Dolichoderus* sp. and *Brachymyrmex* sp. (Oliveira & Pie 1998; Blüthgen *et al.* 2000a). However, other species, such as *Wasmannia auropunctata*, *Pachycondyla villosa*, *Paratrechina* sp. and *Pheidole* sp. are opportunistic in relation to their nesting habits (Blüthgen *et al.* 2000a,b) and *Pachycondyla rostrata* and the Ecitoninae are predators (Davidson 1997; Orivel & Dejean 2001). Several other genera are described as omnivorous, such as *Crematogaster* (Blüthgen *et al.* 2000a; Palmer *et al.* 2000; Vasconcelos & Davidson 2000; Richard *et al.* 2001) and *Azteca* (Blüthgen *et al.* 2000a; Vasconcelos & Davidson 2000). Even though the information on biology and feeding habits of tropical arboreal ant species is rare, Romero and Jaffé (1989), studying the effect of different sampling methods in Venezuelan savannas, did not observe a significant difference between species proportion sampled by tuna or tuna plus honey baited pitfalls.

Regional scale factors may also have influenced the difference between species richness in the two sites. The areas of the two sites are very different (DF has 10000 ha and PP has 200 ha), although the difference would be expected to produce a higher species richness in DF. Another important factor that may have influenced ant species richness in PP is the presence of large soil disturbances caused by people collecting an giant endemic earthworm for fishing bait. This disturbance interferes particularly with the herbaceous stratum of the cerrado vegetation, because the soil is dug in large areas in the search for the earthworms. This activity creates areas inside the PP site with different degrees of disturbance, increasing the natural patchiness of cerrado and benefiting species associated with disturbance.

Processes acting on even larger scales also may influence the difference in ant species richness between the two sampling sites. The distance from areas serving as the source of species may have influenced the observed difference, because the nearer the source areas, the higher the probability of immigration from the source to the studied areas (MacArthur & Wilson 1967).

However, this explanation also does not seem to be valid, because the DF site is located in the core distribution of cerrado vegetation, with several other reserves nearby, whereas PP is located at the edge of cerrado distribution, with few large areas of undisturbed cerrado nearby (Rizzini 1997). Latitudinal patterns of species richness are among the major 'rules' of species diversity (Rosenzweig 1995; Godfray & Lawton 2001), but the observed pattern is opposite to that expected from this pattern. Altitude, however, may be important in the determination of the observed differences (Rosenzweig 1995): DF is located at 1100 m a.s.l. and PP at 734 m a.s.l. Even though latitudinal and altitudinal patterns are well known and described as general rules, the mechanisms behind them are controversial (see more discussion in Rosenzweig 1995). Such disparities in diversity are sometimes explained by different evolutionary histories (Pianka 1989; Ricklefs & Schluter 1993; Godfray & Lawton 2001), and that may be one of the processes involved in the observed differences in ant species richness. There is a low floristic similarity between DF and PP (Balduíno 2001), and this is evidence that the studied areas have different evolutionary histories, which may also be valid for ant communities. In fact, Table 1 shows that the sites share only 26 species, whereas there are 107 species occurring at only one or the other of the sites.

Species richness may be determined by several factors, acting together and on different spatial and temporal scales. Our study showed the importance of tree species richness and density, which are factors acting on local scale, in the determination of arboreal ant species richness. However, other factors acting on larger scales must not be ignored, because our data also indicated their importance in species richness determination.

ACKNOWLEDGEMENTS

We are thankful to Alexander P. C. Balduíno and Jeanine Felfili, who kindly gave access to their data of floristic inventories in PP and DF; our thanks to employees and to the directors of the reserves, who allowed us to use the reserves and facilitated our fieldwork. Renata B. F. Campos, Rogério F. Ribas, Mônica S. da Fonseca and Manoel C. da Silva helped us with the fieldwork. Jacques H. C. Delabie and Ivan C. do Nascimento kindly identified the ants. A previous draft of the paper was commented on by Renata B. F. Campos and Tathiana G. Sobrinho. Alan Andersen, Michael Bull and two anonymous referees gave suggestions that greatly improved the manuscript. C. R. Ribas, S. M. Soares, and M. Pic are supported by CAPES grants. J. H. Schoereder is supported by a CNPq grant. This work was partially supported by a CAPES grant.

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