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Research Article

Removal of Nonmyrmecochorous Seeds by Ants: Role of Ants in Cattle Grasslands

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Livestock production models prevailing in Colombian Andes are simplified treeless pastures for extensive ranching, with the consequent reduction of environmental services, such as seed dispersal, due to lack of primary dispersers, scarcity of adequate sites for seedling establishment and competition with grasses. This study evaluated if, in these harsh environments, ants can promote the colonization of arboreal species through directed dispersion of seeds towards the nests. Ten seeds of each species were offered to ants in six grazing pastures. Ants removed 25% of the seeds (1827) in 48 hours. Preference for arillated and small-to-medium sized seeds, such as *Pithecellobium dulce*, and *Guazuma ulmifolia*, was observed. *Cyphomyrmex major*, *Ectatomma ruidum*, *Solenopsis geminata* and *Atta cephalotes* were the key ant species in seed removal. It was concluded that functional ant groups present in the pastures could contribute to secondary dispersion of seeds with potential for restoration.

1. Introduction

In Latin America, cattle raising is perhaps the productive activity that most contributes to simplification of the landscape. For instance, in Colombia, cattle raising is predominant in more than 80% of the Andean Region, an area inhabited by 70% of the population [1]. The concept of functional diversity relates ecosystemic processes to species diversity through patterns of resource use [2, 3]. Thus, reduction in plant heterogeneity caused by traditional production systems of cattle raising leads to a reduction of both ecosystemic processes and the environmental services they provide [1].

Vegetal regeneration is limited in cattle pastures due to the absence of dispersers, little availability of viable propagules and of adequate sites for germination, and establishment of seedlings [4, 5]. Also, competition for the few nutrients with introduced grasses under rude environmental conditions reduces establishment options for arboreal species.

Ants could play a role in the recovery of disturbed systems potentiating recolonization of plant species in agro ecosystems by removing seeds towards their nests [6, 7]. This interaction could affect the local abundance and distribution

of myrmecochorus and nonmyrmecochorous species [8–10]. In spite of the growing information on the interaction between ants and seeds in neotropical forests [11–14], few studies document the process in neotropical agroecosystems (but see [15–17]). Thus, the role of ants as dispersers of nonmyrmecochorus seeds in pastures is unknown.

The use of diaspores by opportunistic ground dwelling ants can affect the biology of seeds and seedlings of plant species dispersed mainly by vertebrates [18]. The ants can rearrange the rain of seeds produced by primary disperser, facilitate their germination [19, 20], and promote the establishment of their seedlings [21, 22]. The seeds introduced into the nests are not found by predators and remain protected from adverse environmental events, such as burning in ecosystems that experience regular fires [8]. Although nonmyrmecochorous plants produce seeds without specialized adaptations for dispersal by ants, the presence of arils or nutritious tissues is not indispensable for transport to occur [16, 23].

Events of seed removal by ants are influenced by both morphological factors of the seeds and morphological and behavioral traits of the ants. The presence of a nutritious

tissue or aril attracts the attention of ants thereby increasing probability of an encounter [24]. Once the ant locates the seed, removal will depend on its weight and the carrying capacity of the ant [25, 26]. In general, large ants possess a greater carrying capacity in their jaws and can remove seeds greater distances [27, 28]. Nevertheless, small ants usually massively recruit workers towards the seeds and then displace them towards the nests [17, 29].

Characterization of ant-seed interaction under pasture conditions is a first step towards understanding the potential of ants as functional agents in the ecological recovery of cattle pasture by the dispersal of seeds of plants useful for ecological restoration and seeds of interest to peasant farmers (i.e., forage). This study predicted that ants associated with grasslands act as functional agents by removing nonmyrmecochorous seeds from trees that are useful for ecological rehabilitation. Specifically, the following questions were addressed. Do ants in open pastures actively remove seeds of nonmyrmecochorous plant species with a potential for the ecological recovery of pastures? Do these ants exhibit a preference for a certain kind of seed? Which ant species are most frequently involved in removal events? In addition, the implications of the observed interactions were discussed.

2. Materials and Methods

2.1. Study Site. Fieldwork was carried out between September and October 2009 in six cattle pastures located in the flat inter-Andean Cauca River Valley area in the Departments of Valle and Cauca (Southwestern Colombia) covering an area of approximately 627 km². The farms and geographic locations are as follows: I. Department of Cauca, (1) Limonar (03°08'10.1''N; 76°27'42.2''W), (2) La Josefina (3°5'17.3''N; 76°28'18.5''W), (3) Cachimbalito 3°9'1.00''N; 76°27'46.00''W); II. Department of Valle del Cauca, (4) Sachamate (3°16'27.49''N; 76°33'28.00''W), (5) Lituania (3°20'48.5''N; 76°30'30.6''W), (6) Marañón (3°20'48.30''N; 76°31'23.91''W). Over a century ago, dry tropical forest dominated the region [30], but at present only 2.7% of the original forest remains, the remainder having been replaced with great expanses of sugarcane fields and cattle farms [31]. Average annual temperature is 24°C, and average annual precipitation fluctuates between 1000–15000 mm [30] with peaks in March-May and October-December [32]. During the sampling, the pastures averaged temperatures of 29.4 ± 3.7°C and an average relative humidity of 63.4 ± 11%. Each pasture was open, with an average extension of at least two hectares and an arboreal density inferior to 4%. Dominant vegetation consisted of *Cynodon plectostachyus*, an introduced grass, as well as other African grasses like *Brachiaria decumbens*, accompanied by weeds from Malvaceae and Asteraceae families. Inside the pasture, some isolated trees of *Guazuma ulmifolia*, *Pithecellobium dulce*, and *Albizia saman* are allowed by the farmers to provide shade to the cattle and supplement its feed. During the experiments, the cattle were removed from the lot.

Orthodox seeds from five arboreal species commonly found in pastures were used: (1) *Guazuma ulmifolia* Lam. (Sterculiaceae), seeds with hydrophilic mucilage; (2)

Pithecellobium dulce (Roxb.) Benth. (Leguminosae-Mimosoideae), arillated seeds; (3) *Senna spectabilis* (DC.) H. S. Irwin & Barneby (Leguminosae-Caesalpinioideae), nonarillated seeds; (4) *Leucaena leucocephala* (Lam.) de Wit. (Leguminosae-Mimosoideae), seeds without arils, and (5) *Albizia saman* (Jacq.) Merr. (Leguminosae-Mimosoideae) which seeds are usually impregnated with a sweet, oily substance (seeds of *A. saman* used here lack of this substances as they become from a certified seed company provider). Seeds used have a potential for the restoration of livestock systems and with exception of *L. leucocephala* represent part of the native vegetation of open areas. These trees also serve as forage for cattle as they consume the foliage and/or fruit, provide shade for the cattle, protect the ground from erosion, and offer new habitats for other animals. Seeds of *Passiflora ligularis* Juss. (Passifloraceae) was employed as a positive control. Its seeds are intermediate in size, and they are neither orthodox nor recalcitrant [33]. Their removal by ants was verified in previous studies in disturbed habitats such as pastures [16, 34] and mining areas undergoing rehabilitation [17].

In order to sample the ant community, a lineal transect of 190 m with 10 sampling units (SUs), separated 20 m from one another, was established. Each SU consisted of a circle of white paper 12 cm in diameter with 5 g of tuna in oil and approximately 0.5 mL of honey. These were left on the ground for a period of 2 hours. The ants attracted to baits were collected in alcohol (96%), identified to morphospecies, and conserved in a reference collection deposited in the Entomology Museum of the Universidad del Valle (Cali, Colombia). The functional guilds (*sensu* Silvestre et al. [35]) to which the collected ants belonged were identified. Hill N1 and N2 Number Series were calculated [36] for establishing the number of abundant and very abundant species, respectively.

Three transects were simultaneously established in each pasture: a transect that allows ants access to the seeds ("Ant Transect"), a transect that excluded the ants ("Exclusion transect"), and a transect with seeds of *P. ligularis* to which the ants had access (*P. ligularis* Transect). Each transect consisted of 20 seed depots located 10 meters apart. A depot consisted of a disk of white paper 12 cm in diameter containing 10 seeds of each of the five species used in the study and covered by netting to exclude vertebrate activity. In the excluded transect, each depot was isolated by encircling it within a PVC arum, 12 cm in diameter and 6 cm high, the upper edge impregnated with an adhesive substance (tangle foot). In order to guarantee independence, transects were 5 to 10 m apart. Seeds were served at 0700 hours, and the number of seeds of each species removed at 2, 4, 8, 24, and 48 hours after serving the depots was registered. A seed removed out of the depot was considered a removal event. The species of ants observed removing seeds were identified. A total of 2400 seeds of each species in the study and 1200 *P. ligularis* seeds were offered, for a total of 13200 seeds offered during the entire experiment. The response variable was the proportion of seeds removed per depot (P_i). For purposes of analysis, the response variable was transformed by the function $\arcsine \sqrt{P_i}$. To evaluate ant preference for seeds,

a two-factor analysis of variance under a mixed effect model [37] of the following type was carried out:

$$P_{ij}(\text{Removal proportion}) = \mu + \alpha_i(\text{plant species}) + \beta_j(\text{cattle pasture}) + E_{ij}(\text{error}), \quad (1)$$

where types of seeds represent fixed effects and the pastures the random effects. To establish whether the removal events were associated with removal by ants and not other factors, the proportion of seeds removed in Ant Transect and Exclusion Transect were compared. Removal dynamics over time was described for all species. For the two most preferred species, 0, 25, 50, 75, and 100% percentiles were calculated to estimate removal percentages at 2, 4, 8, 24, and 48 hours after offer, respectively.

3. Results

A total of 21 morphospecies distributed in 13 genera and 5 subfamilies for a total of 3471 individuals were collected (Table 1). The most representative genera were *Pheidole* (6 morphospecies and 176 individuals) and *Solenopsis* (four morphospecies and 1315 individuals) (both Myrmicinae). *Crematogaster abstinens* (Myrmicinae), present in six pastures, was the most abundant species with 1774 individuals. The number of ant species found in baits in each pasture fluctuated between 6 and 11. Diversity (H' index between 0.52 and 1.75) and equitability (J' index between 0.29 and 0.51) were also consistently low in all the lots, there being from two to three very abundant species in each pasture (averages values of N1 and N2 estimated as 3 and 2 species, respectively).

The composition of ants attracted to tuna baits was characterized by a predominance of generalist species native to open and degraded habitats. In spite of low richness and equitability, the genera collected represent 8 of the 15 functional guilds described by Silvestre et al. [35] for the Cerrado, Brazil.

Based on ant species composition, the lots do not form agglomerations corresponding to their spatial proximity. In spite of the spacial scale, important variations in ant composition were found (Table 1). But, on a functional level, the pastures contained the same functional guilds.

Ants removed 25% of the seeds, for a total of 1827 seeds removed in 48 hours period. In general, ant preference for seeds with attractive external tissues was found ($F = 17.6$; $P < 0.01$; $gl = 5$). Of the five species of interest to the cattleman, the most preferred was *G. ulmifolia* with 56% removal, followed by *P. dulce* with 25% removal while removal did not surpass 10% for the other species (Table 2).

The presence of ants notably favored the removal of *G. ulmifolia* and *P. dulce*. In the absence of ants (Exclusion Transect), the removal of these species was drastically reduced. Actually, in the case of *P. dulce*, removal was null when the ants were excluded. On the other hand, access of ants to the depots (Ant Transect) did not significantly favor the removal of *S. spectabilis* ($F_{1,5} = 4.35$; $P = 0.09$),

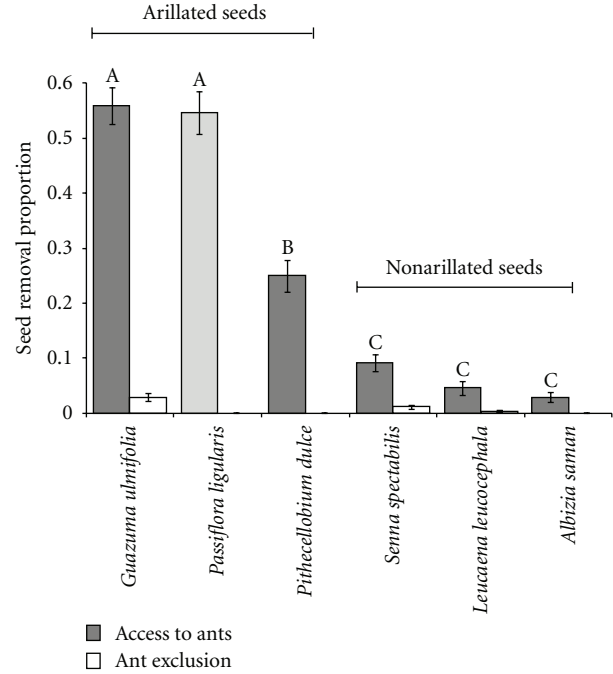


FIGURE 1: Mean (\pm SE) removal of nonmyrmecochorous seeds by ants in cattle grasslands. Letters above columns show different seed preference groups by ants after a Newman-Kewls test ($\alpha = 0,05$).

L. leucocephala ($F_{1,5} = 5.17$; $P = 0.07$), and *A. saman* ($F_{1,5} = 4.37$; $P = 0.09$) (Figure 1). The seeds preferred by the ants were separated into three main groups in the following order of preference: Group A with small *G. ulmifolia* seeds with mucilage, which were preferred as much as the arillated *P. ligularis* seeds in the positive control (*P. ligularis* Transect) ($t = 0.28$; $P = 0.78$). Group B consisted of arillated but heavier *P. dulce* seeds. Group C was made up of smooth covered, nonarillated *S. spectabilis*, *L. leucocephala*, and *A. saman* seeds (Figure 1).

In general, a greater seed removal rate was observed from 8 to 24 hours after initiating the offer (Figure 2), a pattern maintained in each of the cattle pastures sampled. The removal dynamic overtime of the two most preferred seeds suggests an increase in transporting *G. ulmifolia* and *P. dulce* seeds during the night (Table 3).

Very low percentages of removed seeds of *G. ulmifolia* and *P. dulce* seeds were re-located: only 2% and 24%, respectively. The majority of the *G. ulmifolia* and *P. dulce* seeds were removed an average of 20 cm from the depot, and an important part of the seeds were removed a distance of at least 10 cm. However, the final distance of these seeds could not be established. A *Cyphomyrmex major* worker transported a *G. ulmifolia* seed 1.20 m before entering the nest in the ground while an *Ectatomma ruidum* worker transported a *P. ligularis* seed 4.6 m from the depot.

The ant species that most frequently, and in greatest number, approached the tuna baits were, also, those most frequently involved in seed removal events. The ants observed transporting seeds in grasslands belong to three functional groups: (1) a dominant group of small-sized myrmecines

TABLE 1: Composition and total abundance of ant species attracted to tuna and honey baits in each locality. (Sa: Sachamate, LJ: La Josefina, Ca: Cachimbalito, Lit: Lituania, Ma: Maraón, Li: Limonar).

Morphospecies	Sa	LJ	Ca	Lit	Ma	Lim	Total abund.
Myrmicinae							
<i>Atta cephalotes</i>						1	1
<i>Cardiocondyla</i> gr. <i>minutior</i>	7						7
<i>Crematogaster abstinens</i>	73	644	75	56	822	104	1774
<i>Cyphomyrmex major</i>		4	5			3	12
<i>Pheidole ebenina</i>		22					22
<i>Pheidole susanna</i>		26	85	7	8	4	130
<i>Pheidole</i> sp1	1		1				2
<i>Pheidole</i> sp2				5			5
<i>Pheidole</i> sp3			3			2	5
<i>Pheidole</i> sp5						12	12
<i>Solenopsis geminata</i>	213	206	298	72	160	321	1270
<i>Solenopsis</i> sp1	4			35		1	40
<i>Solenopsis</i> sp2	4						4
<i>Solenopsis</i> sp3	1						1
<i>Wasmannia auropunctata</i>	27	43		10		41	121
Formicinae							
<i>Brachymyrmex</i> sp1	6						6
<i>Camponotus</i> sp1				4			4
<i>Nylanderia</i> sp1				8	3		11
Ectatomminae							
<i>Ectatomma ruidum</i>		11	6	11	1	9	38
Ponerinae							
<i>Hypoponera</i> sp1		1					1
Pseudomyrmecinae							
<i>Pseudomyrmex</i> sp1			2	1	1	1	5

TABLE 2: Mean seed removal of nonmyrmecochorous seeds by ants in cattle grasslands. Standard errors are shown for seed weights.

Type of seed	Species	Seed weight (g)	<i>Ant access</i>		<i>Ant exclusion</i>	
			Seeds removed	Removal percentage	Seeds removed	Removal percentage
Arillated	<i>G. ulmifolia</i>	0.005 ± 0.00	672	56.0%	35	2.9
	<i>P. dulce</i>	0.307 ± 0.10	300	25.0%	0	0.0
	<i>P. ligularis</i>	0.16 ± 0.02	656	54.7%	N/A*	N/A
Nonarillated	<i>S. spectabilis</i>	0.026 ± 0.00	109	9.1%	14	1.2
	<i>L. leucocephala</i>	0.062 ± 0.01	55	4.6%	4	0.3
	<i>A. saman</i>	0.233 ± 0.03	35	2.9%	0	0.0
Total			1827	25.4%	53	4.4%

* N/A: Not Applicable. Ant exclusions were not performed in *P. ligularis* transect.

TABLE 3: Percentiles for the total removal percentage of *Pithecellobium dulce* and *Guazuma ulmifolia* nonmyrmecochorous seeds in six cattle pastures in Cauca and Valle.

Percentile	Observation period	Hour of the day	Percentage of seeds removed	
			<i>P. dulce</i>	<i>G. ulmifolia</i>
0%	2 hours	0800 hours	2.17	1.08
25%	4 hours	1200 hours	2.92	1.33
50%	8 hours	1600 hours	16.6	1.92
75%	24 hours	0800 hours	44.8	15.7
100%	48 hours	0800 hours	56.3	25.0

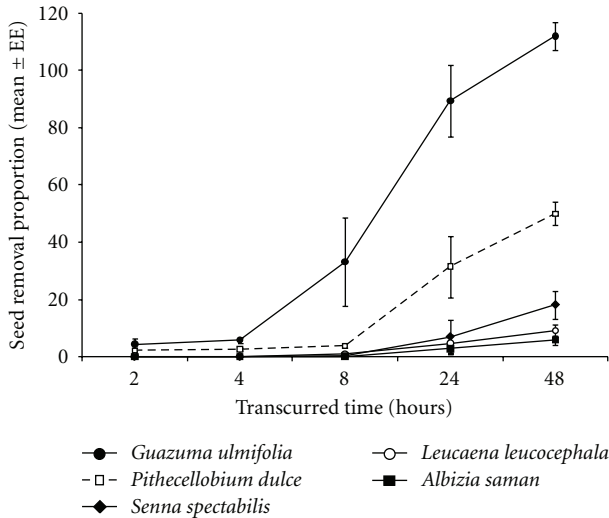


FIGURE 2: Removal of seeds by ants overtime. Average number of seeds removed from depots 2, 4, 8, 24, and 48 hours, after initiating offer, are showed ($n = 6$).

with generalist habits (*Pheidole* spp., *Solenopsis geminata*, and *C. abstinens*); (2) two species of attine, a leaf-cutter (*Atta cephalotes*), and a cryptic fungus grower (*Cyphomyrmex major*) which were the main seed transporters of *P. dulce* and *G. ulmifolia*, respectively; (3) a large epigeal ponerinae (*E. ruidum*), very common and abundant in disturbed lowland habitats (0 to 1500 m.a.s.l.) (Table 4).

Removal activity seems to be occurring throughout the day, with great activity of generalist species during the morning hours such as *E. ruidum* and other small myrmicine, and great activity of attines after 17:00 hours, the activity of *C. major* and *A. cephalotes* increased.

4. Discussion

The ant community associated to cattle pastures in the study area is not very diverse and has a great predominance of only a few species and a relatively predictable composition. The simplification of plant structure in pastures and the surrounding matrix could explain the limited ant diversity [38]. The pattern of diversity found is that expected for the highly fragmented landscape of the biogeographical valley of the Cauca River where pastures and sugar cane fields dominate, and there is only 2% forest cover immersed in a low-quality matrix [39, 40]. The results of this study are consistent with Armbrrecht and Ulloa-Chacón [41] who, one decade earlier, found that ant diversity reduced drastically in the pasturelands with respect to forest fragments. In the same area of this study, they found only 21 species in the productive systems, using six capture methods. In spite of limited diversity, generalist ants in pastures rapidly located and displaced the seeds offered in the depots. Twenty-four percent of the seeds were removed for a total of 1827 removal events during a 48-hour period in treeless pastures with cattle activity and compact, ecologically degraded soil. These removal values are similar to those found by Escobar et al.

[16] who reported a 26% total removal in open grasslands and silvopastoral systems in Valle del Cauca and Quindío, while Zelikova and Breed [15] reported 38.3% removal in open pastureland in Costa Rica. Although total seed removal did not exceed 40%, each removal event as such is of biological importance because it potentiates a possibly effective dispersion event. This is particularly critical in highly disturbed habitats rarely visited by primary dispersers.

Results in the Excluded Transect and direct observation indicate that ants are important seed dispersers of trees useful in ecological recovery of degraded ecosystems. Ants have morphological adaptations which allow them to carrying seeds. Also, their social behavior promotes seed transport from the foraging point to their nests, where conditions may be more favorable for the germination and growth of seedlings. Tendency towards territoriality and the stability of their colonies in the tropics makes removal by ants a permanent ecological service throughout the year. These aspects allow to consider ants as key functional agents, facilitating the distribution of seeds of interest in pasturelands.

Ant preference for seeds with an attractive, nutritious tissue in *G. ulmifolia*, *P. dulce*, and *P. ligularis* was found. This result coincides with the pattern identified for myrmecochorus and nonmyrmecochorous seeds in multiple habitats worldwide [14, 18]. The *G. ulmifolia* species was preferred as much, or more than the *P. ligularis* (positive control) seeds. However, while in the present study, the ants removed 56% of the *G. ulmifolia* seeds, this species was the less preferred in mining areas undergoing rehabilitation [17] in a subxerophytic area where the ants removed only 5% of its seeds. Instead, in the same experiment, ants preferred larger arillated seeds such as *Capparis* sp. (5 mm in diameter) and *Segueira* sp. (4 mm in diameter). In this experiment, the second most preferred seeds (*P. dulce*) are 60 times heavier than *G. ulmifolia* seeds, the lightest in this study. This suggests that the context is an important factor in modeling the way ant-seed interactions occur: the presence of other arillated species that compete for the “transporting energy” of foraging ants as well as the presence of key ant species.

Removal occurred with a great degree of activity of key species such as *E. ruidum*, *S. geminata*, *C. abstinens*, and *Pheidole* spp. during the day while, after 17:00, removal was continued by *C. major* and *A. cephalotes*. The genera observed transporting seeds in the pasturelands (Table 5) coincide with the functional ant guilds exploiting diaspores in flat, sandy forests, and humid tropical forests in the Brazilian lowlands [14, 42]. In these habitats, small myrmicines as well as attine actively interacted with diaspores. Dominguez-Haydar & Armbrrecht [17] identified species of these same functional groups removing seeds. *E. ruidum*, *S. geminate*, and *Acromyrmex octospinosus* were the species that removed the greatest number of seeds from mining lands in early rehabilitation, suggesting that they are key species in the recovery of the ecological function of disturbed areas.

Morphological seed traits, like weight and presence of arils, and foraging strategies in the different ant functional groups are ecologically relevant because they determine how the transport process occur [28]. For example, the foraging of the small-sized myrmicines with generalist habits

TABLE 4: Description of ant species carrying seeds. Body length of workers and its incidence in baits and seed depots (SDs) were recorded, as the seed species they removed. The body length of workers was measured from the posterior margin of clypeus to the posterior end of the last petiole.

Ant species	Workers body length (mm)	Presence		Seed species removed		
		In baits %	In SD %	<i>P. dulce</i>	<i>G. ulmifolia</i>	<i>P. ligularis</i>
<i>Atta cephalotes</i>	12.36 ± 10.9	1.7	1.7	X		
<i>Ectatomma ruidum</i>	5.52 ± 0.12	36.7	35.0		X	X
<i>Solenopsis geminata</i>	2.12 ± 0.01	41.7	16.7		X	
<i>Cyphomyrmex major</i>	1.85 ± 0.11	6.7	36.7		X	
<i>Pheidole susanna</i>	1.67 ± 0.01	20.0	10.0		X	X
<i>Crematogaster abstinens</i>	1.58 ± 0.21	41.7	40.8	X		X

TABLE 5: Ant genus classification of ants attracted to baits into the functional groups established by Silvestre et al. [35].

Item	Functional guild (<i>sensu</i> Silvestre et al. [35])	Genus attracted to baits
(1)	Omnivorous soil dominants	<i>Crematogaster</i> , <i>Pheidole</i> , <i>Solenopsis</i>
(2)	Large epigeal predators	<i>Ectatomma</i>
(3)	Cryptic fungus growers attines	<i>Cyphomyrmex</i>
(4)	Leaf-cutter attines	<i>Atta</i>
(5)	Agile pseudomyrmecinae	<i>Pseudomyrmex</i>
(6)	Soil and vegetation opportunistic	<i>Nylanderia</i>
(7)	Small arboreal ants with massive recruitment	<i>Wasmannia</i>
(8)	Cryptic ponerinae, specialized predators	<i>Hypoponera</i>

is characterized by mass recruiting of workers towards the food resource [35]. The carrying capacity of these ants is limited by their small size, and those seeds that surpass their carrying capacity are foraged on the ground without being displaced [43]. This was observed in the field with species of the *Pheidole*, *Solenopsis*, and *Wasmannia* genera (body length less than 3 mm) that foraged the aril of *P. ligularis* and *P. dulce* seeds without removing them. Nevertheless, small myrmecines also team up to transport heavy seeds. In this study, dozens of *C. abstinens* workers succeeded in moving heavy *P. dulce* seeds from the depots, suggesting that this species is an important functional agent for seed dispersal too.

This study also emphasizes on species of generalist ants considered pests such as *S. geminata*, *E. ruidum*, and attines. The tropical fire ant (*S. geminata*) could be playing a dual role as both predator and seed disperser because, although it is a regular grain collector and eater [44, 45], some seeds could survive and germinate in garbage dumps or soils near the nests [29]. On the other hand, *E. ruidum* has already been identified in Colombia as one of the main seed transporter species in pastures and mining areas under rehabilitation [16, 17, 34]. In Costa Rican agroecosystems, *E. ruidum*, together with *Pheidole fallax*, were responsible for 92% of all observed removal events, *E. ruidum* being the species that removed most seeds in pastures [15]. The greater size of this ant allows a single worker to carry seeds of different sizes thus increasing the range of seeds that can be dispersed by this species.

Finally, attines such as *C. major* and *A. cephalotes* were key transporters of arillated *G. ulmifolia* and *P. dulce* seeds,

respectively. They also acted during evening and nocturnal hours (obs. pers.) thus relaxing competition with other generalist species. These results coincide with the pattern of seed attention described by Rico-Gray & Oliveira [18] and Bas et al. [46] where attines are usually attracted by nonmyrmecochorous diaspores with large arils and low lipid content (<8%). According to the authors, if these diaspores are also light in weight (<0.1 g), they can be transported greater distances (to 10 m), something that could be significant for the lighter *G. ulmifolia* seeds. The hypothesis of directed dispersion [47–49] can be reinforced when seed removal involves species of attines because the seeds are directed towards the nest where appropriate conditions for germination can be provided. Under conditions of dehydration, aridness, and high temperatures, *A. cephalotes* can concentrate foraging activity at night, and its workers can obtain foraging distances of up to 235 m. Genera of cryptic attine, such as *Cyphomyrmex*, usually collect seeds during the dry months, and it is when greater foraging distances are reached by its workers [50].

Despite the low removal distances reported for some functional groups, ants can act as complementary dispersing agents [51] bringing up to their nests seeds that have been dispersed long distances (meters, even kilometers) by primary seed dispersers such as cattle, birds, bats, and rodents [52].

In summary, this study presents evidence supporting the idea of ants as functional agents for the ecological recovery of degraded pastures. The preference pattern of the ants for small-sized seeds with attractive structures was confirmed. In spite of the limited diversity of persistent

ants in the pastures, key species were identified that could provide dispersion service for nonmyrmecochorous species in pastures where barriers to the advance of plant succession exist. The interaction of the different foraging strategies of the participating ants can contribute to the dispersion of seeds through different mechanisms; leaf cutters offer the greatest carrying capacity (quantity and size), and the great majority of seeds will be taken to nests thereby contributing to the reduction of seed competence and depredation by aggregation. Large hunters such as *E. ruidum* removed seed greater distances and feed on the aril instead of the seed. Ant-seed interaction was facultative and generalist instead of an obligatory mutualism specific to one species in particular. Far from being an inconvenience, this generalism opens the way to the use of grassland ants as dispersers of plant species ecologically important. This would also be of interest to producers if seed hauling of economically valuable seeds by ants could be induced, for example, through the simulation of artificial arils in those seeds (Henaó-Gallego et al. [53]). Ant-seed interaction in grasslands can be taken into account for ecological rehabilitation plans by directing this functional diversity. For the rehabilitation of degraded habitats, these facts could mean that, with an abundant although not very diverse ant biota, rehabilitation actions can be initiated, and the plant species chosen will depend on ant preferences and the ecological context of the pasture to be rehabilitated.

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