

Fire effect on ground-foraging ant assemblages in northeastern Argentina

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Abstract Fire is an important component of many natural ecosystems affecting plant communities and arthropods by mortality during combustion and/or indirectly through the modification of the habitat. The Iberá Natural Reserve (INR) is one of the most diverse ecosystems in northern Argentina; it is dominated by grasslands commonly affected by disturbances, such as grazing and fire. The objective of this work was to study the response of ground-foraging ant assemblages, particular species, and functional groups to an extended fire of high intensity in four natural INR habitats with >5 years of cattle exclusion (strict conservation area). A total of 12,798 ant workers of 67 species were captured in 39 sampling stations. The ant fauna was less abundant in burned sites only a few days after the fire; 6 months later, no effect was detected. Richness and abundance of ants differed among unburned habitats. However, fire effect on species richness and composition remained unclear. The rapid recovery of the ant fauna made these insects poor indicators of long-term fire-promoted changes on biodiversity in open habitats

dominated by grassland, though some ant species showed a high level of habitat fidelity mainly in unburned habitats. These results agree with those from other areas of the world, indicating that ants are particularly unreliable biodiversity indicators, with the exception of severe disturbance with long-term habitat restoration. Management decisions at the INR should be oriented to preserve the closed savanna, one of the most diverse and threatened habitat of Argentina.

Keywords Disturbance ecology · Functional groups · Fire · Ant assemblages · Conservation management

Introduction

Many ecosystems, particularly prairie, savanna, chaparral, and conifer forests, have evolved with fire as a necessary contributor to habitat vitality and renewal. Many plant species in naturally fire-affected environments require fire to germinate, establish, or to reproduce. Intentional or prescribed fires are commonly used as a restoration technique to reduce the incidence of invasive and unpalatable plants, favoring a higher productivity of native and/or more palatable species by stimulating the emergence of long-dormant seeds bank (Parsons and Stoltgren 1989; Hobbs and Huenecke 1992; Howe 1994; Parsons and van Wageningen 1996; Klimer and Messer 2001). Thus, fire greatly influences the succession and structure of plant communities (Whelan 1995); however, it might also affect arthropods, such as ants, directly through mortality during combustion and/or indirectly through the modification of the habitat.

Fire effect on ants has been studied in a broad range of habitats. Direct impact on ant colonies is considered to be

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overall relatively small (Andersen and Yen 1985; Warren et al. 1987; Andersen 1991). The fire effect on ants depends mainly on the magnitude of changes in the structure of the vegetation that was burned (Farji-Brener et al. 2002; Parr et al. 2004; Barrow et al. 2007), which is directly related with the type of burned habitat and fire intensity. It is expected that low intense and infrequent fires produce small changes in the structure of the vegetation and associated fauna. The species diversity is maximized when fire intensity and (mainly) frequency is moderate, which favors species coexistence (Roxburgh et al. 2004). The immediate consequence of a high intensity fire is the complete removal of above-ground biomass (vegetation and litter), modifying food supply and nesting sites, increasing insolation, and consequently increasing the temperature and decreasing humidity (Andersen and Yen 1985; New 2000). This drastic change would favor those ant species more adapted to open habitats, such as the dominant fire ants (Tschinkel 2006) or in a case of extreme disturbance by fire would favor to species adapted bare soil in arid or semiarid habitats, such as the Hot-Climates Specialists, which are able to tolerate extremely high temperatures and low levels of humidity (Bestelmeyer 1997).

Dominant species often interfere with the foraging of other ant species (Savolainen and Vepsäläinen 1988; Andersen 1990; Calcaterra et al. 2008); therefore, changes in the abundance of dominant species mediated by variations in the vegetation structure may induce changes in species richness and composition of ant assemblages (Porter and Savignano 1990; Andersen 1990). It is a succession or replacement of species and/or functional groups in the assemblages. Studies conducted in savannas in Australia, Brazil, and Africa reported high resistance and resilience of ground-foraging ants to fire, although they showed changes in ant dominance and functional group composition (Underwood and Fisher 2006).

Wetlands dominated by grasslands are usually influenced by fire during periods of drought. Fire is the primary mode of decomposition in grassland habitats, making it crucial in the recycling of nutrients. Fire plays an important role in the Iberá Natural Reserve (INR), one of the most diverse ecosystems in Argentina and one of the largest freshwater wetlands in South America (The Ramsar Convention on Wetlands 2008; Canziani et al. 2003; Parera 2006). However, nothing is known about the eventual effect of the wildfire on ant assemblages and other taxa. More than 130 native ant species occur in the INR (Calcaterra et al. 2010a, b), several of which were introduced in other countries (Lowe et al. 2000; Pest Directory 2008), such as the red imported fire ant, *Solenopsis invicta*, a serious pest mainly in the United States (Thompson 1990).

The main objective of this work was to study the effect of an extended fire of high intensity on the structure and composition of terrestrial ant assemblages in INR natural grasslands and savannas under strict conservation management. The response of individual ant species and/or functional groups to fire was also investigated because, although controversial, they could be used in additional studies as a proxy or potential indicators of changes in the diversity of other invertebrate groups (Alonso 2000).

Methods

Study area

The INR occupies 1,300,000 ha of the northeastern Corrientes province including a large marsh with lagoons, small rivers, streams, and extensive floating vegetation surrounded by temporary flooded grasslands, savannas, and forests (Neiff and Poi de Neiff 2006; Parera 2006). These terrestrial ecosystems occupied by private ranches are free of exotic plant species (Maturo et al. 2007) and show different degrees of modification through ranching, farming, and wood production (Parera 2006). Ecosystems dominated by grasslands are commonly affected by natural and anthropic disturbances, such as fire and/or grazing. However, natural disturbances are unlikely to occur within these private areas of the INR because of frequent and persistent anthropic modifications. For example, the occurrence of natural fires has greatly decreased since the introduction of domestic cattle (according the ranchers, livestock loads ranged 0.4–4 animals/ha), which reduced the amount of combustible biomass, as has been also documented in other similar habitats of Argentina (Peláez et al. 2003). As a result, tall grasslands were transformed into low grasslands with a higher occurrence of unpalatable grasses and isolated trees or bushes. However, natural fires are an important disturbance in strict conservation areas of the INR.

The study was conducted from February to August 2008 in an area without grazing located 5–40 km southwest of Colonia Pellegrini within the INR. The area shows the following natural habitats with increasing complexity in the vegetation structure: (1) grassland dominated by 1.5 m-high *Andropogon lateralis* (Poaceae) temporarily flooded; (2) open savanna with Caranday palms (*Copernicia alba*, Arecaceae) and other isolated trees, allowing sufficient sun light to support a continuous herbaceous layer; (3) closed savanna, a xerophic woodland dominated by short *Prosopis* and *Acacia* (Fabaceae), Caranday palms, bushes, and grassland dominated by *A. lateralis*; and (4) forest, a closed, narrow, and humid 10–15 m high gallery forest and dominated by Pindó palms (*Syagrus romanzoffiana*,

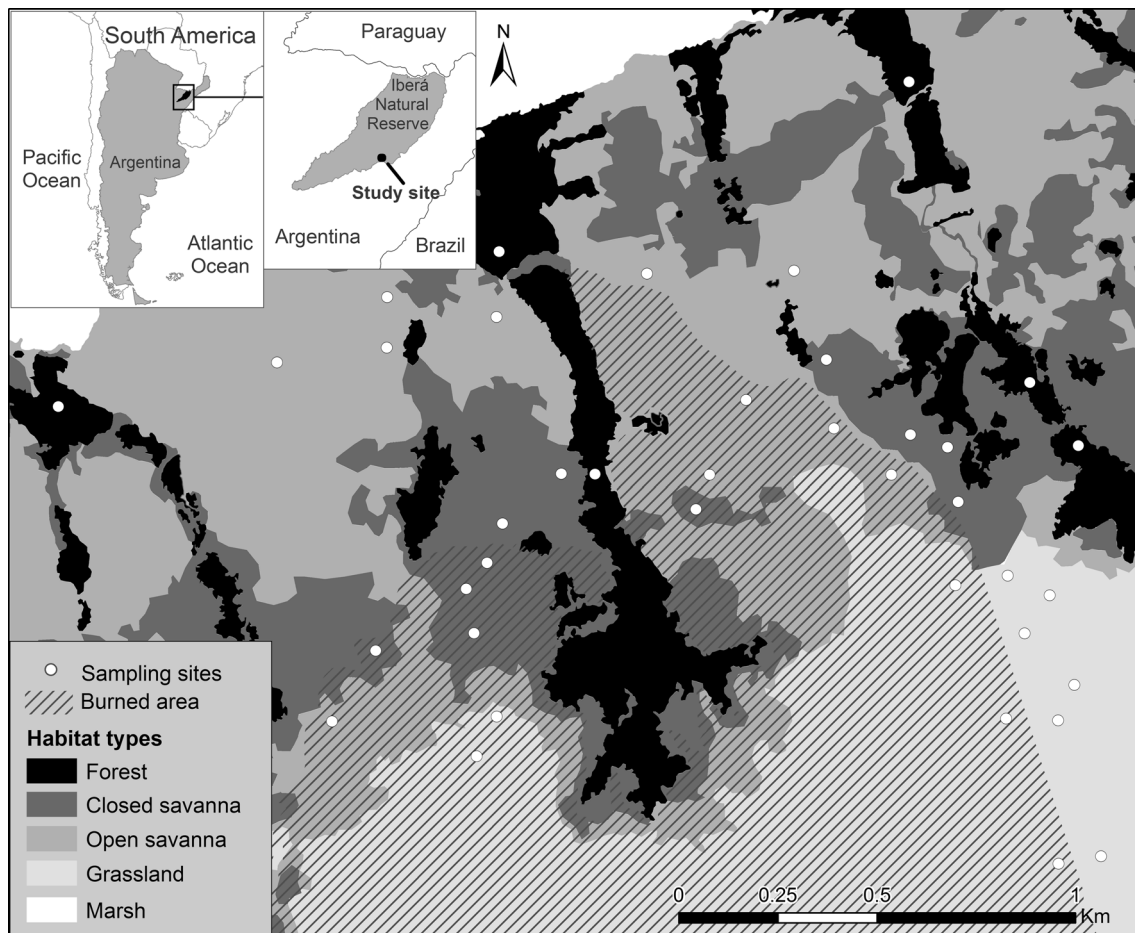


Fig. 1 Study area showing the location of the 39 sampling sites within the Iberá Natural Reserve

Arecacea) and other typical species of the Atlantic forest such as *Blepharocalix salicifolius* (Myrtaceae), *Tabebuia heptaphylla* (Bignoniaceae), *Peltophorum dubium*, and *Holocallix balansae* (Fabaceae) (Cabrera and Willink 1980; Tressens et al. 2002; Neiff and Poi De Neiff 2006; Parera 2006; Maturo et al. 2007).

The climate of the region is humid and subtropical with dry winters (June–September), and also with frequent summer droughts. Mean temperature varies from 15 °C in July to 26 °C in January, and the mean annual rainfall is around 1,500 mm (De Fina 1992; Fontan and Sierra 2004).

Experimental design

We investigated the effect of an intense natural fire that occurred on 6–9 February 2008, on the richness, abundance, and functional composition of the ant assemblages in four natural habitats under strict conservation within the Rincón del Socorro Ranch (RSR) of the Conservation Land Trust Argentina (CLT). The RSR is a 12,400 ha private reserve located in the southeastern portion of the INR. It

had a typical cattle management with a heavy grazing load until 2003, when livestock was removed. Consequently, when fire occurred in 2008, there was a large amount of combustible material (leaf-litter biomass) and fire affected 57 % (~5,700 ha) of the ranch surface. In the study area, the fire burned the 83 % (126 ha), 33 % (57 ha), and 23 % (23 ha) of the grassland, the open savanna, and closed savanna, respectively (Fig. 1). No fire occurred in the gallery forest (the habitat less represented with a surface of 56 ha). The previous fire history at the INR indicated an event in the savannas in September 2006 and in the grasslands in September 2007 (LANDSAT and CBERS-2b satellite images, M.S., unpublished data). However, the selected sampling stations were not affected by these previous fires.

The monitoring was conducted at 39 sampling stations located in a ~5.1 km² mosaic of burned and unburned areas (28°24'S, 57°14'W), >100 m apart in the four habitats to ensure independence of samples. Six sampling stations were established in each of the unburned grassland, open savanna, closed savanna, and forest, and five in each

of the burned grassland, open savanna, and closed savanna. The samplings were conducted a few days after the fire, on 15–19 February 2008 (summer) and then 5–6-months later, on 31 July–3 August 2008 (winter).

Ant sampling

In each station, ants were sampled using 5 unbaited pitfall traps, one in the center and the other four 5 m apart in a squared array following the cardinal points. Each trap consisted of a 50-ml plastic centrifuge tube (3 cm in diameter) buried in the ground and half-filled with soapy water. The traps were open for 48 h as in Calcaterra et al. (2010a, b); then, their content was removed, rinsed with water, and preserved in 96 % alcohol. Ants were separated from other arthropods and identified to species or morphospecies by L.A.C. under a dissecting scope using available key. Specimens of reference were deposited in the FuEDEI entomological collection and voucher specimens at the Instituto-Fundación Miguel Lillo (IFML), Tucumán, Argentina, and at FuEDEI.

Vegetation sampling

To record the impact of the fire and the subsequent restoration process, the vegetation height and cover were monitored in the three burned habitats in February, March, May, and August 2008. The vegetation structure was also recorded in the unburned habitats in August 2008 as a control situation. Unfortunately, vegetation records in unburned habitats were unavailable for February, March, and May 2008. The cover (basal) and height of the herbaceous stratum was estimated in four 1×1 m plots randomly located within the squared sampling stations (which represents around 49 m^2). The basal cover was visually estimated as the percentage of covered ground. Each vegetation variable was averaged over the four quadrants in each site.

Data analysis

The number of ant species was recorded by pooling the five pitfall traps (sampling unit). Seasonal differences in total ant richness and abundance were evaluated using paired *t*-tests. Spatial abundance was measured as the proportion of pitfalls in which a species was present. Numerical abundance was measured as the number of individuals trapped. The effect of the habitat on the richness and abundance of ants and on the height and cover of the vegetation was analyzed using one-way ANOVA or generalized linear model (GLM) with Poisson distribution and log-link function corrected for overdispersion when data did not show Normal distribution, or when the whole normal

model showed a explicative value $R^2 < 0.5$. The effect of habitat, fire, and their interaction on richness and abundance of ant species, and on the number of functional groups were analyzed using two-way ANOVA and, in most cases, a GLM with Poisson distribution and log-link function corrected for overdispersion in STATISTICA v. 7.1 (StatSoft 2005). Means \pm standard errors are reported. Spearman correlation analysis was used to evaluate the relationship between the abundance of the most common ant species trapped.

A two-dimensional ordination of samples was carried out with non-metric multidimensional scaling (NMDS) using the Bray–Curtis distance measure to visually examine the ant assemblage composition in each burned and unburned habitat; this was tested using an analysis of similarity (ANOSIM and post hoc Bonferroni pairwise comparisons; Clark and Green 1988) based on 1,000 permutations. NMDS is appropriated for non-normal data and does not assume linear relationships among variables (McCune and Grace 1999). The Sørensen quantitative similarity index was also used to evaluate the similarity in species composition (Magurran 1988). Indicator species were evaluated following Dufrene and Legendre (1997). This method identifies the typical species of a given habitat with an index, reaching a maximum level (100 %) when all individuals of a species are found in a single habitat and when the species occurs in all sites (or sampling units) of that habitat. The significance of the indicator value for each species was evaluated using a Monte Carlo randomization test (900 iterations and significance level = 0.01). Because rare species may distort the analyses (Smith and Grassle 1977), only species that occurred in four or more sampling units were analyzed. These analyses were performed using PC-ORD 4.0 software (McCune and Mefford 1999).

Functional composition was compared by assigning species to functional groups based on habitat requirements, foraging mode, competitive interactions, and responses to environmental stress and disturbance (Andersen 1995, 1997; Bestelmeyer and Wiens 1996; King et al. 1998; Andersen et al. 2007; van Ingen et al. 2008; Hill et al. 2008; Calcaterra et al. 2010a, b). We followed the classification of functional groups proposed by Bestelmeyer and Wiens (1996) for Argentinean Chaco ants and previously adopted by Calcaterra et al. (2010a, b) for the INR. The following groups were considered in this study: opportunists (unspecialized species that are weak competitors), Specialist Predators (large-body species with small colony size and specialist diet), Subordinate Camponotini (large-body and often nocturnal species, submissive to the dominant species), Attini (fungus-culturing ants including leaf-cutting and detritus-collecting ants), Cryptics (minute species that live mostly in the litter, rotting logs, or soil), Generalized Myrmicinae (small-body species with a

variety of behaviors and habitat requirement that defend resources by recruitment), arboreal (species that nest and forage almost exclusively in trees or shrubs), climate-specialist species (species adapted to specific temperature and humidity conditions), and Army Ants. This later group is considered by other authors as Tropical Climate Specialists or Nomad Ants (Andersen 1997; Silvestre et al. 2003).

Ant species were assigned to these groups based upon habitat and strata occurrence, presence, abundance, and behavior observed at baits; also, other works conducted mainly in South America on these and similar species with known natural history were considered (e.g. Kusnezov 1978; Bestelmeyer and Wiens 1996; Andersen 1997; Silvestre et al. 2003; Andersen et al. 2007; van Ingen et al. 2008; Hill et al. 2008; Calcaterra et al. 2008, 2010a, b; Cuezco and González Campero 2010).

Results

In the 39 sampling stations, 12,798 worker ants were captured, representing 21 genera and 67 species (“Appendix”); 19 (29 %) species were recorded only once (singletons). A total of 11,676 workers (91 %, 62 species) were captured in February, while only 1,122 workers (9 %, 43 species) were captured in August.

The mean number of species per site was 7.7 ± 0.6 in February and 4.2 ± 0.4 species in August ($t = -6.7$, $df = 38$, $P < 0.0001$); the mean number of workers per site was 299.3 ± 95.7 in February and 28.8 ± 8.9 in August ($t = -2.87$, $df = 38$, $P = 0.007$). *Nylanderia fulva*, *S. invicta*, *Wasmannia auropunctata*, and *Nylanderia silvestrii* were numerically dominant with more than 82 % of all workers captured; *Nylanderia* ants accounted for 51 % of all the workers captured. In winter, *Pheidole aberrans* was the second most abundant species after *S. invicta* with 19 % of all workers captured.

Ant assemblages in unburned habitats

Pooling both seasons, the richest unburned natural habitat was the closed savanna with 40 species, 17 of which were exclusive, followed by the grassland with 22 species, 7 exclusive (Fig. 2). Twenty-five (81 %) of the 31 exclusive species were collected in a few sites, with the exception of *Linepithema micans* in the grassland, being recorded in 100 % of the sites in February and in 17 % in August.

The mean species richness differed among (undisturbed) habitats in February (whole model explanation $R^2 = 0.5$; $F_{3,20} = 6.55$, $P = 0.003$) and in August (GLM: Wald $\chi^2 = 10.37$, $df = 3$, $P = 0.016$). Closed savanna was richer than open savanna and forest in February and richer than the grassland and forest in August. Mean abundance

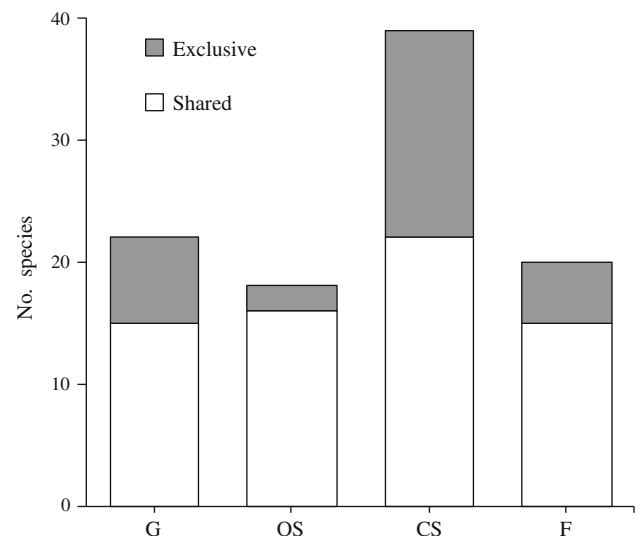


Fig. 2 Total number of ant species (exclusive + shared) recorded in the grassland (G), open savanna (OS), closed savanna (CS), and forest (F) sampled in the Iberá Natural Reserve in February and August 2008

also differed among habitats in February (GLM: Wald $\chi^2 = 9.12$, $df = 3$, $P = 0.028$) and in August (GLM: Wald $\chi^2 = 9.48$, $df = 3$, $P = 0.024$). Open savanna was more abundant than the other three habitats in February and more abundant than the grassland and forest in August.

The highest similarity index was recorded between the open and closed savannas (0.58), followed by the forest and the grassland (0.48), the two habitats with the highest contrast in their structural complexity. The lowest similarity was between the grassland and the open savanna (0.24), the two habitats with the highest grass cover.

Fire effect on ant assemblages

Species richness

In February, mean number of species differed among habitats ($F_{2,27} = 7.441$, $P = 0.003$), but not between burned and unburned sites ($F_{1,27} = 3.901$, $P = 0.059$); the interaction was not significant ($F_{2,27} = 3.04$, $P = 0.061$) (whole model explanation, $R^2 = 0.5$; Fig. 3a). Pooling unburned and burned sites, the closed savanna with 10.5 ± 1.1 species was richer than the grassland with 6.6 ± 0.9 and the open savanna with 6.2 ± 0.9 ($P < 0.05$). In August, the mean number of species was similar in burned and unburned sites (GLM: Wald $\chi^2 = 0.0145$, $df = 1$, $P = 0.904$) and in all habitats (GLM: Wald $\chi^2 = 2.956$, $df = 2$, $P = 0.228$); the interaction was also not significant (GLM: Wald $\chi^2 = 3.696$, $df = 2$, $P = 0.158$) (Fig. 3b).

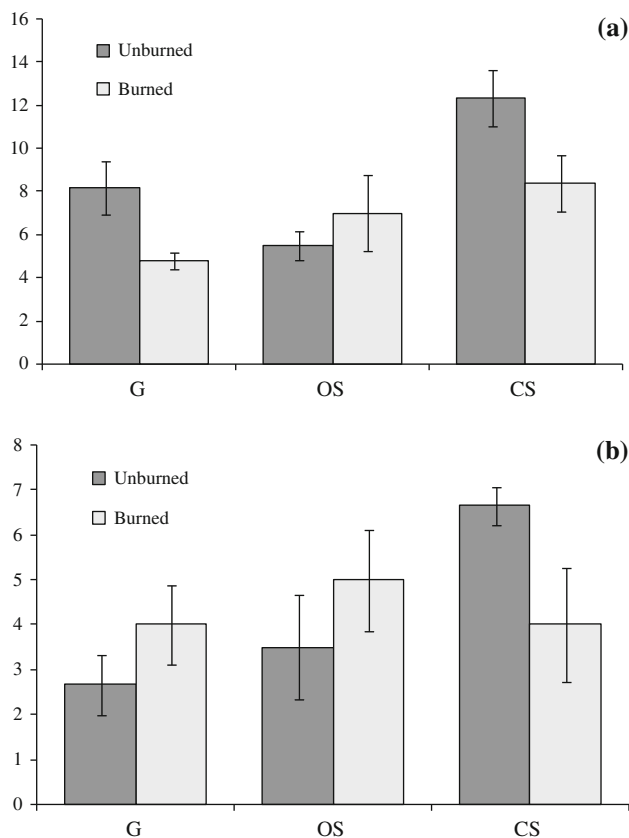


Fig. 3 a, b Mean (SE) species richness recorded at the site level in unburned and burned natural habitats in the Iberá Natural Reserve in February (a) and August (b) 2008

Spatial abundance

In February, most species were more frequent in unburned than in burned stations in each habitat (Table 1). However, this pattern of spatial abundance was less clear in August. *S. invicta* was the most frequently distributed ant in February and in August, being captured in 88 % (29/33) and 73 % (24/33) of the sites, respectively. It was followed by *Crematogaster quadriformis* with 67 % of the sites in February and *P. aberrans* with 42 % in August (though it was absent in the grassland). *S. invicta* spatially co-dominated the unburned and burned savanna habitats with some other few species and it was one of the most common species in the grassland that was dominated by *L. micans* (100 %) in unburned sites and *L. micans* and *N. silvestrii* (both with 80 %) in the burned sites (Table 1).

Numerical abundance

In general, overall abundance of each individual species was higher in unburned than in burned habitats (Table 2). In February, mean abundance was higher in unburned than

in burned sites (GLM: Wald $\chi^2 = 5.013$, $df = 1$, $P = 0.025$), but no differences were found among habitats (GLM: Wald $\chi^2 = 0.921$, $df = 2$, $P = 0.631$); the interaction was also not significant (GLM: Wald $\chi^2 = 4.309$, $df = 2$, $P = 0.116$) (Fig. 4a). On average, unburned sites hold 470 ± 197 workers, whereas burned sites only 88 ± 26 workers. *N. fulva* was the most abundant ant with 5,410 workers (46 %), followed by *S. invicta* with 1,755 (15 %), which was the second most abundant species in all habitats. Pairwise correlations per site among the most frequently captured species revealed a significant positive correlation between overall abundance of *N. silvestrii* and *L. micans* ($r_s = 0.63$, $P < 0.0001$) and between *S. invicta* and *N. fulva* ($r_s = 0.35$, $P < 0.05$). In contrast, a negative relationship was found between abundance of *N. fulva* and both *N. silvestrii* ($r_s = -0.56$, $P < 0.001$) and *L. humile* ($r_s = -0.41$, $P < 0.02$).

In August, the mean number of workers was similar in burned and unburned sites (GLM: Wald $\chi^2 = 2.2848$, $df = 1$, $P = 0.131$) and in all habitats (GLM: Wald $\chi^2 = 4.076$, $df = 2$, $P = 0.130$); the interaction was also not significant GLM: Wald $\chi^2 = 5.490$, $df = 2$, $P = 0.064$ (Fig. 4b). *S. invicta* was the most abundant with 535 workers (48 %), 72 % of them occurred in the unburned open savanna, followed by *P. aberrans* with 192 (17 %), 63 % of them being captured in the closed savanna. Unexpectedly, *P. bison* was the most abundant species in the unburned grassland with 27 % of the workers (Table 2). Overall abundance of *P. aberrans* was positively correlated with *Pheidole spininodis* ($r_s = 0.45$, $P < 0.05$), *Pheidole radoszkowskii* ($r_s = 0.43$, $P < 0.01$), and *Pheidole bergi* ($r_s = 0.40$, $P < 0.05$), whereas *Pheidole* sp. 3 was positively correlated with *N. silvestrii* ($r_s = 0.41$, $P < 0.005$) and *Pheidole* sp. 2 ($r_s = 0.39$, $P < 0.05$).

Species composition

In February, the visual ordination of the samples showed an apparent separation among the grassland and the savannas (Fig. 5a; NMDS: $R^2 = 0.76$, stress = 0.23). However, ANOSIM only showed a moderate segregation between unburned habitats and between both burned open and closed savannas and the unburned grassland, and between unburned open and closed savanna and the burned grassland (ANOSIM: $R^2 = 0.53$, $P < 0.0001$; Bonferroni pairwise comparison, $P < 0.05$). Burned habitats did not show differences. Three species from different subfamilies were typical of the unburned grassland: *L. micans*, with an indicator value of 41.7 %, *Camponotus punctulatus punctulatus* with 39.3 %, and *N. silvestrii* with 38.6 %, whereas three Myrmicinae species were associated with the closed savanna: *P. aberrans* with 66.7 % and *P. radoszkowskii*

Table 1 Number of samples (% of the total) in which the most common ant species were captured at each situation studied in the Iberá Natural Reserve in February and August 2008 (only species present in more than 10 % of the 33 samples; sample size in unburned and burned sites was 6 and 5 samples, respectively)

Species	Grassland		Open savanna		Closed savanna	
	Unburned	Burned	Unburned	Burned	Unburned	Burned
February (1 week after the fire)						
<i>Solenopsis invicta</i>	5 (83)	2 (40)	6 (100)	5 (100)	6 (100)	5 (100)
<i>Crematogaster quadriformis</i>	5 (83)	2 (40)	4 (67)	3 (60)	5 (83)	3 (60)
<i>Nylanderia fulva</i>	0	1 (20)	4 (67)	5 (100)	5 (83)	3 (60)
<i>Camponotus mus</i>	1 (17)	0	4 (67)	2 (40)	2 (33)	4 (80)
<i>Linepithema micans</i>	6 (100)	4 (80)	0	2 (40)	0	1 (20)
<i>Pogonomyrmex cunicularius</i>	0	0	3 (50)	3 (60)	4 (67)	1 (20)
<i>Camponotus punctulatus punctulatus</i>	5 (83)	3 (60)	2 (33)	0	0	0
<i>Nylanderia silvestrii</i>	5 (83)	4 (80)	1 (17)	0	0	0
<i>Camponotus punctulatus cruentus</i>	0	0	4 (67)	2 (40)	1 (17)	2 (40)
<i>Dorymyrmex steigeri platensis</i>	1 (17)	0	3 (50)	3 (60)	0	1 (20)
<i>Cyphomyrmex rimosus</i>	0	1 (20)	0	3 (60)	2 (33)	1 (20)
<i>Nylanderia pubens</i>	2 (33)	3 (60)	2 (33)	0	0	0
<i>Camponotus rufipes</i>	0	1 (20)	1 (17)	0	3 (50)	1 (20)
<i>Pheidole bergi</i>	0	0	3 (50)	1 (20)	1 (17)	1 (20)
<i>Pheidole radoszkowskii</i>	0	0	4 (67)	2 (40)	0	0
<i>Pheidole</i> sp. 3	3 (50)	1 (20)	0	1 (20)	0	0
<i>Pheidole triconstricta</i>	0	0	2 (33)	3 (60)	0	0
<i>Solenopsis</i> sp. 3	0	1 (20)	2 (33)	0	1 (17)	1 (20)
<i>Wasmannia auropunctata</i>	0	0	2 (33)	2 (40)	0	1 (20)
<i>Pheidole aberrans</i>	0	0	4 (67)	0	0	0
<i>Pheidole obscurithorax</i>	1 (17)	0	2 (33)	0	0	1 (20)
August (6 months after the fire)						
<i>Solenopsis invicta</i>	2 (33)	3 (60)	5 (83)	3 (60)	6 (100)	5 (100)
<i>Pheidole aberrans</i>	0	0	2 (33)	3 (60)	6 (100)	3 (60)
<i>Pheidole</i> sp. 2	1 (17)	3 (60)	0	3 (60)	1 (17)	3 (60)
<i>Crematogaster quadriformis</i>	1 (17)	2 (40)	1 (17)	2 (40)	1 (17)	0
<i>Nylanderia silvestrii</i>	3 (50)	2 (40)	1 (17)	0	1 (17)	0
<i>Camponotus punctulatus punctulatus</i>	1 (17)	3 (60)	1 (17)	0	1 (17)	0
<i>Linepithema micans</i>	1 (17)	2 (40)	0	2 (40)	0	0
<i>Nylanderia fulva</i>	0	0	3 (50)	1 (20)	0	1 (20)
<i>Pheidole</i> sp. 3	1 (17)	3 (60)	0	1 (20)	0	0
<i>Pheidole spininodis</i>	0	0	2 (33)	0	3 (50)	0
<i>Pheidole bison</i>	4 (67)	0	0	0	0	0
<i>Pheidole radoszkowskii</i>	0	0	0	0	2 (33)	2 (40)
<i>Solenopsis</i> sp. 2	0	0	2 (33)	1 (20)	1 (17)	0
<i>Wasmannia auropunctata</i>	0	0	1 (17)	0	2 (33)	1 (20)

with 41.7 % in the unburned sites and *Pheidole triconstricta* with 38.6 % in the burned sites.

In August, only an apparent visual separation was observed between the grassland and the savannas (Fig. 5b; NMDS: $R^2 = 0.81$, stress = 0.26). However, only a weak separation was statistically significant between the unburned open savanna and both grassland situations (ANOSIM: $R = 0.32$, $P = 0.0001$; Bonferroni pairwise comparison, $P < 0.05$). Three Myrmicinae species in the *Pheidole* genus, *Pheidole bison* (80 %), *Pheidole laevinota*

(50 %), and *P. aberrans* (37.3 %) were associated with the unburned grassland, unburned closed savanna, and burned open savanna, respectively.

Functional composition

A total of nine functional groups were recorded, 7 in February and 8 in August (Fig. 6a, b). However, the mean number of groups per site was 2.05 ± 0.05 in February, slightly higher than the 1.53 ± 0.06 groups found in

Table 2 Fifteen most abundant ant species captured in February and August 2008 in the Iberá Natural Reserve

Species	Grassland		Open savanna		Closed savanna	
	Unburned	Burned	Unburned	Burned	Unburned	Burned
February						
<i>Nylanderia fulva</i>	0	2 (1.4)	4,998 (84.1)	11 (5.0)	17 (1.5)	382 (39.9)
<i>Solenopsis invicta</i>	289 (21.0)	26 (17.8)	818 (13.8)	104 (47.7)	145 (12.7)	373 (38.9)
<i>Nylanderia silvestrii</i>	954 (69.5)	46 (31.5)	0	0	1 (0.1)	0
<i>Wasmannia auropunctata</i>	0	0	0	1 (0.5)	398 (34.8)	4 (0.4)
<i>Crematogaster quadriformis</i>	8 (0.6)	4 (2.7)	27 (0.5)	9 (4.1)	90 (7.9)	11 (1.1)
<i>Pheidole laevinota</i>	0	0	0	7 (3.2)	124 (10.8)	0
<i>Dorymyrmex steigeri platensis</i>	8 (0.6)	0	0	7 (3.2)	14 (1.2)	59 (6.2)
<i>Camponotus mus</i>	2 (0.1)	0 5 (0.1)	8 (3.7)	68 (5.9)	4 (0.4)	
<i>Pheidole radoszkowskii</i>	0	0	0	0	45 (3.9)	34 (3.5)
<i>Camponotus cruentus</i>	0	0	11 (0.2)	3 (1.4)	33 (2.9)	17 (1.8)
<i>Linepithema micans</i>	24 (1.7)	25 (17.1)	0 4 (1.8)	0	2 (0.2)	
<i>Pheidole bergi</i>	0	0	4 (0.1)	15 (6.9)	21 (1.8)	15 (1.6)
<i>Pogonomyrmex cunicularius</i>	0	0	24 (0.4)	6 (2.8)	9 (0.8)	11 (1.1)
<i>Pheidole obscurithorax</i>	14 (1.0)	0	0	1 (0.5)	25 (2.2)	0
<i>Camponotus punctulatus punctulatus</i>	14 (1.0)	13 (8.9)	0	0	8 (0.7)	0
Others (43 species)	60 (4.4)	30 (20.5)	55 (0.9)	42 (19.3)	147 (12.8)	46 (4.8)
Total worker no.	1,373 (14)	146 (1.5)	5,942 (60.7)	218 (2.2)	1,145 (11.7)	958 (9.8)
August						
<i>Solenopsis invicta</i>	7 (18.9)	52 (47.7)	383 (83.4)	3 (4.1)	44 (17.7)	46 (38.3)
<i>Pheidole aberrans</i>	0	0	20 (4.4)	19 (25.7)	122 (49.2)	31 (25.8)
<i>Pheidole</i> sp. 2	2 (5.4)	19 (17.4)	0	12 (16.2)	1 (0.4)	16 (13.3)
<i>Pheidole bergi</i>	0	0	0	2 (2.7)	30 (12.1)	0
<i>Pheidole</i> sp. 3	7 (18.9)	17 (15.6)	0	4 (5.4)	0	0
<i>Nylanderia fulva</i>	0	0	18 (3.9)	3 (4.1)	0	1 (0.8)
<i>Crematogaster quadriformis</i>	2 (5.4)	7 (6.4)	1 (0.2)	4 (5.4)	2 (0.8)	0
<i>Pheidole spininodis</i>	0	0	6 (1.3)	0	10 (4.0)	0
<i>Pheidole laevinota</i>	0	0	0	14 (18.9)	0	0
<i>Pheidole radoszkowskii</i>	0	0	0	0	4 (1.6)	10 (8.3)
<i>Pheidole nubila</i>	0	0	10 (2.2)	0	3 (1.2)	0
<i>Nylanderia silvestrii</i>	4 (10.8)	5 (4.6)	1 (0.2)	0	2 (0.8)	0
<i>Camponotus punctulatus punctulatus</i>	2 (5.4)	3 (2.8)	1 (0.2)	0	5 (2.0)	0
<i>Solenopsis</i> sp. 3	0	0	8 (1.7)	2 (2.7)	1 (0.4)	0
<i>Pheidole bison</i>	10 (27.0)	0	0	0	0	0
Others (23 species)	3 (8.1)	6 (5.5)	11 (2.4)	11 (14.9)	24 (9.7)	16 (13.3)
Total worker no.	37 (3.5)	109 (10.4)	459 (43.8)	74 (7.1)	248 (23.7)	120 (11.5)

August ($t = 7.39$, $df = 32$, $P < 0.0001$). The most represented group both in February and August was the Generalized Myrmicinae with 24 and 19 species, respectively, followed by Opportunists with 11 species in February, and Attini and Subordinate Camponotini, each with five species in August. Four groups were present in all the sampled situations in February, while only two groups were common in August. The uncommon functional groups displayed an important variation in abundance among situations (Fig. 6a, b).

In February, minimum differences in functional composition were observed among situations (Fig. 6a). These differences were among habitats (GLM: Wald $\chi^2 = 6.426$, $df = 2$, $P = 0.04$), not between burned and unburned sites (GLM: Wald $\chi^2 = 2.468$, $df = 1$, $P = 0.116$); the interaction was also not significant (GLM: Wald $\chi^2 = 2.906$, $df = 2$, $P = 0.234$). Despite differences were not found between fire history, Cryptic species such as *Hylomyrma* sp. and *Solenopsis* spp. were absent in the burned open and closed savannas. However, Hot Climate Specialists did not

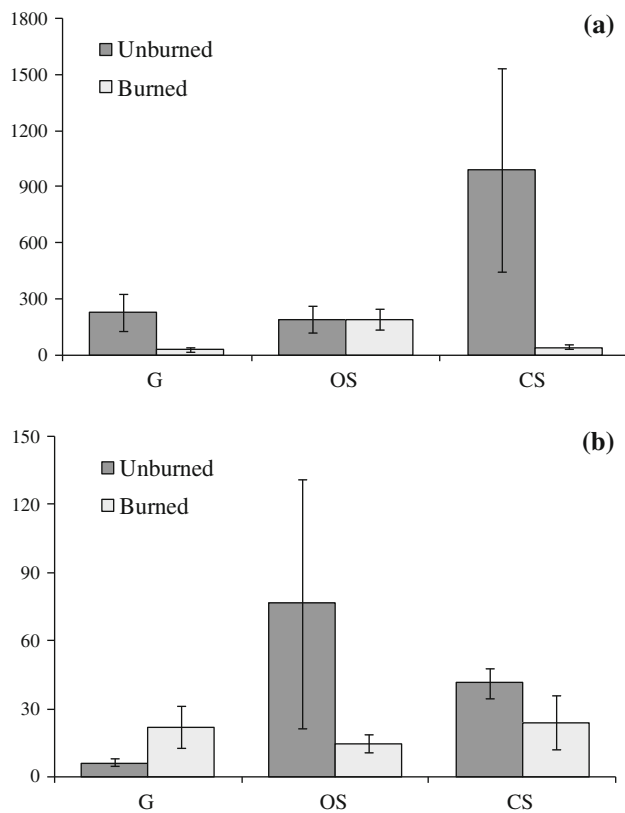


Fig. 4 a, b Mean (SE) number workers recorded at the site level in unburned and burned natural habitats in the Iberá Natural Reserve in February (a) and August (b) 2008

show a clear occurrence pattern. They were present in all situations, except in burned grassland (the most open habitat). *Dorymyrmex thoracicus* occurred in most cases, while *Pogonomyrmex cunicularius* and *Dorymyrmex steigeri platensis* only in savannas and unburned grassland, respectively. Arboreal species were exclusively recorded in the burned open savanna in February.

In August, a clear difference in functional composition was only observed between the unburned and burned closed savanna with 8 and 4 groups, respectively (Fig. 6b). Despite this difference, the mean number of groups was similar in burned and unburned sites (GLM: Wald $\chi^2 = 0.001$, $df = 1$, $P = 0.975$) and in all habitats (GLM: Wald $\chi^2 = 2.779$, $df = 2$, $P = 0.249$); the interaction was also not significant (GLM: Wald $\chi^2 = 3.064$, $df = 2$, $P = 0.216$). Unexpectedly, Cryptic species were only present in the burned open savanna, the habitat with the lowest coverage of litter.

Fire effect on the vegetation structure

The herbaceous stratum was composed mainly of grasses in the Poaceae and Cyperaceae families, broad-leaf herbs, creepers, and ferns. Vegetation height and cover were

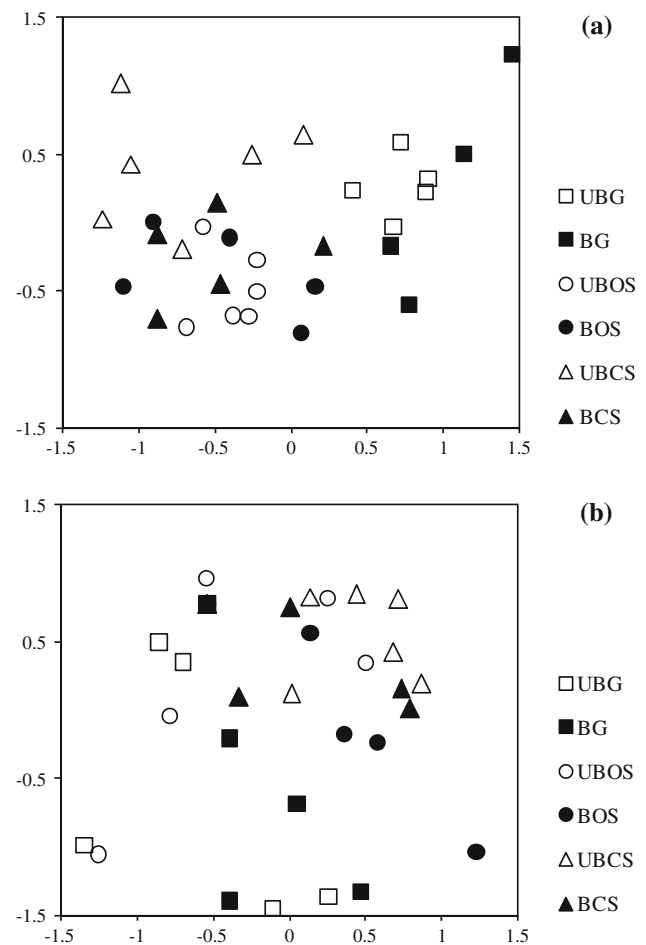


Fig. 5 a, b Non metrical multidimensional scaling ordination plot of samples collected in unburned and burned natural habitats in the Iberá Natural Reserve in February (a) and August (b) 2008

similar in the three habitats soon after the fire (Fig. 7a, b; $F_{1,12} = 0.30$, $P > 0.74$ and $F_{1,12} = 0.09$, $P > 0.91$, respectively). However, the height of the burned grassland recovered more rapidly than the other two burned habitats (Friedman ANOVA $X^2 = 10$, $N = 5$, $df = 2$, $P < 0.007$; Fig. 7a). No differences in the vegetation cover were observed among habitats (Friedman ANOVA $\chi^2 = 0.67$, $N = 5$, $df = 2$, $P > 0.71$; Fig. 7b). It is important to note that none of the three burned habitats reached the height and/or cover of the unburned habitats, with the only exception of the closed savanna cover.

Discussion

Fire effect on ant assemblages

Overall, this study showed that extended fire of high intensity had only a modest and short-term negative effect

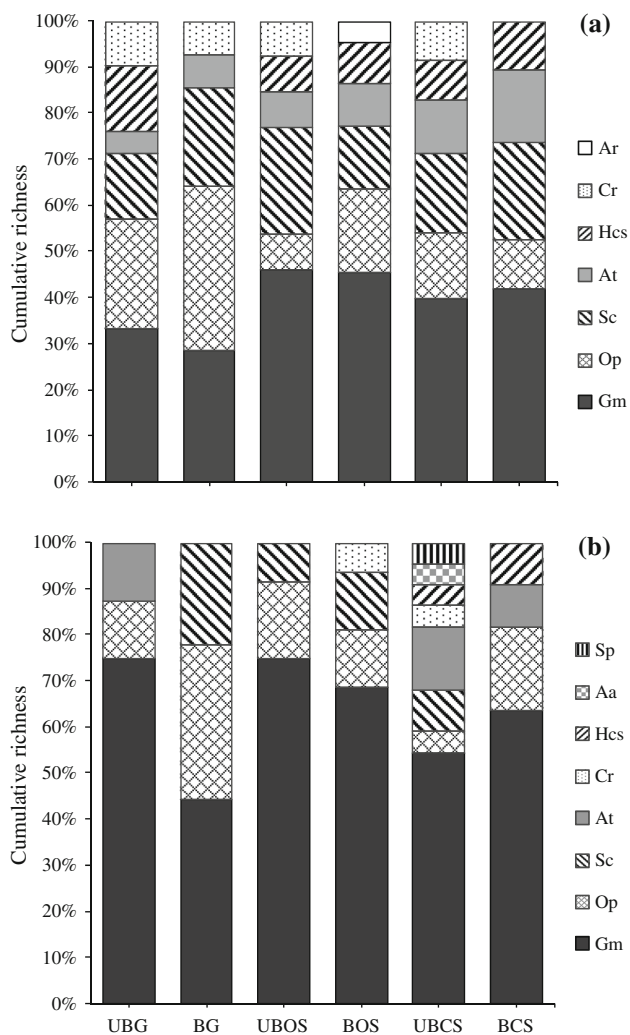


Fig. 6 a, b Functional groups profiles of the ants captured in unburned grassland (UBG), burned grassland (BG), unburned open savanna (UBOS), burned open savanna (BOS), unburned closed savanna (UBCS), and burned closed savanna (BCS). Data are percentage of total species represented by each group: *Ar* Arboreal, *Cr* Cryptic, *Aa* Army Ants, *Sp* Specialist Predators, *Hcs* Hot-Climate Specialist, *At* Attini, *Sc* Subordinate Camponotini, *Op* Opportunists, and *Gm* Generalized Myrmicinae

on the ant abundance in the INR, likely because the extraordinary increase in number of some few species. However, these changes in abundance of dominant species did not stimulate changes in species richness and composition of ant assemblages. It is important to note that 82 % of the individuals captured in this study belong to four species that have invaded other regions of the world, from which *S. invicta* and *W. auropunctata* were listed as two of 100 world's worst invasive alien species (Lowe et al. 2000). *P. aberrans* was the second more abundant species in winter after *S. invicta*. This species may be mainly active in the cool season as reported by Cheli et al. (2010) for the Chubut province in Argentina.

Although the species abundance decreased immediately after the fire, no differences in the diversity indicators were detected 6 months later, suggesting a quick recovery of the ant assemblages, likely as a result of the restoration of the vegetation structure (e.g. plant cover). This agrees with Neumann (1991), Izhaki et al. (2003), Parr et al. (2004), Vasconcelos et al. (2008), Underwood and Quinn (2010), who found full vegetation recovery 3–12 months after a fire.

The ant fauna similarities in all habitats might be then explained by the rapid homogenization effect of the fire on the herbaceous vegetation. Although the vegetation recovery was not complete 6 months after the fire (August), this was probably due to its slower growth during the cold season. An exception of this was observed in the closed savanna where the fire intensity was lower and where the herbaceous vegetation was cold-protected by trees.

We believe that this lack of effect on species richness and species composition was not the consequence of an inadequate sampling design or effort, since most of the expected ant species were actually collected. The 67 species found in this study represented 71 % of the 94 ant species captured by Calcaterra et al. (2010a) in a much larger study area ($\approx 300 \text{ km}^2$), using a combination of several sampling methods in different habitats, and on different strata. The percentage of rare species found here (28 %) is slightly higher than that found by Silvestre et al. (2003) in a much more intensive ant survey (22 % of rare species from 262 samples). This would also indicate that our sampling effort were adequate because, as expected, the number of rare species decreases asymptotically with the sampling effort (Colwell et al. 2006). The lack of effect on species richness agrees with other studies in South African (Parr et al. 2004; Pryke and Samways 2012) and Australian (Parr and Andersen 2008) savannas, which found that ants were remarkably resilient to fire. Its virtual absence of effect might be the consequence of the variability in the performance of ant species in response to fire (Hoffmann and Andersen 2003). The ant composition analyses had high stress values, which would indicate that other significant uncounted factors also contributed to the layout of these NMDS ordinations.

Functional groups of ants also responded to fire in different ways. The ants with leaf-litter nesting habits (e.g. Cryptic species or Specialized predators) should have been the most affected by fire in grassland sites (a habitat with a large accumulation of grass-litter); however, such an effect was not observed for Cryptic species, whereas Specialist Predators (and Army ants) occurred only in the unburned closed savanna in August. The appearance of these groups in winter would represent a colonization event rather than a seasonal occurrence. In contrast, Cryptic species were

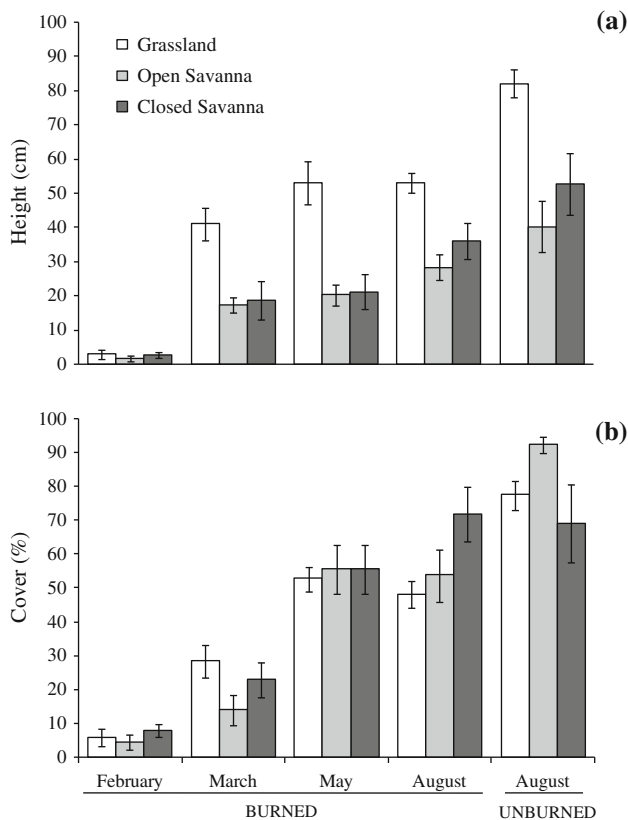


Fig. 7 a, b Mean (SE) height (a) and cover (b) of the vegetation in February, March, May, and August 2008 in three burned habitats in the Iberá Natural Reserve and in the same three unburned habitats in August 2008

absent in burned savannas suggesting an important fire effect on this group. This effect could persist as a consequence of the destruction of nesting sites in this type of habitat (Vasconcelos et al. 2008). Fire might have favored the occurrence of groups associated to open habitats with reduced litter (such as Hot Climate Specialists and Opportunists); however, an increase in the presence and/or abundance of these groups, as reported by Izhari et al. (2003), was poorly observed in the INR. Although Opportunistic ants seemed to increase their presence in burned habitats, this was not the case for Hot Climate Specialists, which were absent in February in burned grassland. Hot Climate Specialists only remained in the unburned and burned closed savanna in August, likely, as mentioned previously, because of its warmer conditions.

The rapid post-fire recovery of the ants community probably also reflected their adaptations to fire regimes in habitats such as savannas (Izhaki et al. 2003; Parr et al. 2004). They avoid direct fire damage by finding refuge in their underground nests, rapidly favoring the post-fire recolonization of the habitats. Several studies in which forests were removed by fire showed positive long-term (>10 years) effect on the ant assemblages (Andersen 1991;

York 2000; Parr et al. 2004; Andersen et al. 2002). However, other studies in more open habitats revealed negative and/or neutral effects (Underwood and Fisher 2006). Thus, these studies seem to indicate that ant response to fire is in fact extremely variable, probably depending on the extension and magnitude of the transformation or replacement of the habitat. The variability in the response could be also explained by the variable behavior observed by some species among habitats, the effect of the seasonality, the spatial variability of the ant assemblages or the level of differences in the whole study systems, such as habitat type and composition of the ant assemblage (Hoffmann and Andersen 2003; Underwood and Fisher 2006).

Abundance of behaviorally dominant ants, such as *S. invicta*, seemed to be more favored in fire-promoted open habitats than those cryptic species associated to closed habitats. Changes in vegetation structure promoted by fire could have positively affected the abundance of *S. invicta*. This pattern was previously reported for *S. invicta* by effect of grazing on the vegetation (Calcaterra et al. 2010b). Changes in its abundance could influence other ecologically similar species, such as *P. obscurithorax* or *P. aberrans*. Further studies are needed to evaluate this hypothesis. The negative correlation between the two *Nylanderia* species could be explicated by the fact that *N. fulva* almost did not occur in the grassland, while *N. silvestrii* was absent in the savanna habitats. However the high abundance of *N. fulva* was mainly because it was over captured in a few traps in the unburned open savanna (92 %). The abundance of these two species very common in summer seemed be strongly affected by the cold. The unexpected association of *P. aberrans* with the burned open savanna could be the consequence of the almost complete vegetation recovery observed in August or simply by a better adaptation to low temperatures in winter.

Response of ants to fire has been used in many studies on the assumption that they are good biodiversity indicators (Hoffmann and Andersen 2003; Underwood and Fisher 2006; Gerlach et al. 2013). However, this assumption is mostly based on the fact that ant richness was correlated with richness of other invertebrate groups in a study conducted in mine sites in Australia (Majer 1983). The true is that no correlations were found between ants and mammals, reptiles and amphibious in most studies conducted until the present; only a significant negative correlation has been reported between ants and birds (Gerlach et al. 2013). Monitoring using multiple taxonomic groups (plants, ants, amphibious, reptiles, birds, and mammals) conducted in the INR has shown a differential taxa response to disturbance, such as grazing (Calcaterra et al. 2010b and L.A.C., personal observation), which was related among other causes to differences in individual species and recovery times.

Fire had only a moderate short-term effect on the abundance of the terrestrial ant assemblages at the INR. Thus, ants seem to be a poor indicator to detect long-term changes in richness and composition in the ecosystem promoted by fire in the INR. Despite the relatively short monitoring time, this study is in agreement with the review conducted by Underwood and Fisher (2006) and Gerlach et al. (2013). Ants seem to be resilient for a wide variety of disturbances (Neumann 1991; Izhaki et al. 2003; Parr et al. 2004; Barrow et al. 2007; Calcaterra et al. 2010b; Pryke and Samways 2012), with some few exceptions, such as the case of severe disturbance produced by mining, which can take a long-term restoration (>10 years) of ecosystems (Majer 1983; Bisevac and Majer 1999) or in systems that burn infrequently, such as forest, which was not affected by fire in this work.

Despite the virtual absence of fire effect, it is important to mention that more ant species were associated with unburned habitats than with burned habitats likely because of the short-term homogenization effect of the fire on the vegetation of the different habitats. Although ants do not seem to be good indicators of changes promoted by fire, they may be useful for conservation prioritization and management (Gerlach et al. 2013). As far as ant species diversity is concerned, further studies are necessary to take management decisions in the INR. At present, management should be oriented to preserve the richest habitats and/or those habitats containing ant species with the highest values for conservation (e.g. endemic or threatened species), rather than determining the fire regime that would favor the occurrence of certain ant species or groups. Conservation efforts in INR should be oriented to protect the close savanna, the most valuable habitat by containing the highest number of species (almost half exclusive) as observed in this work and others (Calcaterra et al. 2010a, b). The closed savanna belongs to the ecoregion or phytogeographical province of the Espinal (Cabrera and Willink 1980), one of the most threatened wooden habitats of Argentina with only 0.26 % of its surface protected (APN 2014); thus, its conservation is essential to ensure the long-term preservation of their associated ant species.

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Appendix

See Table 3.

Table 3 List of ant species captured (functional groups)

<i>Acromyrmex hispidus</i> (At) ^a	<i>Pheidole bergi</i> (Gm)
<i>Atta saltensis</i> (At) ^a	<i>Pheidole bison</i> (Gm)
<i>Atta vollenweideri</i> (At) ^a	<i>Pheidole flavens</i> (Gm) ^a
<i>Atta</i> sp. (At)	<i>Pheidole laevinota</i> (Gm)
<i>Brachymyrmex gauchoi</i> (Op)	<i>Pheidole nitella</i> (Gm)
<i>Brachymyrmex</i> sp. 1 (Op)	<i>Pheidole nubila</i> (Gm)
<i>Brachymyrmex</i> sp. 2 (Op)	<i>Pheidole obscurithorax</i> (Gm) ^a
<i>Brachymyrmex</i> sp. 3 (Op)	<i>Pheidole radoszkowskii</i> (Gm)
<i>Camponotus blandus</i> (Sc)	<i>Pheidole risii</i> Forel (Gm)
<i>Camponotus bonariensis</i> (Sc)	<i>Pheidole rudigenis</i> (Gm)
<i>Camponotus mus</i> (Sc) ^a	<i>Pheidole spininodis</i> (Gm)
<i>Camponotus substitutus</i> (Sc)	<i>Pheidole triconstricta</i> (Gm)
<i>Camponotus punctulatus cruentus</i> (Sc)	<i>Pheidole</i> sp. 1 (Gm)
<i>Camponotus punctulatus punctulatus</i> (Sc) ^a	<i>Pheidole</i> sp. 2 (Gm)
<i>Camponotus rufipes</i> (Sc)	<i>Pheidole</i> sp. 3 (Gm)
<i>Camponotus</i> sp. 1 (Sc)	<i>Pheidole</i> sp. 4 (Gm)
<i>Camponotus</i> sp. 2 (Sc)	<i>Pheidole</i> sp. 5 (Gm)
<i>Crematogaster quadriformis</i> (Gm)	<i>Pheidole</i> sp. 6 (Gm)
<i>Crematogaster</i> sp.(Sc)	<i>Pogonomyrmex cunicularius</i> (Hcs)
<i>Cyphomyrmex rimosus</i> (At) ^a	<i>Pseudomyrmex pallidus</i> (Ar)
<i>Dorimyrmex thoracicus</i> (Hcs)	<i>Solenopsis invicta</i> (Gm) ^a
<i>Dorymyrmex steigeri platensis</i> (Hcs)	<i>Solenopsis magdonaghi</i> (Gm)
<i>Forelius rufus</i> (Hcs)	<i>Solenopsis</i> sp. 1 (Gm)
<i>Gnamptogenys triangularis</i> (Sp)	<i>Solenopsis</i> sp. 2 (Gm)
<i>Hylomyrma</i> sp. (Cr)	<i>Solenopsis</i> sp. 3 (Gm)
<i>Linepithema micans</i> (Op)	<i>Solenopsis</i> sp. 4 (Cr)
<i>Neivamyrmex</i> sp. (Aa)	<i>Solenopsis</i> sp. 5 (Cr)
<i>Nylanderia docilis</i> (Op)	<i>Solenopsis</i> sp. 6 (Cr)
<i>Nylanderia fulva</i> (Op) ^a	<i>Trachymyrmex</i> sp. 1 (At)
<i>Nylanderia pubens</i> (Op) ^a	<i>Trachymyrmex</i> sp. 2 (At)
<i>Nylanderia silvestrii</i> (Op)	<i>Trachymyrmex</i> sp. 3 (At)
<i>Odontomachus chelifer</i> (Op)	<i>Wasmannia auropunctata</i> (Gm) ^a
<i>Pachycondila striata</i> (Op)	<i>Wasmannia</i> sp. (Cr)
<i>Pheidole aberrans</i> (Gm)	

Op Opportunists, Sp Specialist Predators, Sc Subordinate Camponotini, At Attini, Cr Cryptics, Gm Generalized Myrmicinae, Ar Arboreal, Hcs Hot-Climate Specialists, and Aa Army Ants

^a Invasive and/or pest species

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