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Are ant assemblages of Brazilian veredas characterised by location or habitat type?

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(With 4 figures)

Abstract

Wetland areas in the Brazilian Cerrado, known as "veredas", represent ecosystems formed on sandy soils with high concentrations of peat, and are responsible for the recharge of aquiferous reservoirs. They are currently under threat by various human activities, most notably the clearing of vegetation for *Eucalyptus* plantations. Despite their ecological importance and high conservation value, little is known about the actual effects of human disturbance on the animal community. To assess how habitat within different veredas, and plantations surrounding them affect ant assemblages, we selected four independent vereda locations, two being impacted by *Eucalyptus* monoculture (one younger and one mature plantation) and two controls, where the wetland was surrounded by cerrado vegetation. Ant sampling was conducted in May 2010 (dry season) using three complementary methods, namely baits, pitfall traps, and hand collection, in the wetland and in the surrounding habitats. A total of 7,575 ants were sampled, belonging to seven subfamilies, 32 genera and 124 species. Ant species richness and abundance did not differ between vereda locations, but did between the habitats. When impacted by the monoculture, ant species richness and abundance decreased in wetlands, but were less affected in the cerrado habitat. Ant species composition differed between the three habitats and between vereda locations. *Eucalyptus* plantations had an ant species composition defined by high dominance of *Pheidole* sp. and *Solenopsis invicta*, while natural habitats were defined by *Camponotus* and *Crematogaster* species. *Atta sexdens* was strictly confined to native habitats of non-impacted "veredas". *Eucalyptus* monocultures require high quantities of water in the early stages, which may have caused a decrease in groundwater level in the wetland, allowing hypogeic ants such as *Labidus praedator* to colonise this habitat.

Keywords: mesic environments, bioindication, Formicidae, Brazilian savanna, *Eucalyptus*.

Caracterização da assembleia de formigas (Hymenoptera: Formicedae) em veredas impactadas pela monocultura de *Eucaliptus*

Resumo

O ecossistema ribeirinho do Cerrado brasileiro, é conhecido como "vereda", e é formado em solos arenosos com altas concentrações de turfa, além de serem responsáveis pela recarga dos reservatórios dos aquíferos. Atualmente, as veredas estão sob ameaça de várias atividades humanas, especialmente a supressão da vegetação para plantio de *Eucalyptus*. Apesar de sua importância ecológica e elevado valor na conservação, pouco se sabe sobre os efeitos das perturbações humanas sobre a comunidade de animais. Para avaliar como que habitats em diferentes veredas e as plantações circundantes afetam a assembleia de formigas, foram selecionadas quatro "veredas" independentes, sendo duas impactadas pela monocultura de eucalipto (uma jovem e uma madura) e duas controles com a planície de inundação circundada por vegetação de cerrado. A coleta das formigas foi realizada em Maio de 2010 (estação seca) por meio de três métodos complementares, iscas atrativas, armadilhas de pitfall e coleta direta, no habitat de planície alagada, e na área circundante. Foi amostrado um total de 7.575 formigas, pertencentes a sete subfamílias, 32 gêneros e 124 espécies. A riqueza e abundância de formigas não diferiram entre as localidades "veredas", mas sim entre os habitats. Quando impactados pela monocultura, a abundância e a riqueza diminuem nas planícies de inundação, mas os habitats de cerrado foram menos afetados. As plantações de eucalipto têm sua composição de espécies de formigas definida pela alta dominância de *Pheidole* sp. e *Solenopsis invicta*, enquanto os habitats naturais foram definidos por espécies de

Camponotus e *Crematogaster*. *Atta sexdens* foi estritamente relacionada à habitats nativos de "veredas" preservadas. A monocultura de eucalipto requer grandes quantidades de água nos estágios iniciais, o que pode ter provocado a queda no nível do lençol freático nas planícies alagadas, permitindo a colonização deste habitat por espécies de formigas de hábitos hipógeos, como *Labidus praedator*.

Palavras-chave: ambientes mésicos, bioindicação, Formicidae, savana brasileira, *Eucalyptus*.

1. Introduction

Brazilian cerrado is one of the most threatened Neotropical Biomes, suffering loss of biodiversity, invasion of exotic species, soil erosion, and pollution of aquifers (Oliveira-Filho and Lima, 2002). Embedded within the cerrado region, the "veredas" are wetland ecosystems formed on sandy soils with high concentrations of peat, and are responsible for recharge of aquiferous reservoirs; they are particularly endangered as a result of intensified human activity (Eiten, 1994; Alencar-Silva and Maillard, 2007). In addition to their hydrological, social, historical, cultural and economic importance, they are also considered to be of great importance for watershed conservation, which forms almost 80% of headwaters in the northwest of Minas Gerais. The soils are composed of very fine particle sizes, with large amounts of decaying organic matter, resulting in a black matter which is wet and colonised by hydrophilic grasses and the Buriti (*Mauritia flexuosa* L. f. - Arecaceae) palm tree.

The mesic characteristics of "veredas" make them important ecological corridors within the xeric environment, connecting fragments of cerrado and enabling several species populations gene flow to occur (Oliveira and Ferreira, 2007). Thus, when a moderately sized wetland is degraded, this can influence the degradation and possibly cause loss of integrity of hundreds of square kilometers of cerrado (Alencar-Silva and Maillard, 2007). One of the main causes of disorderly destruction of the cerrado is agribusiness, which had its beginning in the late 70's. Currently, planting of *Eucalyptus* is gaining nationwide interest due to the low investment cost and care, and growing market. There is still no consensus on the impacts of this type of monoculture on soil, groundwater and biodiversity, leading to intense debate between the scientific community and farmers' lobby groups, and also in the Brazilian Congress and Senate.

The "veredas" are areas protected under law due their environmental values, such as recharge of aquiferous reservoirs but, even so, tracts of these native areas are gradually being replaced by *Eucalyptus* plantations. *Eucalyptus* was introduced into Brazil at the end of the 19th century for the production of sleepers for railways lines (Mentone et al., 2011). Later, plantations were established for the paper industry. In their early stages, such plantations consume large amounts of water and nutrients (Vezzani et al., 2001; Vital, 2007), and in later stages the litter becomes rich in chemical compounds that slow down its degradation, leading to reduced cycling of nutrients and impoverishment of soil. The scale of these impacts in the veredas is not well understood, but is it in other cerrado phytophysiognomies (Marinho et al., 2002; Tavares et al., 2008). There is an urgent need for studies to assist with conservation measures and to help with the drafting of complementary laws that aim to protect this unique ecosystem in the light of novel land usage policies.

Soil fauna is an important component of such conservation studies, especially for understanding the soil dynamics and the fine-scale aspects of changes in soil features (Majer and Delabie, 1994; Majer et al., 2007), such as soil compaction and the associated lowering of groundwater, a typical problem caused by *Eucalyptus* monocultures (Vital, 2007). Ants, along with termites, worms, and certain other invertebrates, maintain the soil's intrinsic features. These invertebrates promote the formation of channels, pores, and aggregates that influence the transport of gases and water, and they also play important roles in geomorphology and soil formation (Coutinho et al., 2003; Lavelle et al., 2006). Because of their close connection with this stratum, ants are excellent indicators of soil quality (Costa et al., 2010).

The present study examined the assemblages of ant species in different vereda locations, which contain wetland habitats surrounded by cerrado habitats, or by lands where such vegetation has been replaced by *Eucalyptus* monoculture. We predicted that removal of native habitat (cerrado) to plant *Eucalyptus* may favour a few species belonging to generalist guilds, and possibly eliminate populations of rare or specialist species, thus decreasing species diversity.

2. Material and Methods

2.1. Study area

The veredas we studied are located in the northwest region of Minas Gerais state, in a typical cerrado region. The "veredas" are located in the municipalities of São Gonçalo do Abaeté (18°20'16"S and 45°49'58"W), Três Marias (18°15'12"S and 45°15'50"W) and Andréquicé (a district of Três Marias - 18°27'08.69"S and 044°50'51.12"W (see Figure 1). The climate in the region of the high–mid San Francisco river basin is characterised **Aw**, according to Köppen's climatic divisions, being tropical and semi-humid, with an average temperature of 24°C, prevalent rainfall in summer (December until March), dry winters (July until September), and an average rainfall of 1,000 to 1,800 mm.

The field work was carried out in two reasonably well preserved veredas (control locations): Curral das Éguas (Vereda P1) and Lagoa do Inferno (Vereda P2); and in two disturbed veredas (modified locations): Buriti (Vereda

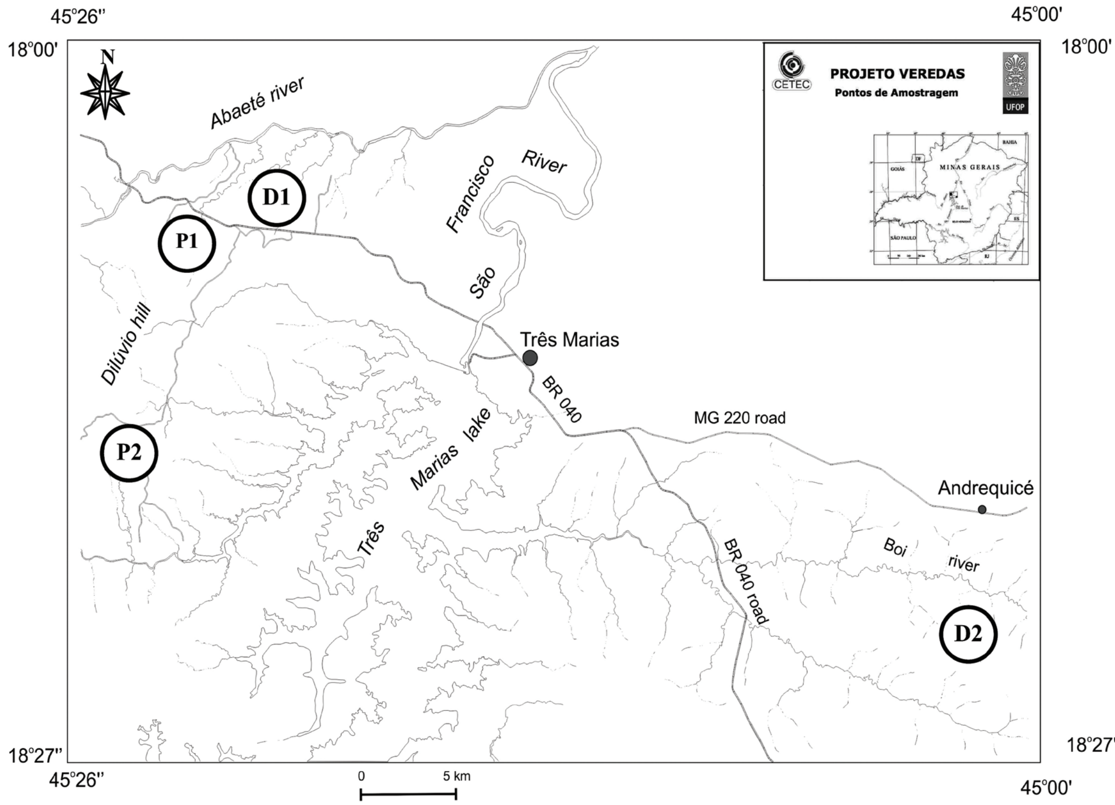

Figure 1. Location of the veredas, near the city of Três Marias. The numbers represent the location of the each vereda, with Vereda P1 and P2 being controls, and Vereda D1 and D2 being planted with eucalypts. Modified from CPRM (2002).

D1 – surrounded by a 3 - year old *Eucalyptus* plantation) and São José (Vereda D2 – surrounded by a 5 - year old *Eucalyptus* plantation) (see Figure 2). The sampled veredas location consisted of the following habitats; the wetland area, the adjacent cerrado (for control habitats) and/or *Eucalyptus* plantation (for modified habitats). In vereda São José (Vereda D2) there was a permanently preserved area of cerrado between the wetland and the *Eucalyptus* plantation. Each vereda therefore consisted of up to three habitats, these being: We – wetland zone, under the direct influence of yearly floods; Ce – cerrado zone, surrounding the wetland; and, if present, Eu – *Eucalyptus* zone. The *Eucalyptus* monoculture was planted on areas where the native vegetation was suppressed and the organic soil layer had been tilled into the ground to prepare the soil for planting. The four vereda locations were considered random blocks (habitat zones: wetland + cerrado; wetland + *Eucalyptus*; wetland + cerrado + *Eucalyptus*), each habitat having three replicated transects (Figure 2).

2.2. Ant sampling

Ant sampling was conducted in May 2010 (dry season) using three methods, namely baits (soil and arboreal), pitfall traps (soil and arboreal), and hand collections. Pairs of 20 m transects situated 10 m apart were replicated in three locations in each habitat (see Figure 2). Pitfall traps and baits were placed 5 m apart along the transect in an alternating fashion. The hand collection was performed for one hour in each habitat. The ground pitfall traps were adapted from the method used by Holway (2005), but traps were left in the ground for three days. Arboreal pitfall traps used the methodology proposed by Majer (1983). The baits followed the method used by Espírito Santo et al. (2012). Sampled ants were sorted and identified to genus level, and then separated into morphospecies or species. The reference collection is stored at the Federal University of Ouro Preto (UFOP), Brazil.

2.3. Data analysis

Abundance and ant species richness were calculated for the combined transects pairs using all the information from all sampling methods together. The ant species richness and abundance data were compared by a nested analysis of variance model, testing the effect of 'habitats' (with levels wetland, cerrado and *Eucalyptus*) nested in 'veredas locations', as random blocks and grouped in a final factor 'conservation' (vereda levels: preserved and disturbed). When necessary, the differences between treatment mean levels were examined using Tukey's post-hoc test.

Non-metric multi-dimensional scaling (NMDS) was performed on ant presence/absence data using the Jaccard similarity measure to produce ordinations of similarity

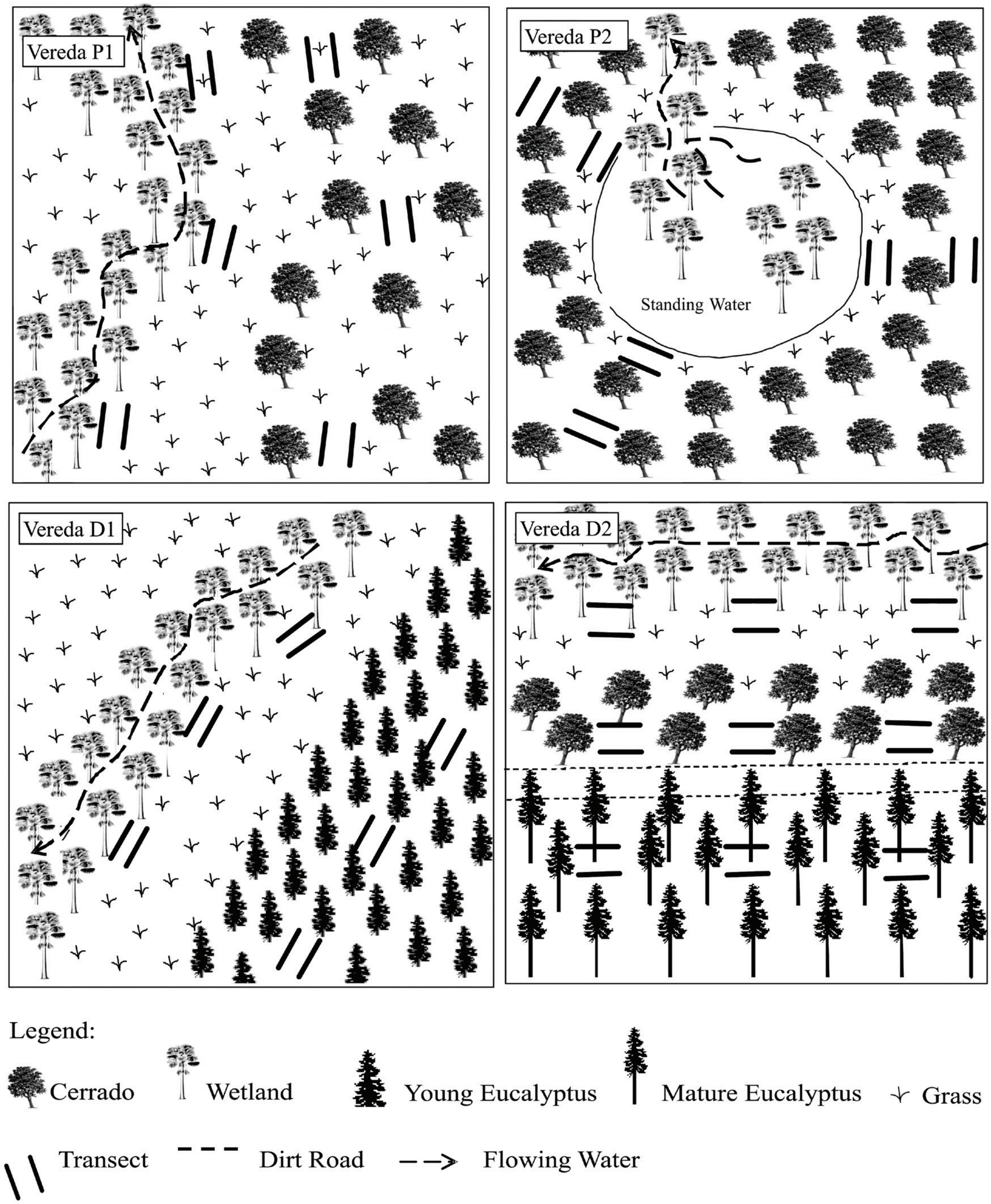

Figure 2. Layout of transects for ant sampling in the veredas, each comprising paired 20 m transects set of 10 m apart.

between transects. Wherever it was possible, 'hulls' were constructed on the ordination diagram to delimit outermost boundaries of each vereda location or habitat. Analyses of similarity (ANOSIM – Two Way) tested for significant differences in ant composition for the factor 'habitat' (with levels wetland, cerrado, eucalypt), and the factor 'vereda location' (with each site as levels). Similarity percentages (SIMPER) identified the contribution of ant species to the dissimilarity between the selected factors. The above analyses were performed using Past version 2.04 (Hammer et al., 2001).

3. Results

Across all areas 7,575 ants were sampled, belonging to seven subfamilies, 32 genera and 125 species. Of this total, 42% of individuals were sampled in the pristine vereda sites, where five genera and 34 species were exclusive. Besides this, 78.1% of genera and 46% of species were common to preserved and disturbed 'veredas locations'. Ant species abundance (from all sampling methods) in each vereda and habitat is shown in Supplementary Table S1.

We sampled two genera and 34 species exclusively in the disturbed "veredas". Myrmicinae and Formicinae were the most speciose subfamilies, with 60 and 30 species, respectively, representing 72% of the total number of species (see Supplementary Table S1). *Pheidole* (Myrmicinae) and *Camponotus* (Formicinae) were the most speciose genera (29 and 24 species, respectively). The most abundant species in these genera were *Pheidole* sp.19 (414 individuals) and *Camponotus crassus* (716 individuals), both of which were present in all "veredas". However, the high total abundances were largely influenced by ants with opportunistic behaviour, such as *Solenopsis invicta* (Myrmicinae), with 1,339 individuals and present in all "veredas". Another pioneer species, with similar opportunistic behaviour, *Linepthema humile*, was also found in the wetland, as well as the *Eucalyptus* monoculture.

There was no significant overall difference in ant abundance or species richness among the 'veredas location' (Nested ANOVA abundance, $F_{(3,18)} = 0.050$, $P = 0.98$; Nested ANOVA richness, $F_{(3;18)} = 1.146$, $P = 0.41$). However, there was a significant CPRM (2002) difference between "habitats" (Nested ANOVA, $F_{(5,18)} = 5.371$, $P = 0.003$), with the wetlands of Vereda D1 and D2 having significantly less ant individuals than the corresponding eucalypt habitat and cerrado of Vereda D2 (see Figure 3a). Although the unbalanced design did not enable us to test the interaction term, the model provided evidence that ant abundance was lower in the impacted wetland than in those that were not surrounded by eucalypt plantations. This trend was reversed in the cerrado habitat, where the highest abundance was in D2 (there was no cerrado in D1). Further, there was an effect of habitat on species richness (Nested ANOVA, $F_{(5,18)} = 3.579$, $P = 0.020$), with all wetlands and eucalypt plantations having lower numbers of species than cerrado, particularly in the cerrado of D2 (see Figure 3b).

The ant species assemblages in Vereda P1, Vereda P2 and Vereda D1 were different from each other, independently of habitats that they comprise (ANOSIM, R = 0.41, $P < 0.0001$; see Figure 4b), but the ant assemblage of Vereda D2 was similar to Vereda P1 (Table S2). The species that most contribute to the separation of the assemblage of the preserved 'veredas location' were *Camponotus* (Myrmobrachys) sp.1 (3.44%), *Ectatomma brunneum* (2%) and *Solenopsis invicta* (1.98%). *Pheidole* sp.24 (1.68%) contribute for the separation of the assemblages in the impacted Vereda D1 and D2, along with *Wasmannia auropuctata* (2.03%) and *Ectatomma planidens* (1.83%). Likewise, the wetland, cerrado and eucalypt "habitats" were different, independently of 'veredas location' were they occurred (ANOSIM, R = 0.34, $P < 0.0001$; see Figure 4a). According to the R and p values provided by ANOSIM (Table S3), all habitats were significantly different from each other. The species most influential in discriminating the cerrado habitats were *Mycocepurus goeldii* (1.62%), *Ectatomma planidens* (1.56%), and *Pheidole* sp.23 (1.52%). *Camponotus rufipes* (2.16%) and *Camponotus melanoticus* (2.25%) had a strong influence in separating wetland habitats, as did *Pheidole* (Flavens) sp.1 (1.68%) and *Pheidole gertrudae* (1.65%) in eucalypt habitats.

It is worth noting that relative species densities of the most abundant species also seem to reflect habitat conditions (see Table S1). In the *Eucalyptus* habitat we sampled 54 species from 1,925 individuals, with 49% of these individuals belonging to the genus *Pheidole* (952 individuals), and 29% to *Solenopsis invicta* (571 individuals). The cerrado and wetland habitats produced 5,633 individuals of ants, belonging to 120 species. Among these species, the most abundant species was *Camponotus crassus* (688 individuals), *Crematogaster torosa* (537 individuals) and *S. invicta* (768 individuals). A further important feature was the high abundance of *Atta sexdens* ("saúvas") (Myrmicinae) in wetland and

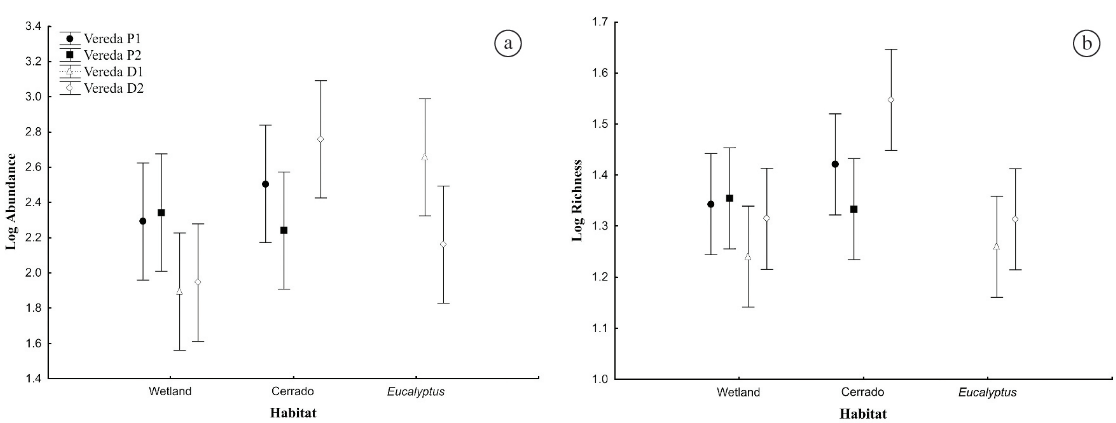

Figure 3. Abundance (a) and richness (b) of ants in habitats for each vereda. Bars are standard deviations.

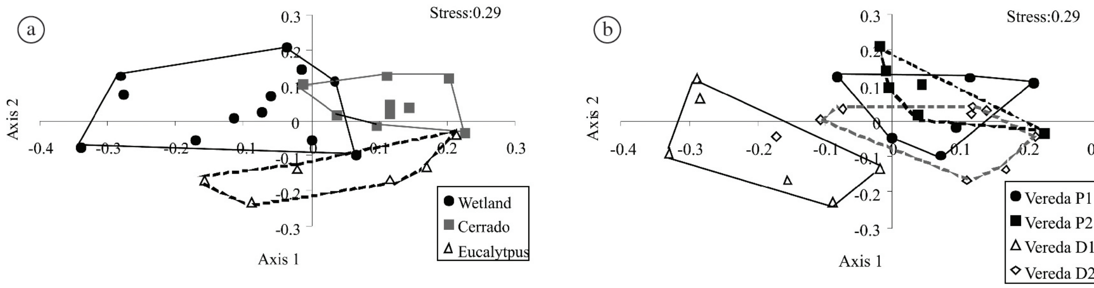

Figure 4. Distribution of (a) habitat and (b) vereda on the NMDS ordination, based on Jaccard similarity measure, using ant presence/absence data. Hulls are drawn around the different habitats in (a) and the veredas in (b).

Table S1. Ant species sampled in the pristine veredas (P) (surrounded by cerrado habitats) and in those impacted by surrounding *Eucalyptus* plantations (D) (We= wetland; Ce= cerrado and Eu= *Eucalyptus*).

Species	Areas								
	Vereda P1		Vereda P2		Vereda D1		Vereda D2		
	We	Ce	We	Ce	We	Eu	We	Ce	Eu
Dolichoderinae									
Azteca sp.1		6					1		
Dolichoderus bispinosus Olivier	1								
Dolichoderus germaini Emery					7	3	6		
Dolichoderus lamellosus Mayr					1				
Dorymyrmex jheringi Forel	330		22	2	16	106	2	1	56
Dorymyrmex spurius Santschi			4		12	77			
Dorymyrmex sp.1		5			1	31		1	
Dorymyrmex sp.2						8			12
Forelius maranhaoensis Cuezzo				4	1				
Gracilidris pombero Wild and Cuezzo	2					2		2	1
Linepihema anathema Wild							3		
Linepithema humile Mayr	79	11	1				14		
Linepithema micans Forel	6	3	108	8			4	1	
Linepithema sp.1			55						
Linepithema sp.4			2	12					
Ecitoninae									
Labidus praedator Smith							5		
Ectatomminae									
Ectatomma brunneum Smith	17	30	11				3	11	5
Ectatomma edentatum Roger	2	1		6			2	11	13
Ectatomma lugens Emery				1					
Ectatomma opaciventre Roger		3						7	7
Ectatomma permagnum Forel		2		2				4	4
Ectatomma planidens Borgmeier		32	2	25			1	28	9
Gnamptogenys acuminata Emery						1			
Gnamptogenys striatula Mayr				1					
Formicinae									
Brachymyrmex sp.1	1	35				9	17	28	
Brachymyrmex sp.2	1					7	1		1
Brachymyrmex sp.3	7				1	1			
Brachymyrmex (*Pallipes* gr.) sp.4				8					
Brachymyrmex sp.5						2			
Camponotus arboreus Smith	5	12		6	1		5		
Camponotus atriceps Smith	4	10		20		1	3	15	1

Table S1. Continued...

Species	Areas								
	Vereda P1		Vereda P2		Vereda D1		Vereda D2		
	We	Ce	We	Ce	We	Eu	We	Ce	Eu
Camponotus blandus Smith	1	137			1	2	3	6	1
Camponotus bonariensis Mayr								1	
Camponotus cameranoi Forel							1		
Camponotus cingulatus Maur		10	5					6	1
Camponotus crassus Mayr	31	145	11	37	4	12	39	421	16
Camponotus leydigi Forel	2							2	
Camponotus melanoticus Emery	4	13	3	8	1		1	18	
Camponotus rufipes Fabricius	12	1	129	20	26	1	26		
Camponotus sericeiventris Guérin-Méneville							1		
Camponotus trapezoideus Mayr							1		
Camponotus (Myrmobrachys gr.) sp.1	9	60	4	1		1	4	81	3
Camponotus (*Myrmothrix* gr.) sp.2	2	11				1		34	
Camponotus (Myrmothrix gr.) sp.3		2							
Camponotus (Myrmothrix gr.) sp.4				1	2				
Camponotus sp.13			1				2	3	
Camponotus sp.16								1	
Camponotus sp.17				1					
Camponotus sp.19			3						
Camponotus sp.21	4								
Camponotus sp.22							1		
Camponotus sp.24				1					2
Camponotus sp.25					1				
Nylanderia nr. *fulva* Mayr	9								
Myrmicinae									
Acromyrmex balzani Emery		1	1	1			1	13	1
Apterostigma sp.1				1				1	
Apterostigma (Pilosum gr.) sp.1			1						
Atta laevigata Smith			1						
Atta sexdens Linneaus	99		24	199				68	
Cephalotes atratus Lineaus				25					
Cephalotes borgmeieri Kempf				3					
Cephalotes eduarduli Forel	1	15							
Cephalotes maculatus Smith F.		3			1		1	1	
Cephalotes pusillus Klug		8	2	11	57		2	2	
Crematogaster acuta Fabricius	14		2		158	14	18		
Crematogaster limata Smith F.	3						1		2
Crematogaster torosa Mayr	10	316	1					210	
Crematogaster nr. *obscurata* Emery		38	1	3					
Crematogaster sp.1			1						
Cyphomyrmex rimosus Spinola			2		2		1	1	
Megalomyrmex sp.1			1						
Mycocepurus goeldii Forel	2	4		4		1		5	8
Mycocepurus smithii Forel								3	
Myrmicocrypta sp.1		1						3	
Pheidole gertrudae Forel	117					287			1
Pheidole (Flavens gr.) sp.1		8		27	1	2		15	27
Pheidole (Flavens gr.) sp.3	1	6							5
Pheidole sp.6			1		2			12	

Table S1. Continued...

Species	Areas								
	Vereda P1		**Vereda P2**		**Vereda D1**		**Vereda D2**		
	We	**Ce**	**We**	**Ce**	**We**	**Eu**	**We**	**Ce**	**Eu**
Pheidole sp.19	2	6		18	4	324	6	22	32
Pheidole sp.20				2					
Pheidole sp.21		1	2						
Pheidole sp.22	4	4	4					7	9
Pheidole sp.23		5	15	13		1	1	23	1
Pheidole sp.24	47	33	4	15		1	15	13	186
Pheidole sp.25	9		2		1				
Pheidole sp.26	3		1			1		6	25
Pheidole sp.27		3						21	
Pheidole sp.28					2	1	17		
Pheidole sp.29								5	
Pheidole sp.30					1				29
Pheidole sp.31								2	9
Pheidole sp.32					2				
Pheidole sp.33					1			3	4
Pheidole sp.34								7	1
Pheidole sp.35					3			1	
Pheidole sp.36					4				
Pheidole sp.37									6
Pheidole sp.40								1	
Pheidole sp.43		1		18				30	
Pheidole sp.45	9	18	1		1			9	
Pheidole sp.46		4	1						
Pheidole sp.47	1								
Pheidole sp.48		1		1	2				
Pogonomyrmex naegelii Emery						1	1		
Sericomyrmex parvulus Forel	1								
Solenopsis invicta Buren	2		179	18		570		569	1
Solenopsis (Geminata gr.) sp.1		2	1			1			
Solenopsis sp.1			34			4	1	2	
Trachymyrmex dichrous Kempf								1	
Trachymyrmex fuscus Emery		2							
Trachymyrmex sp.1								3	1
Wasmannia auropunctata Roger	26		1	24	2		14	36	25
Wasmannia rochai Forel								20	
Xenomyrmex sp.1				19					
Ponerinae									
Hypoponera sp.4			1						
Odontomachus haematodus Emery	1			1	1				
Odontomachus meinerti Forel							2		1
Pachycondyla ferruginea Smith	1								
Pachycondyla obscuricornis Emery	5				3	3	6		
Pseudomyrmecinae									
Pseudomyrmex acanthobius Emery	1		48		2		1		
Pseudomyrmex termitarius Smith		3			2				
Pseudomyrmex nr. *urbanus* Smith		1			1				1
Pseudomyrmex oculatus gr. sp.1									1
Pseudomyrmex sp.2		1							
Pseudomyrmex sp.3							2		

Table S2. Comparison of the variation of similarities (ANOSIM of ant species composition among the four veredas studied.

P – values	Vereda P1	Vereda P2	Vereda D1	Vereda D2
Vereda P1	0	0.0031	0.0016	0.0871
Vereda P2	0.0031	0	0.0022	0.0473
Vereda D1	0.0016	0.0022	0	0.0019
Vereda D2	0.0871	0.0473	0.0019	0

R – values	Vereda P1	Vereda P2	Vereda D1	Vereda D2
Vereda P1	0	0.5444	0.675	0.1565
Vereda P2	0.5444	0	0.6444	0.2128
Vereda D1	0.675	0.6444	0	0.5214
Vereda D2	0.1565	0.2128	0.5214	0

Table S3. Comparison of the variation of similarities (ANOSIM of ant species composition among the three habitats studied.

P – values	Wetland	Cerrado	Eucalyptus
Wetland	0	0.0018	0.0017
Cerrado	0.0018	0	0.0003
Eucalyptus	0.0017	0.0003	0

R – values	Wetland	Cerrado	Eucalyptus
Wetland	0	0.5444	0.675
Cerrado	0.5444	0	0.6444
Eucalyptus	0.675	0.6444	0

cerrado of the Veredas P1 and P2. *Atta sexdens* was absent in the *Eucalyptus* habitat.

4. Discussion

The present study suggests that the ant assemblage is characterised by habitat type, and the ant fauna of the cerrado is resilient to surrounding impacts in terms of species richness but not species composition or relative abundance, thus partially corroborating our hypothesis prediction. The "veredas" are ecosystems under the influence of seasonal water flooding, and they support a unique plant community, based on endemic species such as the Buriti, which has a strong engineering role in the ecosystem. After the Buriti has become established in the area, several other tree and shrub species are able to colonise the flooded margins and stabilise and enrich the soil, creating conditions for further succession, along with the retention of moisture (Rizzini, 1997). The ground and arboreal ant fauna of these "veredas" is directly linked to the phenomena of flooding, the stratification of vegetation, geomorphological evolution and colonisation by other invertebrates. Therefore, ant species responses to habitats may be related to how these habitats evolved and how they are preserved.

Eucalyptus monocultures are poor environments in terms of spatial heterogeneity and species diversity, and they exhibit simplified nutrient cycling and energy dynamics. Such conditions may contribute to reduced numbers of ant species in these environments (Vallejo et al., 1987) and reduce the occurrence of specialist species (Pacheco et al., 2009). The ant species that colonise the area after impact were more aggressive types, and could banish or eliminate the resident species. With all the impact caused by the preparation for the planting of *Eucalyptus*, some rare species or specific habitats may also be eliminated. Accordingly, we found that the diversity of ants in *Eucalyptus* was lower than in pristine habitats, but most species found in *Eucalyptus* were also observed at least somewhere in the cerrado and wetland. This suggests that the preservation of areas surrounded by the plantations may favour the colonisation of ants in environments with low structural complexity, as is the case with the *Eucalyptus* plantation.

Our findings contrast with our predictions that opportunistic and invasive species would dominate in the *Eucalyptus*, forming a completely distinct animal community, and therefore highlight the importance of the legal "Permanent Preservation Areas" attached to each vereda. Besides acting as a source of species that colonise the agro-ecological habitats, such pristine vereda habitats also promote the flow of matter and energy between these environments. The "veredas" are true ecological corridors, functioning as a biological stock, and promoting colonisation of disturbed areas where native vegetation is scarce. On the other hand, the widespread presence of *S. invicta* in the natural habitats of veredas reflects the opposite of this exchange phenomenon, representing decreasing quality of the wetlands and cerrado.

Another interesting indicator of habitat structure dependence was *Atta sexdens* in the surrounding cerrado of Vereda P2. Costa et al. (2010) reported that *Atta* species nests require good, and well-preserved, soil conditions, but are resistant to surrounding impacts, as long as new leaves of pioneer plants are available. More recent works have shown that Attini species are positive engineers of forest biodiversity, and are related to high seed dispersal and seedling survivorship (Leal et al., 2007; Silva et al., 2007; Wirth et al., 2007). Members of the tribe Attini, in particular the genera *Atta* and *Acromyrmex*, have been reported as being abundant in *Eucalyptus* monocultures (Araújo et al., 1997; Cantarelli, 2005), but this was not observed in this study. Due to high leaf concentrations of tannins and other deterrent compounds in *Eucalyptus*, it is an unfavourable habitat for these genera to nest or forage. Indeed, these genera forage in monoculture habitats only in the initial stages, when the native vegetation has just been removed for planting (Bento and Della Lucia, 1993).

It is worth noting that both wetlands and cerrados contained species requiring high quality of arboreal habitats, thus reflecting some resilience and resistance of these ecosystems to the impact of being surrounded by *Eucalyptus*. The presence of certain genera supports this perception, as exemplified by species in cerrado such as *Mycocepurus goeldii* (which nests in soil with rotten logs, and which takes feces of insects, fruit pulp and seeds to grow its fungal gardens - Pizo and Oliveira (2000); Araújo et al. (2002)), and *Ectatomma planidens* plus *E. brunneum* (both aggressive and generalist predators of other arthropods, or scavengers - Silvestre et al. (2003)). Another noteworthy finding in the cerrado habitat (Vereda P2) was a new, as yet undescribed, species of *Xenomyrmex* (Forel 1885). The biology of this genus is little known, but Wheeler and Wheeler (1960) report that this genus builds its colony in tree cavities and suggest that these ants may not be restricted to the trunks of trees, but rather descend to the ground in search of food.

Such woody habitat conditions are part of the wetland ecosystems, and apparently could also be related to the presence of species such *Camponotus rufipes* and *C. melanoticus*. Both species are typical of Brazilian savanna, nesting on the ground or under leaves and are generalist foragers (Silvestre et al., 2003); they were found in both pristine and impacted "veredas". In our study, both species were confined to wetland and cerrado habitats, indicating that the eucalypt habitat doesn't provide conditions for nesting and foraging. Likewise, army ants of the species *Labidus praedator* were only found in the wetland of Vereda D2, reflecting the availability of considerable amounts of invertebrate resources to sustain their vagile colonies. On the other hand, "veredas" have both high availability of food resources and nesting sites, and have proved to be susceptible to establishment by opportunistic species, such as *S. invicta*, *L. humile* and *Wasmannia auropunctata*. These ants have polygynous colonies, territorial, aggressive behaviour and exhibit generalist foraging on the soil and trees. This type of niche promotes rapid colonisation of the environment, with interconnected nests leading to a supercolony of cooperative workers, especially after an environmental disturbance. Once established, colonies displace other species of ants and arthropods, resulting in a general decrease in species richness and abundance (Delabie, 1988; Diehl-Fleig, 2006).

The presence of *S. invicta* in cerrado of Vereda P2 may indicate the presence of secondary impacts in this vereda, such as cattle or other human activities. However, its presence in the cerrado of Vereda D2 indicates that the disturbances could be caused by nearby *Eucalyptus* monoculture areas. The abundance of *S. invicta* at higher levels than that of *W. auropunctata* and *L. humile* in these areas and in the eucalypt habitat of Vereda D1, suggests that *S. invicta* is the ant dominating in this habitat.

The present work is the first large ant survey in the vereda ecosystems, and is the first to provide the background for designing bioindication protocols for diagnosis of the conservation status of these complex wetland habitats within the Brazilian Cerrado. An example of their use is the impact on ant species composition and assemblage structure caused by the plantation. For instance, the number of edaphic ant species in the wetland soils of the "veredas" surrounded by *Eucalyptus* was lower than in the preserved areas. Such species composition suggests an accelerated succession towards a drier ecosystem due to ground water drawdown caused by the monoculture. Based on geomorphologic data, such succession should be happening faster in some of the preserved areas instead. Hence, changes in the distribution of ant species among functional guilds appears to reflect differences in the soil's capacity for water retention, along with variation in micro-spaces between grains in the soil and sediment, and vegetation changes caused by human impacts (CB. Costa-Milanez, unpublished data). This supports the hypothesis that ant assemblages are a sensitive community component, which is potentially a good candidate for bioindication of early impacts caused by land use change.

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