E-Natural History Note

Busy Nights: High Seed Dispersal by Crickets in a Neotropical Forest

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abstract: Among invertebrates, ants are the most abundant and probably most important seed dispersers in both temperate and tropical environments. Crickets, also abundant in tropical forests, are omnivores and commonly attracted to fruits on the forest floor. However, their capability to remove seeds has been reported only once. We compared Marantaceae seed removal by crickets and ants to assess the role of crickets as secondary seed dispersers in Amazonia. Compared with ants, crickets dispersed an equivalent number of seeds and tended to disperse larger seeds farther. However, seed removal by crickets occurs mostly at night, suggesting that removal of arillate seeds by crickets on the tropical forest floor is probably being overlooked or wrongly attributed to other invertebrate groups. One potential consequence of seed dispersal by crickets may be a change in the local spatial distribution of arillate-seed species, due to lower aggregation around ant nests.

Keywords: arillate seeds, Amazonia, seed removal, Orthoptera, Grylloidea, ants.

Introduction

Diplochory is a complex multistage seed dispersion process that relies on two or more dispersal agents (Willson and Traveset 2000; Vander Wall et al. 2005b). Plants that display fleshy diaspores have their dispersal capability enhanced, given the possible presence of animals as dispersal vectors in subsequent phases of diplochory (Jordano et al. 2007; Traveset et al. 2014). In tropical forests, more than 80% of woody plants are primarily dispersed by frugivore vertebrates (Gentry 1982), which, in most cases, are followed by a second movement of seeds by invertebrates (secondary seed dispersal). Secondary seed dispersal by invertebrates is one of the described types of diplochory (Vander Wall and Longland 2004; Christianini and Oliveira 2009;

García-Robledo and Kuprewicz 2009). The combination of multiple biotic dispersers results in complementary processes, given that each vector disperses a different number of seeds to a different microhabitat a different distance away (Beckman and Rogers 2013). Ultimately, the differences in the quantity and distance of seeds dispersed by multiple vectors is reflected in the shape and scale of the seed spatial distribution, or seed shadow (Horvitz and Le Corff 1993; Clark et al. 2005; Cortês and Uriarte 2012). Disentangling the effects of multiple disperser agents is a challenge for seed dispersal ecologists and, essentially, depends on our natural history knowledge of which organisms remove the seeds and how they do so.

As primary dispersers, frugivore vertebrates are key to structuring plant recruitment at different scales, in addition to promoting the colonization of new environments due to their capacity for dispersing seeds farther (>100 m) from the source (Fragoso 1997; Jordano 2007). Occasionally, dispersed diaspores remain in the vicinity of the parent plant or reach the floor with their fleshy part intact, partially consumed, or in vertebrate feces (Jordano and Schupp 2000; Christianini and Oliveira 2009). Those dispersed diaspores become available to the invertebrate community that can either prey on or act as secondary seed dispersers, causing a rearrangement of the vertebrate seed shadows (Vander Wall et al. 2005a). Secondary seed dispersal influences plant population and recruitment on the local scale, enhancing the chances of a plant escaping from predators and reaching the best microsites for seedling establishment (Vander Wall and Longland 2004). Among invertebrate dispersal agents, ants are important primary seed dispersers in both temperate and tropical environments. Myrmecochorous plants are common in arid zones (Bond et al. 1991; Giladi 2006; Boulay et al. 2007) and as herbs in tropical forests (Horvitz 1981). However, for most tropical vegetation, ants act mainly as secondary dispersers of diaspores primarily dispersed by frugivore vertebrates (Pizo et al. 2005; García-Robledo and Kuprewicz 2009; Santana et al. 2013). Seeds bearing lipid-rich arils, a highly attractive struc-

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ture, enhance the removal of seeds by ants on the forest floor (Bieber et al. 2013; Santana et al. 2013). In the past three decades, an increasing number of postdispersal seed removal studies have highlighted the impact of invertebrates in the second phase of seed dispersal.

Given the diversity and abundance of invertebrates on tropical forest floors, it is possible that other invertebrate groups also act as secondary seed dispersers, and some studies already pointed to New Zealand weta, slugs, and crickets as such (Dutie et al. 2006; Türke et al. 2012; Sidhu and Datta 2015). Large-bodied orthopterans called weta (Anostostomatidae) can disperse seeds by endozoochory and enhance seed germination after gut passage (King et al. 2011). Crickets (Orthoptera: Grylloidea) are considered to be omnivores and are commonly attracted to fallen leaves, fruits rich in glucids, and seeds (Szinwelski et al. 2015), but their role as seed dispersers is still poorly explored (but see Sidhu and Datta 2015). The low frequency of records of crickets in seed removal may reflect a bias toward observation periods, given that crickets are mostly active at night (Desutter-Grandcolas 1995), and most seed removal experiments with direct observations of invertebrate-seed interactions focus on diurnal trials. Even so, crickets have been observed interacting with fruits on the floors of tropical forests (Christianini and Oliveira 2010; Bieber et al 2013), but in such interactions they did not remove seeds.

During fieldwork in central Amazonia, frequent interactions between crickets and Marantaceae arillate seeds came to our attention, raising questions about the implications of those interactions on the seed shadow and plant spatial structure. In this study, we compared seed removal by crickets and ants to measure their potential role as secondary seed dispersers of Marantaceae species in Central Amazonia. The study aimed to answer the following questions: (1) Do ants and crickets differ in the number and size of seeds that they remove? (2) Do crickets remove more seeds at night compared to ants? (3) Does the distance of seed removal by ants and crickets differ?

Material and Methods

Study Area

The study was carried out at Reserva Ducke, a 10,000-ha (10 × 10-km) protected area 26 km north of Manaus, Brazil (lat. 02°55′–03°01′S, long. 59°53′–59°59′W), in central Amazonia. The site is covered by terra firme tropical moist forest with a 30- to 37-m-tall canopy. The heterogeneous landscape of Reserva Ducke is formed by a moderately rugged terrain generating a soil gradient from high percentages of clayey yellow latosol in the upland areas (plateau) toward less clayey red-yellow soils on the slopes, until the wet and sandy podzol soils of the valleys, which feature small peren-

nial streams (Chauvel et al. 1987). Mean annual temperature is 26°C, and annual rainfall is ~2,400 mm, with a monthly maximum of ~330 mm in March and a minimum of <100 mm in August (Marques-Filho et al. 1981). The site is subdivided by an 8 × 8-km grid system for long-term ecological studies, with trails spaced 1 km apart.

The present study was carried out in nine 10 × 100-m plots within a 2 × 2-km portion of the grid. Three plots were placed on each of the main topographical microhabitats: plateaus, slopes, and valleys. Although possible seed dispersal variation related to topography is not the main focus of this study, the plot distribution aimed to cover the natural habitat heterogeneity and to avoid any bias in ant and cricket distribution.

Plant Species

Marantaceae is the most conspicuous group within the understory herb community of Reserva Ducke, representing 36.5% of the total herb cover with 22 species (Costa 2006). The diaspores of Marantaceae species are characterized by a seed bearing a lipid-rich aril that is mainly dispersed by ants and birds (Horvitz 1991). We chose four Marantaceae species with contrasting primary dispersal syndromes and seed mass: *Goeppertia altissima* (dispersed by birds) and *Ischnosiphon arouma* (dispersed by unknown vertebrate) produce large seeds (>0.3 g), while *Monotagma densiflorum* and *Monotagma spicatum* (both dispersed by ants) produce small seeds (<0.07 g; fig. 1). Vertebrate frugivores were observed only once, when a thrushlike Schiffornis (*Schiffornis turdina*) was manipulating *G. altissima* seeds (F. D. Santana, unpublished data). The total number of seeds per infructescence differs greatly among species and ranges from 3–10 seeds in *I. arouma*, 7–40 seeds in *G. altissima*, 15–40 seeds in *M. densiflorum*, and 30–70 seeds in *M. spicatum*. However, there is a gradual maturation in the seeds within the infructescence, and just a few become available for dispersal at the same time (F. D. Santana, personal observation).

Seed Removal Experiments

We collected mature seeds (10–20) directly from the infructescence of several individuals, aiming to use them in removal experiments. In each plot, seeds were placed directly on the ground, at least 10 m apart, at three observation points next to adult individuals of the focal species. If a plot did not contain any adult individuals, seeds were placed at random locales respecting the minimum distance of 10 m. The number of seeds per observation point was standardized for each species and ranged between two and five, based on the variable abundance of seeds of the different species. Observations were performed in all plots for 2 h during two periods: diurnal, between 08:00 and 17:00, and nocturnal,

Plant Species	Diaspore characteristic	Potential primary disperser	Weight (g) mean (SD)	Length (cm) mean (SD)	Width (cm) mean (SD)	Seed size	Diaspores
Monotagma densiflorum (Körn.) K.Schum.	dark seed with white aril	ant	0.055 (0.008)	1.341 (0.138)	0.300 (0.061)	small	
Monotagma spicatum (Aubl.) J. F. Macbr.	dark seed with white aril	ant	0.067 (0.014)	0.950 (0.050)	0.264 (0.048)	small	
Goeppertia altissima (Poepp. & Endl.) Borchs. & S. Suárez	Blue seed with white aril in an orange capsule	bird	0.347 (0.052)	1.090 (0.142)	0.853 (0.109)	large	
Ischnosiphon arouma (Aubl.) Körn.	dark seed with white aril and strong smell	small mammal or bat	0.348 (0.053)	2.253 (0.153)	0.570 (0.094)	large	

Figure 1: Summary of the main characteristics of the four Marantaceae plant species used in this study. Diaspores are represented in the same scale.

between 18:30 and 01:00. To facilitate visualization during night trials, all seeds were painted with a solution of fluorescent pigment powder diluted in acetone (Reiter et al. 2005) the day before the experiment. A previous experiment showed that painted seeds did not affect how they were treated by ants and crickets (figs. 2*A*, A1; figs. A1, D1 available online). Observation points were constantly monitored by an observer who took notes of all interactions between invertebrates and seeds. In a seed removal event, the invertebrate was followed until the deposition of the seed in the ground, the animal reached its nest (in the case of ants), or the seeds were lost from sight. Measurement of the removal distance was between the observation point and the last known location of the seed at the end of the 2 h of observation. One specimen from each ant and cricket species involved in seed removal was collected whenever possible. We also used images of the seed removal events to help in the identification of species in cases when it was not possible to collect a specimen.

Statistical Analysis

We used generalized linear mixed models (GLMM) available in the gamlss package of R 3.2.3 (R Core Team 2016) to answer our three questions. The fixed effects in the models were disperser agent (ant or cricket), seed weight (representing the mean weight value of each plant species as presented in fig 1), and period of day (day or night). In model 1, we evaluated whether the number of seeds removed was explained by the dispersal agent, the mean weight of seeds, and their interaction. In model 2, we evaluated whether the number of seeds removed was explained by the dispersal agent, the period of day, and their interaction. In model 3, we evaluated whether the distance of seed removal was explained by the dispersal agent, the mean weight of seeds, and their interaction. We fitted GLMMs with Poisson error distribution for models 1 and 2 and gamma error distribu-

tion for model 3. Data analyzed in this manuscript are deposited in the PPBio, MetaCat Repository: https://ppbiodata.inpa.gov.br/metacatui/#view/PPBioAmOc.56.6 (Santana and Costa 2016).

Results

We used 648 seeds of the four Marantaceae species in the removal experiments, and 21% ($n = 136$) of those seeds were removed by ants and crickets. Besides those removed by ants and crickets, 5 seeds were removed by other invertebrates such as cockroaches ($n = 4$) and spiders ($n = 1$), but those records were not included in data analyses. Seed removal was performed by 16 ant and 6 cricket species (table B1, available online). The removal behavior of ants varied according to the species, being basically of two types: (i) seed removal followed by aril consumption out of the nest performed by ant species that recruit to food source, such as *Pheidole* and *Solenopsis*; and (ii) seed removal to the nest by solitary foragers of *Ectatomma* and *Pachycondyla* species. Cricket species varied greatly in morphology and body size (fig. 2), but their behavior toward seeds was remarkably similar. Generally, crickets removed seeds and then consumed the aril (fig. 2*C*–2*F*; video C1, available online), and the predation of seed after removal was observed in only a single event.

Among crickets, *Luzarida lata* removed most of the seeds, followed by *Luzaridella* sp. Crickets and ants were sometimes seen simultaneously at the same observation point during the experiments, and in some events, they removed the same seed at different times. The crickets' maximum dispersal distance was 80 cm, which was around half the maximum distance observed for seeds dispersed by ants (fig. 3*A*).

Ants and crickets removed seeds of all four studied plant species (fig. 3*B*), and the proportion of removal events was approximately the same, around 56.6% ($n = 77$) by ants
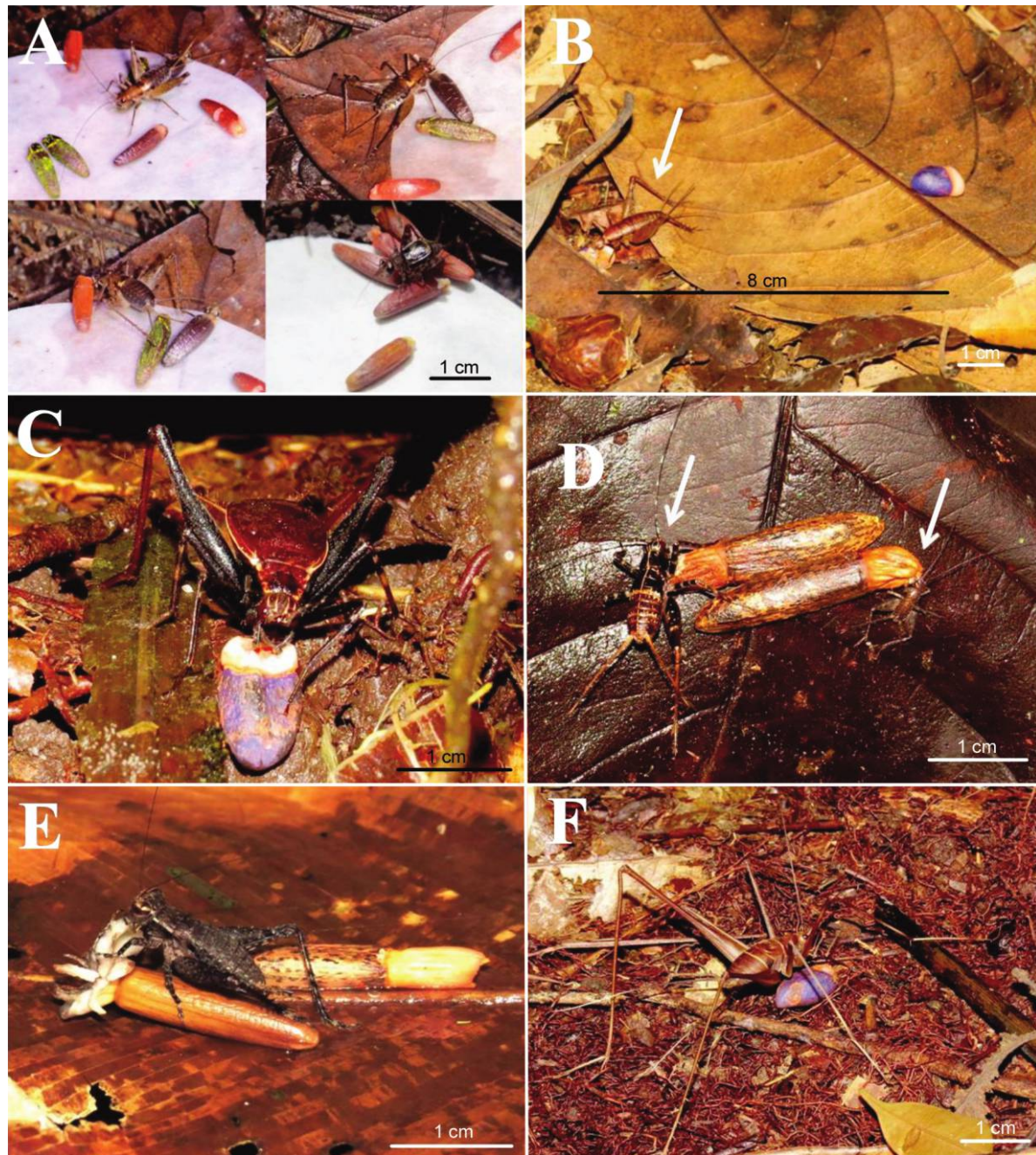
Figure 2: Interactions between crickets and seeds of Marantaceae species. *A,* Trial experiment using *Monotagma spicatum* seeds that showed that the painted seeds with fluorescent ink did not interfere with the disperser-seed interactions (see also app. C for further details). *B,* Seed removed by female of *Luzaridella sussura* cf.; distance = 8 cm. *C,* Male of *Luzarida lata* and *Goeppertia altissima* seed. *D, Hygronemobius* sp. and *Luzarida* sp. cf. with *Ischnosiphon arouma* seeds; *E, Hygronemobius* sp. cf. with *I. arouma* seeds; *F, Phalangopsis* sp. and seed of *G. altissima.* Photos by F. D. Santana.

and 43.4% ($n = 59$) by crickets ($\chi^2 = 36$, df $= 30$, $P = .208$). Seed removal was not, however, evenly distributed among plant species. Ants removed more seeds of *Monotagma densiflorum* (small seed) and *Ischnosiphon arouma* (large seed), while crickets removed more seeds of *Goeppertia*

altissima (large) and *Monotagma spicatum* (small; fig. 3*B*). Seed weight influenced seed removal, and both disperser groups tended to remove more small seeds (table 1, model 1; fig. D1*A*). There was a tendency for crickets to remove larger seeds more frequently than ants (fig. 1*D*); however, the interaction be-

Table 1: Summary of the generalized linear mixed models comparing seed removal by ants and crickets in an Amazonian forest

Model, variable	Coefficient B	$\Pr(>|t|)$
Model 1:		
(Intercept)	1.17	<.01**
Disperser	−.54	.04*
Weight	−5.03	.01*
Disperser : weight	1.77	.17
Model 2:		
(Intercept)	5.82	.001***
Disperser	−4.92	.001***
Period	−3.41	.001***
Disperser : period	2.79	.001***
Model 3:		
(Intercept)	6.35	.001***
Disperser	−2.10	.001***
Weight	−13.18	.001***
Disperser : weight	7.81	.001***

Note: Plant species was set as a random factor in all models.

* $P < .05$.

** $P < .01$.

*** $P \leq .001$.

tween seed weight and crickets was not significant (table 1). Crickets removed more seeds at night compared to ants (fig. 3*C*). Indeed, the time of day was an important effect for explaining the number of seeds removed (table 1, model 2) by each disperser group (fig. D1*B*). On average, ants removed seeds longer distances (mean = 39.31 cm, range = 2–226 cm) than crickets (mean = 13.83 cm, range = 3–80 cm; fig. 3*D*). However, the distance of seed removal by crickets and ants also differed according to plant species and seed size (table 1, model 3; fig. D1*C*), ants moved small seeds farther than crickets, and crickets moved large seeds farther than ants (fig. 3*D*).

Discussion

Crickets are known predators of fallen leaves, fruits, and seeds (Szinwelski et al. 2015), and records of seed removal by crickets are rare and involve one particular species (Sidhu and Datta 2015). However, to our knowledge, the role of assemblages of crickets acting as secondary seed dispersers has not been reported. Our study showed that crickets consume only the aril of arillate seeds and abandon the seed in another location, acting as secondary dispersers. Crickets removed the same amount of seeds as ants of all four studied Marantaceae species, indicating that seed removal by crickets on the forest floor is common. The number of seeds removed by crickets was not affected by seed weight for the studied species, but crickets removed larger seeds farther than ants.

The role of crickets as seed dispersers remains little explored or is largely unknown. The New Zealand weta is the only orthopteran group widely recognized as seed dispersers (Dutie et al. 2006). However, wetas consume the entire seed, and some of them escape from the gut passage in conditions to germinate (Dutie et al. 2006). In a recent report, Sidhu and Datta (2015) showed that the Indian cricket *Brachytrupes* sp. was responsible for approximately 30% of secondary seed removal. Seeds removed by crickets were buried underground and had a higher germination rate when compared to seeds found by rodents, which acted as seed predators (Sidhu and Datta 2015). Our data suggest that at least six cricket species act as dispersers, removing seeds from the surface of the leaf litter after they fall directly from the parent plant. Sidhu and Datta (2015) used in their experiments seeds with the aril removed, and therefore, they were not able to observe aril consumption as shown here. Consumption of the aril can be considered a benefit for plant species with fleshy diaspores when this activity decreases seed attack by fungi and pathogens (Ohkawara and Akino 2005).

Our study shows that there is a temporal partitioning of seed removal by ants and crickets. Although some ant species of Ectatomminae and Ponerinae subfamilies forage more actively at night (Pizo et al. 2005; Santana et al. 2013), most of the species that interacted with the seeds during this study were more frequently observed during the day. Conversely, we recorded a higher occurrence of crickets during nocturnal seed removal experiments. Therefore, increasing the number of experiments for direct observation of seed removal by invertebrates in the nocturnal period will probably generate a better picture of the role of crickets in seed dispersal of arillate seeds.

On average, crickets did not transport seeds farther than ants. However, there was indication that large seeds of *G. altissima* and *I. arouma* were removed greater distances by crickets (fig. 3*D*). These results suggest that crickets may affect the local seed distribution of herb species that produce seeds too heavy to be carried by ants (Gómez et al. 2005), changing their dispersal kernel. Body size of crickets may vary 16 mm among species and around 5 mm within the same species during their life cycle (Mews and Sperber 2008; Gorochov 2014), so their effects on dispersal distance may be more variable than we report here. Invertebrates such as ants and crickets act at local scales (mean radius <5 m), but their seed removal distances, even if apparently small, represent enough escape from under the parent canopy for herbs that are mostly ~1 m high (except for *I. arouma*, which averages 2 m high). For some plant species, habitat quality where seeds arrive is more important than dispersal distance per se (Schupp et al. 2010), especially in patchier environments such as tropical forests.

Besides their differences in distance of seed removal, ants and crickets also disperse seeds differently. It is known
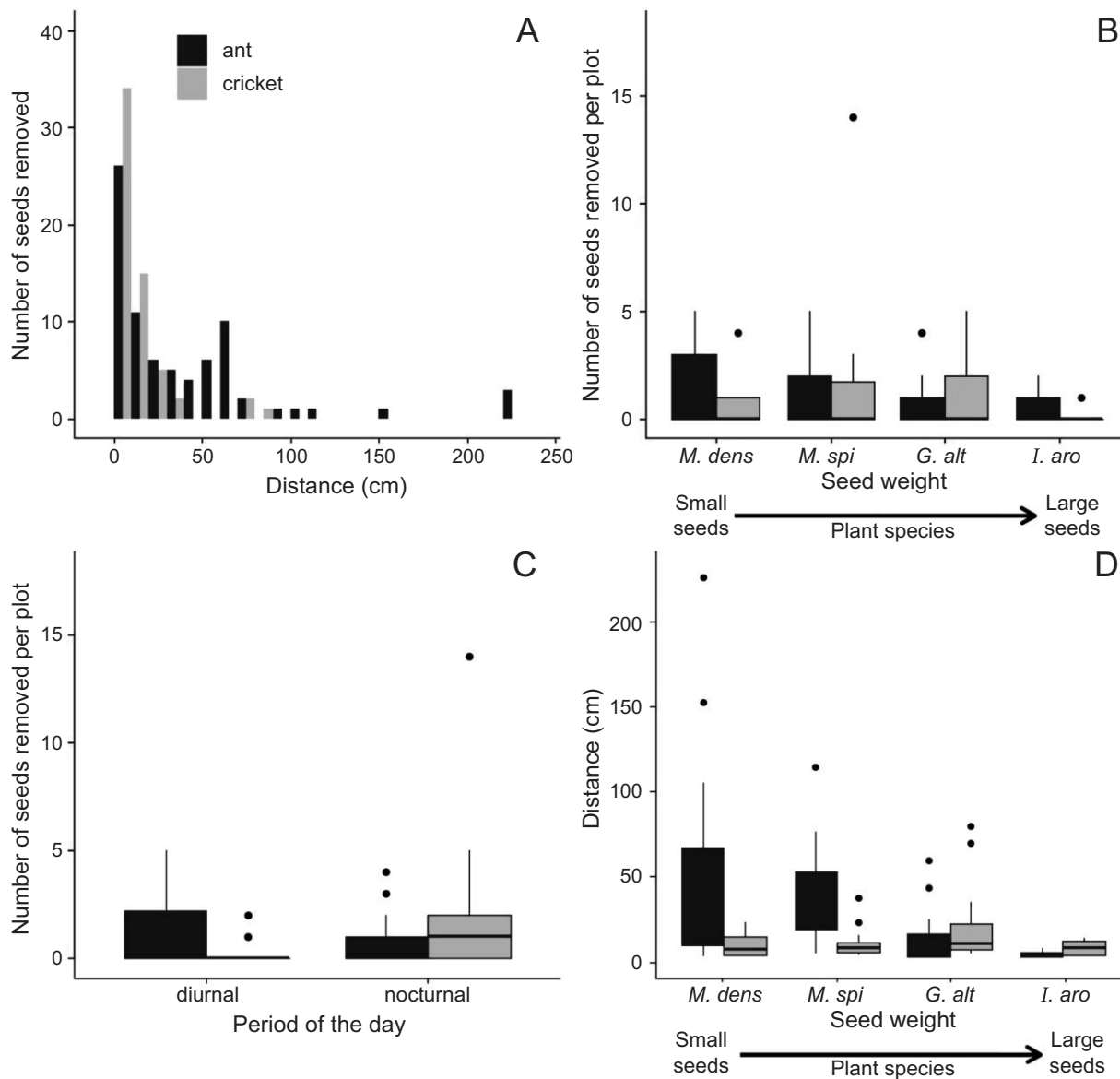
Figure 3: Seed dispersal by ants and crickets in the Amazonian forest. *A*, Range of seed removal distances. *B*, Number of seeds removed per plot among plant species. *C*, Differences in number of seeds removed during each period. *D*, Variation in seed removal distance among plant species. The line near the middle of the boxplot represents the median, and those at the bottom and top of the box represent the 25th and 75th percentiles, respectively. Extreme data are represented by black circles. Plant species are ordered by seed mean weight values. *M. dens* = *Monotagma densiflorum*; *M. spi* = *Monotagma spicatum*; *G. alt* = *Goeppertia altissima*; *I. aro* = *Ischnosiphon arouma*.

that in the ant-seed interaction, the final destination of the seed tends to be the ant nest (Leal et al. 2007; Servigne and Detrain 2008), resulting in plant recruitment concentrated around nests (Horvitz and Schemske 1994; Passos and Oliveira 2002). This generates an aggregated spatial pattern at small scales. The impacts of seed aggregation were not specifically explored for our studied species, however, aggregated seed dispersal may in some cases be responsible for

increases in denso-dependent mortality caused by the spread of pathogens (Spiegel and Nathan 2010; Beckman and Rogers 2013). Crickets, however, forage individually and have an errant behavior, resulting in a multidirectionally scattered seed shadow, which may be advantageous in decreasing the negative effects of seed aggregation. However, ant nests may provide a better germination site (Passos and Oliveira 2002), so the consequences of the combination of ant and cricket

dispersal for plant recruitment should still be examined. As seen here, crickets may have a complementary role on the dispersal process of vertebrate- and ant-dispersed species, potentially modifying spatial population patterns.

Our results show that crickets remove similar amounts of arillate seeds compared to ants, suggesting that the removal of arillate seeds by crickets on the tropical forest floor is being overlooked or wrongly attributed to other invertebrate groups. Given that interactions between crickets and seeds involved more than one species and the high diversity and abundance of cricket species in Neotropical forests (Desutter-Grandcolas 1992), it is possible that additional cricket and plant species interactions will be identified, especially if nocturnal experiments become a common practice.

Acknowledgments

Literature Cited

Beckman, N. G., and H. S. Rogers. 2013. Consequences of seed dispersal for plant recruitment in tropical forests: interactions within the seedscape. Biotropica 45:666–681.

Bieber, A. G. D., P. S. D. Silva, and P. S. Oliveira. 2013. Attractiveness of fallen fleshy fruits to ants depends on previous handling by frugivores. Ecoscience 20:85–89.

Bond, W. J., R. Yeaton, and W. D. Stock. 1991. Myrmecochory in Cape fynbos. Pages 448–462 in C. R. Huxley and D. F. Cutler, eds. Ant-plant interactions. Oxford University Press, New York.

Boulay, R., J. Coll-Toledano, A. J. Manzaneda, and X. Cerdá. 2007. Geographic variations in seed dispersal by ants: are plant and seed traits decisive? Die Naturwissenschaften 94:242–246.

Chauvel, A., Y. Lucas, and R. Boulet. 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. Experimentia 43:234–241.

Christianini, A. V., and P. S. Oliveira. 2009. The relevance of ants as seed rescuers of a primarily bird-dispersed tree in the Neotropical cerrado savanna. Oecologia (Berlin) 160:735–745.

———. 2010. Birds and ants provide complementary seed dispersal in a Neotropical savanna. Journal of Ecology 98:573–582.

Clark, C. J., J. R. Poulsen, B. M. Bolker, E. F. Connor, and V. T. Parker. 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. Ecology 86:2684–2694.

Cortês, M. C., and M. Uriarte. 2012. Integrating frugivory and animal movement: a review of the evidence and implications for scal-ing seed dispersal. Biological Reviews of the Cambridge Philosophical Society 88:255–272.

Costa, F. R. C. 2006. Mesoscale gradients of herb richness and abundance in central Amazonia. Biotropica 38:711–717.

Desutter-Grandcolas, L. 1992. Les Phalangopsidae de Guyane française (Orthoptères, Grylloidea): systématique, éléments de phylogénie et de biologie. Bulletin du Muséum national d'Histoire naturelle 14: 93–177.

———. 1995. Toward the knowledge of the evolutionary biology of phalangopsid crickets (Orthoptera: Grylloidea: Phalangopsidae): data, questions and evolutionary scenarios. Journal of Orthoptera Research 4:163–175.

Dutie, C., G. Gibbs, and K. C. Burns. 2006. Seed dispersal by weta. Science 311:1575.

Fragoso, J. M. V. 1997. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. Journal of Ecology 85:519–529.

García-Robledo, C., and E. K. Kuprewicz. 2009. Vertebrate fruit removal and ant seed dispersal in the Neotropical ginger *Renealmia alpinia* (Zingiberaceae). Biotropica 41:209–214.

Gentry, A. H. 1982. Patterns of Neotropical plant species diversity. Pages 1–84 in M. K. Hecht, B. Wallace, and E. T. Prance, eds. Evolutionary biology. Vol. 15. Springer, Boston.

Giladi, I. 2006. Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. Oikos 3:481–492.

Gómez, C., X. Espadaler, and J. M. Bas. 2005. Ant behaviour and seed morphology: a missing link of myrmecochory. Oecologia (Berlin) 146:244–246.

Gorochov, A. V. 2014. Classification of the Phalangopsinae subfamily group, and new taxa from the subfamilies Phalangopsinae and Phaloriinae (Orthoptera: Gryllidae). Zoosystematica Rossica 23:7–88.

Horvitz, C. C. 1981. Analysis of how ant behaviors affect germination in a tropical myrmecochore *Calathea microcephala* (P. & E.) Koernicke (Marantaceae): microsite selection and aril removal by Neotropical ants, *Odontomachus*, *Pachycondyla*, and *Solenopsis* (Formicidae). Oecologia (Berlin) 51:47–52.

———. 1991. Light environments, stage structure, and dispersal syndromes of Costa Rican Marantaceae. Pages 463–485 in C. R. Huxley and D. F. Cutler, eds. Ant-plant interactions. Oxford University Press, New York.

Horvitz, C. C., and J. Le Corff. 1993. Spatial scale and dispersion pattern of ant- and bird-dispersed herbs in two tropical lowland rain forests. Pages 351–362 in T. H. Fleming and A. Estrada, eds. Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer Academic, Belgium.

Horvitz, C. C., and D. W. Schemske. 1994. Effects of dispersers, gaps, and predators on dormancy and seedling emergence in a tropical herb. Ecology 75:1949–1958.

Jordano, P. 2007. Frugivores, seeds and genes: analysing the key elements of seed shadows. Pages 229–251 in A. Dennis, R. Green, E. W. Schupp, and D. Wescott, eds. Frugivory and seed dispersal: theory and applications in a changing world. CABI, Wallingford.

Jordano, P., C. García, J. Godoy, and J. L. García-Castaño. 2007. Differential contribution of frugivores to complex seed dispersal patterns. Proceedings of the National Academy of Sciences of the USA 104:3278–3282.

Jordano, P., and E. W. Schupp. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. Ecological Monographs 70:591–615.

King, P., L. Milicich, and K. C. Burns. 2011. Body size determines rates of seed dispersal by giant king crickets. Population Ecology 53:73–80.

Leal, I. R., R. Wirth, and M. Tabarelli. 2007. Seed dispersal by ants in the semi-arid Caatinga of north-east Brazil. Annals of Botany 99: 885–894.

Marques-Filho, A. O., M. N. G. Ribeiro, H. M. Santos, and J. M. Santos. 1981. Estudos climatológicos da Reserva Florestal Ducke. IV. Precipitação. Acta Amazônica 11:759–768.

Mews, C. M., and C. F. Sperber. 2008. Two new species of *Phalangopsis* Serville, 1831 (Orthoptera: Grylloidea: Phalangopsidae) from Brazilian Amazon Forest. Annals of the Brazilian Academy of Sciences 80:647–655.

Ohkawara, K., and T. Akino. 2005. Seed cleaning behavior by tropical ants and its anti-fungal effect. Journal of Ethology 93–98.

Passos, L., and P. S. Oliveira. 2002. Ants affect the distribution and performance of seedlings of *Clusia criuva*, a primarily bird-dispersed rain forest tree. Journal of Ecology 90:517–528.

Pizo, M. A., L. Passos, and P. S. Oliveira. 2005. Ants as seed dispersers of fleshy diaspores in Brazilian Atlantic forests. Pages 315–329 *in* P.-M. Forget, J. E. Lambert, P. E. Hulme, and S. B. Vander Wall, eds. Seed fate: predation, dispersal, and seedling establishment. CABI, Wallingford.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/.

Reiter, J., E. Curio, B. Tacud, H. Urbina, and F. Geronimo. 2005. Tracking bat-dispersed seeds using fluorescent pigment. Biotropica 38:64–68.

Santana, F. D., E. Cazetta, and J. H. C. Delabie. 2013. Interactions between ants and non-myrmecochorous diaspores in a tropical wet forest in southern Bahia, Brazil. Journal of Tropical Ecology 29:71–80.

Santana, F. D., and F. Costa. 2016. Data from: Seed removal experiments by invertebrates of four Marantaceae species. PPBio, Meta Cat repository, PPBioAmOc.56, https://ppbiodata.inpa.gov.br/metacatui/#view/PPBioAmOc.56.6.

Servigne, P., and C. Detrain. 2008. Ant-seed interactions: combined effects of ant and plant species on seed removal patterns. Insectes Sociaux 55:220–230.

Schupp, E., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188:333–353.

Sidhu, S., and A. Datta. 2015. Tracking seed fates of tropical tree species: evidence for seed caching in a tropical forest in northeast India. PLoS ONE 10:e0134658.

Spiegel, O., and R. Nathan. 2010. Incorporating density dependence into the directed-dispersal hypothesis. Ecology 91:1538–1548.

Szinwelski, N., C. S. Rosa, R. R. de C. Solar, and C. F. Sperber. 2015. Aggregation of cricket activity in response to resource addition increases local diversity. PLoS ONE 10:e0139669.

Traveset, A., R. Heleno, and M. Nogales. 2014. The ecology of seed dispersal. Pages 62–93 *in* R. S. Gallagher, ed. Seeds: the ecology of regeneration in plant communities. CABI, Wallingford.

Türke, M., K. Andreas, M. M. Gossner, E. Kowalski, M. Lange, S. Boch, S. A. Socher, et al. 2012. Are gastropods, rather than ants, important dispersers of seeds of myrmecochorous forest herbs? American Naturalist 179:124–131.

Vander Wall, S. B., and W. S. Longland. 2004. Diplochory: are two seed dispersers better than one? Trends in Ecology and Evolution 19:155–161.

Vander Wall, S. B., K. M. Kuhn, and M. J. Beck. 2005a. Seed removal, seed predation, and secondary dispersal. Ecology 86:801–806.

Vander Wall, S. B., K. M. Kuhn, and J. R. Gworek. 2005b. Two-phase seed dispersal: linking the effects of frugivorous birds and seed-caching rodents. Oecologia (Berlin) 145:282–287.

Willson, M., and A. Traveset. 2000. The ecology of seed dispersal. Pages 85–110 *in* M. Fenner, ed. Seeds: the ecology of regeneration in plant communities. CABI, Wallingford.

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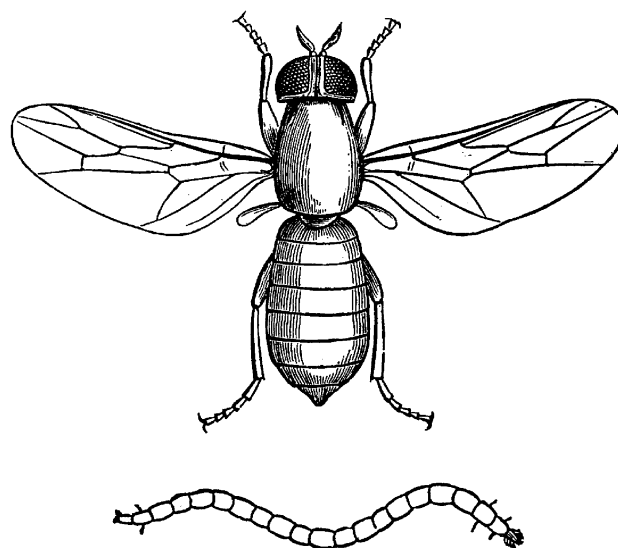
"We turn to a comparatively unknown insect, which has occasionally excited some distrust in the minds of housekeepers. It is the Carpet-fly, *Scenopinus pallipes* Say [*above*], which, in the larva state, is found under carpets, on which it is said to feed. The worm [*below*] has a long, white, cylindrical body, divided into twelve segments, exclusive of the head." From "A Chapter on Flies" by A. S. Packard Jr. (*The American Naturalist* 1869, 2:586–596).