

# Effects of land-use changes on ecosystem services: decrease in ant predation in human-dominated landscapes in central Brazil

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## Abstract

Anthropogenic disturbances often affect the abundance and diversity of ants (Hymenoptera: Formicidae) but relatively few studies have explored the implications of such changes on the ecosystem services mediated by these insects. Here, we evaluated how the transformation of Cerrado savanna habitats into crop plantations affects the abundance, diversity, and the predatory activity of ants. A survey of the ant faunas foraging above- and belowground was performed in six crop and six non-crop (i.e., native vegetation) sites. Above- and belowground rates of ant predation were estimated at these same sites using mealworms, *Tenebrio molitor* L. (Coleoptera: Tenebrionidae), as baits, simulating crop herbivores. Belowground predation rates were significantly greater in the non-crop sites, despite the lack of difference in overall abundance and species richness of ants foraging belowground between the crop vs. non-crop sites. In contrast, we did not detect any significant difference in aboveground predation rates between crop vs. non-crop sites even though there were significantly more species of ants foraging aboveground in the non-crop sites. Army ants (subfamily Dorylinae) were the main predatory species belowground, and their abundance was significantly greater in non-crop sites. In contrast, the main predators aboveground were omnivore ants of the genera *Pheidole* and *Solenopsis*, which had similar abundances in the crop and non-crop sites. Overall, our results indicate that transformation of native Cerrado habitats into crop plantations reduces the abundance of some important predatory species, notably those that forage belowground, and this may negatively affect the potential for ants to provide pest control services in agroecosystems.

## Introduction

Ecosystem services are the economic benefits that nature provides to people (Millennium Ecosystem Assessment, 2005). Insects, due to their sheer number of individuals and species, and their great variety of feeding habits and ecological niches, are involved in many ecosystem services (Losey & Vaughan, 2006). Some of these services, including especially pollination, decomposition, weed seed predation, and pest suppression, are also important to farming (Isaacs et al., 2009). For instance, insect pollinators supply a valuable input to agricultural production that

can increase both the size and quality of harvests (Ricketts et al., 2008). Anthropogenic activities that threaten the maintenance of insect diversity are thus of great concern – not only from a conservation point of view, but also economically –, as the loss of beneficial insects directly affects the ecosystem services they provide. In fact, several authors have recommended that land-management decisions should take into account the ecosystem services performed by insects (Losey & Vaughan, 2006).

Ants are an abundant and ecologically important group of insects in many terrestrial ecosystems (Hölldobler & Wilson, 1990). Because predation forms part of the foraging strategy of most ant species, ants are thought to play a key role in animal community regulation (Philpott & Armbrrecht, 2006; Kaspari et al., 2011), with potential for

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controlling agricultural pests and acting as biological control agents (Risch & Carroll, 2008; Morris et al., 2015). Although the economic value of these ant services has not been quantified it is probably high, as the annual value of pest control attributed to all predatory insects (including ants) combined is around US\$ 4.5 billion in the USA alone (Losey & Vaughan, 2006).

There is relatively little information about the factors that affect the predation services provided by ants in agricultural landscapes and especially if ant biodiversity per se is a driver of these services (but see De la Mora et al., 2015). Also, very little is known about predation services by ants that nest or forage in different soil strata, notably those that forage belowground. The subterranean ant fauna has been regarded by some as the 'final frontier' in the study of the biodiversity of the Formicidae (Wilkie et al., 2007). This fauna includes a relatively large number of species with cryptobiotic morphology (i.e., small body, reduced or absent eyes) (Andersen & Brault, 2010). One group that seems to be highly abundant underground is the army ants (Berghoff et al., 2002; Wilkie et al., 2007). Army ants are considered keystone predators given their disproportional impact on the diversity and abundance of other arthropods (Hölldobler & Wilson, 1990; Kaspari & O'Donnell, 2003).

Land-cover and land-use changes often affect the structure of ant communities (Majer, 1983; Andersen & Majer, 2004; Hoffmann, 2010), and thus potentially also the rate at which ant services are delivered. In particular, ant services may be severely affected by the expansion and intensification of modern agriculture, which is known to cause heavy biodiversity losses (Pimm & Raven, 2000) and induces a simplification and homogenisation of biological communities (Pacheco et al., 2013; Solar et al., 2016). Over the past 50 years, the largest and richest savanna region of South America – the Cerrado, in central Brazil – has witnessed a rapid process of conversion into intensive, large-scale agricultural fields, especially those devoted to the production of soybeans (Ratter et al., 1997; Myers et al., 2000). The conversion of large tracts of natural Cerrado vegetation into soybean plantations was found to have strong negative impacts on the diversity of ground-dwelling ants (Frizzo & Vasconcelos, 2013; Pacheco et al., 2013). However, the consequences of such conversion on the predatory activity of ants remain unclear.

In this study, we evaluated whether land-use changes in the Cerrado affect the predatory services provided by ants. In addition, we evaluated which characteristics of the ant communities are correlated with rates of ant prey removal. For this, we determined the abundance, species richness, and functional composition of the ant faunas foraging above- and belowground in different crop and non-crop

(i.e., native vegetation) sites, and estimated the rates of prey removal above- and belowground at these same sites.

## Materials and methods

### Study sites

The study was conducted on six farms located near the cities of Uberlândia (18°56'S, 48°18'W) and Monte Alegre de Minas (18°52'S, 48°52'W), in the western region of Minas Gerais state, Brazil. This region is characterised by a tropical climate with a dry winter (May–September) and a rainy summer (October–April). The mean annual temperature and precipitation are 22 °C and 1 650 mm, respectively.

Within each farm, we selected one crop and one non-crop site located immediately adjacent to each other. The crop sites were either soybean (four sites), maize (one site), or sorghum (one site); all were large-scale commercial plantations, with  $\geq 600$  ha of cultivated area. In our study area these three crops are commonly cultivated in a rotational scheme and all three have a similar structure. The non-crop habitats consisted of remnants of natural Cerrado vegetation, varying in size from 39 to 149 ha (mean = 83 ha), and their vegetation was either open savanna (i.e., a savanna with scattered trees and a grassy understory; two sites) or dense woodland savanna (i.e., a savanna dominated by trees and almost no grasses; four sites). These types of savannas are the most common ones in our study region. For a more detailed description of the study sites see Pacheco et al. (2013).

### Estimating ant abundance and diversity

We used conventional pitfall traps to sample ants that forage on the soil surface and subterranean traps to sample ants that forage belowground (Pacheco & Vasconcelos, 2012). Ant sampling was conducted once in each site between December 2008 and March 2009. The conventional pitfall traps consisted of 300-ml plastic cups, buried so that the opening of the trap was level with the soil surface. Subterranean traps consisted of closed 250-ml plastic containers, with four 1-cm and four 0.5-cm holes on their side, buried to a depth of 20 cm (Pacheco & Vasconcelos, 2012). Both types of traps were filled to one-third of their volume with a mixture of ethanol (70%) and glycerine.

In each non-crop site the traps were distributed along seven parallel 180-m-long transects, located at 3, 20, 40, 60, 100, 140, and 180 m from the edge between the non-crop and the crop site. The transect established at the furthest distance (180 m from the edge) was located approximately in the centre of the non-crop site. One non-crop site was not large enough to accommodate all the seven transects and in this case only six transects were established

(at the same distances as described before, except the distance of 180 m). Along each transect, we installed a total of 10 traps (five subterranean and five conventional pitfall traps). We kept a minimum distance of 20 m between any two traps, and of 40 m between two traps of the same type. We used exactly the same protocol to sample ants in the adjacent crop sites. However, because crop plantations occupied a much larger area than the remnants of natural vegetation, in each crop we established three additional transects, located at 260, 340, and 420 m from the edge between the crop and non-crop site. Therefore, in each crop site a total of 100 traps were installed (50 of each type), whereas in each non-crop site 60–70 traps were installed (see Figure S1).

All traps were baited with sardine mixed with vegetable oil and kept in the field for seven consecutive days. Collected specimens were sorted to morphospecies and named (whenever possible) following Bolton's catalogue for species classification (Bolton et al., 2007). Voucher specimens of all species were deposited at the Zoological Collection of the Federal University of Uberlandia (UFU) in Brazil.

The ant species collected in the general survey were assigned to functional groups based on the classification of Silvestre et al. (2003), and on knowledge about the feeding and nesting biology of the collected species (Baccaro et al., 2015). The ant species were classified as: (1) arboreal (e.g., *Azteca* and *Camponotus* spp.), (2) fungus-growing (all ants of the tribe Attini), (3) army ants (predatory ants with nomadic habits), (4) other predators (mostly poneromorph ants), (5) cryptic (species collected mostly belowground with cryptobiotic morphology), or as (6) omnivore (e.g., *Pheidole* and *Solenopsis* spp.).

#### Ant predation experiments

Estimates of ant predation rates were performed 1 week after the general ant sampling. To estimate rates of ant predation above- and belowground we adopted the live-bait trap methodology developed by Yamaguchi & Hasegawa (1996). The traps consisted of a sealed plastic container (250 ml) baited with one live mealworm larva, *Tenebrio molitor* L. (Coleoptera: Tenebrionidae). Eight holes (0.5 mm) were made around the wall of each container (close to the lid). In a preliminary test, we found that the *Tenebrio* larvae were unable to climb the walls of the plastic container and escape, whereas ants could easily get in or out of the containers.

In total, 60–70 traps with live baits were placed in each non-crop site, and 100 traps in each crop site. The spatial arrangement of traps with live baits was the same as described above for sampling the ant fauna. Half of the traps with live baits were buried so that the entrance holes

were located 20 cm below the soil surface, and half were only partially buried so that the entrance holes were very close to the soil surface. The traps were left in the field for 48 h and, after this period, we counted the traps in which the larva was removed or partially eaten. We also collected and identified any ants that were present within the traps. No other type of predatory insect was found in our traps, so we assumed that all missing larvae were removed by ants.

#### Data analysis

The rate of ant predation in each site was estimated by the proportion of the total number of mealworms that were missing or were partially eaten by ants. Separate estimates were made for live-bait traps placed near the soil surface and for those placed 20 cm belowground ( $n = 30\text{--}50$  mealworms per site in each soil stratum). Estimates of ant species richness at these same sites were based on the data obtained during the general ant sampling. For this, we calculated the mean number of species found in each subterranean trap and the mean number of species found in each conventional pitfall trap, for a total of 30–50 traps of each type per site (all transects combined). As an estimate of aboveground ant abundance in each site we used the mean number of ants per pitfall trap. The number of ants per trap was  $\log(x + 1)$  transformed before calculating mean values.

We used t-tests to test for differences between crop and non-crop sites in the number of species per trap, the overall abundance of ants per trap, the abundance of ants from different functional groups, and predation rates. We used analysis of covariance (ANCOVA) to evaluate the relationship between ant species richness per trap and predation rates, and to evaluate whether differences in ant predation between crop and non-crop habitats were maintained when controlling for differences in ant abundance and richness. The response variable was proportion of mealworms removed by ants and separate analyses were performed for ant predation above- and belowground. Habitat type (crop or non-crop) was the main factor, whereas species richness was treated as the covariate. Similarly, ANCOVA was used to evaluate the relationship between ant abundance and ant predation rates above- and belowground. In total, four ANCOVA models were run. For all analyses we used SYSTAT v.10.2 (Systat Software, San Jose, CA, USA).

#### Results

During the general survey, we found a total of 200 ant species in the non-crop sites (192 species aboveground and 60 belowground) and 101 species in the crop sites (96 above- and 37 belowground). The most abundant species in the

non-crop sites were *Labidus mars* (Forel), *Pheidole oxyops* Forel, *Pheidole fimbriata* Roger, and *Neivamyrmex bruchi* (Forel), whereas *Solenopsis saevissima* (Smith) was the most abundant species in the crop sites (Table 1) (the complete species list is available from the authors upon request).

The mean number of ant species per trap was greater in the non-crop than in the crop sites for ants foraging aboveground ( $t = 2.67$ , d.f. = 10,  $P = 0.032$ ), whereas for those foraging belowground the difference between non-crop and crop sites was not significant ( $t = 0.48$ , d.f. = 10,  $P = 0.64$ ). Overall ant abundance did not differ between crop and non-crop sites (aboveground:  $t = 1.37$ , d.f. = 10,  $P = 0.22$ ; belowground:  $t = 2.25$ , d.f. = 10,  $P = 0.06$ ). However, fungus-growing ants and ants classified as ‘other predators’ foraging aboveground were more abundant in the non-crop than in the crop sites. In addition, we found that army ants foraging belowground were more abundant in non-crop sites (Figure 1). Belowground ant predation rates were higher in the non-crop sites ( $t = 2.44$ , d.f. = 10,  $P = 0.035$ ), whereas aboveground

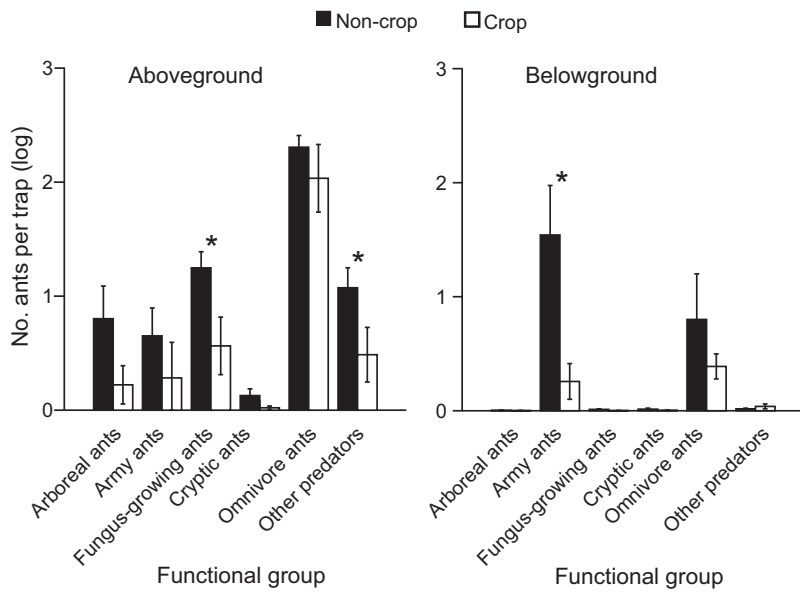
rates of ant predation did not differ between crop and non-crop sites ( $t = 1.55$ , d.f. = 10,  $P = 0.16$ ).

In both the crop and non-crop habitats, rates of ant predation increased as ant species richness (number of species per trap, recorded during the general ant survey) increased (aboveground:  $F_{1,9} = 6.44$ ,  $P = 0.032$ , belowground:  $F_{1,9} = 5.96$ ,  $P = 0.037$ ; Figure 2). Similarly, rates of ant predation increased as the overall abundance of ants increased (aboveground:  $F_{1,9} = 6.83$ ,  $P = 0.024$ , belowground:  $F_{1,9} = 6.44$ ,  $P = 0.032$ ; Figure 2). The observed difference in belowground predation rates between crop and non-crop habitats was maintained when controlling for inter-habitat differences in belowground species richness ( $F_{1,9} = 6.44$ ,  $P = 0.030$ ), but not when controlling for differences in overall abundance ( $F_{1,9} = 1.30$ ,  $P = 0.28$ ).

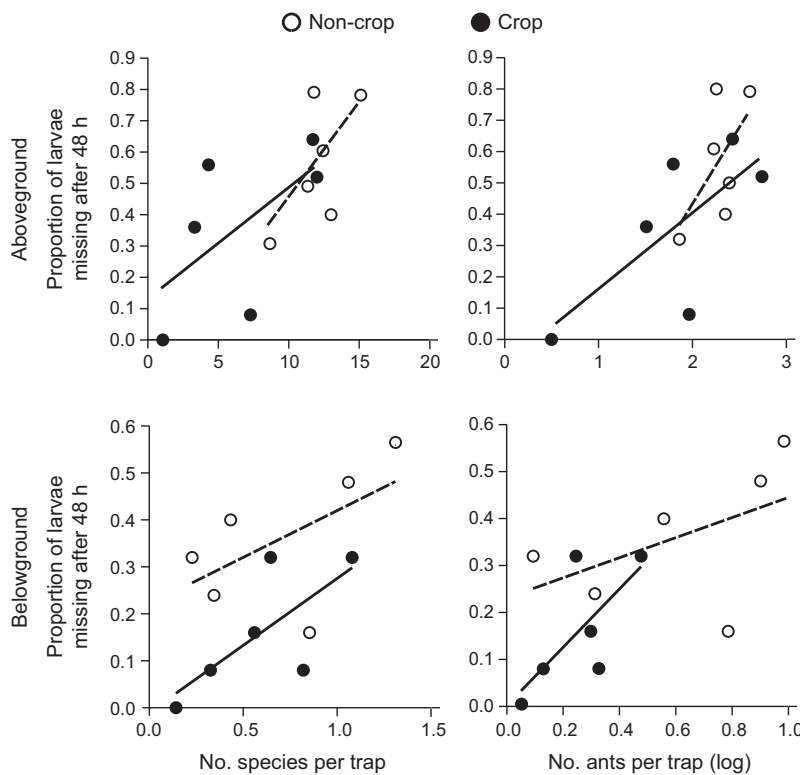
*Pheidole fimbriata*, *Pheidole* gr. *diligens* sp. 1, and *N. bruchi* were the species most frequently found preying on mealworm larvae in the non-crop sites (Table 1), whereas *S. saevissima* was the main predatory species in the crop sites (Table 1).

**Table 1** The most abundant ant species within each functional group found in the crop and non-crop sites. Data represent the mean ( $\pm$  SD) number of ant workers in pitfall traps (placed aboveground) or in subterranean traps. The numbers in parentheses indicate the number of times a species was found attacking mealworms in the live bait traps

Functional group	Ant species	Non-crop		Crop	
		Aboveground	Belowground	Aboveground	Belowground
Arboreal ants	<i>Camponotus sericeiventris</i> (Guérin-Méneville)	10.5 $\pm$ 34.2	0	0.23 $\pm$ 2.6	0
	<i>Cephalotes pusillus</i> (Klug)	0.48 $\pm$ 2.8	0.01 $\pm$ 0.1	0	0
	<i>Crematogaster nitidiceps</i> Emery	3.6 $\pm$ 22.4 (1)	0	0	0
	<i>Crematogaster rudis</i> Emery	1.3 $\pm$ 11.4 (1)	0	1.2 $\pm$ 8.1	0.003 $\pm$ 0.06
Fungus-growing ants	<i>Atta laevigata</i> (Smith)	17.6 $\pm$ 80.9	0.005 $\pm$ 0.07	2.7 $\pm$ 12.9	0
	<i>Acromyrmex molestans</i> Santschi	0.68 $\pm$ 5.3	0	2.3 $\pm$ 8.4	0.003 $\pm$ 0.06
	<i>Acromyrmex subterraneus</i> (Forel)	1.7 $\pm$ 9.7	0	0.19 $\pm$ 2.4	0
Army ants	<i>Mycocepurus goeldii</i> (Forel)	0.36 $\pm$ 2.6	0.01 $\pm$ 0.14	0.86 $\pm$ 2.0	0
	<i>Labidus coecus</i> (Latreille)	1.7 $\pm$ 13.7 (1)	0.01 $\pm$ 0.14 (2)	8.1 $\pm$ 80.6 (2)	0.36 $\pm$ 3.5 (4)
	<i>Labidus mars</i> (Forel)	0.005 $\pm$ 0.07	81.5 $\pm$ 840.8 (4)	0	1.1 $\pm$ 17.1 (3)
Other predators	<i>Neivamyrmex bruchi</i> (Forel)	3.6 $\pm$ 49.7 (1)	38.2 $\pm$ 373.2 (9)	0.004 $\pm$ 0.06	0.04 $\pm$ 0.39
	<i>Neivamyrmex punctaticeps</i> (Emery)	0 (1)	7.79 $\pm$ 53.37 (1)	0	0.003 $\pm$ 0.06
	<i>Ectatomma brunneum</i> Smith	0.49 $\pm$ 3.8	0	2.3 $\pm$ 6.9	0.07 $\pm$ 0.74
Cryptic ants	<i>Ectatomma lugens</i> Emery	3.13 $\pm$ 6.55	0	0	0
	<i>Ectatomma planidens</i> Borgmeier	1.8 $\pm$ 12.9	0	0.36 $\pm$ 2.4	0
	<i>Ectatomma</i> sp. 5	4.9 $\pm$ 10.8	0.01 $\pm$ 0.14	0.18 $\pm$ 1.00	0.003 $\pm$ 0.06
	<i>Carebara brevopilosa</i> Fernandez	0.34 $\pm$ 1.2	0.01 $\pm$ 0.1	0.004 $\pm$ 0.06	0.003 $\pm$ 0.06
Omnivore ants	<i>Carebara urichi</i> (Wheeler)	0.04 $\pm$ 0.23	0	0	0.003 $\pm$ 0.06
	<i>Cryptopone guianensis</i> (Weber)	0	0.020 $\pm$ 0.28	0	0
	<i>Prionopelta punctulata</i> (Mayr)	0.005 $\pm$ 0.07	0	0.05 $\pm$ 0.26 (5)	0.003 $\pm$ 0.06
	<i>Pheidole fimbriata</i> Roger	15.1 $\pm$ 84.8 (6)	38.0 $\pm$ 350.0 (12)	0	0
Omnivore ants	<i>Pheidole oxyops</i> Forel	70.3 $\pm$ 159.8 (1)	0.19 $\pm$ 1.4	46.9 $\pm$ 159.7	0.19 $\pm$ 0.84 (1)
	<i>Pheidole</i> gr. <i>diligens</i> sp. 1	9.8 $\pm$ 26.1 (4)	0.21 $\pm$ 1.3 (4)	19.6 $\pm$ 80.5 (1)	0.07 $\pm$ 0.72
	<i>Solenopsis saevissima</i> (Smith)	3.9 $\pm$ 38.3 (1)	1.1 $\pm$ 13.3 (5)	72.1 $\pm$ 219.3 (19)	1.0 $\pm$ 6.2 (14)



**Figure 1** Functional composition of the above- and belowground ant assemblages in the crop and non-crop habitats. Values represent log-transformed mean ( $\pm$  SE) numbers of ants per trap. Asterisks denote significant differences between mean values (t-tests:  $P < 0.05$ ).



**Figure 2** Above- and belowground ant predation rates in the crop and non-crop habitats in relation to variation in species richness (mean no. species per trap; panels on the left) and ant abundance (log-transformed mean no. ants per trap; panels on the right). Each point represents a sampling site. Lines represent the fitted regression lines. Note the scale differences.

**Discussion**

Pest suppression has been highlighted as one of the main ecosystem services provided by ants (Philpott et al., 2008; Morris et al., 2015). In spite of this, relatively few studies have examined the effect of land use changes on ant predation rates. Our results showed that belowground

predation rates were significantly greater in the non-crop sites, whereas the overall abundance and species richness of ants foraging belowground did not differ between the crop and non-crop sites. Similarly, Gray et al. (2015) reported that rates of protein bait removal by ants were higher in forests than in plantations, even though the number of ant workers and species attracted to the baits



was not different between the two habitats. These authors attributed the observed difference in bait removal rates between forests and plantations to inter-habitat differences in the mean mass of bait removed per ant individual (Gray et al., 2015). Although we cannot discard the possibility that a similar mechanism operates in our study system (i.e., that the mean rate of predation per ant individual across all species in the community was greater in the non-crop habitat), we also detected important inter-habitat differences in the functional composition of ant communities belowground. Notably, we have found that army ants of the genus *Labidus* and *Neivamyrmex* were much more abundant in the non-crop than in the crop sites. Not surprisingly thus, the frequency with which we found *Neivamyrmex* and *Labidus* attacking mealworm larvae belowground was  $2.3\times$  higher in the non-crop than in the crop sites. Army ants are important predators of other arthropods (Kronauer, 2009; Kaspari et al., 2011), including agricultural insect pests (Monteiro et al., 2008). Why army ants were less abundant in the crop than in the non-crop sites is not clear. However, there is evidence that army ants are sensitive to habitat destruction and degradation (Boswell et al., 1998; Kumar & O'Donnell, 2009). Furthermore, it is known that some army ant species (notably those that forage belowground) have a relatively low thermal tolerance (Baudier et al., 2015).

In both the crop and non-crop habitats, and both above- and belowground, ant predation rates were positively correlated to the overall abundance and species richness of ants. Sites in which predation rates were comparatively high also tended to support more ant species and more ant workers. Positive effects of ant diversity on ant-mediated ecosystem services have also been found in studies that evaluated predation rates in coffee plants (De la Mora et al., 2015) or scavenging rates on the forest floor (Fayle et al., 2011; but see Gray et al., 2015). However, here, the observed difference in aboveground species richness between the crop and non-crop habitats did not translate into significant differences in aboveground predation rates.

Our observations indicate that omnivore ants are the main ant predators aboveground. However, omnivore ants presented similar abundances in both the crop and non-crop habitats. Furthermore, the most abundant omnivore ant in the crop sites was a fire ant (*S. saevissima*), and previous studies indicate that fire ants are highly effective in controlling arthropod populations (Risch & Carroll, 2008). Together, these findings may help to explain why, on average, aboveground predation rates did not differ between the crop and non-crop habitats. In addition, it is important to point out the limitations of our study design, as it involved sampling in different types of crops and in different types of natural (non-crop) habitats.

In spite of these limitations, to the best of our knowledge, this is the first study to evaluate how land use changes in the Cerrado affect the predatory services provided by ground-dwelling ants. We have found that transformation of natural Cerrado savanna habitats into monocultures of soy, maize, or sorghum caused a concomitant decrease in ant predation belowground. We attributed these differences in belowground predation to differences in the functional composition of ant communities. Army ants were among the main ant predators belowground and they were significantly more abundant in the non-crop than in the crop sites. We did not detect any difference between the crop and non-crop sites in aboveground ant predation rates, possibly because the abundance of the main group of predators aboveground (omnivore ants of the genera *Pheidole* and *Solenopsis*) also did not differ between the crop and non-crop sites. In this sense, crop management practices that limit the persistence and/or activity of predatory ants (e.g., soil tillage; Pereira et al., 2010) are likely to result in decreased predation services.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Spatial arrangement of the pitfall traps in transects established at different distances from the edge between a crop and a non-crop site.