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Habitat and Grazing Influence on Terrestrial Ants in Subtropical Grasslands and Savannas of Argentina

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ABSTRACT The maintenance of species diversity in modified and natural habitats is a central focus of conservation biology. The Iberá Nature Reserve (INR) protects highly diverse ecosystems in northeastern Argentina, including one of the largest freshwater wetlands in South America. Livestock grazing is one of the major disturbances to these ecosystems; however, its effect on ant diversity is poorly known. The objective of this work was to study the effect of savanna versus grassland and grazing on the structure and composition of subtropical terrestrial ants focusing on the particular response of the native red imported fire ant, Solenopsis invicta Buren. Unbaited pitfall traps were used to capture worker ants in 25 grazed and 20 nongrazed sites. Fifty ant species were collected. The savanna showed more species, individuals, biomass, and functional groups of ants than the grassland. S. invicta was the most frequently captured (61.4%) and numerically dominant species; however Camponotus punctulatus punctulatus Mayr showed the highest biomass. Grazing simplified vegetation structure in both habitats, but its impact on vegetation seemed only to promote a higher total biomass especially in the grassland, and/or functional groups, favoring occurrence of hot-climate specialists in the savanna. This study revealed that habitat type strongly affected the organization of the terrestrial ant assemblages at the INR. However, as in other studies, we did not find clear evidence that habitat modification by grazing significantly affected terrestrial ant assemblages. The weak grazing influence could be the consequence of the short enclosure time as to recover the original ant communities, the differential response of ant species to habitat type, and/or the resilience of ants.

KEY WORDS richness, species composition, disturbance, vegetation structure, Solenopsis invicta

Ants represent a high proportion of the biomass and diversity on earth. They constitute an important part of the edaphic mesofauna that enriches the soil, disperses seeds, tends homopterans, and controls insects (Wilson 1971, Fittkau and Klinge 1973, Holldobler and Wilson 1990). The structure and composition of ant communities are influenced by competition, natural enemies, resource availability, habitat, and disturbance (Wilson 1971; Holldobler and Wilson 1990; Bestelmeyer and Wiens 1996, 2001; Andersen 1997; Kaspari and Majer 2000).

Habitat degradation and biological invasions are the two greatest threats to global biodiversity. The maintenance of species diversity in modified and natural habitats is a central focus of conservation biology. In this regard, the Iberá Nature Reserve (INR) represents a unique system of 1,300,000 ha in northeastern Argentina that protects one of the largest freshwater wetlands in South America (Canziani et al. 2003, Parera 2006, The Ramsar Convention on Wetlands 2008). The reserve includes a large marsh with lagoons, small rivers, streams, and extensive floating vegetation, surrounded by a diverse mosaic of terrestrial ecosystems, such as temporary flooded grasslands, savannas, and forests (Neiff and Poi de Neiff 2006, Parera 2006). These terrestrial ecosystems show different degrees of modification through ranching, agriculture, and wood production (Parera 2006). More than 100 native ant species occur in the INR (Calcaterra et al. 2010), several of which are invasive in other countries (Lowe et al. 2000, Pest Directory 2008), such as the red imported fire ant, Solenopsis invicta Buren, which was accidentally introduced into the United States from northeastern Argentina in the early 1900s. This species occurs in several natural habitats of the INR (Calcaterra et al. 2010).

Natural and anthropogenic disturbances observed in the INR, such as floods, fires, or grazing, are essential factors affecting species structure and composition, as in many natural ecosystems (Cooperrider 1991, Suarez et al. 2001, Adis and Junk 2002, Parera 2006). As one of the most extensive forms of land use (FAO 1996), cattle grazing is one of the main potential threats to biodiversity in the INR. Its effect on...
many biological components of wetlands has been widely studied in other regions (Reeves and Champion 2004, Marty 2005, Casanova 2008); however, few studies investigated its effect on ant fauna in different habitat types. Depending on grazing intensity, habitat complexity, and hierarchies in the ant community (Farji-Brener et al. 2002), grazing may have positive or negative effects on ants (Bestelmeyer and Wiens 1996, 2001; Kerley and Whitford 2000; Woinarski et al. 2002; Hoffmann and Andersen 2003; Ratchford et al. 2005). Many studies have reported that intensive grazing affects habitat structure facilitating the dominance of highly competitive species (such as the invasive ant *S. invicta*), but with scarce consequences on the organization of assemblages of ants (Orians 1986, Deyrup et al. 2000, Hoffmann and Andersen 2003). To know whether the presence of livestock grazing affects the organization of the ant assemblages of the INR, it is essential to establish future management policies that contribute to the biodiversity maintenance of this protected area.

The main objective of this work was to study the influence of the habitat type (savanna versus grassland) and grazing (nongrazed versus moderate to very heavy grazing) on the structure and composition of subtropical terrestrial ant assemblages of the INR. We also investigated the response of the invasive *S. invicta* to grazing to confirm whether or not this fire ant is more abundant in disturbed (grazed) habitats in its native range, as has been reported for its introduced range, mainly in North America (King and Tschinkel 2006, 2008; Tschinkel 2006; Hill et al. 2008).

### Materials and Methods

#### Study Area.

The study was conducted in June (late fall) and November (spring) 2007 and September (late spring) 2008 in an area of ~300 km² mostly located in the southeast of the INR, 5 km southwest of Colonia Pellegrini (Fig. 1). Study sites were located in two habitats: 1) savanna, an open forest belonging to the “Espinal” ecoregion, with short *Prosopis L.* and *Acacia (Tourn.)* trees, bushes, and grasses (Tressens et al. 2002); and 2) grassland, a temporarily flooded grassland, typical of the “Campos y Malezales” ecoregion, dominated mainly by *Andropogon lateralis* Nees (Tressens et al. 2002, Neiff and Poi de Neiff 2006, Parera 2006). In each habitat, we sampled both grazed and nongrazed areas with cattle exclusion for >5 yr (strict conservation areas). Besides cattle, the region harbors wild grazers such as capybara (*Hydrochaeris hydrochaeris* L.), plains viscacha (*Lagostomus maximus* Desmarest), marsh deer (*Blastocerus dichotomus* Illiger), and brocket deer (*Mazama gouazoupira* Fischer).

The climate in the region is humid and subtropical with drier winters. Mean temperature varies from 15°C in July to 26°C in January. Mean annual rainfall is 1,500 mm (De Fina 1992, Fontan and Sierra 2004).
Sampling Design. In total, 45 sampling stations were established as follows: 1) nongrazed savanna: 10 stations; 2) grazed savanna: 14 stations; 3) nongrazed grassland: 10 stations; and 4) grazed grassland: 11 stations (Fig. 1). The nongrazed savanna stations and those in the grassland were located in two private reserves owned by The Conservation Land Trust within the INR, whereas all the grazed savanna stations were located in Paraje Uguay (eight stations), and El Porvenir Ranch (six stations), 30 km south from the other sampling areas (not included in Fig. 1).

All stations were located at least 1–2 km apart and >300 m away from habitat limits (ecotones), roads and trails to avoid border effect. According to the ranchers, the average livestock loads during the past 5 yr were as follows: Paraje Uguay, four animals per ha (very heavy grazing; cows, sheep, and horses); El Porvenir Ranch, 0.8 animal per ha (heavy grazing; cows); and Iberá Ranch, 0.4 animal per ha (moderate grazing; cows). Thus, the savanna presented eight sites with very heavy grazing and six with heavy grazing, and the grassland had all 11 sites with moderate grazing. To evaluate the effect of grazing on vegetation richness and structure (height and cover) and on the ant assemblage structure, we used original data from a vegetation survey carried out by Maturo et al. (2007) in 25 of the 45 sampling stations used in this study, mainly located in the savanna. This vegetation analysis did not include information from El Porvenir Ranch.

Ant Survey. Ants were sampled using unbaited pitfall traps following Calcaterra et al. (2010). At each station, one trap was set up every 10 m along a linear transect and exposed for 48 h. Each trap consisted of a 50-ml plastic centrifuge tube (~3 cm in diameter) buried in the ground and half-filled with soapy water. In total, five traps were considered the sampling unit. After 48 h, the content of the traps was removed, rinsed with water, and preserved in 96% ethanol. All stations were sampled once. Thus, in total 45 sampling units (225 pitfalls traps) were considered. Although the habitats were sampled simultaneously, the sampling effort differed (Tables 1 and 2).

Table 1. Number of sampling units (five traps) per habitat in Iberá

| Sampling period | Savanna | Grassland | Total |
|-----------------|---------|-----------|-------|
|                 | Nongrazed | Grazed | Nongrazed | Grazed | Nongrazed | Grazed | Total |
| June 2007 (late fall) | 2 | 3 | 3 | 3 | 11 |
| Nov. 2007 (spring) | 3 | 5 | 3 | 4 | 15 |
| Sept. 2008 (late winter) | 5 | 6 | 4 | 4 | 19 |
| Total | 10 | 14 | 10 | 11 | 45 |

Table 2. Sampling effort and diversity indicators in Iberá

| No. stations (or samples) | Savanna | Grassland | Total |
|---------------------------|---------|-----------|-------|
| Pitfall traps | 50 | 70 | 50 | 55 | 225 |
| Expected species | 44 | 68 | 27 | 24 | 75 |
| Observed species (% expected) | 25 (57) | 35 (51) | 16 (59) | 13 (54) | 50 (67) |
| Max. species per sample | 8 | 10 | 7 | 5 | 10 |
| Common species | 5 | 11 | 4 | 5 | 5 |
| Rare species | 13 | 20 | 8 | 7 | 18 |
| Exclusive species | 5 | 14 | 2 | 5 | 5 |
| Invasive species | 6 | 8 | 7 | 3 | 10 |

Data Analysis. We used a combination of diversity indices (ant species richness, relative abundance, biomass, Shannon, dominance, similarity, and composition) to study the effects of habitat and livestock grazing on ant assemblages. Because we were not interested in temporal effects on the ant assemblages, sampling periods did not cover all seasons and samples were grouped for the analysis. The number of ant species at each station was recorded by pooling five pitfalls traps (sampling unit). Spatial abundance was measured as the proportion of units in which a species was present. Numerical abundance was measured as the number of individuals trapped. Ants were separated from other arthropods and identified to species or morphospecies by L.A.C. and F.C. under a dissecting scope and by using keys as in Calcaterra et al. 2010. Voucher specimens were deposited at the Instituto-Fundación Miguel Lillo (IFML), Tucumán, Argentina, and at the South American Biological Control Laboratory (SABCL).
dominant species. A chi-square test was used to evaluate the influence of grazing on the total number of workers in each habitat.

The total numbers of species found in each habitat and grazing history was visually compared using sampled-based species accumulation curves (Gotelli and Colwell 2001) by entering occurrence data in a two-way matrix (species × sample) and using the EstimateS 8.0 software (Colwell 2006). Curves were obtained after 500 randomizations. To quantitatively ensure that sampling effort was similar in the four treatments, the total number of species observed in each situation was divided by the total number of species expected to occur in each situation according to the nonparametric second-order Jackknife richness estimator (henceforth Jack2) (Table 2). This estimator was selected because of its best performance under a wide range of sample sizes.

A two-dimensional ordination of samples was carried out with nonmetric multidimensional scaling (NMDS) by using the Sørensen distance measure to visually examine the ant assemblage composition; this was tested using an Analysis of Similarity (ANOSIM and post hoc Bonferroni pairwise comparisons; Clarke and Green, 1988) based on 1,000 permutations. NMDS is well suited for non-normal data and does not assume linear relationships among variables (McCune and Grace 2002). The Sørensen similarity index also was used to evaluate the similarity in species composition (Magurran 1988). Because rare species may distort the analyses, only species with more than four individuals occurring in more than one sample were considered for the analyses, which were performed using PCORD 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; Hill et al. 2008; van Ingen et al. 2008; Calcaterra et al. 2010). We followed the classification of functional groups proposed by Bestelmeyer and Wiens (1996) for Argentinean Chaco ants and previously adopted by Calcaterra et al. (2010) for the INR. This classification was considered more appropriate for our study than that proposed by Andersen (1995) for Australian ant communities. 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-bodied species with a variety of behaviors and habitat requirement that defend resources by recruitment), arboreals (species that nest and forage almost exclusively in trees or shrubs), and climate-specialist species (species adapted to specific temperature and humidity conditions). Dominant Dolichoderinae (active and dominant ants) was not recorded in this study. 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 (Kusnezov 1978; Bestelmeyer and Wiens 1996; Andersen 1997; Silvestre et al. 2003; Andersen et al. 2007; Calcaterra et al. 2008, 2010; Hill et al. 2008; van Ingen et al. 2008; Cuezzo and González Campero 2010). A two-way ANOVA was used to examine the influence of habitat type, grazing history, and their interaction on the number of functional groups (square-root + 0.5 transformed) and the number of species (square-root + 0.5 transformed) in each functional group. A one-way ANOVA was used to examine whether different grazing intensities in the savanna (nongrazed, Rincón del Socorro Ranch; heavy grazed, El Porvenir Ranch; and very heavy, Paraje Uguay) affect the richness, abundance, diversity, dominance, biomass, and functional group number of ants. Means ± SE are reported.

**Results**

**Species Richness.** In total, 1,163 ants belonging to 50 species or morphospecies in 16 genera were captured (Appendix 1). The most represented genera were *Pheidole* Westwood with 16 species (32%) and *Solenopsis* Westwood with seven (14%). Forty-three species were captured in the savanna and 24 species in the grassland. Grazed and nongrazed sites showed 41 and 30 species, respectively. Because none of the curves approached the asymptotic level, more species (mainly rare species) should be expected to occur in all situations (Fig. 2). However, according to the most stable richness estimator (Jack2), the percentages of expected species were relatively similar in all treatments, ranging from 51% for the grazed savanna (the richest treatment) to 59% for nongrazed grassland conditions.
The mean number of species captured per station was $6 \pm 0.4$ in the savanna and $2.7 \pm 0.4$ in the grassland ($R^2 = 0.48$; $F_{1,41} = 32.96$; $P < 0.001$) (Table 3). In contrast, grazing history ($F_{1,41} = 0.31$; $P = 0.582$) and the interaction habitat-grazing history ($F_{1,41} = 1.57$; $P = 0.218$) were not significant. In the savanna, the mean ant richness was similar under different grazing intensities ($F_{2,21} = 1.44$, $P = 0.26$) (Table 4).

Although the Shannon ($F_{1,41} = 17.25$, $P < 0.001$) and dominance ($F_{1,41} = 9.65$, $P < 0.004$) indices indicated a significant difference in the diversity and dominance of ant species between habitats (Table 3), the variance explained by the whole model were relatively low ($R^2 = 0.32$ and 0.21, respectively). Again, grazing history and the interaction were not significant for these two indices ($P > 0.35$ in all the cases). Shannon and dominance indices were also similar under different grazing intensities in the savanna ($F_{2,21} = 0.23$; $P = 0.8$ and $F_{2,21} = 0.25$; $P = 0.78$, respectively).

**Spatial Abundance.** *S. invicta* was the most widely distributed ant, being captured in 64% (29/45) of the stations, followed by *Paratrechina fulva* (Mayr) (31%) and *Pheidole laevinota* Forel (29%). Also, *S. invicta* dominated all habitats except the nongrazed grassland, which were codominated by *P. fulva* and *P. laevinota* (40%) (Table 5). *Pheidole aberrans* Mayr (29%) and *Pheidole obscurithorax* Naves (22%) occurred exclusively in the savanna. Only five (10%) of the 50 species captured occurred at >20% of the stations (Table 5).

**Numerical Abundance.** *S. invicta* was the most abundant with 309 workers (27%), followed by *P. laevinota* with 148 (13%), whereas *Camponotus punctulatus punctulatus* Mayr showed the highest biomass with 95.9 mg (32%), followed by *Camponotus punctulatus cruentus* Santschi with 55.4 mg (19%) and *S. invicta* with 45.7 mg (15%). *S. invicta* and other 11 species represented >80% of the total workers captured and almost 90% of the total biomass (Table 6). Nongrazed savanna sites were dominated by *S. invicta* with 46% of the workers and 36% of the biomass (Table 6). Grazed savanna was codominated by *Dorymyrmex steigert platensis* Santschi (17%, it occurred only in this situation), *P. laevinota* (16%), and *S. invicta* (15%), but only by *C. punctulatus cruentus* (40%) in terms of biomass. Nongrazed grassland sites were codominated by *P. fulva* (21%) and *P. laevinota* (20%), and by *Camponotus rugosus* (F.) in biomass (51%). *Solenopsis invicta* (37%) and *C. punctulatus punctulatus* (32%) codominated in the grazed grassland; in addition, *C. punctulatus punctulatus* was clearly the dominant species in biomass (80%).

Overall abundance of *S. invicta* was positively related to *P. aberrans* and negatively to *C. punctulatus punctulatus* ($r_s = 0.36$; $P = 0.014$ and $r_s = -0.41$; $P = 0.006$, respectively). Abundance of *P. fulva* was negatively related to this latter species ($r_s = -0.33$; $P = 0.029$).

The mean number of workers per station was $34.3 \pm 4.9$ in the savanna and $16.1 \pm 4.1$ in the grassland ($F_{1,41} = 10.99$; $P < 0.002$) (Table 3), but grazing history was only marginally significant ($F_{1,41} = 3.85$; $P = 0.057$) and the interaction was not significant.
No difference in biomass was detected between habitats, grazing history and the interaction ($P_{H11022} = 0.25$ in all the cases). Variation in grazing intensity in the savanna did not affect the mean number of workers ($F_{2, 21} = 1.24; P = 0.31$) or the mean biomass ($F_{2, 21} = 0.26; P = 0.77$) of ants.

At the species level, a significant difference was detected in numerical abundance of *S. invicta* between habitats ($F_{1, 41} = 8.69; P = 0.005$), although the variance explained by the whole model was low ($R^2 = 0.20$). Grazing history ($F_{1, 41} = 0.20; P = 0.659$) and the interaction ($F_{1, 41} = 1.95; P = 0.171$) were not significant. The fire ant averaged 15 workers per station in the savanna and only nine in the grassland. Abundance of other species common to both habitats, such as *P. laevinota* ($H_{3, 45} = 3.6; P = 0.31$), *C. punctulatus punctulatus* ($H_{3, 45} = 3.6; P = 0.31$).
latus \((H_{\text{a},35} = 0.53; P = 0.767)\), and *P. fulva* \((H_{\text{a},45} = 1.07; P = 0.79)\) was similar and unrelated to grazing. No differences were found for *C. punctulatus crucetus* \((H_{1,24} = 0.02; P = 0.88)\), *P. aberrans* \((H_{1,24} = 1.38; P < 0.24)\), and *P. obscivirhorax* \((H_{1,24} = 0.18; P < 0.67)\) between the nongrazed and grazed savanna.

Although an association was not detected between grazing and numerical abundance at the station and species levels, the total number of workers (adjusted to the sample size) was significantly higher in the grazed than in the nongrazed savanna sites \((\chi^2 = 23.88; df = 1; P < 0.0001)\) and grassland sites \((\chi^2 = 53.69; df = 1; P < 0.0001)\) (Table 6).

**Species Composition.** The visual ordination of samples did not show separation among the stations of each treatment (NMDS: \(R^2 = 0.67, \text{stress} = 0.23\)). However, a weak segregation (ANOSIM: \(R = 0.35, P < 0.001\)) in species composition was detected between both grazed situations (Bonferroni pairwise comparison, \(P < 0.05\)). Dissimilarity between the grazed savanna and grassland was 71%, whereas that of nongrazed habitats was 56%. The highest similarity was within the savanna situations with 56%, whereas grassland situations showed only a similarity of 41%.

The number of functional groups was significantly higher in the savanna \((R^2 = 0.30; F_{1,41} = 13.32; P < 0.001)\); grazing history and the interaction were not significant. Variation in grazing intensity in the savanna did not affect the mean number of functional groups \((F_{1,21} = 0.87; P = 0.44)\).

The most represented functional group was generalized Myrmicinae with 21 species, followed by opportunists and Attini with seven species (Appendix 1). Grazed savanna sites were the richest with eight functional groups (six shared with the nongrazed savanna sites), whereas the grazed grassland was the poorest with only three functional groups (Fig. 3). Specialist predator species occurred exclusively in savanna sites, whereas climate specialists (specifically hot-climate species) in the grazed savanna. Arboreal, cryptic, and Attini species also were absent in the grazed grassland. Generalized myrmicines had the highest proportions in the four situations (33.3–57.1% of total species); however, differences in mean number of species were found only between habitats \((R^2 = 0.46; F_{1,41} = 33.75; P < 0.001)\). Grazing history \((F_{1,41} = 0.86; P = 0.36)\) and the interaction \((F_{1,41} = 0.30; P = 0.59)\) were not significant. Attini was the second most common group in the nongrazed savanna (16%), whereas subordinate Camponotini and opportunistic were the next most common in the grazed savanna (14.3%) and grassland (28.6%). In nongrazed grassland, Attini species codominated with generalized myrmicines (33.3%).

**Vegetation Structure.** Significant differences were detected in the vegetation structure of the savanna as an effect of grazing. As expected, plant height was six-fold shorter in grazed than in the nongrazed stations \((F_{1,15} = 6.81; P = 0.02)\), whereas plant cover was 22% lower in grazed than in nongrazed stations \((t = -2.6, df = 13, P = 0.02)\). A similar pattern was observed in the grassland, but significant differences were not detected mainly because of the lower sample size. Mean number of plant species was similar in the four habitats \((H_{1,24} = 2.68; P = 0.44)\) (Table 3).

The mean plant height was negatively related to ants abundance \((r = -0.47, P = 0.02)\) and biomass \((r = -0.42, P = 0.04)\), whereas plant cover was negatively related to the dominance index \((r = -0.42, P = 0.04)\). Only the numerical abundance of *P. obscurithorax* was positively related to plant cover in the savanna \((r_a = 0.42, P = 0.039)\).

**Discussion**

Most diversity indicators showed a clear distinction between habitats, with the savanna showing more species, individuals, biomass, and functional groups of ants than the grassland. It agrees with other studies showing that habitats with a more complex vegetation structure and primary productivity support more diverse and dense ant assemblages (Andersen 1997, Kaspari et al. 2000, Sart et al. 2006, Vasconcelos and Vilhena 2006, Calcaterra et al. 2010). Contrarily, we did not find clear evidence that habitat modification by grazing affected the structure and composition of terrestrial ant assemblages at the INR.

Diversity indicators neither showed differences attributable to the variation in the grazing pressure observed in the savanna. After 5 yr of enclosure, ant assemblages in the savanna were similar in nongrazed, heavy grazed and very heavy grazed sites. These results are consistent with studies conducted
in the Argentine Chaco semiarid woodland (Bestelmeyer and Wiens 1996), in North American desert grassland (Bestelmeyer and Wiens 2001), and in semiarid and desert habitats in Australia (Hoffmann and Andersen 2003). The lack of effect might be the consequence of the variable behavior observed for some ant species among habitats, as has been reported by Hoffmann and Andersen (2003); they did not find a consistent positive or negative response to grazing for individual species, except the effects on hot-climate specialists, as in our study.

However, the higher overall numerical abundance (and biomass) recorded in grazed savanna and grassland might indicate some grazing effect on the ant assemblage structure. This is supported by the fact that grazing affects vegetation structure, which is associated with changes in the mean abundance, biomass, and dominance of ants.

Species Richness. The savanna was almost two-fold richer in species than the grassland, when grazed and nongrazed sites were pooled, but it was only a third richer if only ungrazed sites of both habitats are considered. This relationship between natural habitats is consistent with a recent study by Calcaterra et al. (2010), except that the expected richness for the grassland was much higher (42) than that reported in this work (27). This discrepancy could be attributed to weather differences during the samplings in both studies, and/or to temporary flooding or fire recorded in some grassland sites. A similar pattern was observed for diversity–dominance indices. The savanna was more diverse, whereas the grassland showed higher values of species dominance.

The 40% higher total number of species observed in the grazed compared with the nongrazed savanna was a consequence of the higher number of stations used in this habitat (40%) and the fact that grazed savanna sites were located in two separated areas, increasing the total richness by replacement of species (beta diversity). This also could explain, at least in part, the higher number of exclusive and rare species found in the grazed savanna compared with the other habitats. However, the lower number of expected species obtained for the nongrazed savanna could suggest a positive grazing effect in the savanna. This should be confirmed with more enclosure experiments in new areas within this habitat type.

Species Abundance. Grazing promoted higher number of workers and biomass both in the grassland (three-fold) and the savanna (two-fold) mainly because of the additive increasing abundance of some ant species. Only 12 species represented ≈85% of the workers and 95% of the biomass captured. Although not significant, the grazing effect was more evident for S. invicta and C. punctulatus punctulatus in the grassland and for P. laevi nota, D. steigeriplatensis, and C. punctulatus cruentus in the savanna. As a consequence, an inverse relationship was found between richness and abundance between nongrazed and grazed sites in the grassland (Table 3). Overall, grazed grassland had fewer species, but they were more abundant than the total species in nongrazed grassland.

The presence and abundance of S. invicta was strongly influenced by habitat. This was the only species that showed higher abundance in nongrazed compared with grazed savanna sites. This agrees with Calcaterra et al. (2010), who reported that S. invicta was strongly (62%) associated to the nonmodified savanna in the INR. However, it is in contrast with the results from studies conducted in the United States where fire ants were more abundant in modified habitats, being almost absent in nondisturbed natural habitats (Graham et al. 2004; King and Tschinkel 2006, 2008; Tschinkel 2006). Our results from the grassland, however, were more consistent with the situation in the United States where S. invicta is considered a disturbance specialist.

Overall, S. invicta was the most common and numerically dominant species with almost 27% of total individuals captured, but representing only 15% of the total biomass. This is in great contrast, for example, with the findings in intensively grazed pastures in Mississippi, where S. invicta accounted for >88% of the ant biomass (Hill et al. 2008). This contrast is consistent with Porter et al. (1992, 1997) who reported that densities of fire ants in South America average 1/5–1/10 of those in the United States. This difference has been mainly explained by the presence of natural enemies and/or a more intense competitive pressure in South America compared with the United States (Tschinkel 2006, LeBrun et al. 2007, Calcaterra et al. 2008).

These results concur with studies in semiarid and desert environments in the United States (Bestelmeyer and Wiens 2001, Nash et al. 2004), where live-stock grazing only impacted the abundance of some ants and functional groups rather than on species richness and composition. However, their observation was made for a desert grassland situation and a transitional zone between the short grass steppe and the Chihuahuan desert biomes.

Both the negative relationships between plant height and abundance of workers and between plant cover and dominance index could explain the higher species dominance observed in the grassland compared with the savanna. C. punctulatus punctulatus and S. invicta showed several times more individuals and biomass in the grazed than in the nongrazed grassland. The subordinate C. punctulatus punctulatus was practically the only ant captured in grassland sites more frequently flooded (abandoned rice cultivation sites).

The higher abundance of S. invicta in the grazed grassland could be the consequence of the important reduction in plant height (from 130 to 44.2 cm), allowing higher insolation and temperature for colony thermoregulation. This pattern was previously reported for S. invicta in Argentina and United States (Hölldobler and Wilson 1990, Bestelmeyer and Wiens 1996, Tschinkel 2006) and for Solenopsis substituta Santschi in Brazil (Vasconcelos et al. 2008). The dominance of S. invicta in grazed grass-
land also could be favored by the absence (or probable scarce presence) of its main competitors, such as *P. obscurithorax* (LeBrun et al. 2007; Calcaterra et al. 2008, 2010) or potential competitors such as *P. aberrans*.

**Species and Functional Composition.** Although a weak distinctive species composition was only observed between grazed savanna and grazed grassland, and despite the 2–10 times higher livestock load in the savanna, dissimilarity indices suggest a stronger grazing influence on community composition of the grassland (59%) compared with the savanna (44%). The overall grazing intensity in the INR (moderate to very heavy) was relatively similar to those reported for other studies and regions (Bestelmeyer and Wiens 2001, Hoffmann and Andersen 2003, Hill et al. 2008). Ant species composition in Mojave Desert was not affected under different grazing intensities but relative abundance of several species and functional groups did change (Nash et al. 2004). This agrees with our observations in the savanna, where stations with different grazing intensities (from nongrazed to very heavy) and separate locations overlapped in the ordination analysis, which reveals a similar species composition.

The little influence of grazing on functional groups detected in the INR is congruent with studies conducted in grasslands and arid and semiarid rangelands in the United States and Australia (Hoffmann and Andersen 2003, Underwood and Christian 2009). According to Hoffmann and Andersen (2003), functional groups responses to disturbance will depend on the specific combinations of types of habitats and disturbances. In the INR, habitat type strongly influenced the occurrence of functional groups. Savanna possessed with twice as many functional groups than the grassland.

Although nongrazed and grazed habitats were spatially and numerically dominated with generalized myrmicines, they were codominated by different groups. As reported by Bestelmeyer and Wiens (1996), generalized myrmicines were apparently unaffected by grazing in the Chaco savanna, but in grassland situations, they increased in numbers and replaced arboreal and cryptic species. However, this “replacement” should be better explicated by the absence of niche (trees and leaf litter) for these groups in the grassland. A pattern of substitution of Attini and subordinate Camponotini species by opportunistic ants was also observed in the two habitats and was probably as a consequence of grazing. Generalized myrmicines and opportunists are groups particularly sensitive to competitive interactions (Hoffmann and Andersen 2003). The strong effect of the very heavy cattle load on the vegetation structure in the Paraje Uguay (savanna) favored the occurrence of hot-climate specialists, agreeing with the functional group model developed for arid-adopted Australian ants (Andersen 1995, 1997; King et al. 1998). This model predicts an increase of opportunistic and hot-climate specialists in structurally simplified habitat by effect of disturbance such as grazing or fire (Greenslade 1978, Bestelmeyer and Wiens 1996, Hoffmann and Andersen 2003). Hot-climate specialists prefer open environments with scarce vegetation coverage and therefore prefer grazed sites. Specialist predators [*Gnamptogenys triangularis* (Mayr) and *Anochetus neglectus* Emery] were exclusively associated with the savanna in INR. This group, similar to cryptic species, had highly specific habitat requirements (Hoffmann and Andersen 2003). Three species (*Anochetus neglectus*, *Acromyrmex lundi* Guerin, and *Solenopsis macdonaghi* Santschi) were recorded for the first time at INR, which brings the total number of ant species recorded for this macroecosystem to 108 species (Calcaterra et al. 2010).

**Vegetation Structure.** Livestock grazing simplified vegetation structure mainly by reducing overall plant height in both habitats. However, this variation did not explain the variation observed in ant species richness. Although the height reduction was (unexpectedly) higher in the habitat with the lowest cattle load, the grassland (86 cm), than in the savanna (55 cm), the height of the vegetation was a third lower in the grazed savanna (11.1 cm) than in grazed grassland (44.3 cm), which should explain at least the occurrence of the hot-climate specialist species. As in the Brazilian savanna (Vasconcelos et al. 2008), grass cover variation did not explain the variation observed in species richness either. These variables were only weakly associated to the number of workers and biomass (in the case of the plant height) and dominance index (plant cover) in the savanna. This is consistent with Bestelmeyer and Wiens (2001), who found a strong grazing effect on the vegetation in a semiarid landscape but scarce consequences on the ants.

The virtual absence of grazing effect on ant assemblages also could be explained by the fact that livestock grazing had no real impact on the vegetation above the background levels of natural grazing. This assumption seems to be supported by the fact that the presence of cattle, mainly in Paraje Uguay, negatively affected the occurrence of wild fauna (Di Bitetti et al. 2009). However, the relative higher load of native herbivoros estimated by photographic records with camera-traps (Di Bitetti et al. 2009) in nongrazed sites (enclosure sites) did not compensate the much higher total load of herbivorous (native and exotic) recorded in the grazed sites (M. Di Bitetti, personal communication).

In conclusion, this study showed that habitat (differences) strongly influenced the ant structure and composition at the INR. Clearly, the savanna showed a higher diversity of species and functional groups than the grassland. Although grazing resulted in a simplified vegetation structure, its (indirect) influence on ant species richness and composition was not significantly detected. Grazing impact on vegetation structure seemed to affect only some individual species, promoting a higher total abundance of workers (and biomass) especially in the grassland, and/or functional groups, favoring mainly the occurrence of hot-climate specialists in the savanna.
S. invicta was dominant in most of the situations without showing the highest biomass. Though numerically dominant, S. invicta seemed not to affect the organization of ant assemblages. Its occurrence and abundance seemed to be favored by grazing only in the habitat with the less complex vegetation structure (grassland), as in its introduced range, but independently of grazing, it was more abundant in the savanna.

In terms of biodiversity conservation, these findings revealed that habitat type strongly affected the organization of the terrestrial ant assemblages at the INR, whereas grazing had an insignificant effect. Thus, disturbance by grazing does not seem to be a key factor that threatens the maintenance of ant diversity in the INR. However, the scarce grazing influence could be the consequence of the short enclosure time as to recover the original and distinctive ant communities, the differential response of ant species according to the habitat type, and/or the resilience of ants. This study needs to be replicated in new areas and in the long-term in the INR to test these hypotheses.

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Appendix 1. List of ant species captured in Iberá (functional group*)

| Species Name | Functional Group |
|--------------|------------------|
| Acromyrmex lundi Guerin (At) | Acromyrmex sp. 1 (At) |
| Acromyrmex sp. 2 (At) | Acromyrmex sp. 2 (At) |
| Anochetus neglectus Emery (Sp) | Linepithera micans (Forel) (Op) |
| Atta colombica Forel (At) | Neomyrmex sp. (Ar) |
| Brachymyrmex isanensis Santschi (Op) | Paratrechina docilis (Forel) (Op) |
| Paratrechina fulva (Mayr) (Op) | Paratrechina pubens (Forel) (Op) |
| Camponotus bonariensis Mayr (Sc) | Paratrechina silvestrii (Emery) (Op) |
| Camponotus mus Roger (Sc) | Pheidole aberrans Mayr (Gm) |
| Camponotus punctulatus cruenus Santschi (Sc) | Pheidole bergi Mayr (Gm) |
| Camponotus punctulatus punctulatus Mayr (Sc) | Pheidole bison Wilson (Gm) |
| Camponotus rufipes (F.) (Sc) | Pheidole fastifrons Roger (Gm) |
| Camponotus sp. (Sc) | Pheidole laeviceps Forel (Gm) |
| Crematogaster quadrifrons Roger (Gm) | Pheidole nitida Wilson (Gm) |
| Cyphomyrmex olitor Forel (At) | Pheidole obscurithorax Naves (Gm) |
| Cyphomyrmex rimosus (Spinola) (At) | Pheidole vulgarekowskii Mayr (Gm) |
| Dorymyrmex steigeri platensis Santschi (Hcs) | Pheidole rufa Wilson (Gm) |

* Op, opportunists; Sp, specialist predators; Sc, subordinate camponotini; At, Attini; Cr, cryptics; Gm, generalized Myrmicinae; Ar, arboreals; and Hcs, hot-climate species.

* Invasive and/or pest species.