

Diversity of Arboreal Ants In a Brazilian Tropical Dry Forest: Effects Of Seasonality and Successional Stage

by

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ABSTRACT

In tropical systems, habitat heterogeneity and resource availability have been reported as important factors driving ant species richness and composition. For this reason, these variables have been widely used as indicators of forest disturbance. The aim of this study was to compare the composition and richness of arboreal ants between the dry and wet seasons in three successional stages of a tropical dry forest at the Parque Estadual da Mata Seca, northern Minas Gerais state, Brazil. Ant sampling was performed in 15 plots in three different forest secondary stages: early, intermediate and late. Ants were sampled during the wet and dry seasons, using five pitfall traps per plot. We collected 43 ant species, distributed in 19 genera. Our results indicated a change on ant species composition along the successional gradient ($p < 0.05$). However, ant species richness did not differ between stages and seasons ($p > 0.05$) and was not affected by the variables used here as surrogates to habitat heterogeneity (tree richness) and resource availability (tree density) ($p > 0.05$). Ant composition did not change significantly between the dry and wet seasons for the early successional stage, but plots from the intermediate and late stages were clearly segregated according to seasons. We suggest that

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it is likely that 25 years of forest regeneration are enough to restore most of the arboreal ant communities in tropical dry forests, strengthening the importance of secondary habitats to biodiversity maintenance.

Key-words: habitat heterogeneity, resource availability, secondary succession, species richness, species composition.

INTRODUCTION

Ants represent an important group of terrestrial organisms due to their high taxonomic diversity and dominance in many ecosystems (Erwin 1983, Tobin 1997). Moreover, ants occupy various trophic levels and make substantial contributions to ecosystem processes (Hölldobler & Wilson 1990, Jouquet *et al.* 2006). In tropical systems, habitat heterogeneity and resource availability have been reported as important factors driving ant species richness (Bestelmeyer & Wiens 2001, Ribas *et al.* 2003, Armbrecht *et al.* 2004, Ribas & Schoereder 2007). For these reasons, ants are considered to be sensitive to seasonal and landscape structure variations (Reddy & Venkataiah 1990, Lindsey & Skinner 2001). Further, ants have been suggested as tools to assess the response of animal biodiversity to forest regeneration after disturbance (Castro *et al.* 1990, Leal *et al.* 1993, Bustos & Ulloa-Chacón 1996, Estrada & Fernández 1999, Vasconcelos 1999, Nichols & Nichols 2003, Schnell *et al.* 2003, Ottonetti *et al.* 2006, Silva *et al.* 2007, Santos *et al.* 2008).

In tropical forests, post-disturbance plant succession is characterized by an increase in the habitat structural complexity, together with resource quantity and diversity (Brown 1994, Aide *et al.* 1996, Guariguata & Ostertag 2001, Kalácska *et al.* 2004, Madeira *et al.* 2009). For arthropod communities, species diversity has been found to be positively associated with habitat complexity (Hansen 2000, Ribas *et al.* 2003, Sperber *et al.* 2004, Lassau *et al.* 2005, Lassau & Hochuli 2005). Thus, it is likely that ant diversity will increase during forest regeneration, and this group can be potentially used as indicator of forest successional condition (Santos *et al.* 2008).

In the Americas, Tropical Dry Forests (TDFs) have been the preferred ecosystems for human settlements (Murphy & Lugo 1986, Sanchez-Azofeifa *et al.* 2005). Activities such as wood extraction, agriculture, pasture, forestry, mining practices and urbanization processes have severely disturbed TDFs (Denevan 1992, Guariguata & Ostertag 2001, Miles *et al.* 2006, Quesada *et*

al. 2009). Further, tropical dry forests are considered the most threatened of all tropical ecosystems (Janzen 1986, Sánchez-Azofeifa *et al.* 2005). The land cover matrix of this ecosystem is characterized by exploited areas that are abandoned after short time after clear-cutting resulting on a combination of primary and secondary fragments (Kalacska *et al.* 2004, Arroyo-Mora *et al.* 2005, Quesada *et al.* 2009).

In TDFs, the marked seasonality significantly affects ecosystem structure and function (Murphy & Hugo 1986). These forests are highly deciduous due to the prolonged dry season, which limits plant productivity to 3-5 months per year, when rainfall is very concentrated (Sánchez-Azofeifa *et al.* 2005). In response to this strong seasonal variation in resource availability, fluctuations in abundance and species richness have been documented for some Neotropical insect groups (Janzen 1984, Basset *et al.* 2003). Seasonality is known to influence ant activity in Mexican TDFs (Gove *et al.* 2005) but there have been no studies designed to investigate this in South America.

Successional and seasonal changes in insect species diversity and composition have rarely been documented for TDFs (see Lewinson *et al.* 2005). Given the potential use of ants as bioindicators (Alonso 2000, Alonso & Agosti 2000, Delabie *et al.* 2006) of habitat disturbance, understanding their spatial and temporal distributions across regeneration gradients can be very helpful to TDFs conservation. In this study, we aimed to test the following hypotheses in a TDF in southeastern Brazil: (I) the arboreal ant composition changes and their richness increases along a successional gradient; (II) the arboreal ant composition changes and their richness decreases from the wet to the dry season; (III) habitat heterogeneity (indicated by tree species richness) and resource availability (indicated by tree density) positively influence arboreal ant species richness.

MATERIAL AND METHODS

Study Area

This study was conducted in the Parque Estadual da Mata Seca (hereafter PEMS), a conservation unit of integral protection managed by the Instituto Estadual de Florestas (IEF- State Forestry Institute). The PEMS has an area of 10,281 ha and is located in the valley of the São Francisco River, Minas Gerais state, Brazil, between 14°48'36" – 14°56'59" S and 137 43°55'12" –

44°04'12" W. The original vegetation of the park is seasonally dry tropical forests, growing on plain and nutrient-rich soils (IEF, 2000). These forests are dominated by deciduous trees, with almost 90-95% of leaf drop during the dry season (May-October) (Pezzini *et al.* 2008). The climate of the region is tropical semi-arid (Köppen's classification), characterized by a severe dry season during the winter months. The average temperature of the study region is 24 °C (Antunes 1994), and the average annual precipitation is 818 ± 242 mm (Madeira *et al.* 2009). The main economic activities in the area before protection were cattle raising and bean and corn plantations. Approximately 1,525 ha of the PEMS are covered with abandoned pasture fields in different regeneration stages, and the remaining area supports secondary and primary dry forests (Madeira *et al.* 2009).

Study Plots

Ants were sampled in 15 plots of 50 x 20 m (0.1 ha each) in early, intermediate and late forest stages of natural regeneration (five plots per stage). All plots were located along a 7 km transect encompassing all stages, and were placed inside an area in which management practices were similar for all pasturelands in the last 30 years, when the property belonged to the same owner. The early regeneration stage is characterized by a forest area composed of sparse patches of woody vegetation, shrubs, herbs and grasses with a single stratum of tree crowns composing a very open canopy up to 4 meters. This area was used as pasture for at least 20 years and abandoned in 2000. Intermediate successional stages have two vegetation layers: the first one is composed of deciduous trees 10-12 m in height and some emergent trees up to 15 m. The second layer is formed by a dense understory with many young trees and abundant lianas. This area was used as pasture for an unknown period and was abandoned in late 1980's. The late successional stage is also characterized by two strata, the first stratum is composed by taller deciduous trees which form a closed canopy 18-20 m high, the second stratum is formed by a sparse understory with reduced light penetration and low density of young trees and lianas. There are no records of clear-cutting in this area for the last 50 years (Madeira *et al.* 2009). Plots from the same regeneration stage were located approximately 0.2-1.0 km from each other. For a detailed description of the study plots see Madeira *et al.* (2009).

Ant Sampling

Ants were sampled twice during the study, in February 2007 (289.5 mm of rain), which represents the end of the wet season, and September of the same year (no rain since May), the end of the dry season. Ant sampling was conducted using pitfall traps attached to the tree trunk, at 1.3 meters above the ground (see Ribas *et al.* 2003, Campos *et al.* 2006). In each plot, 5 traps were placed in different trees (regardless of the species) with circumference at breast height ≥ 15 cm, at least 6 m apart from each other. Traps were baited with honey and sardine and stayed in the field for 48 hours. After this period, pitfalls were removed and taken to the laboratory, where the collected specimens were counted and identified. We calculated ant species richness per plot for each season and the accumulated richness for both sampling periods. Voucher specimens were deposited in the Entomological Collection of the Laboratório de Biologia da Conservação at Universidade Estadual de Montes Claros, Montes Claros, and in the collection of the Laboratório de Mirmecologia, Centro de Pesquisa do Cacau, Ilheus, under the reference number #5506.

Data Analyses

Variations in ant community composition between season and successional stages were analyzed through a detrended correspondence analysis (DCA, Bestelmeyer & Wiens 1996). We used ant species composition in each plot at each season as the grouping parameter between plots. The effects of seasonality and successional stage on ant species composition were analyzed using general linear models (GLMs) (Crawley 2002). The scores obtained for each plot in the axis 1 and 2 of the DCA were used as response variables (see Santos & Thomaz 2007, Basset *et al.* 2008), and the season and successional stages were used as explanatory variables in the GLMs. We also tested the influence of season and successional stages on ant species richness using a GLM.

We used tree species richness at each plot as a surrogate of habitat heterogeneity, and tree density (number of tree individuals with a diameter at breast height ≥ 5 cm) in each plot as a surrogate of resource availability to arboreal ants (see Ribas *et al.* 2003). These data were obtained from a floristic study conducted in 2006 by Madeira *et al.* (2009). To evaluate the effects of habitat heterogeneity and resource availability on ant species richness, we used a

GLM with accumulated ant species richness as response variable and the tree richness and density as explanatory variables.

All GLMs were submitted to residual analyses, so as to evaluate adequacy of error distribution (Crawley 2002). If significant, factor levels (stages) were compared through contrast analysis by aggregating level and comparing deviance change (Crawley 2002). If the level of aggregation did not alter significantly the deviance explained by the model, the levels were pooled together (amalgamation), simplifying the model. The complete models were simplified by stepwise omission of non-significant terms. The DCA analysis was performed using the statistical package PC-ORD v3.15 for Windows (McCune & Mefford 1997) and the other analyses were conducted with the software R (R Development Core Team 2008).

RESULTS

We collected 43 ant species, distributed in 19 genera. The most speciose subfamily was Myrmicinae (17 species) followed by Formicinae (11 species), Dolichoderinae and Pseudomyrmecinae (five species each), Ponerinae (four species) and Ecitoninae contained only one species (Table 1). The *Camponotus* genera exhibited the higher richness, with nine species (21% of the total). Only four species occurred in the three successional stages, in both seasons: *Camponotus atriceps*, *C. melanoticus*, *C. sericeiventris* and *Pheidole fowleri* (Table 1). The species *C. renggeri* occurred in the three stages only in the wet season, and five species (*C. arboreus*, *C. crassus*, *C. vittatus*, *Cephalotes pusillus* and *Crematogaster erecta*) occurred in the three stages only in the dry season (Table 1).

In total, we collected 31 ant species in the plots at early successional stage, 28 in intermediate and 29 in late plots. Six species were restricted to early stage plots, whereas three species were sampled exclusively in the intermediate stage and only one species occurred solely in the late stage. In the early stage, we recorded 24 species in each season, with moderate changes in the species composition between seasons (Table 1). At intermediate stage we collected 19 species in the wet season and 21 in the dry season. In late stage 16 species were recorded in the wet season and 21 in the dry season. In the intermediate and late stages the similarities in species composition between seasons were reduced (Table 1). In the early stage, 48 % of the species were collected in both seasons, decreasing to 38 % in the intermediate stage and to 28 % in the late stage.

Table 1. Species of arboreal ants sampled at the Parque Estadual da Mata Seca during the wet and dry seasons, in three successional stages.

Species	Stage/Season					
	Early		Intermediate		Late	
	wet	dry	wet	dry	wet	dry
Subfamily Myrmicinae						
<i>Acromyrmex subterraneus subterraneus</i> (Forel)	X	X		X		X
<i>Cephalotes atratus</i> L.			X	X	X	
<i>Cephalotes eduarduli</i> (Forel)			X		X	
<i>Cephalotes minutus</i> (Fabricius)		X				
<i>Cephalotes nilpiei</i> De Andrade	X	X				X
<i>Cephalotes pellans</i> De Andrade			X			
<i>Cephalotes pusillus</i> (Klug)	X	X		X	X	X
<i>Crematogaster erecta</i> Mayr	X	X	X	X		X
<i>Crematogaster obscurata</i> Emery	X					X
<i>Crematogaster victima</i> Smith	X	X			X	
<i>Pheidole fowleri</i> Wilson	X	X	X	X	X	X
<i>Pheidole rufipilis</i> Forel	X		X			
<i>Pheidole scalaris</i> Wilson	X					
<i>Pheidole</i> sp.1	X					
<i>Solenopsis</i> sp.1			X	X		
<i>Wasmannia auropunctata</i> (Roger)	X			X		X
<i>Wasmannia rochai</i> Forel				X		X
Subfamily Dolichoderinae						
<i>Azteca alfari</i> Emery						X
<i>Dolichoderus voraginosus</i> Mackay		X				
<i>Dorymyrmex</i> sp.1	X	X			X	
<i>Forelius pusillus</i> (Santschi)		X	X			
<i>Tapinoma</i> sp.1	X	X				
Subfamily Formicinae						
<i>Brachymyrmex</i> sp.1	X			X		
<i>Brachymyrmex</i> sp.2				X		
<i>Camponotus arboreus</i> (Smith)		X	X	X	X	X

Table 1. Species of arboreal ants sampled at the Parque Estadual da Mata Seca during the wet and dry seasons, in three successional stages (continued).

Species	Stage/Season					
	Early		Intermediate		Late	
	wet	dry	wet	dry	wet	dry
<i>Camponotus atriceps</i> (Smith)	X	X	X	X	X	X
<i>Camponotus cingulatus</i> Mayr				X		X
<i>Camponotus crassus</i> Mayr	X	X	X	X		X
<i>Camponotus melanoticus</i> Emery	X	X	X	X	X	X
<i>Camponotus novogranadensis</i> Mayr				X		X
<i>Camponotus renggeri</i> Emery	X	X	X		X	
<i>Camponotus sericeiventris</i> (Guerin)	X	X	X	X	X	X
<i>Camponotus vittatus</i> Forel		X	X	X	X	X
Subfamily Ecitoninae						
<i>Neivamyrmex</i> sp.1		X		X		
Subfamily Ponerinae						
<i>Ectatomma suzanae</i> Almeida			X		X	
<i>Gnamptogenys sulcata</i> (Smith)	X					
<i>Odontomachus bauri</i> Emery			X		X	
<i>Pachycondyla villosa</i> (Fabricius)			X	X		X
Subfamily Pseudomyrmecinae						
<i>Pseudomyrmex gracilis</i> (Fabricius)	X	X			X	X
<i>Pseudomyrmex schuppi</i> (Forel)	X	X	X		X	
<i>Pseudomyrmex</i> sp.1	X	X		X		X
<i>Pseudomyrmex</i> sp.2	X	X				X
<i>Pseudomyrmex termitarius</i> Smith		X				
Total	24	24	19	21	16	21

The DCA ordinate the plots according to the successional gradient (axis 1, eigenvalue = 0.38) and seasonality (axis 2, eigenvalue = 0.21) (Fig. 1). Three statistically different groups of plots were formed, based on arboreal ant species composition (Fig. 1, Table 2): the axis 1 separated the early stage plots from the others, regardless of the season. The axis 2 separated the plots from intermediate and late stages in two groups, according to the season. Thus

Table 2. Analyses of deviance of the minimal adequate models showing the effects of season and successional stages on the scores from axis 1 and 2 obtained from a detrended correspondence analysis (DCA).

Response variable	Explanatory variable	d.f.	F	P
Score (axis1)	Successional stage	1	21.5	< 0.001
Score (axis2)	Season	1	26.66	< 0.001
	Successional stage	1	8.8	< 0.01
	Interaction season: successional stage	1	16.55	< 0.001

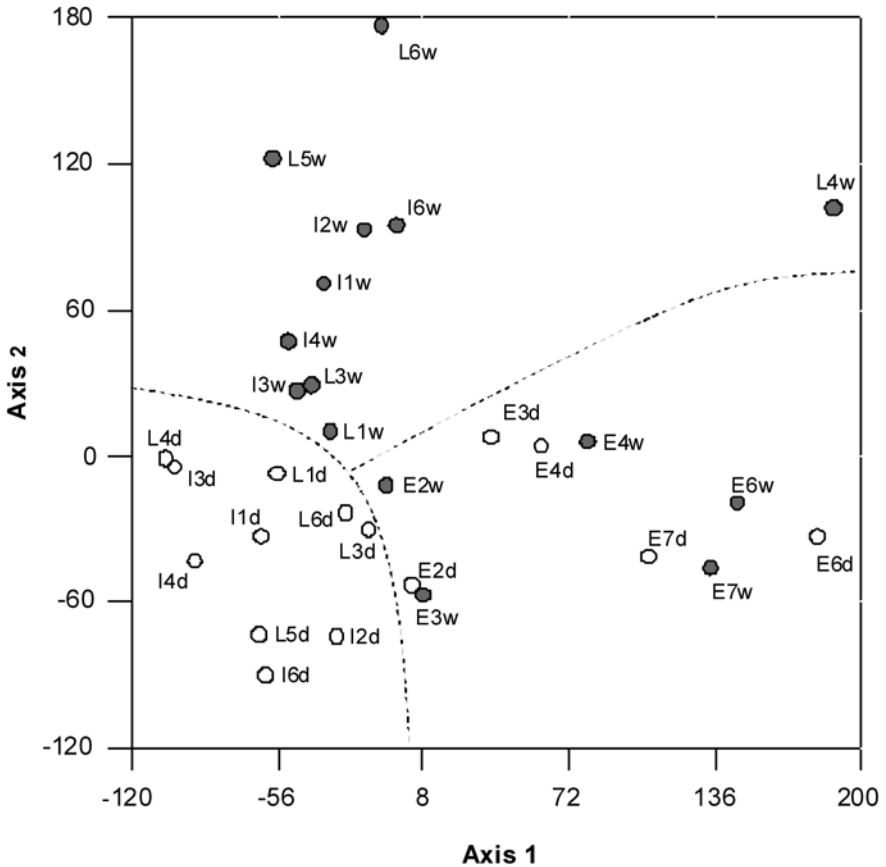


Fig. 1. Plot ordination of the arboreal ant composition sampled in wet (filled circles) and dry (open circles) seasons in early (E), intermediate (I) and late (L) successional stages, using detrended correspondence analysis (DCA). Dashed lines separate statistically distinct groups ($p < 0.05$) through the analysis of the scores obtained from the DCA.

our results indicate that ant communities are affected by forest succession from early to advanced stages, and the effects of seasonality are stage-dependent, affecting only intermediate and late forests.

We did not verify any influence of seasonality and successional stage on ant richness ($p > 0.05$, Fig. 2). Also, the variables used here as surrogates for habitat heterogeneity (tree richness) and resource availability (tree density) did not affect the accumulated richness of arboreal ant in each plot ($p > 0.05$).

DISCUSSION

We verified substantial changes in ant community composition along STDF succession, especially from early to intermediate-late stages. From the forty-three sampled species, only ten (23.3%) occurred in all stages and six species

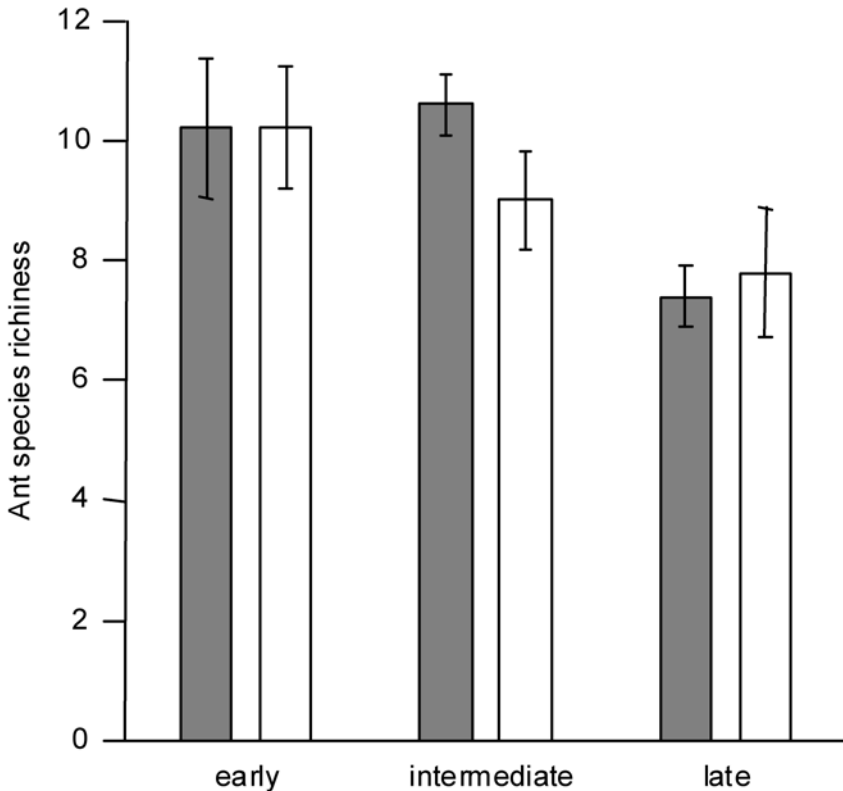


Fig. 2. Mean (\pm SE) arboreal ant richness per plot in wet (gray bars) and dry (white bars) seasons in early ($p > 0.05$), intermediate and late successional stages ($p > 0.05$).

collected in the early stages were not collected in the intermediate and late stages. A similar result was found for terrestrial and arboreal ants in Mexican TDF's (Gove *et al.* 2005), with ant assemblages differing between conservation habitat types and having similar composition between regrowth and forest assemblage. This result shows that ant species are probably affected by habitat changing across a secondary succession in TDFs, with several arboreal ants showing preference for intermediate-late stages (see Gove *et al.* 2005).

The high similarity between arboreal ant communities in intermediate and late stages suggests that approximately 25 years of forest regeneration may be enough to restore most ant diversity to pre-disturbance levels. This time is the same recorded for the recovery of ant species in tropical rain forests (Dunn 2004, Coelho *et al.* 2009), which vary from 20 to 40 years. We concluded that secondary TDFs can provide suitable habitats for forest ant species (see Laurance 2007), contradicting a recent study conducted by Bihn *et al.* (2008) on epigeic and hypogeic ants at an Atlantic Rain Forest fragment in southern Brazil, which showed that secondary forests do not act as refuges for ants.

Though ant species composition varied substantially between stages, the same was not observed for species richness. The absence of successional effects on ant richness was already reported for a tropical rain forest in Brazil (Schmidt 2008, Coelho *et al.* 2009). The same trend was verified for arboreal ants in Mexican TDFs (Gove *et al.* 2005), in which ant species richness did not differ between habitats with different perturbation levels. It is possible that the greatest structural complexity of the late stages in the PEMS (see Madeira *et al.* 2009) provide an adequate habitat for the establishment of large colonies of aggressive species, forming dominance mosaics typically observed in the canopy of tropical wet forests (Dejean & Corbara 2003, Primack & Corlett 2005, Blüthgen & Stork 2007, Sanders *et al.* 2007). In fact, some ant species sampled here, such as those belonging to *Azteca*, *Camponotus* and *Crematogaster* genera can influence the distribution of less competitive species in tropical canopies (Dejean *et al.* 2003, Dejean & Corbara 2003). Alternatively, it is possible that a higher ant richness in the early stage is a consequence of ground-nesting ants foraging in trees, a phenomenon not observed in the late stage. Thus, trees in early successional stages would be occupied by both ground-nesting and arboreal ants, whereas exclusive arboreal ants predominate in late-stage trees. A similar result was observed

for the ant community of a tropical system (Dejean *et al.* 2003), where not ground-nesting but arboreal-foraging species were initially favored during early succession. In late successional stages, ants with this type of behavior decreased in importance (see Dejean *et al.* 2003, Dejean & Corbara 2003).

No significant effect of either tree species richness (used as a surrogate of habitat heterogeneity) or tree density (surrogate of resource availability) on ant richness was observed. These results contradict several previous studies suggesting that ant richness is a good indicator of habitat disturbance status (e. g. Armbrecht *et al.* 2004, Corrêa *et al.* 2006, Vargas *et al.* 2007). However, Lassau & Hochuli (2004) verified higher ant richness in less complex habitats in Australia. The authors proposed several possible explanations for this pattern, including increased foraging and nest construction efficiency, facilitated chemical orientation and lower soil moisture and shadow levels. Thus, further studies are necessary to understand the mechanisms driving arboreal ant species richness along complexity gradients such those observed during tropical dry forest succession.

We did not verify seasonal differences in arboreal ant species richness in this study. This result contradicts several studies in tropical regions that recorded higher ant diversity during the wet season (Reddy & Venkataiah 1990, Lindsey & Skinner 2001). Given the drastic change in vegetation structure and cover between rainy and dry periods, TDFs were expected to present the greatest seasonal fluctuations in ant richness, a pattern already recorded for litter-dwelling and ground-foraging ants in the Argentinean Chaco (Delsinne *et al.* 2008), arboreal and terrestrial ants (Gove *et al.* 2005) and dung beetles (Andersen 2005, 2008) in Mexican TDFs. The same factors that might explain the highest ant diversity in less complex habitats can account for the slightly higher richness recorded during the dry season for all successional stages. The lack of leaves causes habitat structural simplification and decreases humidity and shadow levels, which can facilitate ant foraging and nest construction (Lassau & Hochuli 2004).

In spite of that, there were marked changes in ant community composition between rainy and dry seasons, especially for intermediate and late stages. In these advanced stages, environmental conditions are deeply altered, mainly in the forest floor, going from low temperature and light exposure and high humidity during the wet season to the extreme opposite during the dry season.

Severe leaf drop in the onset of the dry season brings not only a shift in environmental conditions, but also changes the resource availability for arboreal ants in the canopy, such as extrafloral nectar and honeydew produced by trophobionts (Delabie 2001, Dejean & Corbara 2003). Such alterations are attenuated in early successional stages, where the canopy is low and discontinuous. Probably, the ant species occurring in the arboreal stratum in this stage are opportunistic and already adapted to open areas. In contrast, intermediate and late stages probably support a highly forest-specialized ant community during the wet season, which can be colonized by more generalist ant species during the dry season. Thus, arboreal ant communities in advanced stages of TDFs may form mosaics of dominant species during the wet season, when conditions are highly favorable, precluding epigeic ants foraging on trees. In the dry season, arboreal ant species' dominance can be weakened, allowing the occurrence of epigeic ants that thrive better in exposed soil and increased litterfall conditions. However, information on the ecology of most species collected here is lacking, preventing more precise conclusions. Further studies on the biology of individual species of Brazilian TDFs may help explain the changes in community composition both spatially and temporally.

Our results indicate that ant community composition may be a better indicator of habitat quality in tropical forests than species richness. Based in the successional patterns observed in the TDF studied here, it is likely that 25 years of forest regeneration are enough to restore arboreal ant communities, strengthening the importance of secondary habitats to biodiversity maintenance in these ecosystems. It is likely that certain components of TDF structure, such as plant species richness and density, have less influence on ant richness and community composition than in Cerrado. In TDFs, the pronounced effects of seasonality can break dominance mosaics and constitute a strong determinant of ant diversity, particularly in advanced regeneration stages.

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REFERENCES

- Aide, T.M., J.K. Zimmerman, M. Rosario & H. Marcano. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica* 28: 537-548.
- Alonso, L.E. 2000. Ants as indicators of diversity. In D. Agosti, J.D. Majer, L.E. Alonso, & T.R. Schultz (Ed.). *Ants: standard methods for measuring and monitoring biodiversity*, pp. 80-88. Smithsonian Institution, Washington, USA.
- Alonso, L.E. & D. Agosti. 2000. Biodiversity studies, monitoring, and ants: an overview. In D. Agosti, J.D. Majer, L.E. Alonso & T.R. Schultz (Ed.). *Ants: Standard methods for measuring and monitoring biodiversity*, pp. 1-8. Smithsonian Institution Press, Washington, USA.
- Andresen, E. 2005. Effects of season and vegetation type community organization of dung beetles in a tropical dry forest. *Biotropica* 37: 291-300.
- Andresen, E. 2008. Dung beetle assemblages in primary forest and disturbed habitats in a tropical dry forest landscape in western Mexico. *Journal Insect Conservation* 12: 639-650.
- Antunes, F.Z. 1994. Caracterização Climática - Caatinga do Estado de Minas Gerais. *Informe Agropecuario* 17: 15-19.
- Armbrecht, I., I. Perfecto & J. Vandermeer. 2004. Enigmatic biodiversity correlations: Ant diversity responds to diverse resources. *Science* 304: 284-286.
- Arroyo-Mora, J.P., G.A. Sánchez-Azofeifa, B. Rivard & J. Calvo. 2005. Quantifying successional stages of tropical dry forests using Landsat ETM+. *Biotropica* 37: 497-507.
- Basset, Y., V. Novotny, S.E. Miller, & Kitching, R.L. 2003. *Arthropods of Tropical Forests - spatio-temporal dynamics and resource use in the canopy*. University Press, Cambridge, UK.
- Basset, Y., O. Missa, A. Alonso, S.E. Miller, G. Curletti, M. Meyer, C. Eardley, O.T. Lewis, M.W. Mansell, V. Novotny & T. Wagner. 2008. Choice of metrics for studying arthropod responses to habitat disturbance: one example from Gabon. *Insect Conservation and Diversity* 1: 55-66.

- Bestelmeyer, B.T. & J.A. Wiens. 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. *Ecological Application* 6: 1225–1240.
- Bestelmeyer, B.T. & J. A. Wiens. 2001. Ant biodiversity in semiarid landscape mosaics: The consequences of grazing vs. natural heterogeneity. *Ecological Application* 11: 1123-1140.
- Bihn, J.H., M. Verhaagh & R. Brand. 2008. Ecological stoichiometry along a gradient of forest succession: Bait preferences of litter ants. *Biotropica* 40: 597-599.
- Blüthgen, N. & N.E. Stork. 2007. Ant mosaics in a tropical rainforest in Australia and elsewhere: A critical review. *Austral Ecology* 32: 93–104.
- Brown, V.K. 1994. The effects of changes in habitat structure during succession in terrestrial communities. In: S.S. Bell, E.D. McCoy, H.R. Mushinsky, (Ed.). *Habitat structure: The physical arrangement of objects in space*, pp. 141–168. Chapman and Hall, London, UK.
- Bustos, J.H. & P. Ulloa-Chacón. 1996. Mirmecofauna y perturbación en um bosque de nieblina neotropical (Reserva Natural Hato Viejo, Valle del Cauca, Colombia). *Revista de Biología Tropical* 44/45: 259-266.
- Campos, R., H.L. Vasconcelos, S.P. Ribeiro, F.S. Neves & J.P. Soares. 2006. Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. *Ecography* 29: 482-450.
- Castro, A.G., M.V.B. Queiroz & L.M. Araújo. 1990. O papel do distúrbio na estrutura de comunidades de formigas (Hymenoptera-Formicidae). *Revista Brasileira de Entomologia* 34: 201-213.
- Coelho, M.S, G.W. Fernandes, J.C. Santos & J.H.C. Delabie. 2009. Ants (Hymenoptera: Formicidae) as Bioindicators of Land in a Brazilian Atlantic Forest Fragment. *Sociobiology* 54: 51-63.
- Corrêa, M.M., W.D. Fernandez & I.R. Leal. 2006. Diversidade de formigas epigéicas (Hymenoptera: Formicidae) em Capões do Pantanal Sul Matogrossense: Relações entre riqueza de espécies e complexidade estrutural da área. *Neotropical Entomology* 35: 724–730.
- Crawley, M.J. 2002. *Statistical computing – an introduction to data analysis using s-plus* pp. 761. John Wiley & Sons, London, UK.
- Dejean, A., B. Corbara, F. Fernández & J.H. Delabie. 2003. Mosaicos de hormigas arbóreas en bosques y plantaciones tropicales. In F. Fernández (Ed.). *Introducción a las hormigas de la región Neotropical*, pp. 149-158. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Co.
- Dejean, A. & B. Corbara. 2003. A review of mosaics of dominant ants in rainforests and plantations. In Y. Basset, V. Novotny, S. E. Miller, and R. L. Kitching. (Ed.). *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*, pp. 341-347. Cambridge University Press, Cambridge, UK.
- Delabie, J.H.C. 2001. Trophobiosis between Formicidae and Hemiptera (Sternorrhyncha and Auchenorrhyncha): an overview. *Neotropical Entomology* 30: 501-516.

- Delabie, J.H.C., V.R.L.M. Paim, I.C. Nascimento, S. Campiolo & C.S.F. Mariano. 2006. As formigas como indicadores biológicos do impacto humano em manguezais da costa sudeste da Bahia. *Neotropical Entomology* 35: 602-615.
- Delsinne, T., M. Leponce, L. Theunis, Y. Braet & Y. Roisin. 2008. Rainfall Influences Ant Sampling in Dry Forests. *Biotropica* 40: 590-596.
- Denevan, W.M. 1992. The pristine myth: The landscape of the Americas in 1492. *Annals of the Association of American Geographers* 82: 369-385.
- Dunn, R.R. 2004. Recovery of faunal communities during tropical forest regeneration. *Conservation Biology* 18: 302-309.
- Estrada, M.C. & C.F. Fernández. 1999. Diversidad de hormigas (Hymenoptera: Formicidae) en un gradiente sucesional del bosque nublado (Nariño, Colombia). *Revista de Biología Tropical* 47: 189-201.
- Erwin, T. 1983. Tropical forest canopies: the last biotic frontier. *Bulletin of the Entomological Society of America* 29: 14-19.
- Gove, A.D., J.D. Majer & V. Rico-Gray. 2005. Methods for conservation outside of formal reserve systems: The case of ants in the seasonally dry tropics of Veracruz, Mexico. *Biological Conservation* 126: 328-338.
- Guariguata, M.R. & R. Ostertag. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148: 185-206.
- Hansen, R.A. 2000. Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology* 81: 1120-1132.
- Holldobler, B. & E.O. Wilson. 1990. The ants, pp. 746. Bellknap Press, Cambridge, UK.
- IEF - Instituto Estadual De Florestas. 2000. Parecer técnico para a criação do Parque Estadual da Mata Seca. - Instituto Estadual de Florestas, Belo Horizonte, BR.
- Janzen, D.H. 1984. Two ways to be a tropical big moth: Santa Rosa saturniids and sphingids. *Oxford Surveys in Evolutionary Biology*. 1: 85-140.
- Janzen, D.H. 1986. Mice, big mammals and seeds: it matters who defecates what where. In A. Estrada, and T. H. Fleming. (Ed.). *Frugivores and seed dispersal*, pp. 251-271. Dr W. Junk Publishers, Dordrecht, NL.
- Jouquet, P., J. Dauber, J. Lagerlo, P. Lavelle & M. Lepage. 2006. Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. *Applied Soil Ecology* 32: 153-164
- Kalácska, M., G.A. Sanchez-Azofeifa, J.C. Calvo-Alvarado, M. Quesada, B. Rivarda & D.H. Janzen. 2004. Species composition, similarity and diversity in three successional stages of a seasonality dry tropical forest. *Forest Ecology Management* 200: 227-247.
- Lassau, S.A & D.F. Hochuli. 2004. Effects of habitat complexity on ant assemblages: can we generalise across scale? *Ecography* 27: 157-164.
- Lassau, S.A & D.F. Hochuli. 2005. Wasp community responses to habitat complexity in Sidney sandstone forests. *Austral Ecology* 30: 179-187.

- Lassau, S.A., D.F. Hochuli, G. Cassis & C.A.M. Reid. 2005. Effects of habitat complexity on forest beetle diversity: do trophic groups respond consistently? *Diversity and Distributions* 11: 73-82.
- Laurance, W.F. 2007. Have we overstated the tropical biodiversity crisis? *Trends in Ecology and Evolution*. 22: 65–70.
- Leal, I.R., S.O. Ferreira & A.V.L. Freitas. 1993. Diversidade de formigas de solo em um gradiente sucessional de Mata Atlântica, ES, Brasil. *Biotemas* 6: 42-53.
- Lindsey, P.A. & J.D. Skinner. 2001. Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo. *Journal of Arid Environments* 48: 551–568.
- Madeira, B.G., M.M. Espírito-Santo, S. Dangelo Neto, Y.R.F. Nunes, G.A. Sanchez-Azofeifa, G. W. Fernandes & M. Quesada. 2009. Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. *Plant Ecology* 291: 291-304.
- Mccune, B. & M.J. Mefford. 1997. *Multivariate Analysis of Ecological Data*, Version 3.15. MJM software Gleneden Beach, Oregon, USA.
- Miles, L.A.C., R.S. Newton, C. Defries, I. Ravilious, S. May, V. Blyth, Kapos & J.E. Gordon. 2006. A global overview of the conservation status of tropical dry forests. *Journal of Biogeography* 33: 491-505.
- Murphy, P.G. & A.E. Lugo. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67-88.
- Nichols, O.G. & F.M. Nichols. 2003. Long-term trends in faunal recolonization after bauxite mining in the Jarrah Forest of Southwestern Australia. *Restoration Ecology* 11: 261–272.
- Ottonetti, L., L. Tucci & G. Santini. 2006. Recolonization patterns of ants in a rehabilitated lignite mine in Central Italy: Potential for the use of Mediterranean ants as indicators of restoration processes. *Restoration Ecology* 14: 60–66.
- Pezzini, F.F., D.O. Brandão, B.D. Ranieri, M.M. Espírito-Santo, C.M. Jacobi & G.W. Fernandes. 2008. Polinização, dispersão de sementes e fenologia de espécies arbóreas no Parque Estadual da Mata Seca. *MG Biota*: 37-45.
- Primack, R. & R. Corlett. 2005. *Tropical Rain Forests: An Ecological and Biogeographical Comparison*, pp 319. Blackwell Publishing, Oxford, UK.
- Quesada, M., G.A. Sanchez-Azofeifa, M. Alvarez-Anorve, K.E. Stoner, L. Avila-Cabadilla, J. Calvo-Alvarado, A. Castillo, M.M. Espírito-Santo, M. Fagundes, G.W. Fernandes, J. Gamon, M. Lopezaraiza-Mikel, D. Lawrence, P. Morellato, J. Powers, F.S. Neves, V. Rosas-Guerrero, R. Sayago & G. Sanchez-Montoya. 2009. Succession and Management of Tropical Dry Forests in the Americas: Review and new perspectives. *Forest Ecology and Management* 258: 1014–1024.
- R Development Core Team. 2008. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Reddy, M.V. & B. Venkataiah. 1990. Seasonal abundance of soil-surface arthropods in relation to some meteorological and edaphic variables of the grassland and tree-planted areas in a tropical semi-arid savanna. *International Journal of Biometeorology* 34: 49–59.
- Ribas, C.R., J.H. Schoereder, M. Pic & S.M. Soares. 2003. Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology* 28: 305–314.
- Ribas, C.R. & J.H. Schoereder. 2007. Ant communities, environmental characteristics and their implications for conservation in the Brazilian Pantanal. *Biodiversity Conservation* 16: 1511–1520.
- Sánchez-Azofeifa, G.A., M. Kalacska, M. Quesada, J. Calvo, J. Nassar & J.P. Rodriguez. 2005. Need for integrated research for a sustainable future in tropical dry forests. *Conservation Biology* 19: 285–286.
- Sanders, N.J., G.M. Crutsinger, R.R. Dunn, J.D. Majer & J.H.C. Delabie. 2007. An ant mosaic revisited: Dominant ant species disassemble arboreal ant communities but co-occur randomly. *Biotropica* 39: 422–427.
- Santos, A.M. & S.M. Thomaz. 2007. Aquatic macrophytes diversity in lagoons of a tropical floodplain: The role of connectivity and water level. *Austral Ecology* 32: 177–190.
- Santos, C.S., J.H.C. Delabie & G.W. Fernandes. 2008. A 15-year post evaluation of the fire effects on ant community in an area of Amazonian forest. *Revista Brasileira de Entomologia* 52: 82–87.
- Schmidt, F.A. 2008. Resposta de comunidades de formigas a um gradiente de sucessão. MSc Dissertation. Universidade Federal de Viçosa, Viçosa, Brazil.
- Schnell, M.R., A.J. Pik & J.M. Dangerfield. 2003. Ant community succession within eucalypt plantations on used pasture and implications for taxonomic sufficiency in biomonitoring. *Austral Ecology* 28: 553–565.
- Silva, F.A.B., M.I.M. Hernández, S. Ide & R.C. Moura. 2007. Comunidade de escarabeíneos (Coleoptera: Scarabaeidae) copro-necrófagos da região de Brejo Novo, Caruaru, Pernambuco, Brasil. *Revista Brasileira de Entomologia* 51: 228–233.
- Sperber, C.F.S., K. Nakayama, M.J. Valverde & F.S. Neves. 2004. Tree species richness and density affect parasitoid diversity in cocoa agroforestry. *Basic and Applied Ecology* 5: 241–245.
- Tobin, J.E. 1997. Competition and coexistence of ants in a small patch of rainforest canopy in Peruvian Amazonia. *Journal of New York Entomological Society* 105: 105–112.
- Vargas, A.B., A.J. Mayhé-Nunes, J.M. Queiroz, G.O. Souza & E.F. Ramos. 2007. Efeitos de fatores ambientais sobre a mirmecofauna em comunidade de Restinga no Rio de Janeiro, RJ. *Neotropical Entomology* 36: 28–37.
- Vasconcelos, H.L. 1999. Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. *Biodiversity and Conservation* 8: 409–420.