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The Importance of Poneromorph Ants for Seed Dispersal in Altered Environments

FS Almeida¹, AJ Mayhé-Nunes², JM Queiroz^{1,2}

1 - Universidade Federal Rural do Rio de Janeiro, Três Rios, Rio de Janeiro, Brazil.

2 - Universidade Federal Rural do Rio de Janeiro, Seropédica, Rio de Janeiro, Brazil.

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Corresponding author

Jarbas M. Queiroz

Depto. de Ciências Ambientais

Instituto de Florestas/UFRRJ

BR 465, Km 7, Seropédica, RJ, Brazil

E-Mail: jarquiz@gmail.com

Abstract

Changes in species composition and an increase in the probability of local or regional extinctions alone are considered alarming consequences of human disturbances. However, these changes bring other damages that have passed unnoticed by scientists, such as the loss of ecological interactions. In the present study, we assessed fragments of secondary forest and pastures focusing on two aspects of the seed dispersal process: removal rate and dispersal distance. We collected data in forest fragments named Forest 1 (6 ha), Forest 2 (36 ha), and Forest 3 (780 ha), and in a pasture in the municipality of Vassouras, Rio de Janeiro, southeastern Brazil. In each site, we established 40 observation stations containing six seeds of *Carica papaya* L. (papaya) and monitored seed removal for 2 h at each station. Seventeen ant species removed a total of 316 seeds (32.92% of the seeds). The species that removed the highest number of seeds was *Pachycondyla striata* Fr. Smith, followed by *Odontomachus chelifer* (Latreille). The seed removal rate was significantly higher ($P < 0.05$, Tukey test) in the forest fragment where larger species were more frequent. The average removal distance was significantly longer in two out of three forest fragments ($P < 0.05$, Tukey test). Larger ants removed more seeds and for longer distances. Hence, seed dispersal was increased by the presence of large-bodied ant species and their high frequency in forest fragments seed dispersal.

Introduction

Seed dispersal is important for plants, as it reduces mortality by seed parasites and predators and decreases intraspecific competition (Janzen, 1970; Howe & Smallwood, 1982). Seed dispersal by animals, also known as zoochory, can be carried out by ants that nest in the ground and remove seeds to their nest or its surroundings (Pizo et al., 2005). The habit of feeding on seeds (granivory) or of collecting seeds to remove their appendages occurs in several species (Hölldobler & Wilson, 1990). Seed consumption rate and removal distance vary according to ant behavior and morphology (Ness et al., 2004; Zelikova & Breed, 2008).

In South American tropical forests, poneromorph ants *Pachycondyla striata* Fr. Smith and *Odontomachus chelifer* (Latreille) feed on the seeds of a wide variety of native plants (Pizo & Oliveira, 1998; Passos & Oliveira, 2003). These ants have a relatively large size and can remove diaspores up to

13 m (Passos & Oliveira, 2003). Small ants, mainly of the genera *Pheidole* and *Solenopsis*, are frequently found consuming diaspores in tropical forests. These ants explore the resource where they find it, instead of taking it to the nest, as observed in *Solenopsis* ants (Pizo & Oliveira, 1998; Passos & Oliveira, 2003; Leal et al., 2007). In general, large-bodied species forage at larger distances than small-bodied ants (Gomez & Espadaler, 1998) and can more easily carry seeds individually (Zelikova & Breed, 2008).

Forest fragmentation may change the composition of ant communities, since small fragments may be invaded by generalists ants and parasites of mutualistic systems (Puntilla et al., 1994; Gibb & Hochuli, 2002; Ness et al., 2004; Schorereder et al. 2004). In many cases, forest fragments are more susceptible to biological invasions (Ness et al., 2004). Although these changes in community composition caused by environmental disturbances are relatively well documented, the consequences of these alterations for ecological processes



are still poorly known.

The impact of environmental changes on seed-dispersing ants may compromise the seed dispersal process and plant species that depend on animals for this process (Guimarães-Jr & Cogni, 2002; Ness et al., 2004; Cordeiro et al., 2009). Starting from the assumption that environmental changes, for instance forest fragmentation, affect the composition of ant communities, it is relevant to analyze the relationship between the guild of ants that consume seeds and the seed dispersal process in altered environments. In the present study, we assessed fragments of secondary forest and a pasture, and monitored two aspects of the seed dispersal process: removal rate and dispersal distance. We aimed at testing the following hypotheses: (1) changes in ant community structure cause changes in the rate and distance of seed dispersal; (2) the ant body size affects the number of seeds removed and the removal distance.

Material and Methods

Study area

We collected data in the municipality of Vassouras, state of Rio de Janeiro, southeastern Brazil. The region is located within the domain of the Atlantic Forest and the vegetation is classified as semi-deciduous seasonal forest. In the municipality of Vassouras, red-yellow argisols predominate and the landscape is broadly dominated by pastures (60.2%) and also by secondary forests (35.3%) (Francelino et al., 2012). According to the Köppen system, the climate of the region is humid mesothermal (Cwa) (Francelino et al., 2012), with average annual rainfall of 1,280 mm; rainfall is higher in summer than in winter. The average temperature in the coldest month may be below 18 °C (July) and in the warmest month, above 23 °C (February) (EMBRAPA, 2011).

To measure seed removal rate, dispersal distance, ant body size, and the guild of ants that consume seeds, we chose three secondary forest fragments of different sizes and a pasture. The smallest fragment (Forest 1) had an area of 6 ha and a perimeter of 1,056 m (22° 27' 41" S; 43° 38' 57" W); the intermediate fragment (Forest 2) had an area of 36 ha and a perimeter of 4,464 m (22° 27' 3" S; 43° 38' 40" W), and the largest fragment (Forest 3) had an area of 780 ha and a perimeter of 37,571 m (22° 27' 11" S; 43° 39' 47" W). The pasture (Pasture) (22° 27' 30" S; 43° 39' 29" W), used for raising bovine cattle, was covered by *Brachiaria decumbens* Stapf. and was located at approximately 200 m from the largest fragment (Forest 3). The altitude in the region is approximately 600 m a.s.l.

Assessment of seed removal by ants

To quantify the rate and distance of seed removal by ants, we used seeds of *Carica papaya* L. (papaya) (Zelikova

& Breed, 2008). Although seed size and weight affect removal by ants (Pizo & Oliveira, 2001), the characteristics of the papaya seeds used in the present study can be considered intermediate within the range of native seeds used by ants in tropical forests (Passos & Oliveira, 2003). The average weight of fresh papaya seeds was 0.09 ± 0.01 g, the average length was 0.63 ± 0.06 cm and the average width was 0.47 ± 0.05 cm (N = 100 seeds). To avoid the introduction of papaya in the study sites, we pierced the seeds used in the experiment with a pin, making three perforations to make them unviable. To confirm that the seeds were unviable, we placed 100 pierced seeds and 100 non-pierced seeds in trays with sterile moist sand. After 60 days of observation no pierced seed germinated, but 48% of the non-pierced seeds germinated, a high value considering that no treatment to break dormancy was applied (Tokuhisa et al., 2007).

In October and November 2009, we installed four groups of 10 observation stations in each environment. The distance between stations was 10 m and between groups, 30 m. Each station consisted of a 10 x 10 cm white paper on which we placed six papaya seeds. Each station was observed for 120 min, between 07:00 and 17:00 h. The ants were monitored until they dropped the seeds; we collected the ants that carried the seeds for more than 5 cm, which was considered a removal event (Zelikova & Breed, 2008). Whenever possible, we observed whether the seeds were taken to inside the nest or nest surroundings (at least 20 cm from the nest entrance).

We placed the ants collected in identified plastic vials containing alcohol 70%. We deposited voucher specimens in the entomological collection Coleção Entomológica Ângelo Moreira da Costa Lima (CECL), Instituto de Biologia/UFRRJ, and the numbers used to refer to morphospecies are the same used in CECL.

As a measurement of ant size we used head width (Kaspari & Weiser, 1999), measured in up to six workers of each species. Next, we calculated the average size of each species. The measurements were taken in a light chamber coupled to a stereomicroscope.

Data analysis

We described the guild of ant species that removed the experimental seeds in each study site in terms of seeds removed, removal distance, and ant body size. We classified the ant species collected in each environment by body size and counted for each size class the number of stations where the ants removed seeds. We used simple linear regressions to test for a relationship between ant size, number of seeds removed, and removal distance. In the regression between ant size and removal distance we considered only species that removed four or more seeds. We used a chi-squared test (Zar, 1999) to compare the proportion of stations with at least one seed removed among the three forest environments.

To compare seed removal rate and average removal distance in different environments we used an analysis of variance (ANOVA) and a Tukey test.

Results

Seventeen ant species removed seeds in our experiment; *Pheidole* was the ant genus with the largest number of species (9). We collected eight species in Forest 1, six species in the Pasture and in Forest 3, and five species in Forest 2. The ant species that removed seeds in forest fragments did not occur in the pasture and vice-versa (Table 1). In total, 316 seeds were removed, which represents a removal rate of 32.9%. Among the five species that most removed the experimental seeds, three occurred in forest fragments: *P. striata* (29.1% of all seeds removed), *O. chelifer* (25%), and *Ectatomma edentatum* Roger (10.1%); and two in the pasture: *Pheidole fallax* Mayr (11.7%) and *Pheidole radoszkowskii* Mayr (5.4%).

Table 1. Number of papaya seeds removed by ants in different environments of Vassouras, Rio de Janeiro, southeastern Brazil.

Species	Number of seeds removed				Total
	Pasture	Forest 1	Forest 2	Forest 3	
<i>Pachycondyla striata</i> Fr. Smith		3	11	78	92
<i>Odontomachus chelifer</i> (Latreille)		20	21	38	79
<i>Pheidole fallax</i> Mayr	37				37
<i>Ectatomma edentatum</i> Roger		14	8	10	32
<i>Pheidole radoszkowskii</i> Mayr	17				17
<i>Pheidole</i> sp.1			7	6	13
<i>Pheidole</i> sp.53				12	12
<i>Pheidole</i> sp.52		11			11
<i>Solenopsis</i> sp.12	10				10
<i>Pheidole gertrudae</i> Forel			3	1	4
<i>Pachycondyla verena</i> (Forel)	2				2
<i>Trachymyrmex prox. oetkeri</i>		2			2
<i>Camponotus rufipes</i> (Fabricius)	1				1
<i>Crematogaster</i> sp.11	1				1
<i>Pheidole sensitiva</i> Borgmeier		1			1
<i>Pheidole</i> sp.49		1			1
<i>Pheidole</i> sp.51		1			1
Total	68	53	50	145	316
Number of species	6	8	5	6	17

Of all seeds removed by *P. fallax*, 86.5% were transported to the nest surroundings. The percentage of seeds taken to the nest surroundings was 84.4% for *E. edentatum*, 89.9% for *O. chelifer*, and 87.0% for *P. striata*. In the Pasture and in Forest 1, most stations were visited by small ants. The number of stations visited by large ants was higher in Forest 3 than in the other environments (Figure 1).

The longest seed removal distances were observed for *O. chelifer*, followed by *P. striata*. These two species had also larger body size (Table 2). Larger ants removed more seeds ($r^2 = 0.44$; $P = 0.003$; Figure 2) and for longer distances ($r^2 =$

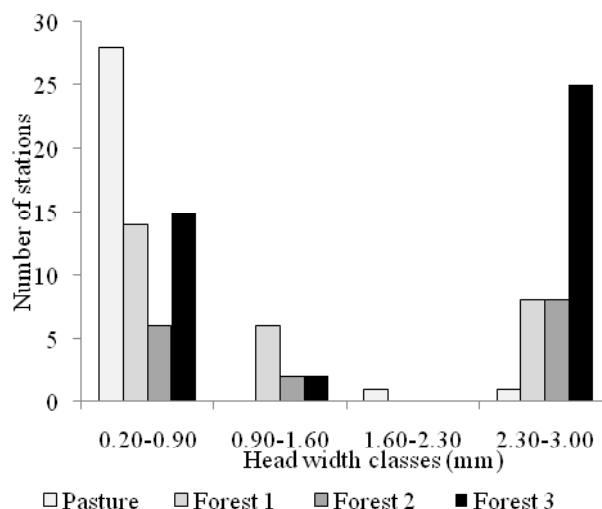


Figure 1. Number of stations containing papaya seeds where ants, classified according to head width categories, removed seeds in different environments.

0.60; $P = 0.01$; Figure 3). More than half of the seeds in the Pasture were removed by *P. fallax*. For the three forest environments, the proportion of stations with at least one seed removed by *E. edentatum* or *O. chelifer* in each forest did not differ from the proportion expected by chance (*E. edentatum*: $\chi^2 = 2.00$; $df = 2$; $P = 0.37$ and *O. chelifer*: $\chi^2 = 0.74$; $df = 2$; $P = 0.69$), but *P. striata* was more frequent in the largest fragment ($\chi^2 = 19.19$; $df = 2$; $P < 0.01$). The average rate of seed removal differed only between the largest fragment and the other environments (Tukey test, $P < 0.05$; Figure 4). However, the average removal distance was significantly longer in Forest 2 and Forest 3 than in the other environments (Tukey test, $P < 0.05$; Figure 5).

Table 2. Average and maximum removal distance (\pm SE) of papaya seeds by each ant species, including information on average head width of ants.

Species	Removal distance (m)		Head width (mm)
	Average	Maximum	
<i>Odontomachus chelifer</i>	2.35 \pm 1.17	5.20	2.77
<i>Pachycondyla striata</i>	1.69 \pm 0.93	4.31	2.67
<i>Trachymyrmex prox. oetkeri</i>	1.25 \pm 0.38	1.60	1.17
<i>Pheidole gertrudae</i>	1.23 \pm 0.37	1.60	0.61
<i>Pheidole sensitiva</i>	1.10 \pm 0.00	1.10	0.55
<i>Pheidole fallax</i>	1.03 \pm 0.07	1.60	0.53
<i>Pheidole</i> sp.1	0.98 \pm 0.08	1.25	0.50
<i>Crematogaster</i> sp.11	0.96 \pm 0.00	0.96	0.65
<i>Camponotus rufipes</i>	0.90 \pm 0.00	0.90	2.31
<i>Pachycondyla verena</i>	0.84 \pm 0.46	1.30	1.85
<i>Pheidole radoszkowskii</i>	0.82 \pm 0.04	1.05	0.49
<i>Ectatomma edentatum</i>	0.74 \pm 0.37	1.62	1.53
<i>Pheidole</i> sp.53	0.74 \pm 0.40	1.20	0.54
<i>Pheidole</i> sp.49	0.35 \pm 0.00	0.35	0.43
<i>Pheidole</i> sp.52	0.30 \pm 0.03	0.47	0.61
<i>Pheidole</i> sp.51	0.26 \pm 0.00	0.26	0.42
<i>Solenopsis</i> sp.12	0.12 \pm 0.02	0.21	0.65

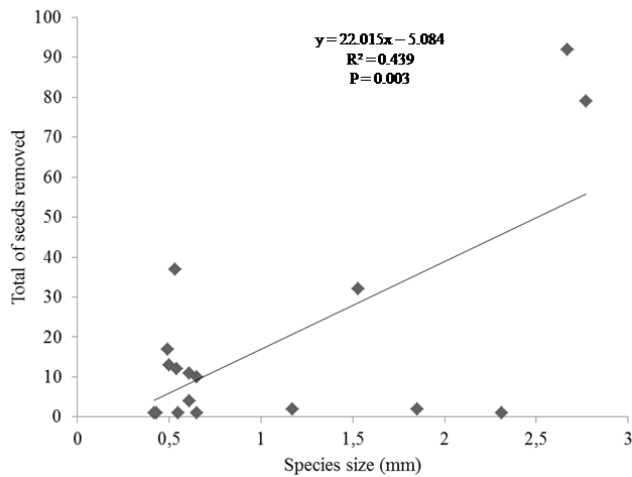


Figure 2. Relationship between ant size and number of experimental seeds of *Caryca papaya* removed.

Discussion

Previous studies on ant-seed interactions in forests of southeastern Brazil focused mainly on large tracts of Atlantic rain forest (e.g. Passos & Oliveira, 2002; Passos & Oliveira, 2004; Bottcher 2006; Costa et al. 2007, but see Guimarães & Cogni, 2002). Our focus in this study was the fragments of second-growth semi-deciduous forest. The original cover of semi-deciduous forest in southeastern Brazil has been drastically reduced, but the remaining or second-growth fragments still harbor high biodiversity and endangered species (Ribeiro et al., 2009; Dan et al., 2010). In the fragments of secondary forest monitored in the present study, the species *P. striata*, *O. chelififer*, and *E. edentatum* stood out in seed removal. These species are common in semi-deciduous seasonal forests (Santos et al., 2006; Castilho et al., 2011), as well as in other forest types of South America (Antonialli Jr. & Giannotti, 2001; Schütte et al., 2007; Silva-Melo, 2008) and Central America (Kempf, 1972). The species *P. fallax* and *P. radoszkowskii*, which removed most seeds in the pasture, occur in several habitat types in South and Central America, mainly altered environments, and their interaction with seeds have already been studied by other authors (Hölldobler & Wilson, 1990; Zelikova & Breed, 2008, Lobo et al., 2011).

The highest seed removal rate found in Forest 3 may be explained by the presence of large ants in most stations, mainly *P. striata*. Large ants are able to carry seeds individually, whereas small ants need the help of other ants (Pizo & Oliveira, 1998; Zelikova & Breed, 2008). However, behavioral characteristics of ants should also be taken into account to assess seed dispersal (Zelikova & Breed, 2008).

The removal distance was also longer in environments where more visits by large-bodied ants occurred. Indeed there was a positive relationship between ant size and removal distance. This result contrasts with Zelikova & Breed (2008), who did not find a relationship between ant

size and removal distance. This difference in results is related to ant behavior. *Ectatomma ruidum*, the large species that removed most seeds in the study by Zelikova & Breed (2008), removes seeds at a smaller distance than *Pheidole fallax*, a small ant. On the other hand, *P. striata* and *O. chelififer*, the largest species found in the present study, removed seeds at greater distances than *P. fallax*, which was found in

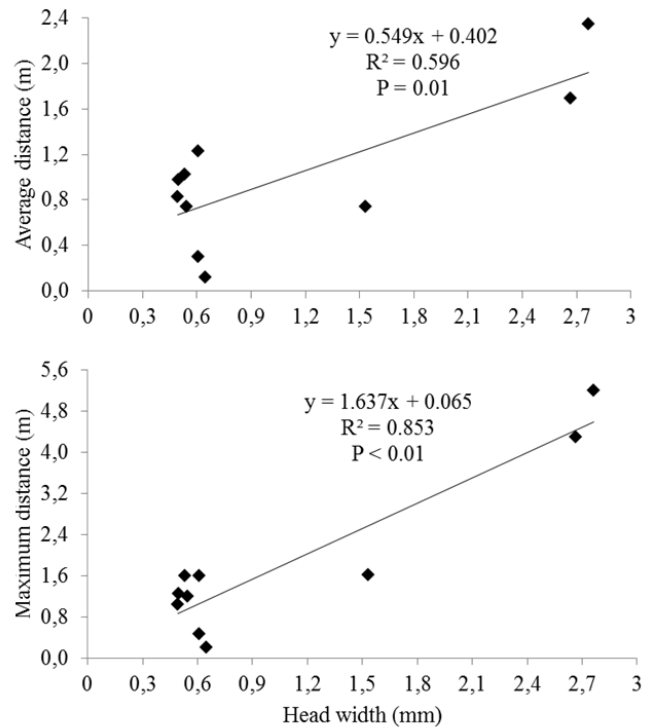


Figure 3. Relationship between removal distance of papaya seeds (average and maximum) and head width of ant species (n = 10). Note: we considered only species that removed at least four seeds.

the pasture. *Ectatomma edentatum*, which is also a large ant, removed seeds at a distance similar to *E. ruidum*. Hence, we conclude that, although *Ectatomma* species are large-bodied, they are not as good dispersers as *P. striata* and *O. chelififer*. The highest removal rates and distances found in the largest fragment are mainly related to a higher frequency of interactions involving *P. striata*.

In several tropical forests of South America, the species *O. chelififer* and *P. striata* seem to play important roles in seed dispersal. In addition, the activities of *O. chelififer* and *P. striata* increase nutrient concentration in the surroundings of the nest and potentialize the recruitment of dispersed plants (Passos & Oliveira, 2002; Bottcher, 2006). Hence, these ants are ecosystem engineers (*sensu* Jones et al., 1994) and may contribute to the maintenance of biodiversity in the forests where they occur, which is very important to threatened ecosystems, such as semi-deciduous seasonal forests (Dean 2002; MMA, 2007). However, we suggest that the effect of ants may depend not only on occurrence, but also on abun-

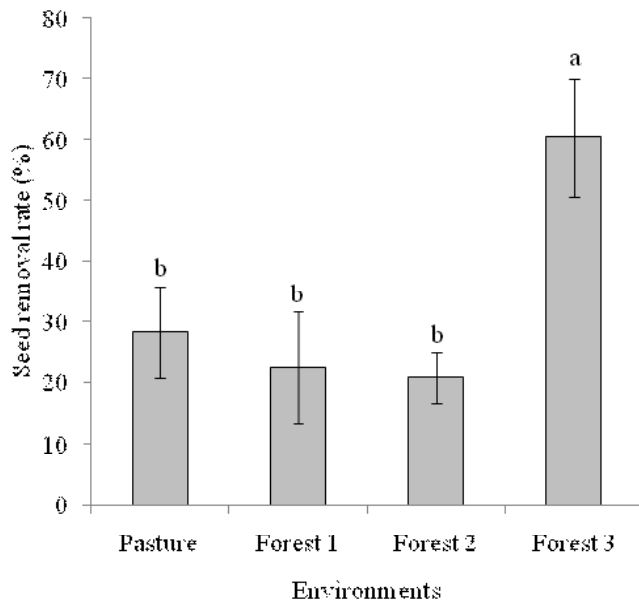


Figure 4. Average removal rate (\pm SE) of papaya seeds per plot ($n = 4$) in different environments of Vassouras, Rio de Janeiro, southeastern Brazil. Note: different letters indicate significant differences identified in the Tukey test, $\alpha = 5\%$.

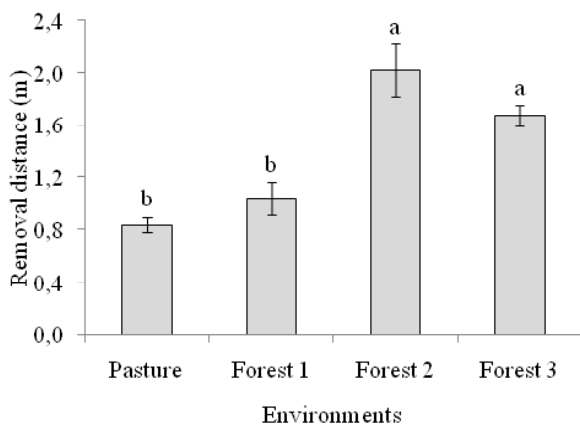


Figure 5. Average removal distance (\pm SE) of papaya seeds in different environments of Vassouras, Rio de Janeiro, southeastern Brazil. Note: different letters indicate significant differences identified in the Tukey test, $\alpha = 5\%$.

dance. Hence, a greater effort is required to understand which mechanisms are responsible for the differences in abundance between ant species in forests.

Since seed removal was performed mainly by a small number of species in each environment, local extinctions or decreases in population size may decrease the seed removal rate. This may put at risk plant species that depend on zoochory for germination and establishment. Taking into account that forest fragmentation influences the composition and structure of ant communities (Gibb & Hochuli, 2002, Schoederer et al., 2004), we can also assume that it affects seed dispersal by ants too.

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