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Attractiveness of fallen fleshy fruits to ants depends on previous handling by frugivores[1]

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Abstract: Interactions between ants and vertebrate-dispersed fleshy fruits are common on the floor of tropical forests. These interactions are considered beneficial to seeds if ants clean the seed (which may prevent fungal contamination and/or increase germination success) or act as secondary fine-scale dispersers (depositing the seed in nearby nutrient-enriched nest sites). Benefits to seeds, however, may be constrained by limited ant access to fruits. Here, we experimentally tested whether ant access to fallen fleshy fruits of *Psychotria suterella* (Rubiaceae) can be affected by previous handling (including ingestion) by birds. We found that mandibulated fruits and fruits embedded in feces are more prone to be visited by ants compared to entirely intact fruits. Moreover, the number of ant species per station was higher for vertebrate-handled fruit categories. We suggest that ongoing vertebrate loss in tropical forests may affect this highly opportunistic and potentially mutualistic interaction.
Keywords: ant–seed interaction, Atlantic forest, frugivory, *Psychotria suterella*, seed dispersal, vertebrate loss.

Résumé : Les interactions entre les fourmis et les fruits charnus dispersés par les vertébrés sont importantes dans les forêts tropicales. Ces interactions sont considérées comme avantageuses pour les graines si les fourmis nettoient la graine (ce qui peut empêcher la contamination fongique et/ou augmenter le succès de germination) ou si elles agissent comme agents secondaires de dissémination à petite échelle (en déposant la graine dans des nids environnants enrichis de nutriments). Les bénéfices pour les graines peuvent cependant être contraints par l'accès des fourmis aux fruits. Nous avons évalué de façon expérimentale si l'accès des fourmis aux fruits charnus de *Psychotria suterella* (Rubiaceae) tombés au sol peut être influencé par une manipulation antérieure (incluant l'ingestion) par des oiseaux. Nous avons constaté que les fruits ayant été percés et qui sont mélangés à des fèces ont plus tendance à être utilisés par les fourmis que les fruits entièrement intacts. De plus, le nombre d'espèces de fourmis par station était plus élevé pour les catégories de fruits ayant été manipulés par des vertébrés. Nous suggérons que la perte d'espèces vertébrées en cours dans les forêts tropicales pourrait nuire à cette interaction très opportuniste et potentiellement mutualiste.
Mots-clés : dispersion de graines, forêt atlantique, frugivorie, interaction graine-fourmi, perte d'espèces vertébrées, *Psychotria suterella*.

Nomenclature: Bolton *et al.*, 2007; Lista de Espécies da Flora do Brasil, 2012.

Introduction

Generally, when talking about ants attracted to plant diaspores, we think of seeds with a lipid-rich appendage known as elaiosome. Such an appendage is typical among the ant-dispersed seeds of true myrmecochores (Beattie, 1985). Nonetheless, ants are often recorded at non-myrmecochoric diaspores, which do not present adaptations to dispersal by ants (Rico-Gray & Oliveira, 2007). Many ant species are known to visit a broad assemblage of fleshy diaspores found on the ground of tropical rainforests and savannas (Pizo & Oliveira, 2000; Christianini, Mayhé-Nunes & Oliveira, 2007). Moreover, ants are also attracted to seeds within feces of vertebrates (*e.g.*, Roberts & Heithaus, 1986; Kaspari, 1993; Martínez-Mota, Serio-Silva & Rico-Gray, 2004). Broadly, fleshy diaspores found by ants on the ground may be classified into 3 different conditions: completely intact diaspores, diaspores mandibulated/manipulated by vertebrates, and diaspores embedded within vertebrate feces (Rico-Gray & Oliveira, 2007).

In a 2-y survey of ant–fruit interactions in the Brazilian Atlantic forest, Pizo and Oliveira (2000) found that some hard-coated diaspore species were exploited by ants only if previously crushed by vertebrates, thus making the fleshy part accessible (*e.g.*, *Astrocaryum aculeatissimum* [Arecaceae], *Garcinia gardneriana* [Clusiaceae], *Abuta selloana* [Menispermaceae], *Posoqueria latifolia* [Rubiaceae]). A number of studies have shown that previous handling by vertebrates of relatively soft-coated fruits may also facilitate oviposition by invertebrate seed predators such as fruit flies and bruchid beetles (see Sallabanks & Courtney, 1992; Silvius & Fragoso, 2002; and included references). Unlike fruit flies and bruchids, ants in tropical forests are commonly regarded as seed mutualists, acting as secondary fine-scale dispersers through seed deposition

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in nearby nutrient-enriched nest sites (Böhning-Gaese, Gaese & Rabemanantsoa, 1999; Passos & Oliveira, 2002; Christianini & Oliveira, 2010) or cleaning the seed *in situ* and thus preventing fungal contamination (Oliveira *et al.*, 1995). Attraction of ants to fallen fleshy diaspores is known to vary with attributes of both ant and diaspore species (Pizo & Oliveira, 2001). Given the variable conditions of fallen fleshy diaspores (see above), it is likely that their attractiveness to ants and the resulting ant-derived benefits may also vary.

Here, we experimentally examine whether ant access to fleshy diaspores can be affected by previous handling (including ingestion) by frugivores. We hypothesized that ant visits to fleshy fruits would differ in accordance with the state of the fruits on the forest floor. Specifically, fruits previously mandibulated by vertebrate frugivores, or within their feces, should be more prone to be visited by ants compared to entirely intact ones. To test this hypothesis, we used fruits of a primarily bird-dispersed species, *Psychotria suterella* (Rubiaceae), as our model. This work is part of a broader study assessing how interactions between ants and fleshy fruits are affected by forest fragmentation (Bieber, 2012). Previous studies with fallen fleshy diaspores have already demonstrated ant-derived benefits for seed germination and seedling establishment (see Rico-Gray & Oliveira, 2007). Indeed, pulp removal by ants from *Psychotria* fruits has been documented in Brazilian forests and savannas, and such "seed cleaning" activity has been demonstrated to increase germination success in *P. stachyoides* (Leal & Oliveira, 1998). Here, we test whether fruits not handled by vertebrates (a possible outcome of forest fragmentation) are less attractive to ants compared to those previously manipulated by frugivores. We discuss our findings in the context of habitat fragmentation and current loss of vertebrate frugivores.

Methods

Field work was carried out in an Atlantic forest remnant at Tapiraí (23°54'44"s, 47°28'47"w), São Paulo State, in southeast Brazil. The native vegetation in the region is classified as lower montane rainforest, and the study site comprises 91 ha of second-growth forest. Monthly mean temperatures vary from 15 to 22 °C (mean annual temperature of 19 °C), and annual rainfall is *ca* 1800 mm (for further information, see Banks-Leite, Ewers & Metzger, 2010).

Fruits of *Psychotria* spp. are commonly dispersed by birds in tropical habitats (Snow, 1981), including the Atlantic rainforest (Galetti, Pizo & Morellato, 2011). Many fruits, however, fall to the ground with pulp material still attached, and "seed cleaning" by ground-dwelling ants can improve germination, as reported for *P. stachyoides* in the Brazilian savanna (Leal & Oliveira, 1998). Our model species, *P. suterella*, is a common understory treelet in the study area, and its fruits are frequently exploited by ants on the forest floor (Bieber, 2012). The fruits are medium-sized, purple, succulent berries (diameter: 12.65 ± 1.86 mm, mean ± SD; *n* = 8) containing 2 seeds (length: 4.85 ± 0.45 mm; width: 2.35 ± 0.12 mm; *n* = 10). The fruit coat is not considered hard (A. G. D. Bieber, pers. obs.; see Denslow & Moermond, 1982 for other species in this genus).

Intact fruits of *P. suterella* were collected on the ground or directly from trees. These fruits were randomly subjected to 1 of 3 procedures in order to simulate the 3 most common conditions in which they are encountered on the ground: intact, opened by vertebrates (either manipulated or mandibulated), and embedded in vertebrate feces. "Intact" fruits presented no marks or holes of any kind and received no additional treatment. "Mandibulated" fruits were produced by making an opening with a forceps to simulate the mark left by the beak of a bird. We mimicked fruit passage through bird guts (fruits "embedded" in feces) by smashing an intact *P. suterella* fruit and mixing it with fresh feces of curassows (*Crax* spp. and *Mitu* spp.; Cracidae), which are large birds that include fruits of many species of Rubiaceae in their diet (Muñoz & Kattan, 2007). Although this treatment may not appropriately mimic the physicochemical effects of gut passage on seeds (*e.g.*, for germination experiments), it does mimic the condition in which ants encounter seeds after gut passage (*i.e.*, embedded in feces). Bird feces were obtained from captive individuals fed a fruit-based diet (mainly banana, apple, and papaya; no seeds) at a local private zoo.

Experimental fruits were placed on the leaf litter at stations 5 m apart from each other along 1 transect in the forest. The distance of 5 m may be considered adequate to ensure the independence of sampling units on the forest floor (Pizo & Oliveira, 2000). At each station, 3 fruits subjected to the above treatments (1 for each treatment) were placed separately on pieces of filter paper (4 × 4 cm), about 1 m from one another. The relative location of experimental fruits was switched across stations to avoid any visitation bias due to proximity to the transect. Proximity of stations to fruiting trees was not avoided, as *P. suterella* treelets are highly abundant in the understory. Fallen fruits found near the stations, however, were removed before the experiment. Fruits were set at 9:00, after which the attracted ants and their behaviour were recorded in 4 scan samples taken at 1-h intervals from 10:00 to 13:00. Samplings were performed on 2 consecutive days under similar weather conditions (February 2009); 20 stations were established each day. On the second day, to avoid spatial pseudoreplication, the stations were established on a different part of the transect. Ant voucher specimens are deposited in the Museu de Zoologia of the Universidade de Estadual de Campinas.

Data from all 4 scan samplings of ant visitation to stations were pooled to evaluate differential attractiveness among fruit treatments. The number of stations with ant visitors at each treatment was compared with a *G* test of independence, applying Williams' correction (Sokal & Rohlf, 1995). Ant species per station (*i.e.*, species density) in each fruit treatment was compared using a two-way ANOVA without replication (*i.e.*, a design similar to the method of randomized complete blocks) (Sokal & Rohlf, 1995). A Tukey *post hoc* test was used to determine which treatments significantly differed from one another (Sokal & Rohlf, 1995). Stations at which none of the 3 fruits were discovered by ants were removed from the analyses (4 cases). Statistical tests were performed in the software STATISTICA v 8.0 (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

Overall, 23 ant species were attracted to the fruits of *Psychotria suterella* (Appendix I). The myrmicine species *Pheidole* sp. 3 and *Wasmannia affinis* were the most frequently registered visiting the fruit stations. Eleven species were captured just once. The great majority of the species exploited the fruits on the spot. The only ant species seen removing seeds from feces was the leaf-cutter *Acromyrmex* sp. 1, which also removed fecal parts. Ants recorded on "mandibulated" fruits were seen mostly exploiting the exposed pulp (63% of the records).

As predicted, there is a significant difference among fruit treatments in the number of stations with ant visitors. Fruits "embedded" in feces and "mandibulated" fruits presented higher frequencies of ant visitation (26 and 23 stations, respectively) than "intact" fruits (12 stations) (G_{adj} = 10.93, df = 2, $P < 0.005$; see Appendix I). In addition, species density at "intact" fruits was significantly lower than in the other fruit treatments (F = 7.90, df = 2, 70, $P < 0.001$; Figure 1), with no significant difference among experimental stations (F = 0.85, df = 35, P = 0.70).

Discussion

Although many studies have registered ants visiting a wide variety of non-myrmecochoric diaspore species on the ground of tropical habitats (Rico-Gray & Oliveira, 2007, and included references), our field experiment suggests that fruit attractiveness to ants may depend on previous handling by frugivores, which likely facilitates ant access to fruit rewards or detection of the fruits by volatile emission. So far, however, the idea of volatiles eliciting ant attraction via olfaction has not been supported in the literature (Sheridan, Iversen & Itagaki, 1996). Our results suggest that the mandibles of most ant species were not able to penetrate (*i.e.*, tear) the coat of intact *P. suterella* fruits. The exposed pulp of "mandibulated" fruits, on the other hand, was easily accessible by many ant species. Moreover, in the "embedded" treatment, ants had full access not only to the fruit reward per se (*i.e.*, pulp and seeds), but to the feces constituents as well. Some ant species may be more attracted to vertebrate feces than to the fruit itself, while others are much more interested in the pulp rewards (see Kaspari, 1993; Levey & Byrne, 1993; Pizo, Guimarães & Oliveira, 2005).

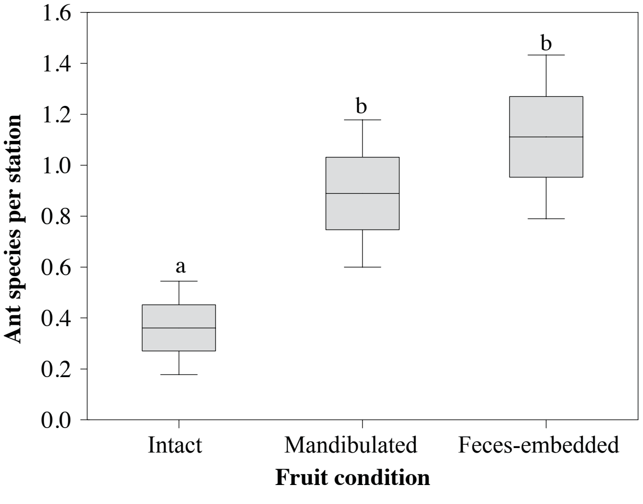

FIGURE 1. Density of ant species attracted to *Psychotria suterella* fruits subjected to 3 different treatments (intact, mandibulated, and embedded in feces) in an Atlantic forest remnant in southeast Brazil (n = 36 sampling stations). Central lines and borders in each box plot indicate the mean ± SE, whereas whiskers indicate the 95% confidence interval range. Different letters denote significant differences ($P < 0.05$).

Due to the short observation period, seed cleaning on the spot was not observed. Moreover, given the size of the fruits, ants were unable to carry whole *Psychotria suterella* fruits to their nests. Investigation of the ant-derived benefits to seeds of *P. suterella* was beyond the scope of this work; however, previous studies have demonstrated positive impacts from ants on seed germination and establishment for many non-myrmecochoric species (*e.g.*, Passos & Oliveira, 2002; 2004). Ant visits to *Psychotria* fruits have been recorded in lowland Atlantic rainforest (Pizo & Oliveira, 2000) and in sandy coastal forest (Passos & Oliveira, 2003). In cerrado savanna, removal of pulp material from fallen fruits by recruited ants ("seed cleaning") has been shown to increase germination success in *P. stachyoides* (Leal & Oliveira, 1998). The high frequency of ant visitation and the wide variety of ants at vertebrate-handled fruits suggest that attendance by ant species capable of providing important services such as seed cleaning and/or removal is likely (Rico-Gray & Oliveira, 2007).

Although our experiment focused on only 1 species, a preference by ants for vertebrate-handled fruits should be expected for other plant species whose fruits are soft-coated berries or drupes (A. G. D. Bieber, pers. obs.). At the community level, the great variability in coat toughness observed among tropical fleshy fruits (Snow, 1981) generates a gradient of varying resistance to ant access. For instance, while the hard-coated fruits of *Posoqueria latifolia* are only accessible to ants when crushed by vertebrates (Pizo & Oliveira, 2000), our data on *Psychotria suterella* fruits revealed that ants are capable of exploiting these fruits even when intact, although less frequently. The current study highlights the importance of taking into account fruit condition in future investigations of ant visits to non-myrmecochoric fleshy fruits. Intact fruits must be clearly distinguished from even slightly mandibulated fruits, as the latter condition has been proven to be more attractive to ants.

Our results suggest that ongoing changes in the structure of vertebrate communities (*e.g.*, lower abundance, alteration in species composition, loss of specialist species) due to hunting and habitat fragmentation in tropical forests (Silva & Tabarelli, 2000; Terborgh *et al.*, 2001; Cordeiro & Howe, 2003) might indirectly affect opportunistic interactions between ants and fleshy diaspores. Vertebrate-impoverished forest fragments probably present lower frequencies of previously manipulated fallen fruits (especially large diaspores), thus reducing the chances of ant–diaspore interactions. If still intact when they fall, the fruits of many diaspore species are likely to be inaccessible (or less attractive) to a number of potentially beneficial ant species.

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Appendix 1

APPENDIX I, TABLE I. Ant species visiting fruits of *Psychotria suterella* (Rubiaceae) subjected to 3 different treatments (intact, mandibulated, and embedded in feces) in an Atlantic forest remnant in southeast Brazil. Records refer to ant visits to fruits at 40 sampling stations (40 fruits per category). Species are in alphabetical order within subfamilies.

	Records at experimental fruits			
Subfamily Ant species	Intact	Mandibulated	Feces-embedded	Total
Formicinae				
Brachymyrmex sp. 4	1	0	0	1
Heteroponerinae				
Heteroponera inermis	0	2	1	3
Myrmicinae				
Acromyrmex sp. 1	0	2	1	3
Basiceros disciger	0	0	1	1
Cyphomyrmex rimosus	0	1	2	3
Megalomyrmex iheringi	1	0	0	1
Pheidole sp. 1	1	2	5	8
Pheidole sp. 3	2	5	8	15
Pheidole sp. 4	1	2	0	3
Pheidole sp. 5	1	2	1	4
Pheidole sp. 7	0	0	1	1
Pheidole sp. 8	1	1	2	4
Pheidole sp. 14	0	1	0	1
Pheidole sp. 18	0	0	2	2
Pheidole sp. 19	0	0	1	1
Pheidole sp. 20	0	0	1	1
Pheidole sp. 21	0	0	1	1
Pheidole sp. 25	0	0	1	1
Solenopsis sp. 3	0	1	0	1
Solenopsis sp. 7	0	3	3	6
Solenopsis sp. 9	1	1	1	3
Wasmannia affinis	3	7	6	16
Ponerinae				
Pachycondyla striata	0	0	1	1
Number of ant records	12	30	39	81
Number of ant species	9	13	18	23
Number of stations with ants	12	23	26	61