Received: 26 May 2020 | Revised: 29 September 2020 | Accepted: 6 November 2020

DOI: 10.1111/btp.12904

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

ORIGINAL ARTICLE

Can variation in seed removal patterns of Neotropical pioneer tree species be explained by local ant community composition?

Selina A. Ruzi[1] | Paul-Camilo Zalamea[2,3] | Daniel P. Roche[4] | Rafael Achury[5] | James W. Dalling[1,3,6] | Andrew V. Suarez[1,5,7]

[1]Program in Ecology, Evolution, and Conservation Biology, University of Illinois, Urbana, Illinois, USA

[2]Department of Integrative Biology, University of South Florida, Tampa, Florida, USA

[3]Smithsonian Tropical Research Institute, Ancon, Republic of Panama

[4]Wildlife and Fisheries Resources Program, West Virginia University, Morgantown, West Virginia, USA

[5]Department of Entomology, University of Illinois, Urbana, Illinois, USA

[6]Department of Plant Biology, University of Illinois, Urbana, Illinois, USA

[7]Department of Evolution, Ecology, and Behavior, University of Illinois, Urbana, Illinois, USA

Correspondence
Selina A. Ruzi, Program in Ecology, Evolution, and Conservation Biology, University of Illinois, Urbana, IL, USA.
Email: sruzi24@gmail.com

Present address
Selina A. Ruzi, Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina, USA

Funding information
United States Department of Agriculture; National Science Foundation, Grant/Award Number: 120205, 1069157 and 1701501; Dissertation Travel Grant from the University of Illinois

Associate Editor: Jennifer Powers
Handling Editor: Eric Fuchs

Abstract

Many plants depend on animals for seed dispersal, and ants commonly fill this role. We examined whether heterogeneity in ant community composition among sites, between above- and belowground foraging guilds, or between seasons predicts observed variation in seed removal rates for 12 nonmyrmecochorous Neotropical pioneer tree species on Barro Colorado Island, Panama. We also investigated whether ants associated with removing seeds differed in specific morphological characters from the larger ant community. We observed ant–seed interactions at caches to determine which ants removed seeds of 12 tree species. We also sampled ant community composition by placing 315 pitfall traps and 160 subterranean traps across the five sites where seed removal rates were quantified. Aboveground ant community composition varied by site but not season. Among-site variation in ant composition did not predict seed removal patterns at these same sites. Belowground ant communities differed from aboveground ant communities but were not structured by either site or seed cache type. Finally, ants that removed seeds did not differ morphologically from the broader ant community. Overall, our results suggest ant communities vary over relatively small spatial scales but exhibit a high degree of functional redundancy in terms of seed removal services provided for Neotropical pioneer tree species.

Abstract in Spanish is available with online material.

KEYWORDS
Barro Colorado Island, Formicidae, myrmecochory, Panama, pioneer plants, plant communities, secondary dispersal

1 | INTRODUCTION

Dispersal is a key life-history constraint for many species, especially sessile organisms such as plants (Nathan & Muller-Landau, 2000). Neotropical pioneer tree species produce large quantities of small seeds (Dalling et al., 2002), which require high light microsites such as canopy gaps to germinate and grow (Hubbell et al., 1999; Swaine & Whitmore, 1988). Seeds reach these spatially heterogeneous gaps (Martinez-Ramos et al., 1988) either through dispersal or for some species by remaining viable in the soil seed bank for decades (Dalling & Brown, 2009) until a treefall occurs. Seeds in the soil seed bank retain their mobility (Ruzi et al., 2017), experiencing secondary dispersal via animal vectors (e.g., Mull & MacMahon, 1997; Sanchez-Cordero & Martinez-Gallardo, 1998). However, due to differences in seed characteristics that affect their attractiveness to animal vectors (Fornara & Dalling, 2005) and the heterogeneous distribution of seed dispersers (Mull & MacMahon, 1997; Sanchez – Cordero & Martinez-Gallardo, 1998), it is difficult to predict secondary dispersal distributions for Neotropical pioneer trees (Dalling et al., 2002).

Ants are important seed dispersers in many ecosystems (Beattie, 1985; Handel & Beattie, 1990). Ants play a role in both short-distance dispersal and long-distance dispersal (Gómez & Espadaler, 2013), removing seeds from the soil surface where they are more likely to be eaten by granivores (Bond & Slingsby, 1984; Christian & Stanton, 2004; O'Dowd & Hay, 1980), and providing suitable microsites for germination and growth (Culver & Beattie, 1980; Davidson & Morton, 1981; Hanzawa et al., 1988). Some plants encourage seed dispersal by providing an elaiosome attached to their seeds, while others participate in ant-mediated dispersal without providing a food reward (e.g., Anjos et al., 2020; Barroso et al., 2013; Christianini & Oliveira, 2010; Passos & Oliveira, 2002; Pizo & Oliveira, 1998; Magalhães et al., 2018). Even among ants that use seeds as resources, not all ants are attracted equally to seeds of different plant species. In some communities, individual ant species that forage for seeds have disproportionally large effects on plant communities through their dispersal services (Barroso et al., 2013; Youngsteadt et al., 2009).

Vertical stratification of ant communities is well-documented in tropical forests (Weiser et al., 2010; Yanoviak & Kaspari, 2000). In addition to differences between arboreal and surface ant assemblages, ant communities vary greatly among samples collected from the soil surface, the leaf litter, and within the top layers of soil (Jacquemin et al., 2016; Ryder Wilkie et al., 2007, 2010). These assemblages differ in key traits including food preferences (Hahn & Wheeler, 2002; Yanoviak & Kaspari, 2000), mode of resource defense (Yanoviak & Kaspari, 2000), and morphology (e.g., body size distribution; Kaspari & Weiser, 1999). Variation in ant microhabitat preferences, morphological, and ecological traits could result in widely different patterns of seed dispersal over small scales. For example, in addition to varying with microhabitat preference (Kaspari & Weiser, 1999), ant body size is often correlated with seed size (Kaspari, 1996; Pfeiffer et al., 2006) and seed dispersal distance (Gómez & Espadaler, 2013; Ness et al., 2004). Due to differences in ant morphological traits in different microhabitats, ant-mediated seed dispersal should vary both by tree species and the microhabitat in which ants interact with seeds.

In a recent study of 12 Neotropical pioneer species, Ruzi et al. (2017) found that secondary seed removal rates varied among tree species both for seeds deposited on the soil surface and in the topsoil. However, removal rates did not vary between the wet and dry seasons. Here, we combine the observations of seed removal by ants from Ruzi et al. (2017) with a characterization of the foraging above- and belowground ant communities at the same five sites to determine whether seed removal patterns are associated with local ant community structure. Specifically, we ask the following: (a) Does the foraging ant community differ between wet and dry seasons? We predict no change in community composition given the lack of a seasonal effect on seed removal rates (Ruzi et al., 2017); (b) Does variation in ant community composition between microhabitats (soil surface vs. belowground) or among sites correspond with observed variation in seed removal rates? We predict that different microhabitats will have different ant communities based on previous literature demonstrating vertical stratification of ant communities; and (c) Does ant species identity or morphology correspond to variation in seed removal rates among tree species? We predict that associations between ant and tree species will result from variation in morphology, chemistry, and primary dispersal type, and will be reflected in ant morphological characteristics. Overall, we test whether data on ant community composition would be able to accurately predict seed removal in this system, allowing for future studies to make inferences about seed removal with only ant community information.

2 | METHODS

2.1 | Study site and species

The study was performed at five sites on Barro Colorado Island (BCI) (9°10'N, 79°51'W) in the Republic of Panama. BCI is characterized as a seasonal semi-deciduous forest with average annual rainfall of 2,600 mm/year with a pronounced dry season starting late December or early January until late April or early May (Windsor, 1990). Each site was located along a range of soil types in either old growth or secondary deciduous forest (Ruzi et al., 2017; Sarmiento et al., 2017; Zalamea et al., 2015).

We used previously reported data on seed removal from Ruzi et al. (2017). Here, we briefly summarize the methods used to collect those data. We also complemented the data from Ruzi et al. (2017) with observations of ants removing seeds, and collections of both above- and belowground ant communities. Ripe fruits were collected from below parent trees of 12 pioneer species (Table 1). Seeds of these Neotropical pioneer tree species are not known to have elaiosomes or other ant attractants (except for *Guazuma ulmifolia* whose seeds produce mucilage which may be an ant attractant; Escobar-Ramírez et al., 2012). The seeds of these tree species also vary in several characteristics including defense

TABLE 1 Tree species used in the different experiments (A = aboveground, B = belowground), seed traits, and seed removal percentages (mean and standard error) per tree species (aboveground: pooled over dry and wet seasons; belowground: wet season only) for each experiment. Fruit, pulp, or fibers were removed from seeds prior to conducting the experiments

Tree species (species code)	Experiment	Primary dispersal mode	Dormancy type	Fruit/pulp/fibers removed	Seed mass (mg)	Seed persistence (18 months)	Aboveground seed removal mean ± *SE* (%)	Belowground seed removal mean ± *SE* (%)
Apeiba membranacea Aubl. (Ape)	AB	Animal	Physical[a]	x	13.58 ± 1.23	0.75	75.50 ± 6.43	78.00 ± 6.11
Cecropia longipes Pitt. (Cec)	AB	Animal	Quiescent[b]	x	0.9 ± 0.07	0.85	47.00 ± 9.65	63.00 ± 8.44
Cochlospermum vitifolium Willd. (Coc)	A	Wind	Physical[b]	x	24.2 ± 2.27	0.24	20.00 ± 7.81	–
Ficus insipida Willd. (Fic)	A	Animal	Quiescent[b]	x	1.56 ± 0.12	0.46	43.00 ± 9.46	–
Guazuma ulmifolia Lam. (Gua)	A	Animal	Physical[a]		3.38 ± 0.28	0.86	71.00 ± 8.24	–
Hieronyma alchorneoides Allemão (Hie)	A	Animal	Physiological[a]	x	6.55 ± 0.33	0.98	32.50 ± 8.55	–
Jacaranda copaia (Aubl.) D. Don. (Jac)	AB	Wind	Quiescent[b]		1.16 ± 0.18	0.33	20.00 ± 7.40	27.00 ± 8.23
Luehea seemannii Triana and Planch. (Lue)	A	Wind	Physical[a]		1.85 ± 0.3	0.88	12.00 ± 4.84	–
Ochroma pyramidale Urb. (Och)	AB	Wind	Physical[a]	x	5.73 ± 0.29	0.88	66.89 ± 8.01	65.00 ± 10.67
Trema micrantha (L.) Blume "*black*" (TrBl)	AB	Animal	Physiological[a]	x	3.2 ± 0.21	0.97	16.50 ± 6.08	81.00 ± 9.24
Trema micrantha (L.) Blume "*brown*" (TrBr)	A	Animal	Quiescent[b]	x	1.71 ± 0.1	1.00	21.00 ± 7.61	–
Zanthoxylum ekmanii (Urb.) Alain (Zan)	AB	Animal	Physiological[b]		16.2 ± 0.81	1.00	85.50 ± 5.35	41.00 ± 11.87

[a] Sautu et al. (2007).

[b] Zalamea et al. (2018)

syndromes, mass, primary dispersal mode, and dormancy type (Ruzi et al., 2017; Zalamea et al., 2018; Table 1). Fruit, pulp, and fibers were manually removed from seeds prior to presenting them on forest floor (Table 1).

2.2 | Aboveground seed removal and ant community sampling

The aboveground seed removal experiment was conducted once in the dry season and once in the wet season of 2013 following methods in Fornara and Dalling (2005) (see Ruzi et al., 2017). At each of five sites, seeds of the 12 pioneer tree species were placed in seed caches every meter along a 12-m linear transect (dry season, 13-m transect in the wet season) along the edge of a rectangular plot (9 m by 15 m; Figure S1a). Plots were at least 350 m apart (average approx. 800 m) and were at least 20 m away from conspecific adults of the species used in the study. The order the seeds of each tree species were presented along the transect was randomized. Each cache consisted of an inverted Petri dish lid (90 mm diam, 8 mm deep) with 10 seeds of one of the 12 different tree species or 10 silica beads as a control (mass 30.5 ± 0.038 mg, mean ± *SE*; wet season only). Caches were placed under transparent plastic shelters (1.0 m wide x 1.0 m long x 0.5 m tall) to reduce passive removal of seeds by raindrops and forest debris. We replicated this setup twice at each of the five sites in both the dry season and the wet season. Therefore, over both trials, each site had 24 (dry season, no silica bead control cache) to 26 caches (wet season, silica bead control cache included), two caches for each of the 12 tree species, for a total of 120 caches in the dry season and 130 caches in the wet season.

Caches at each site were observed over a 47-hr period. Observations were initiated at 10:00 h on the first day and retrieved at 09:00 h on the third day. Observations of ant removal and number of seeds remaining were recorded hourly on the first and second days from 10:00 h to 16:00 h . Hand samples of ants were collected once ants exited the inverted Petri dish lid or if they were present in large numbers. As a result of collecting ant samples, it is possible that overall removal rates were reduced (see Kaspari, 1993). As observations spanned the 12- to 13-m transect, some seed removal was likely missed. However, the lip of the Petri dish prevented ants from quickly exiting with a seed, increasing handling time and the probability that seed removal would be observed.

We used pitfall traps to sample the aboveground foraging ant community in each of the five sites. Pitfall traps consisted of 50-ml conical centrifuge tubes (28 mm diam. opening) buried so that the lip was flushed to the soil surface and contained 20 ml of preserving fluid (aqueous saturated NaCl solution with a drop of detergent). Each site was sampled twice during the wet season (2013) and twice during the dry season (2014). During each sample period, we placed 15–16 pitfall traps inside the experimental plots. These traps were located within four subplots in a grid pattern (Figure S1a). The traps were collected after 48 hr, and all ants preserved in 95% ethanol. Traps were pooled by site within a season, as the sampling locations within the site were the same and not independent of each other. From here on, we refer to the aboveground ant community as the ants captured by these pitfall traps, though we recognize that pitfall trapping is biased toward collecting ants that walk on the soil surface and not necessarily in the litter itself (Bestelmeyer et al., 2000). Despite this bias in types of ants collected, pitfall trapping allows for easy comparison across multiple sampling sites and investigators. Wet season pitfall traps had small plastic cups inverted and affixed over the trap entrance (but not touching the surrounding soil or leaf litter) to help prevent traps from overflowing with rainwater.

2.3 | Belowground seed removal and ant community sampling

The belowground seed removal experiment was conducted once in the wet season (2013) and used seeds of six tree species (Table 1; Ruzi et al., 2017). At each of the five sites, seven seed caches were buried in random order along a randomly chosen edge of the same rectangular plots in the previous section and left for four weeks. Each cache consisted of a 2 cm deep-by-2.5 cm wide hole that contained 10 seeds of one of the tree species or 10 silica beads covered with sieved sterile soil (autoclaved at 121°C for 2 hr; Figure S1b). We replicated this set up twice at each of the five sites; each site had a total of 14 caches, two for each of six tree species and the silica bead control cache, for a total of 70 caches across all sites.

Belowground seed caches do not allow for direct observations of ants interacting with seeds of each tree species. To sample ants that are potentially responsible for seed removal, we placed two subterranean traps within 10 cm of each cache (Figure S1b). We placed an additional two subterranean traps 1 m away from the seed caches as unbaited controls. We had a total of 16 traps each sample period, or 32 total subterranean traps at each of the five sites. Subterranean traps consisted of 50-ml conical centrifuge tubes with eight approximately 2- to 4-mm holes equidistantly spaced around the side of the tube approximately 2 cm below the top of the lid. The traps were buried so that the cap was flush with the soil surface and contained 20 ml of preserving fluid. Traps were placed at the same time as the seed caches and left out for four weeks (July 12–August 24, 2013). After collection, all ants were preserved in 95% ethanol.

2.4 | Ant identification and size measurements

Ants were identified to genus using Palacio and Fernández (2003), and to species whenever possible using published keys, online resources for identifying ants of Costa Rica (Longino, 2010), and AntWeb.org (2020). For each of the most common species or morphospecies at the soil surface (found in at least 10% of the pitfall

traps at a single site when the seasons were pooled), we measured head width (across the eyes – HW), head length (HL), eye position (EP; calculated as head width minus intraocular width – OW), mandible length (ML), scape length (SL), eye width (EW), eye length (EL), hind femur length (HF), and Weber's length (WL) (Figure S2). These measurements relate to specific ecological functions and how these ants interact with their environment (summarized in Table 2). Each measurement was repeated for at least two ants of each species and three times per specimen, with the average value across all measurements used in analyses (Table S1). All ant species observed removing seeds at the soil surface had the same measurements recorded in the same way. All measurements were done on point-mounted individuals using a Semprex Micro-DRO digital stage micrometer that was accurate to 0.005 mm (Semprex Corporation) connected to a stereomicroscope (Leica MZ 12.5). For dimorphic species (e.g., *Pheidole* spp.), only minors were measured as they are the caste that recruited to the seeds. For polymorphic species, workers were haphazardly picked to be measured. While this sampling is insufficient to capture intraspecific variation, two individuals will still capture meaningful interspecific variation for most ant measurements (Gaudard et al., 2019).

2.5 | Statistical analyses

All statistical tests were conducted in R (version 3.6.1, R Core Team, 2019). Here, ant communities are characterized as the frequency of presence of ants in traps (i.e., the number of traps a forager was present in divided by the number of traps placed) either at the site level (pitfall traps) or per cache type per site (subterranean traps). This considers both the identity of ant species present and the relative activity of foraging ants as higher frequencies of presence (i.e., closer to 1) indicate a more common or more active ant species.

We determined the completeness of sampling of ant species by generating rarefaction and extrapolation estimates for species richness and sample coverage using the *iNEXT* package with q Hill number set to 0 (version 2.0.19, Chao et al., 2014; Hsieh et al., 2016; Hsieh et al., 2019). We also generated species richness estimates using the *ChaoSpecies* function in the *SpadeR* package (version 0.1.1, Chao et al., 2016). Both sample coverage and species richness estimates indicated that adding more samples would have captured more species, though the adequacy of sampling within a season was dependent on site (Figures S3, S4). For all analyses, we use the raw data and not the estimated species richness.

The composition of ant communities collated by season (aboveground experiment only), location within the soil seed bank (wet season only), and tree species (above- and belowground separately) was compared using nonmetric multidimensional scaling (NMDS) and the multi-response permutation procedure (MRPP, with 999 permutations). NMDS and MRPP were conducted using the *metaMDS* and *mrpp* functions in the *vegan* package, respectively (version 2.5–6, Oksanen et al., 2019). The distance matrix was compiled using frequency of presence of ant species in traps and the Bray–Curtis index. As the number of hand-collected samples of ant species observed removing species was low, hand samples of ants removing seeds were not included in NMDS or MRPP analyses except for the aboveground analysis of ant community composition by tree species. The frequency of presence in a hand sample community

TABLE 2 Ant morphological traits and their proposed ecological functions based on the literature (summarized in Parr et al., 2017 and references within). Eigenvectors were calculated from the log-transformed morphological measurements as well as the standard deviation, contribution, and total observed variation for the first two principal components (PCs)

		Principal components	
Trait	**Related function**	**PC1**	**PC2**
Head width (HW)	Indicative of how much musculature there is for the mandibles, worker body size, and the size gaps workers can pass through	−0.3386	−0.2386
Head length (HL)	May relate to diet and also indicates worker body size	−0.3370	−0.2818
Eye position (EP; calculated as HW – intraocular width)	Indicative of hunting ability and habitat used	−0.3300	0.2843
Mandible length (ML)	Related to diet	−0.3311	−0.3982
Scape length (SL)	Sensory ability	−0.3385	0.0192
Eye width (EW)	Food searching behavior and activity times	−0.3284	0.4697
Eye length (EL)	Food searching behavior and activity times	−0.3157	0.5746
Hind femur (HF)	Foraging speed and complexity of habitat	−0.3383	−0.1574
Weber's length (WL)	Corresponds to worker body size which also related to metabolic traits	−0.3416	−0.2199
Standard deviation	–	2.8745	0.6699
Proportion of variance	–	0.9181	0.04987
Cumulative proportion	–	0.9181	0.9679

was calculated by taking the number of time periods in which a forager of an ant species was observed removing a seed and dividing by the total number of time periods in which there was a change in daytime (between 10:00 h and 16:00 h) hourly seed count. Based on this definition, the total number of time periods foragers could have been present varied depending on the tree species, site, and season.

To determine whether ant community composition can predict seed removal, we used partial least squares regression (PLS-R, Mevik & Wehrens, 2007) using the *plsr* function in the *pls* package (version 2.7–2, Mevik et al., 2019). The frequency of presence of foragers of each ant species in traps was used as the predictor variables (where each ant species was a different variable) with the percent of seed removal as the response variable. PLS-R reduces the number of predictor variables into components that explain as much variation in the response variable as possible, making it robust to many predictor variables with few observations (StatSoft, 2013). Additional components were added if they increased the amount of explained variance of the response variable by at least 5% to maximize the predictive ability of the models, while keeping the root-mean-square error of prediction (RMSEP) low. RMSEP values have the same units as the response variable; therefore, both RMSEP and the response variable range from 0 to 100. Higher RMSEP values indicate lower accuracy and reduced utility of predicting the response variable of future tests.

To assess whether ant communities at sites were clustered, we used agglomerative hierarchical cluster analyses using the beta-flexible method (b = −0.25) and the Bray–Curtis index. These analyses used the *agnes* function in the *cluster* package (version 2.1.0, Maechler et al., 2019). Final dendrograms were visualized using *ggplot2* (version 3.2.1, Wickham, 2016), *ggdendro* (version 0.1–20, de Vries & Ripley, 2016), and *dendextend* (version 1.13.2, Galili, 2015) packages. Once visual groups were determined with the dendrogram, MRPPs were conducted to determine whether the visual groupings were significantly different from each other.

Morphological traits for ant species were reduced to two principal components (PCs) using a principal component analysis (PCA) using the *prcomp* function in the base *stats* package. All nine morphological measurements were included in the PCA and were log-transformed and standardized prior to analyses. The ant species were categorized into two groups: (a) those removing seeds and (b) those common in pitfall traps (present in at least 10% of traps at one site when seasons were pooled) but not observed removing seeds. To determine whether there were morphological differences between groups, an analysis of variance (ANOVA) was conducted on the loadings on the first two principal components separately using the *aov* function.

3 | RESULTS

We identified 69 ant species belonging to 30 genera and 6 subfamilies from samples taken of ants removing seeds (dry and wet season, 13 species), pitfall traps (dry and wet seasons, 59 species), and subterranean traps (wet season only, 20 species) (Table S2). There were 158 daytime (between 10:00 h and 16:00 h) intervals that had a recorded change in hourly seed count (5.89% of all daytime intervals with seeds remaining). Ants were present at 75 of these 158 (47.5%) times and observed removing seeds 61 of these 158 (38.6%) times.

3.1 | Effect of season and microhabitat on ant communities

There was no effect of season on the ant communities captured in pitfall traps during the dry and wet season (five sites) (NMDS: stress = 0.075; MRPP: strata = fixed by site, A = 0.003, p = 0.06; Figure S5).

There was an effect of microhabitat (i.e., pitfall traps aboveground versus subterranean traps belowground) on ant community composition (5 pitfall sites versus 36 cache types across 5

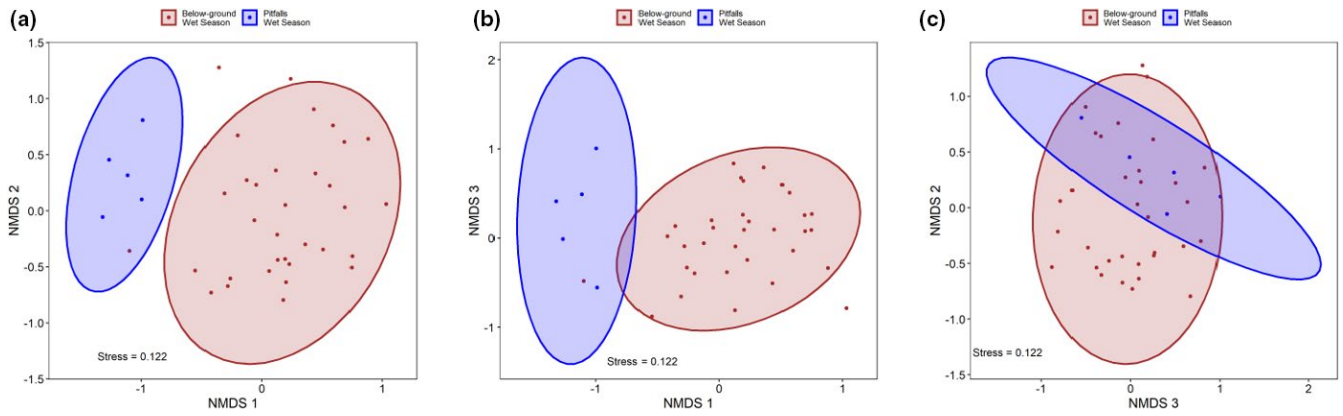

FIGURE 1 Nonmetric multidimensional scaling (NMDS) depicting the relationship between ant communities (points) found in the wet season pitfall or subterranean traps for NMDS axes 1 and 2 (a), axes 1 and 3 (b), and axes 2 and 3 (c). Ellipses represent the 95% CI based on the multivariate t distribution

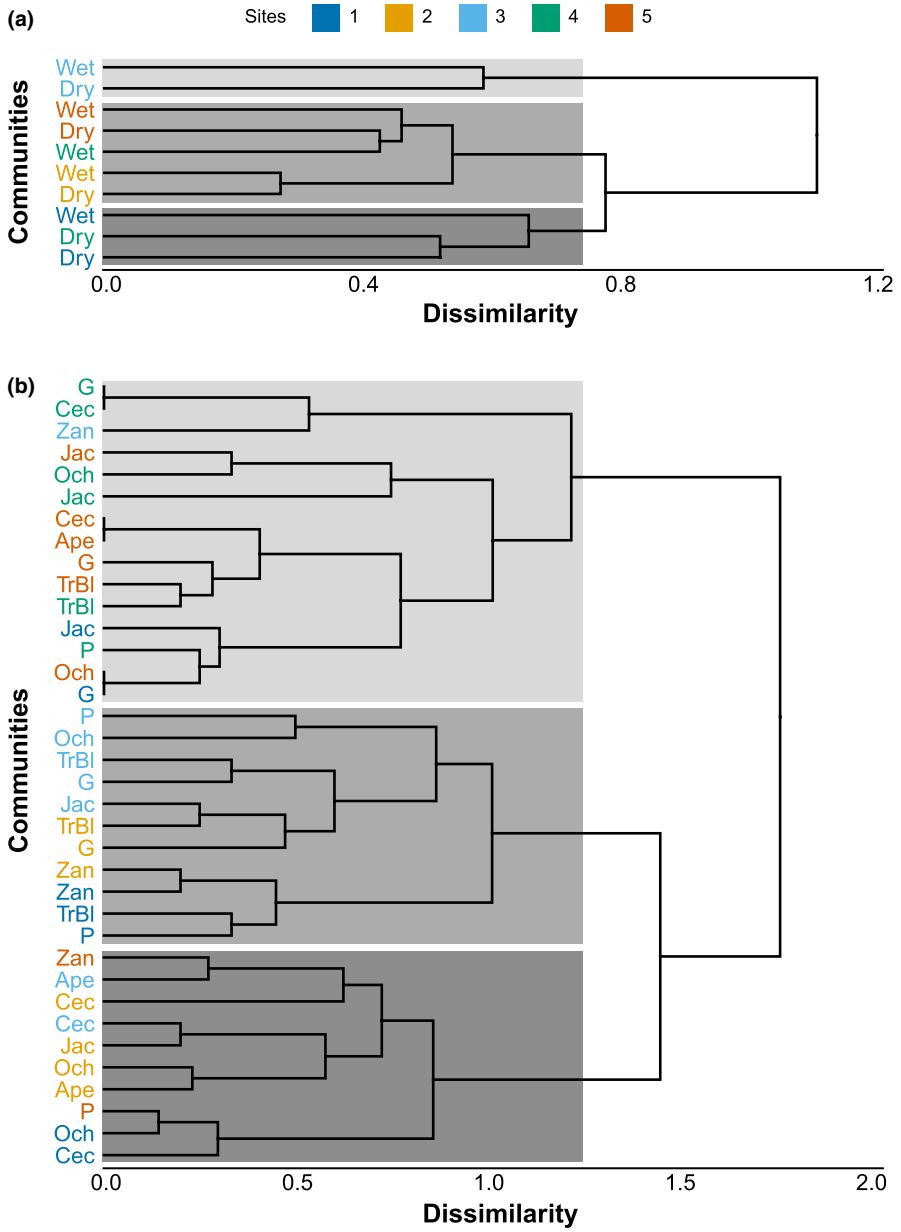

FIGURE 2 Hierarchical clustering analyses with beta-flexible method ($b = -0.25$) using the Bray–Curtis index on ant communities aboveground (a), and belowground (b) with colored boxes to indicate different groups. For aboveground, leaves represent communities at the site level with the leaf indicating the season. For belowground, leaves represent communities captured in different cache types per site with the leaf indicating the cache type. Cache: Ape = *Apeiba membranacea*, G = silica bead controls, Cec = *Cecropia longipes*, Jac = *Jacaranda copaia*, Och = *Ochroma pyramidale*, TrBl = *Trema micrantha* "black," P = unbaited controls, Zan = *Zanthoxylum ekmanii*

belowground sites) during the wet season (NMDS: stress = 0.122; MRPP: strata = fixed by site, A = 0.08, $p = 0.001$; Figure 1). The seven most common ant species found aboveground (based on the frequency of presence out of all pitfall traps placed at all sites over both seasons) were *Ectatomma ruidum* (60.0% of pitfall traps), *Pachycondyla harpax* (30.0%), *Pheidole multispina* (18.8%), *Sericomyrmex amabilis* (13.1%), *Labidus praedator* (11.2%), *Pheidole* sp. 002_016 (11.2%), and *Solenopsis* cf. *vinsoni* (11.2%). The five most common ant species found belowground (based on the frequency of presence out of all subterranean traps placed at all sites and all cache types) were *Labidus coecus* (22.5%), *S.* cf. *vinsoni* (17.5%), *Tranopelta gilva* (16.9%), *Solenopsis* cf. *bicolor* (15.6%), and *P.* sp. 002_016 (3.75%) (Table S2).

3.2 | Effect of site on seed removal and ant community composition

PLS-R analyses used a subset of the variation in ant community composition to explain 93% and higher (all tree species pooled and each tree species separately) and 74.5% of the variation in above- and belowground seed removal, respectively (Table S3). In all cases, RMSEP

values remained high, indicating low predictive power of using ant composition data alone to predict seed removal.

Hierarchical cluster analyses and MRPP determined three clusters for ant communities both at the soil surface (MRPP: strata = fixed by season, A = 0.19, p = 0.004; Figure 2a) and within the topsoil (MRPP: A = 0.21, p = 0.001; Figure 2b). Groupings within the topsoil contained communities collected from traps at different sites and different cache types.

3.3 | Seed identity and ant species

Of the 13 ant species observed removing seeds from the surface caches (dry and wet season pooled), nine were also collected in pitfall traps with only four species unique to hand samples (Table 3). The five most common ant species observed removing seeds during time intervals when there was a change in seed number were *E. ruidum* (24 intervals), *Paratrachymyrmex cornetzi* (11), *Pheidole sussanae* and *Paratrachymyrmex bugnioni* (4 each), and *S. amabilis* (3). Tree species varied in the number of time intervals when ants were collected removing seeds (Table 3). Ants removing the most commonly visited tree species (with at least three ant samples at a given site: *G. ulmifolia*, *Ochroma pyramidale*, and *Zanthoxylum ekmanii*) were distinct from the ant communities captured in pitfall traps at those same sites (NMDS: stress = 0.080; MRPP: strata = fixed by site, A = 0.10, p = 0.005; Figure 3a). These three tree species also differed from one another and from pitfall samples in terms of ant identity visiting the caches when not pooled (MRPP: A = 0.13, strata = fixed by site, p = 0.006; Figure 3b). Four ant species – *Aphaenogaster araneoides*, *E. ruidum*, *P. bugnioni*, and *P. cornetzi* – significantly separate out the assemblages at the different tree species and pitfall samples. Pitfall traps and hand samples of ants observed removing *Z. ekmanii* seeds had a higher abundance of *E. ruidum* and occasionally a higher abundance of *A. araneoides*. Hand samples of ants observed removing

TABLE 3 Ant species that had foragers associated with seeds of the different tree species and the number of time periods in which ants had been observed removing seeds (aboveground)

Tree species code	No. of time periods ants observed removing seeds	Ant species	
		Hand samples	Subterranean traps
Ape	2	*Ectatomma ruidum*, *Paratrachymyrmex cornetzi*	*Labidus coecus*, *Neivamyrmex macrodentatus*, *Pachycondyla harpax*, *Pheidole* sp. 002_016, *Rogeria foreli*, *Solenopsis* cf. *bicolor*, *Solenopsis* cf. *vinsoni*, *Tranopelta gilva*
Cec	1	*Pheidole susannae*	*Labidus coecus*, *Pachycondyla harpax*, *Pheidole* sp. 002_016, *Solenopsis* cf. *bicolor*, *Solenopsis* cf. *castor*, *Solenopsis* cf. *vinsoni*, *Tranopelta gilva*, *Wasmannia auropunctata*
Coc	0		
Fic	1	*Pheidole simonsi*	
Gua	20	*Cyphomyrmex rimosus*, *Ectatomma ruidum*, *Paratrachymyrmex bugnioni*, *Paratrachymyrmex cornetzi*, *Wasmannia auropunctata*	
Hie	0		
Jac	0		*Ectatomma ruidum*, *Labidus coecus*, *Pheidole* sp. 001_014_023, *Pheidole* sp. 002_016, *Pheidole pugnax*, *Solenopsis* cf. *bicolor*, *Solenopsis* cf. *pollux*, *Solenopsis* cf. *vinsoni*, *Tranopelta gilva*
Lue	0		
Och	13	*Ectatomma ruidum*, *Mycetomoellerius isthmicus*, *Paratrachymyrmex bugnioni*, *Paratrachymyrmex cornetzi*, *Pheidole multispina*, *Sericomyrmex amabilis*, *Wasmannia auropunctata*	*Labidus coecus*, *Pachycondyla harpax*, *Pheidole* sp. 002_016, *Phedole colobopsis*, *Solenopsis* cf. *bicolor*, *Solenopsis* cf. *vinsoni*, *Tranopelta gilva*
TrBl	3	*Mycetomoellerius isthmicus*, *Mycetomoellerius zeteki*, *Paratrachymyrmex bugnioni*, *Paratrachymyrmex cornetzi*, *Sericomyrmex amabilis*	*Carebara urichi*, *Labidus coecus*, *Pheidole glomericeps*, *Solenopsis* cf. *bicolor*, *Solenopsis* cf. *vinsoni*, *Tranopelta gilva*
TrBr	3	*Paratrachymyrmex cornetzi*, *Pheidole susannae*	
Zan	18	*Aphaenogaster araneoides*, *Ectatomma ruidum*, *Paratrachymyrmex cornetzi*, *Pheidole* sp. 025, *Pheidole simonsi*, *Phedole susannae*	*Labidus coecus*, *Neivamyrmex macrodentatus*, *Nylanderia* sp. 001, *Pachycondyla harpax*, *Pheidole* sp. 002_016, *Pheidole pugnax*, *Solenopsis* cf. *bicolor*, *Solenopsis* cf. *vinsoni*, *Tranopelta gilva*

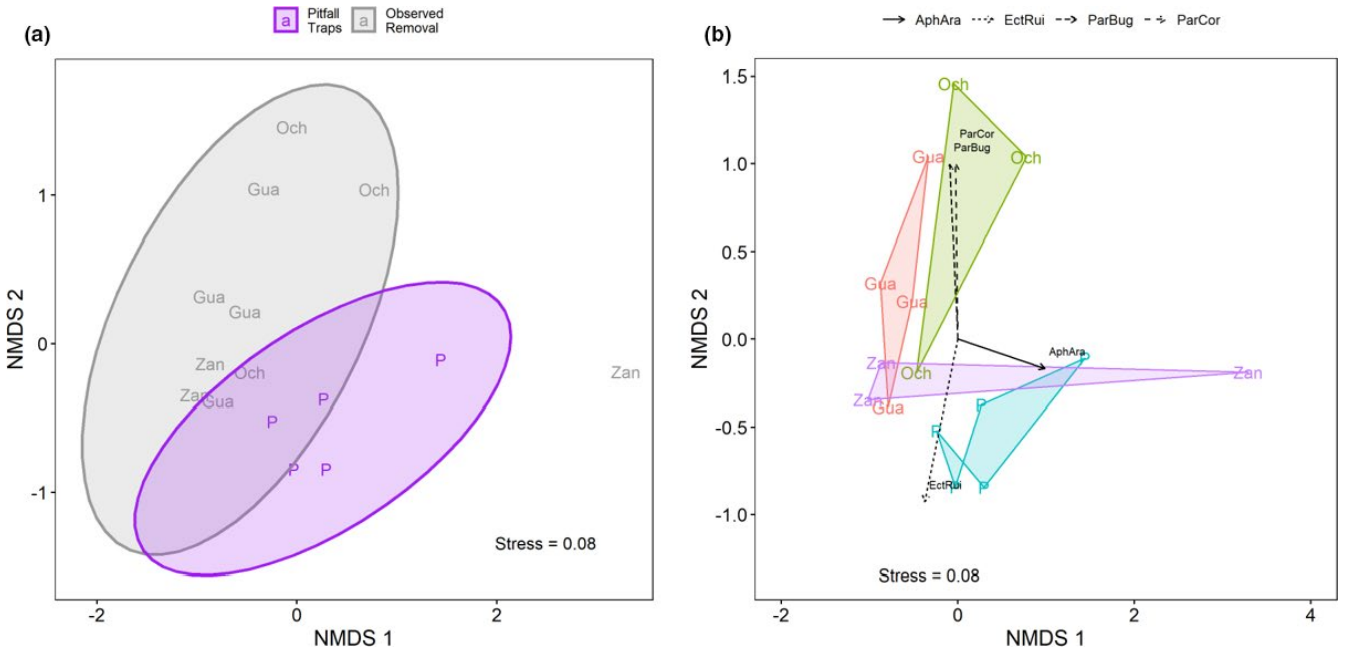

FIGURE 3 NMDS depicting the relationship between ant assemblages collected removing seeds of tree species (Gua, Och, and Zan) pooled and those found at pitfall traps (a) and with species separated (b). Both figures have the same axes shown. Ellipses represent the 95% CI based on the multivariate t distribution (a) or are polygons of the data (b). P = pitfalls, Gua = *Guazuma ulmifolia*, Och = *Ochroma pyramidale*, Zan = *Zanthoxylum ekmanii*, AphAra = *Aphaenogaster araneoides*, EctRui = *Ectatomma ruidum*, ParCor = *Partrachymyrmex cornetzi*

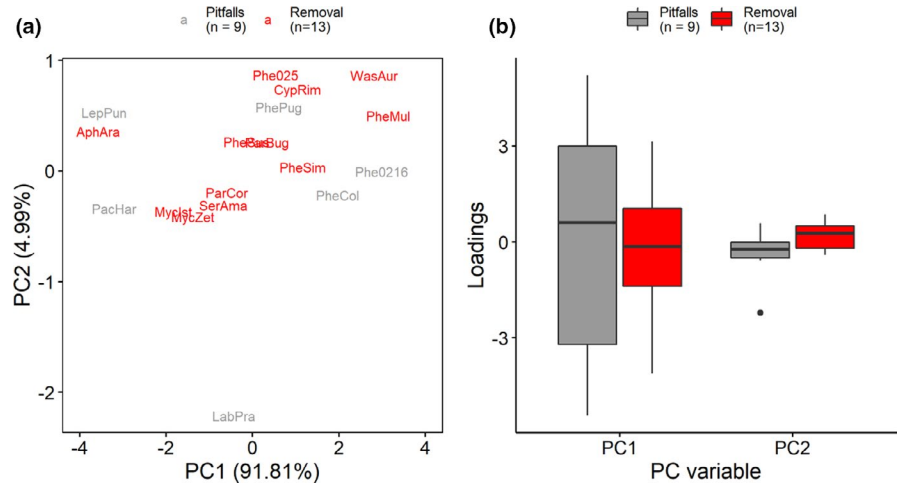

FIGURE 4 Principal component analysis (PCA) of the ant species found in at least 10 percent of pitfall traps at one site (dry and wet seasons pooled) and all the ant species observed removing seeds at the soil surface categorized into two groups: (1) those removing seeds and (2) those common in pitfall traps but not observed removing seeds (a), and box plots of the loadings on the first two principal components (PCs; b)

seeds of *G. ulmifolia* and *O. pyramidale* had higher abundances of both *P. bugnioni* and *P. cornetzi*.

We used subterranean traps to detect differences in ant communities near the different caches. Eighteen out of the 20 ant species captured in subterranean traps were found in traps associated with seed caches, with two additional species found in traps associated with bead controls or not associated with any seed cache (Table 3). Eight of the ant species collected in traps associated with seed caches were associated with multiple tree species (range: 2–6; mean: 4.6), while the remaining 10 were associated with one seed species. We found no differences in the community of ants collected at subterranean traps placed next to specific tree species caches (NMDS: stress = 0.087; MRPP: A = −0.04, strata = fixed by site, p = 0.48, Figure S6). Rarefaction and extrapolation of all sites pooled suggest that the subterranean traps had the same species richness regardless of whether the traps were next to seeds or control caches

(Figure S3). The six most common ant species found in subterranean traps associated with seed caches (all seed caches pooled = 120 samples) were *L. coecus* (25.8%), *T. gilva* (16.7%), *S.* cf. *vinsoni* (15.8%), *S.* cf. *bicolor* (14.2%), and *Pachycondyla harpax* and *Pheidole* sp. 02_16 (4.17% each). The four most common ant species found in silica beads / unbaited traps (all control traps pooled = 40 samples) – *S.* cf. *vinsoni* (22.5%), *S.* cf. *bicolor* (20.0%), *T. gilva* (17.5%), and *L. coecus* (12.5%) – were all also common in traps associated with seed caches.

3.4 | Morphological traits of ants removing seeds

PC1 weighted all morphological characters in similar amounts and accounted for 91.81% of the variation in the morphological data (Table 2). PC2 accounted for only 4.99% of variation in the data and mainly consisted of eye width, eye length, and mandible length. Ant morphological traits did not differ with respect to whether ants were categorized as removing seeds or common in pitfall traps without being observed removing seeds (ANOVA: PC1 loadings, $F_{1,20} = 0.24$, $p = 0.63$; PC2 loadings, $F_{1,20} = 4.26$, $p = 0.052$; Figure 4).

4 | DISCUSSION

Many tropical plant species depend on ants for seed dispersal and ants can influence patterns of seed recruitment following disturbance (Gallegos et al., 2014). Here, we show that seed removal rates by ants at the soil surface differed among focal tree species and study sites, and was primarily attributed to the activities of just four ant species. In contrast, ant communities associated with belowground seed caches did not vary among sites or tree species. Here, we explore whether these results reflect differences in plant traits, the heterogeneous distribution of ant species, or differences in ant traits.

4.1 | Plant species identity explains seed removal

Previous examination of plant traits in this experiment found that seed mass and seed persistence were uncorrelated with seed removal, while primary dispersal mode and dormancy type were only related to seed removal when tree species identity was not included as a random effect (Ruzi et al., 2017). Further, tree species identity accounted for the greatest amount of explained variation in seed removal, followed by site in the forest, while other variables accounted for little variation on their own. These results suggest that ants are using species-specific cues that are independent of traits typically associated with commonly measured characteristics such as seed size or dispersal mode. We suggest that seed chemistry, which varies among species and is associated with plant defense (Dalling et al., 2020), is a likely source of this variation in dispersal rates in this system.

4.2 | Ant communities vary spatially, but not temporally

We found variation in the aboveground ant communities among sites, which clustered into three groups regardless of the sampling season. These spatial differences could influence dispersal services plants receive at local scales (e.g., Horvitz & Schemske, 1986). While ant community composition accounted for substantial variation in seed removal rates among sites, it had low accuracy and may therefore not be a useful measure for predicting seed dispersal at other locations. Belowground ant communities also clustered, but not based on cache type (clustering together regardless of site) or site (clustering together regardless of cache type).

4.3 | Ant characteristics do not predict seed removal

Ant diet is variable and can depend on colony needs (e.g., Dussutour & Simpson, 2009). Of the most common ant taxa at seed caches in our surveys, two are generalists and the other three grow fungus. *Ectatomma ruidum* consumes insects and plant-based resources (Pratt, 1989; Lachaud, 1990), and is often observed moving seeds (e.g., Escobar-Ramírez et al., 2012; Zelikova & Breed, 2008). *Paratrachymyrmex cornetzi*, *P. bugnioni*, and *S. amabilis* are all members of the fungus-growing Attini tribe, collecting fresh and decaying plant material and insect frass to feed their fungal gardens (de Fine Licht & Boomsma, 2010). It is unknown how important seeds are as provisions for their fungi. *Pheidole* spp. in general are omnivorous and include many seed harvesters that consume most of the seeds they move (Levey & Bryne, 1993). However, some seeds are placed in refuse piles where seedlings have lower mortality and increased growth relative to seedlings in nearby soil (Levey and Bryne 1993). While ants were observed removing seeds aboveground, we lacked direct observations of belowground ant–seed interactions. It is likely that ants belowground are passively encountering seeds rather than actively searching for seeds given the general lack of known seed specialists in the community of ants captured within the topsoil; four of the six most common ant species collected in subterranean traps associated with seed caches were also common in the control traps. The most commonly collected ant species in subterranean traps was the army ant *Labidus coecus*. Army ants are important predators and are commonly found raiding underground in tropical forests (O'Donnell et al., 2007; Ryder Wilkie et al., 2010).

Ant species differ in their effectiveness as seed dispersers based on their size (Gómez & Espadaler, 2013; Ness et al., 2004). However, the ants observed removing seeds from the soil surface in our study were not morphologically distinct from ants not observed removing seeds. This lack of association could be due to the seeds being removed by generalists rather than specialist seed predators. For example, chemical cues used by plants to attract ants to seeds could attract scavenging or insectivorous species even though they

are incapable of consuming them (e.g., Youngsteadt et al., 2010). Consequently, many of the ants would likely share morphological features with other generalist or predatory species in the community. Even ants in this system that are seed predators might not have distinct morphological characteristics. For example, small worker body size could be offset by communal foraging (e.g., *Pheidole sussanae* worked together to carry *Z. ekmanii* seeds up a tree; observation, March 27, 2013). Morphological traits could be determined by other factors that take precedence over making ants good seed removers. The fungus-growing ants (*Cyphomyrmex*, *Mycetomoellerius*, *Paratrachymyrmex*) that carried seeds likely have their morphology driven or constrained by factors related to their specialized lifestyle. However, this does not preclude fungus-growing ants from being important seed dispersers; in the Brazilian cerrado, fungus-growing ants increase seed germination by removing fruit pulp and arils (Leal & Oliveira, 1998). Additionally, the use of pitfall traps could have constrained the morphological diversity of ants captured as pitfall traps are good for collecting ants walking at the soil surface but not those that walk in the leaf litter. Other sampling methods may have collected a wider range of ant species (e.g., on BCI: Berlese extractions and baiting = 127 species, Levings, 1983; Berlese extractions = 98 species, Donoso, 2014). Future work linking morphological traits to diet (e.g., through stable isotope analyses) will help elucidate the role of functional groups on variation in seed removal rates.

5 | CONCLUSIONS

Our results suggest that ant community composition, as estimated by pitfall traps, varied over small spatial scales but does not accurately predict seed removal at a given location. Additionally, ant species observed at seed caches did not exhibit a strong trait-based association with seed removal. Ant communities may therefore exhibit functional redundancy in terms of seed removal services provided for Neotropical pioneer tree species, most likely through opportunistic foraging by common ants. However, there could be lasting effects of disperser identity on post-dispersal seed fate depending on if the disperser provides directed dispersal or alters germination microsite characteristics (e.g., Magalhães et al., 2018). Therefore, future work aimed at examining the fates of these seeds once they are moved by ants should be a priority.

ACKNOWLEDGMENTS

This work was supported by the United States Department of Agriculture (Project Number ILLU 875-952), National Science Foundation (Grants: 120205 to JWD, 1069157 to AVS, and 1701501 to AVS and SAR), and a Dissertation Travel Grant from the University of Illinois. We thank the Smithsonian Tropical Research Institute for permission to conduct the research and for logistical support. We thank Abigail C. Robison for help in the field and Adam S. Davis for advice on statistical analyses. We thank Jack Longino for his expertise in identifying *Pheidole*. Finally, we thank Eric Fuchs and three anonymous reviewers for their comments.

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTION

SAR, PCZ, DRP, JWD, and AVS conceptualized the data, designed methodology, involved in project administration, and provided resources; SAR, PCZ, DPR, and RA curated the data and investigated the data; SAR and RA involved in formal analysis; SAR, JWD, and AVS acquired funding; SAR provided software, validated the data, and visualized the data; PCZ, JWD, and AVS supervised the data; SAR and AVS wrote the original draft; SAR, PCZ, DPR, RA, JWD, and AVS wrote, reviewed, and edited the manuscript.

DATA AVAILABILITY STATEMENT

Data available are from the Dryad Digital Repository: https://doi.org/10.5061/dryad.n2z34tmvj (Ruzi et al., 2020).

ORCID

Selina A. Ruzi https://orcid.org/0000-0003-1973-8526
Paul-Camilo Zalamea https://orcid.org/0000-0002-0987-4164
Rafael Achury https://orcid.org/0000-0003-0435-3594
James W. Dalling https://orcid.org/0000-0002-6488-9895
Andrew V. Suarez https://orcid.org/0000-0002-2257-3366

REFERENCES

Anjos, D. V., Leal, L. C., Jordano, P., & Del-Claro, K. (2020). Ants as diaspore removers of non-myrmecochorous plants: A meta-analysis. *Oikos*, *129*(6), 775–786. https://doi.org/10.1111/oik.06940

AntWeb. (2020). Retrieved from https://www.antweb.org

Barroso, Á., Amor, F., Cerdá, X., & Boulay, R. R. (2013). Dispersal of non-myrmecochorous plants by a "keystone disperser" ant in a Mediterranean habitat reveals asymmetric interdependence. *Insectes Sociaux*, *60*(1), 75–86. https://doi.org/10.1007/s00040-012-0268-0

Beattie, A. J. (1985). *The evolutionary ecology of ant-plant mutualisms* (p. 196). Cambridge University Press.

Bestelmeyer, B. T., Agosti, D., Alonso, L. E., Brandão, C. R. F., Brown, W. L. Jr, Delabie, J. H. C., & Silvestre, R. (2000). Field techniques for the study of ground-dwelling ants. In D. Agosti, J. D. Majer, L. E. Alonso, & T. R. Schultz (Eds.), *Ants: Standard methods for measuring and monitoring biodiversity* (pp. 122–144). Smithsonian Institution Press.

Bond, W., & Slingsby, P. (1984). Collapse of an ant-plant mutualism: The Argentine ant and myrmecochorous Proteacae. *Ecology*, *65*(4), 1031–1037.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Chao, A., Ma, K. H., Hsieh, T. C., & Chiu, C.-H. (2016). *SpadeR: Species-richness prediction and diversity estimation with R*. R package version 0.1.1. Retrieved from http://chao.stat.nthu.edu.tw/wordpress/software_download/

Christian, C. E., & Stanton, M. L. (2004). Cryptic consequences of a dispersal mutualism: Seed burial, elaiosome removal, and

seed-bank dynamics. *Ecology*, *85*(4), 1101–1110. https://doi.org/10.1890/03-0059

Christianini, A. V., & Oliveira, P. S. (2010). Birds and ants provide complementary seed dispersal in a Neotropical savanna. *Journal of Ecology*, *98*(3), 573–582. https://doi.org/10.1111/j.1365-2745.2010.01653.x

Culver, D. C., & Beattie, A. J. (1980). The fate of *Viola* seeds dispersed by ants. *American Journal of Botany*, *67*(5), 710–714. https://doi.org/10.1002/j.1537-2197.1980.tb07701.x

Dalling, J. W., & Brown, T. A. (2009). Long-term persistence of pioneer seeds in tropical rain forest soil seed banks. *The American Naturalist*, *173*(4), 531–535. https://doi.org/10.1086/597221

Dalling, J. W., Davis, A. S., Arnold, A. E., Sarmiento, C., & Zalamea, P.-C. (2020). Extending plant defense theory to seeds. *Annual Review of Ecology, Evolution, and Systematics*, *51*, 123–141. https://doi.org/10.1146/annurrev-ecolsys-012120-115156

Dalling, J. W., Muller-Landau, H. C., Wright, S. J., & Hubbell, S. P. (2002). Role of dispersal in the recruitment limitation of Neotropical pioneer species. *Journal of Ecology*, *90*(4), 714–727. https://doi.org/10.1046/j.1365-2745.2002.00706.x

Davidson, D. W., & Morton, S. R. (1981). Myrmecochory in some plants (*F. chenopodiaceae*) of the Australian arid zone. *Oecologia*, *50*, 357–366. https://doi.org/10.1007/BF00344976

de Fine Licht, H. H., & Boomsma, J. J. (2010). Forage collection, substrate preparation, and diet composition in fungus-growing ants. *Ecological Entomology*, *35*(3), 259–269. https://doi.org/10.1111/j.1365-2311.2010.01193.x

de Vries, A., & Ripley, B. D. (2016). *ggdendro: Create dendrograms and tree diagrams using 'ggplot2'*. R package version 0.1-20. Retrieved from https://CRAN.R-project.org/package=ggdendro

Donoso, D. A. (2014). Assembly mechanisms shaping tropical litter ant communities. *Ecography*, *37*(5), 490–499. https://doi.org/10.1111/j.1600-0587.2013.00253.x

Dussutour, A., & Simpson, S. J. (2009). Communal nutrition in ants. *Current Biology*, *19*(9), 740–744. https://doi.org/10.1016/j.cub.2009.03.015

Escobar-Ramírez, S., Duque, S., Henao, N., Hurtado-Giraldo, A., & Armbrecht, I. (2012). Removal of nonmyrmecochorous seeds by ants: Role of ants in cattle grasslands. *Psyche*, *2012*, 1–8. https://doi.org/10.1155/2012/951029

Fornara, D. A., & Dalling, J. W. (2005). Post-dispersal removal of seeds of pioneer species from five Panamanian forests. *Journal of Tropical Ecology*, *21*(1), 79–84. https://doi.org/10.1017/S026646740400197X

Galili, T. (2015). dendextend: An R package for visualizing, adjusting, and comparing trees of hierarchical clustering. *Bioinformatics*, *31*(22), 3718–3720. https://doi.org/10.1093/bioinformatics/btv428

Gallegos, S. C., Hensen, I., & Schleuning, M. (2014). Secondary dispersal by ants promotes forest regeneration after deforestation. *Journal of Ecology*, *102*(3), 659–666. https://doi.org/10.1111/1365-2745.12226

Gaudard, C. A., Robertson, M. P., & Bishop, T. R. (2019). Low levels of intraspecific variation in a keystone invertebrate group. *Oecologia*, *190*(4), 725–735. https://doi.org/10.1007/s00442-019-04426-9

Gómez, C., & Espadaler, X. (2013). An update of the world survey of myrmecochorous dispersal distances. *Ecography*, *36*(11), 1193–1201. https://doi.org/10.1111/j.1600-0587.2013.00289.x

Hahn, D. A., & Wheeler, D. E. (2002). Seasonal foraging activity and bait preferences of ants of Barro Colorado Island. *Panama. Biotropica*, *34*(3), 348–356.

Handel, S. N., & Beattie, A. J. (1990). Seed dispersal by ants. *Scientific American*, *263*(2), 58–64. https://doi.org/10.1038/scientificamerican0890-76

Hanzawa, F. M., Beattie, A. J., & Culver, D. C. (1988). Directed dispersal: Demographic analysis of an ant-seed mutualism. *The American Naturalist*, *131*(1), 1–13. https://doi.org/10.1086/284769

Horvitz, C. C., & Schemske, D. W. (1986). Seed dispersal of a Neotropical myrmecochore: Variation in removal rates and dispersal distance. *Biotropica*, *18*(4), 319–323. https://doi.org/10.2307/2388575

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

Hsieh, T. C., Ma, K. H., & Chao, A. (2019). *iNEXT: iNterpolation and EXTrapolation for species diversity*. R package version 2.0.19 Retrieved from http://chao.stat.nthu.edu/tw/blog/software-download/

Hubbell, S. P., Foster, F. B., O'Brien, S. T., Harms, K. E., Condit, R., Wechsler, B., Wright, S. J., & Loo de Lao, S. (1999). Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science*, *283*(5401), 554–557. https://doi.org/10.1126/science.283.5401.554

Jacquemin, J., Rosen, Y., & Leponce, M. (2016). Spatio-temporal variation in ant communities in leaf-litter and soil layers in a premontane tropical forest. *Myrmecological News*, *22*, 129–139.

Kaspari, M. (1993). Removal of seeds from Neotropical frugivore droppings. *Ant Responses to Seed Number. Oecologia*, *95*(1), 81–88. https://doi.org/10.1007/BF00649510

Kaspari, M. (1996). Worker size and seed size selection by harvester ants in a Neotropical forest. *Oecologia*, *105*(3), 397–404. https://doi.org/10.1007/BF00328743

Kaspari, M., & Weiser, M. D. (1999). The size-grain hypothesis and interspecific scaling in ants. *Functional Ecology*, *13*(4), 530–538. https://doi.org/10.1046/j.1365-2435.1999.00343.x

Lachaud, J- P. (1990). Foraging activity and diet in some Neotropical ponerine ants. I. *Ectatomma ruidum* Roger (Hymenoptera, Formicidae). *Folia Entomologica Mexicana*, *78*, 241–256.

Leal, I. R., & Oliveira, P. S. (1998). Interactions between fungus-growing ants (Attini), fruits and seeds in cerrado vegetation in Southeast Brazil. *Biotropica*, *30*(2), 170–178.

Levey, D. J., & Byrne, M. M. (1993). Complex ant-plant interactions: Rain forest ants as secondary dispersers and post-dispersal seed predators. *Ecology*, *74*(6), 1802–1812. https://doi.org/10.2307/1939938

Levings, S. C. (1983). Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: Some causes of patchy species distributions. *Ecological Monographs*, *53*(4), 435–455. https://doi.org/10.2307/1942647

Longino, J. T. (2010, September 17). *Ants of Costa Rica*. Retrieved from https://ants.biology.utah.edu/AntsofCostaRica.html

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., & Hornik, K. (2019). *Cluster: Cluster analysis basics and extensions*. R package version 2.1.0.

Magalhães, V. B., Espíritosanto, N. B., Salles, L. F. P., Soares, H. Jr, & Oliveira, P. S. (2018). Secondary seed dispersal by ants in Neotropical cerrado savanna: Species-specific effects on seeds and seedlings of *Siparuna guianensis* (Siparunaceae). *Ecological Entomology*, *43*(5), 665–674. https://doi.org/10.1111/een.12640

Martinez-Ramos, M., Alvarez-Buylla, E., Sarukhan, J., & Pinero, D. (1988). Treefall age determination and gap dynamics in a tropical forest. *Journal of Ecology*, *76*(3), 700–716. https://doi.org/10.2307/2260568

Mevik, B.-H., & Wehrens, R. (2007). The pls package: Principal component and partial least squares regression in R. *Journal of Statistical Software*, *18*(2), 1–23.

Mevik, B.-H., Wehrens, R., & Liland, K. H. (2019). *pls: Partial least squares and principal component regression. R package version 2.7-2*. Retrieved from https://CRAN.R-project.org/package=pls

Mull, J. F., & MacMahon, J. A. (1997). Spatial variation in rates of seed removal by harvester ants (*Pogonomyrmex occidentalis*) in a shrub-steppe ecosystem. *The American MIdland Naturalist*, *138*(1), 1–13. https://doi.org/10.2307/2426649

Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, *15*(7), 278–285. https://doi.org/10.1016/S0169-5347(00)01874-7

Ness, J. H., Bronstein, J. L., Andersen, A. N., & Holland, J. N. (2004). Ant body size predicts dispersal distance of ant-adapted seeds: Implications of small-ant invasions. *Ecology*, *85*(5), 1244–1250. https://doi.org/10.1890/03-0364

O'Donnell, S., Lattke, J., Powell, S., & Kaspari, M. (2007). Army ants in four forests: Geographic variation in raid rates and species composition. *Journal of Animal Ecology*, *76*(3), 580–589. https://doi.org/10.1111/j.1365-2656.2007.01221.x

O'Dowd, D. J., & Hay, M. E. (1980). Mutualism between harvester ants and a desert ephemeral: Seed escape from rodents? *Ecology*, *61*(3), 531–540.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Wagner, H. (2019). *vegan: Community Ecology Package*. R package version 2 Retrieved from 6. https://CRAN.R-project.org/package=vegan

Palacio, E. E., & Fernández, F. (2003). Clave para las subfamilies y géneros. In F. Fernández (Ed.), *Introduccíon a las horigas de la region Neotropical* (pp. 233–260). IAvH.

Parr, C. L., Dunn, R. R., Sanders, N. J., Weiser, M. D., Photakis, M., Bishop, T. R., Fitzpatrick, M. C., Arnan, X., Baccaro, F., Brandao, C. R. F., Chick, L., Donoso, D. A., Fayle, T. M., Gomez, C., Grossman, B., Munyai, T. C., Pacheco, R., Retana, J., Robinson, A., … Gibb, H. (2017). *GlobalAnts:* A new database on the geography of ant traits (Hymenoptera: Formicidae). *Insect Conservation and Diversity*, *10*(1), 5–20. https://doi.org/10.1111/icad.12211

Passos, L., & Oliveira, P. S. (2002). Ants affect the distribution and performance of *Clusia criuva* seedlings, a primarily bird-dispersed rainforest tree. *Journal of Ecology*, *90*(3), 517–528. https://doi.org/10.1046/j.1365-2745.2002.00687.x

Pfeiffer, M. J., Nais, J. & Linsenmair, K. E., (2006). Worker size and seed size selection in 'seed'-collecting ant ensembles in primary rain forests on Borneo. *Journal of Tropical Ecology*, *22*(6), 685–693. https://doi.org/10.1017/S0266467406003622

Pizo, M. A., & Oliveira, P. S. (1998). Interaction between ants and seeds of a nonmyrmecochorous Neotropical tree, *Cabralea canjerana* (Meliaceae), in the Atlantic forest of southeastern Brazil. *American Journal of Botany*, *85*(5), 669–674.

Pratt, S. C. (1989). Recruitment and other communication behavior in the ponerine ant *Ectatomma ruidum*. *Ethology*, *81*(4), 313–331.

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Ruzi, S. A., Roche, D. P., Zalamea, P.-C., Robison, A. C., & Dalling, J. W. (2017). Species identity influences secondary removal of seeds of Neotropical pioneer tree species. *Plant Ecology*, *218*(8), 983–995. https://doi.org/10.1007/s11258-017-0745-7

Ruzi, S. A., Zalamea, P. C., Roche, D. P., Achury, R., Dalling, J. W., & Suarez, A. V. (2020). Data from: Can variation in seed removal patterns of Neotropical pioneer tree species be explained by local ant community composition? *Dryad Digital Repository*, https://doi.org/10.5061/dryad.n2z34tmvj

Ryder Wilkie, K. T., Mertl, A. L., & Traniello, J. F. A. (2007). Biodiversity below ground: Probing the subterranean ant fauna of Amazonia. *Naturwissenschaften*, *94*(9), 725–731. https://doi.org/10.1007/s00114-007-0250-2

Ryder Wilkie, K. T., Mertl, A. L., & Traniello, J. F. A. (2010). Species diversity and distribution patterns of the ants of Amazonian Ecuador. *PLoS One*, *5*(10), e13146. https://doi.org/10.1007/s00114-007-0250-2

Sanchez-Cordero, V., & Martinez-Gallardo, R. (1998). Postdispersal fruit and seed removal by forest-dwelling rodents in a lowland rainforest in Mexico. *Journal of Tropical Ecology*, *14*(2), 139–151. https://doi.org/10.1017/S0266467498000121

Sarmiento, C., Zalamea, P.-C., Dalling, J. W., Davis, A. S., Stump, S. M., U'Ren, J. M., & Arnold, A. E. (2017). Soilborne fungi have host affinity and host-specific effects on seed germination and survival in a lowland tropical forest. *PNAS*, *114*(43), 11458–11463. https://doi.org/10.1073/pnas.1706324114

Sautu, A., Baskin, J. M., Baskin, C. C., Deago, J., & Condit, R. (2007). Classification and ecological relationships of seed dormancy in a seasonal moist tropical forest, Panama, Central America. *Seed Science Research*, *17*(2), 127–140. https://doi.org/10.1017/S0960258507708127

StatSoft Inc. (2013). *Electronic statistics textbook*. StatSoft.

Swaine, M. D., & Whitmore, T. C. (1988). On the definition of ecological species groups in tropical rain forests. *Vegetatio*, *75*(1–2), 81–86. https://doi.org/10.1007/BF00044629

Weiser, M. D., Sanders, N. J., Agosti, D., Andersen, A. N., Ellison, A. M., Fisher, B. L., Gibb, H., Gotelli, N. J., Gove, A. D., Gross, K., Guénard, B., Janda, M., Kaspari, M., Lessard, J.-P., Longino, J. T., Majer, J. D., Menke, S. B., McGlynn, T. P., Parr, C. L., … Dunn, R. R. (2010). Canopy and litter ant assemblages share similar climate-species density relationships. *Biology Letters*, *6*(6), 769–772. https://doi.org/10.1098/rsbl.2010.0151

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis* (p. 212). Springer.

Windsor, D. M. (1990). Climate and moisture variability in a tropical forest: Long-term records from Barro Colorado Island, Panama. *Smithsonian Contributions to the Earth Sciences*, *29*, 1–145.

Yanoviak, S. P., & Kaspari, M. (2000). Community structure and habitat template: Ants in the tropical forest canopy and litter. *Oikos*, *89*(2), 259–266.

Youngsteadt, E., Baca, J. A., Osborne, J., & Schal, C. (2009). Species-specific seed dispersal in an obligate ant-plant mutualism. *PLoS One*, *4*(2), e4335. https://doi.org/10.1371/journal.pone.0004335

Youngsteadt, E., Bustios, P. G., & Schal, C. (2010). Divergent chemical cues elicit seed collecting by ants in an obligate multi-species mutualism in lowland Amazonia. *PLoS One*, *5*(12), e15822. https://doi.org/10.1371/journal.pone.0015822

Zalamea, P.-C., Dalling, J. W., Sarmiento, C., Arnold, A. E., Delevich, C., Berhow, M. A., Ndobegang, A., Gripenberg, S., & Davis, A. S. (2018). Dormancy-defense syndromes and tradeoffs between physical and chemical defenses in seeds of pioneer species. *Ecology*, *99*(9), 1988–1998. https://doi.org/10.1002/ecy.2419

Zalamea, P.-C., Sarmiento, C., Arnold, A. E., Davis, A. S., & Dalling, J. W. (2015). Do soil microbes and abrasion by soil particles influence persistence and loss of physical dormancy in seeds of tropical pioneers? *Frontiers in Plant Science*, *5*, 799. https://doi.org/10.3389/fpls.2014.00799

Zelikova, T. J., & Breed, M. D. (2008). Effects of habitat disturbance on ant community composition and seed dispersal by ants in a tropical dry forest in Costa Rica. *Journal of Tropical Ecology*, *24*(3), 309–316. https://doi.org/10.1017/S0266467408004999

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Ruzi SA, Zalamea P-C, Roche DP, Achury R, Dalling JW, Suarez AV. Can variation in seed removal patterns of Neotropical pioneer tree species be explained by local ant community composition?. *Biotropica*. 2021;53:619–631. https://doi.org/10.1111/btp.12904