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Do herbivores exert top-down effects in Neotropical savannas? Estimates of biomass consumption by leaf-cutter ants

Costa, Alan N.[1]**; Vasconcelos, Heraldo L.**[1]**; Vieira-Neto, Ernane H.M.**[1] **& Bruna, Emilio M.**[2*]

[1]*Institute of Biology, Federal University of Uberlândia (UFU), C.P. 593, 38400-902, Uberlândia, MG, Brazil*
[2]*Department of Wildlife Ecology and Conservation & Center for Latin American Studies,*
University of Florida, Gainesville, FL 32611-0430, USA;
[*]*Corresponding author; Fax +1 352 3926984; E-mail embruna@ufl.edu*

Abstract

Question: Plant communities in Paleotropical savannas are regulated by a combination of bottom-up and top-down effects. However, the paucity of ungulates and other large herbivores in Neotropical savannas has led to speculation that these communities are primarily structured by physical factors such as fire, precipitation and soil chemistry. We addressed the following question: How much plant biomass is consumed by leaf-cutter ants in Neotropical savannas, and is it comparable to the amount of biomass consumed by herbivores in Paleotropical savanna sites?

Location: Our study was conducted at the Estação Ecológica do Panga, located 30 km south of Uberlândia, Minas Gerais, Brazil. All field work was conducted in the vegetation type known as cerrado *sensu stricto*.

Methods and Results: Using direct measurements of herbivory, coupled with estimates of plant productivity and ant colony density, we found that leaf-cutter ants (*Atta* spp.) consume 13-17% of the foliar biomass produced annually by woody plants in a Neotropical savanna (Brazilian cerrado). Although comparisons with other savanna systems are complicated by methodological differences among studies, the proportion of biomass consumed by *Atta* species is about 25% of that consumed by the entire ungulate community in some African savannas and greater than or comparable to the total herbivory observed in some terrestrial ecosystems.

Conclusions: We hypothesize that this intense biomass consumption by *Atta* will have important ecological consequences for the cerrado ecosystem, because leaf-cutter abundance increases in fragmented or degraded habitats. These effects are likely to be exacerbated as anthropogenic pressure in this biodiversity hotspot increases.

Keywords: *Atta laevigata*; *Atta sexdens*; Biodiversity hotspot; Brazil; Cerrado; Herbivory.

Introduction

Savannas are one of the most widespread ecosystems in the tropics, occupying 65% of Africa, 60% of Australia and 45% of South America (Huntley & Walker 1982). Decades of research have demonstrated that plant communities in Paleotropical savannas are regulated by a combination of pervasive bottom-up effects, such as precipitation and soil nutrient levels, and top-down effects such as fire and mammalian herbivory (e.g. Cumming 1982; Roques et al. 2001; Augustine et al. 2003). In contrast, the paucity of ungulates and other large herbivores in Neotropical savannas has led to speculation that these plant communities are primarily structured by physical factors such as fire, precipitation and soil chemistry (reviewed in Mistry 1998; Ruggiero et al. 2002). While the importance of abiotic drivers in Neotropical savannas is indisputable, the available evidence suggests that asserting their primacy is premature. Empirical studies quantifying the impacts of herbivores in Neotropical savannas such as Brazil's cerrado are very rare (e.g. Klink 1994; Marquis et al. 2002), making it difficult to assess the relative importance of top-down and bottom-up effects. Furthermore, although mammalian grazers and browsers are indeed rare in Neotropical savannas (Marinho-Filho et al. 2002), these ecosystems contain a diverse and abundant community of herbivorous insects (Marquis et al. 2001). This community includes species such as leaf-cutter ants (*Atta* spp.), which are conspicuous throughout much of tropical and subtropical America and are the dominant herbivores in many locations (Bucher 1982; Cherrett 1989). Only by evaluating the impacts of these and other consumers can we elucidate the relative importance of factors influencing plant population and community structure.

We investigated whether leaf-cutter ants in a Brazilian cerrado site could harvest amounts of plant biomass comparable to those consumed by herbivores in mammal-dominated savannas, which would suggest that these insects may play an important and underappreciated role in structuring these communities. To do so, we addressed the following four questions. 1. What is the size and density of leaf-cutter ant nests in our cerrado field site? 2. How much plant biomass is harvested by individual leaf-cutter ant colonies in this location? 3. What is the relationship between nest size and plant consumption? 4. How much biomass is produced over the course of one year by the plant community in this location, and what proportion of this biomass is consumed by leaf-cutter ants?

Material and Methods

The study was conducted at the Estação Ecológica do Panga (19º10' S, 48º23' W), a 404-ha reserve located 30 km south of Uberlândia, Minas Gerais, Brazil (Costa & Araújo 2001). The region is characterized by a subtropical climate with two well-defined seasons: a dry winter (May to September) and a rainy summer (October to April). The mean annual temperature and precipitation are 22 ºC and 1650 mm, respectively; soils at the site are primarily red latosols that vary from moderately to strongly acidic (Embrapa 1982). Our fieldwork was conducted in an 18.65-ha portion of the reserve dominated by the vegetation type known as cerrado *sensu stricto* (Oliveira-Filho & Ratter 2002). The study area has a relatively dense canopy cover (61 ± 2%; mean ± SE, based on 60 measurements with a spherical densiometer); consequently, cover of native grasses locally is sparse. The tree and shrub canopy reaches a height of ca. 6 m and the dominant species are *Miconia albicans* (*Melastomataceae*), *Matayba guianensis* (*Sapindaceae*) and *Qualea grandiflora* (*Vochysiaceae*) (H.L. Vasconcelos & E.M. Bruna unpubl. data).

Estimating Atta colony density and biomass consumption

The dominant leaf-cutter in our site is *Atta laevigata* (Fr. Smith), although there are also colonies of its congener *A. sexdens rubropilosa* (Forel). To estimate the density of *Atta* colonies in our study area, we surveyed the entire 18.65-ha plot and marked all active colonies with nest mounds ≥ 2.0 m^2 (i.e. colonies with an easily-recognized nest mound and producing the soldier caste necessary for species identification). We then estimated the area of each nest mound using the formula for an ellipse.

We used the ‘foraging activity method’ (Fowler et al. 1990) to estimate the amount of plant biomass harvested by each of eight *A. laevigata* colonies. These focal colonies were chosen from eight pre-established nest size classes, with one colony randomly selected from among all those in each size class. The foraging activity method requires remaining at a fixed point along a colony’s foraging trail (close to the entrance/exit hole) and collecting all of the plant fragments transported by workers during a 3 min interval. Because *A. laevigata* builds underground foraging galleries, with trails extending from the entrances to these galleries along the soil surface to the plants being cut, we used a modified version of the method described by Fowler et al. (1993) to confirm what trails belonged to which focal colony. To do so, we searched for all entrance/exit holes within a 50-m radius of each nest mound; previous work with *A. sexdens* and *A. laevigata* indicates that most entrance/exit holes are located 10-20 m from the nest (Silva 1975). We then placed fragments of plastic sheeting (1 cm^2; 0.1 mm thick) coated with a solution of human urine and water (1:1) as an attractant on all foraging trails. Fragments were numbered with a permanent marker and we used a unique number for each trail. After the ants removed the fragments, they deposited them on top of the nest mound, allowing us to determine which trails were associated with each of the focal colonies.

Once we had confirmed trails belonged to distinct colonies, we used a fine forceps to collect plant fragments every 2 h over the course of 24 h (12 collections per trail per day). To avoid disturbance of the ants during the night collections, we never pointed the light source directly towards the trail. One colony was monitored at 15-day intervals for an entire year (23 observation days from April 2003 to March 2004), while the remaining seven colonies were monitored at 30-day intervals over a period of up to 4 months (1 to 4 observation days). These seven colonies were monitored at different times of the year (18 observations during the wet season and 16 observations during the dry season) and over a relatively long period (January 2004 to August 2006) to minimize any possible effects of seasonal variation in plant consumption by ants. Material collected during each observation was sorted (categories: fresh leaves, dead leaves from the leaf-litter, grasses, twigs, flowers, fruits), dried at 60 ºC for 3 days, and weighed to the nearest 0.0001 g. During each observation day each colony was monitored for a total of 36 min, therefore the biomass collected during this period was multiplied by 40 to estimate the amount of biomass collected per day (i.e. in 1440 min). The biomass harvested annually by each colony was estimated by multiplying mean daily values by 365 (Fowler et al. 1990).

Estimates of plant biomass production

We estimated the annual production of leaf-litter in our site using 10 litter traps (0.55 m × 0.55 m, 1 mm mesh) that were monitored for an entire year (March 2004-February 2005). A pilot study showed that the variability in leaf-litter capture among traps was low (given that the 95% confidence limit of the mean amount of litter collected per trap was < 10% of the mean, cf. Proctor 1983), suggesting that 10 traps should be sufficient to provide a good estimate of leaf fall throughout the study plot. The traps were placed 0.5 m above the ground at regular intervals along a 250 m transect. To reduce the influence of ant activity on leaf-litter production, the transect was located within the study plot ca. 200 m from the focal colonies in an area of very low leaf-cutter ant activity. The plant material accumulating in the traps was collected at monthly intervals, separated, dried at 60 ºC for 3 days, and weighed to the nearest 0.001 g. We multiplied the biomass of leaves collected in traps by 1.068 to correct for the fact that 6.8% of cerrado leaves are consumed by other insect herbivores prior to abscission (based on instantaneous measurements of damage on leaves in plant crowns, Marquis et al. 2001).

Results

We found 85 *Atta laevigata* nests and four *A. sexdens rubropilosa* nests in our study site, resulting in an average density of 4.8 nests/ha. The largest nest mound we found was 37.5 m^2 (mean ± 95% confidence intervals = 9.6 ± 1.6 m^2; median = 7.6 m^2, Fig. 1). Plant biomass consumption (BC, in kg/year) varied strongly among the eight focal *A. laevigata* colonies, ranging from 51.0 to 500.0 kg.a^{-1}. Most of the variation in biomass consumption among colonies was explained by differences in nest mound size (NS, in m^2), a surrogate of colony size (Fowler et al. 1986) that was strongly and positively correlated with plant biomass consumption ($BC = 62.76 + 11.43*NS$; $R^2 = 0.871$, $F_{1,6} = 40.55$, $P = 0.001$; Fig. 2). Fresh leaves represented 67.6 ± 9.2% of the total biomass harvested by our focal colonies (mean ± 95% CI; n = 8 colonies), while dead leaves from the leaf-litter were 18.5 ± 6.5% of the biomass consumed. Leaf-cutter ants also harvested twigs (6.6 ± 2.2 %), flowers (4.7 ± 4.6%), fruits (2.0 ± 2.1%), and grasses (0.6 ± 0.4%).

Using the regression equation relating colony size to biomass consumption (Fig. 2), we estimated that the 89 colonies found in our study sites collectively harvested 15,387 kg of plant biomass per year, or 825.6 kg.ha^{-1}.a^{-1}. As indicated above, fresh leaves removed from plants represent 67.6 ± 9.2% of the total biomass harvested by our focal colonies; therefore we estimated the total consumption of fresh leaves in our site to be 558.1 ± 76.0 kg.ha^{-1}.a^{-1}. This is 15.0 ± 2.0% (mean ± 95% CI) of the estimated 3731.3 kg.ha^{-1}.a^{-1} of leaves produced by the trees, shrubs, and vines in our study area (see App. 1).

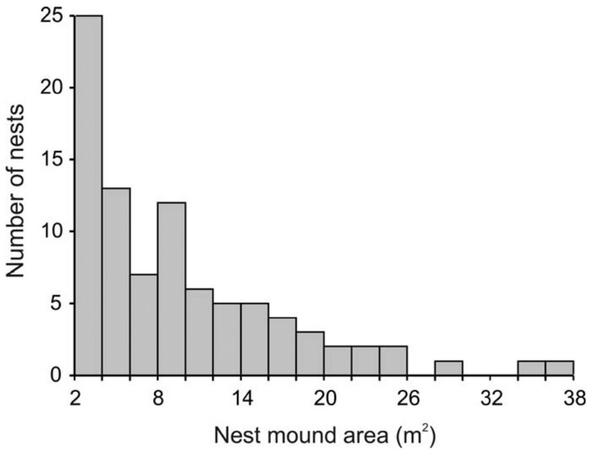

Fig. 1. Frequency distribution of nest sizes for all leaf-cutter ant nests (mound area ≥ 2 m^2) found in an 18.65 ha plot of cerrado vegetation in central Brazil. Nest mounds size ranged from 2.0 to 37.5 m^2 (mean = 9.6 ± 0.8 SE m^2), with most nests smaller than 10 m^2.

Discussion

Our estimate of herbivory by leaf-cutter ants is 1.3-3.7 times greater than that by all other cerrado insects combined (range 4.6-9.3%, Fowler & Duarte 1991, Marquis et al. 2001), and 5.2-6.8 fold greater than estimates of leaf consumption by *Atta* in tropical rain forests (range 1.6-2.5%, Haines 1978; Wirth et al. 2003, but see Cherrett 1989). Our estimate of biomass consumption by leaf-cutter ants is even more remarkable when compared to values of herbivory in African savannas. Although comparisons must be made with caution given the methodological differences among

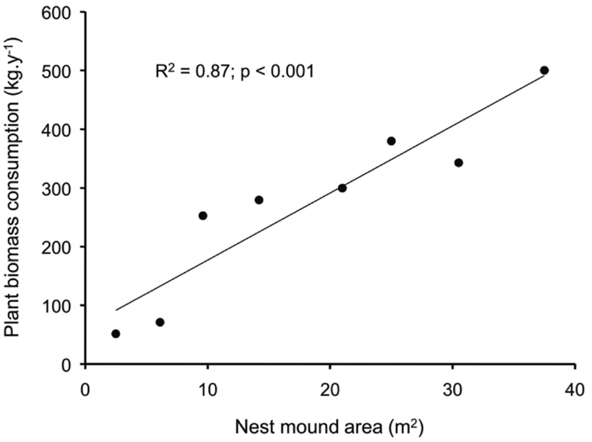

Fig. 2. Relationship between nest mound size and plant biomass consumption by colonies of the leaf-cutter ant *Atta laevigata*. Each symbol represents a different colony.

studies, it is estimated that the 31 species of ungulate herbivores in the Serengeti collectively remove ca. 60% of total above-ground primary produced over the course of the year (range = 17-94%, McNaughton 1985, see also Frank et al. 1998). Estimates of primary productivity consumed by individual browser species are rare, but the 15% of foliar biomass consumed by *Atta* species in our site appears proportionately comparable to the impacts of species such as kudus (*Tragelaphus strepsiceros*) and impalas (*Aepyceros melampus*) (Owen-Smith & Cooper 1987). Indeed, our estimate of the proportion of foliar productivity consumed is greater than or comparable to the total herbivory observed in many other terrestrial ecosystems (Frank et al. 1998).

Additional studies in other locations are clearly needed to establish the generality of our results. Nevertheless, we believe that our results can be cautiously extended to other cerrado areas for three reasons. First, leaf production in our site is comparable to that in other South American savannas with similar tree cover (Dezzeo & Chacon 2006; Nardoto et al. 2006). Second, our estimate of the average annual biomass consumption by an *Atta* colony is well within the range reported in similar studies conducted in other tropical habitats (Wirth et al. 1997; Herz et al. 2007). Finally, leaf-cutter ants are distributed throughout the Brazilian cerrado (Gonçalves 1960), and *Atta* nest density in our study site is within the range of values reported for other cerrado areas (2.7-6.0 nests per ha, Schoereder & Coutinho 1990; Viana et al. 2004). The higher nest densities in the cerrado are probably why our estimates of biomass consumption by *Atta* spp. are far greater than those reported for other tropical ecosystems – they are substantially higher than the 0.5 -1.7 nests per ha reported in tropical forests (Cherrett 1989; Wirth et al. 2003; Herz et al. 2007). Indeed, a recent study conducted on Panama's Barro Colorado Island (BCI), found that leaf-cutter ants consume 1.7% of annual leaf production, but the density of leaf-cutter ants on BCI is only 0.5 nests/ha (Herz et al. 2007). If *Atta* density on BCI were the same as that in our study plot (4.8 nests/ha), the estimate of annual leaf production consumed by *Atta* colonies on BCI would be 16.3% – a value comparable to the 15.0 ± 2.0% we estimate for our cerrado site.

The dominant paradigm is that herbivory has only minimal effects on cerrado vegetation structure (e.g. Gardner 2006). However, levels of biomass consumption equivalent to those we observed have profound ecological consequences in Paleotropical savannas (Frank et al. 1998). We therefore suggest that herbivory by *Atta* spp. has important and heretofore underappreciated ecological impacts for the structure and dynamics of vegetation in the Cerrado, whose distribution of 2 million km^2 makes it South America's second largest biome. Indeed, it is somewhat surprising that the potential impacts of *Atta* spp. have been largely overlooked (but see Bucher 1982; Coutinho 1984), given that they have long been recognized as the dominant herbivore – both numerically and in terms of plant biomass consumed – in many tropical and subtropical ecosystems (reviewed in Wirth et al. 2003). Studies in these ecosystems have shown that defoliation by leaf-cutter ants negatively affects the growth, reproduction, and survival of preferentially-consumed plant species (Rockwood 1973; Vasconcelos & Cherrett 1997), and there is evidence that *Atta* herbivory can drive shifts in plant community composition (Rao et al. 2001). We are currently addressing these hypotheses with experiments evaluating the impact of *Atta* herbivory on plant demography and seedling community composition.

In addition to population and community-level consequences, the transfer of tons of plant biomass below ground by ants may alter the spatiotemporal dynamics of carbon stocks, nutrient availability, susceptibility to fire, and other ecosystem properties (Haridasan 2001; Moutinho et al. 2003). Given that the abundance of *Atta* colonies increases in fragmented or degraded locations (Rao 2000; Vasconcelos et al. 2006) the magnitude of these effects is likely to increase as anthropogenic pressure in this biodiversity hotspot is exacerbated (Klink & Machado 2005). Continuing to elucidate the natural history of *Atta* in the Cerrado, along with quantifying spatiotemporal variation in their ecological impacts, will greatly enhance our understanding of how top-down and bottom-up forces interact to structure this and other savanna ecosystems.

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For App. 1, see below (online version)
also available at JVS/AVS Electronic Archives;
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App. 1. Photos of cerrado at Estação Ecológica do Panga (Minas Gerais, Brazil) with (**A**) limited *Atta* activity and (**b**) high *Atta* activity. Note the amount of greenfall to the surface where leaf-cutter ants are foraging (photos by Heraldo Vasconcelos).

A

B

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