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Post-Dispersal Seed Removal in a Large-Seeded Palm by Frugivore Mammals in Western Ecuador

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Abstract

Post-dispersal seed removal by ground-foraging frugivores promotes secondary dispersal of large seeds, reducing seed predation and increasing recruitment and regeneration. We studied how habitat disturbance influences seed removal patterns in the large-seeded palm *Phytelephas aequatorialis* within three habitats forming a continuum of disturbance (agroforestry system, disturbed forest, and less-disturbed forest) using seed removal experiments and camera trapping. We tested whether seed removal rates, and both richness and composition of seed remover communities varied between the habitats. On average, 15 seeds were removed under each tree in the agroforestry system over seven days, which was significantly lower compared to the disturbed forest (18) and the less-disturbed forest (19). Eight mammal species were identified removing seeds in the three habitats. On average, one mammal species removed seeds at each station in the agroforestry system, which was significantly lower than the two species observed in the two forests. The composition of seed remover communities was significantly different between the three habitats. Our results suggest that the loss of forest cover in the agroforestry system has reduced the richness of seed removers, which subsequently caused decreased removal rates. Nevertheless, this habitat could still maintain effective seed dispersal events because spiny rats were important seed removers. Our camera trap data should be taken as preliminary because we could only identify less than half of the animals responsible for seed removal. This study highlights the importance of medium- and large-sized rodents for the removal and effective dispersal of large seeds in disturbed tropical habitats.

Keywords

Arecaceae, camera trapping, habitat disturbance, Neotropics, recruitment, scatter-hoarding rodents, seed dispersal

Most tropical woody plants produce fleshy fruits adapted for animal consumption, and therefore, depend extensively on frugivore animals for the effective dispersal of their seeds (Howe, 2016; Howe & Smallwood, 1982; Jordano, 1995). Seed dispersal is important because it increases offspring survival and recruitment by reducing seed accumulation around parental and conspecific plants, where density- and distance-dependent mortality is high (Comita et al., 2010; 2014; Connell, 1971; Hardesty et al., 2006; Janzen, 1970; Johnson et al., 2014; Peters, 2003; Sezen et al., 2009). Seed escape from high-mortality areas and posterior establishment in turn shape patterns of plant species diversity in species-rich tropical forests (Comita et al., 2010; Harms et al., 2000; Wandrag et al., 2017).

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In addition, seed dispersal over long distances promotes genetic connectivity between populations, colonization of new available sites, and changes in species ranges to follow climate change (Howe, 2016; Nathan, 2006; Nathan et al., 2008). Thus, the future permanence of tropical plant communities is linked to the maintenance of the dispersal services provided by frugivore animal communities (Caughlin et al., 2015; Howe, 1984).

Habitat disturbance may alter the diversity and the composition of animal communities (Alroy, 2017; Morris, 2010; Newbold et al., 2015), which in turn, affects negatively seed dispersal dynamics in tropical forests. A decrease in the richness and abundance of animal seed dispersers reduces seed removal rates and the distance that seeds are dispersed (Blackham & Corlett, 2015; Galetti et al., 2006; Lehouck et al., 2009; Ramírez et al., 2009; Wright et al., 2000; Wright & Duber, 2001). Exceptions can occur when a highly effective disperser is introduced in disturbed habitats, allowing higher rates of seed removal and dispersal than in less-disturbed habitats with higher animal richness (da Silva et al., 2011). Changes in the composition of animal disperser communities can maintain seed removal rates and dispersal over short distances because small-sized generalist animals can provide these services in the absence of larger animals (Farwig et al., 2017; Neuschulz et al., 2011). However, rare dispersal events over long distances may decrease in habitats with communities of small and generalist animals because certain plants, such as those with large seeds, rely on larger and specialized animals for this purpose (Farwig et al., 2017; González-Varo, 2010; Howe, 2016).

Effective seed dispersal depends on the removal of seeds followed by their deposition in places with favorable conditions for germination, establishment, survival, and ultimately recruitment to become reproductive adults (Schupp et al., 2010). Because of their size, the effective dispersal of large seeds (4–10 cm in diameter) relies on ground-foraging animals that remove the seeds from the ground after they have fallen by the action of gravity or tree-foraging animals (Vander Wall, 2001; Vander Wall et al., 2005). The falling of seeds could imply horizontal displacement and be considered as primary dispersal, while the posterior removal of seeds (i.e. post-dispersal seed removal) promotes either secondary dispersal or seed predation (Vander Wall et al., 2005). Many generalist animals may only feed on the fleshy fruit and do not provide effective dispersal for large seeds (Howe, 2016). Some rodent species are considered effective secondary dispersers of large seeds because they promote directed dispersal to specific microsites, and may scatter-hoard seeds in shallow caches for further consumption (Aliaga-Rossel et al., 2008; Brodin, 2010; Campos et al., 2017; Carvajal & Adler, 2008; Choo et al., 2012; Dittel et al., 2015; Haugaasen et al., 2010; Jansen

et al., 2012; Kuprewicz & García-Robledo, 2019; Sunyer et al., 2013; Vander Wall et al., 2005). Seeds that are not recovered from such caches can germinate and establish because seed burial reduces seed predation (Crawley & Long, 1995; Forget et al., 1994), increasing plant recruitment and regeneration (Dunham, 2011). Scatter-hoarding by rodents even promote dispersal of large seeds for distances over 100 m, potentially contributing to plant population connectivity (Jansen et al., 2012). Therefore, it is expected that the presence of rodents, and particularly those that scatter-hoard seeds, would ensure effective dispersal for large-seeded plants.

Here, we study post-dispersal seed removal of the large-seeded palm *Phytelephas aequatorialis* and the fauna associated with this process in three habitats with different degrees of disturbance. Palms are keystone species in tropical forests and they have been much studied to determine the effect of habitat disturbance and degradation on seed dispersal dynamics (Carvajal & Adler, 2008; da Silva et al., 2011; Dittel et al., 2015; Galetti et al., 2006; Ramírez et al., 2009; Wright et al., 2000; Wright & Duber, 2001). *Phytelephas aequatorialis* is widely distributed in western Ecuador, which is a highly threatened region because of high rates of deforestation and land conversion (Sierra, 2013). The fruits and seeds of *P. aequatorialis* are an important food resource for many animals in the forest (Brokamp et al., 2014). In addition, the seeds of this palm are widely commercialized in the region for their white and hard endosperm also known as vegetable ivory (Barfod et al., 1990; Escobar et al., 2019; Montúfar et al., 2013). All this makes *P. aequatorialis* a suitable biological model for the study of how animal communities influence the removal of large seeds in disturbed habitats. We studied seed removal within three common habitats in the study area, which represent a gradient of disturbance from an agroforestry system, over a disturbed forest to a less-disturbed forest. We emphasize that we studied seed removal and not seed dispersal because we did not follow seed fate after removal (Christianini & Galetti, 2007; Vander Wall et al., 2005). We, therefore, use an exploratory approach to quantify the contribution of different animal species to seed removal by counting the number of seeds removed by each species in captured videos and pictures. We also explore how seed removal rates, the numbers of different species of seed removers, and the composition of seed remover communities vary between the three studied habitats. We expect that seed removal rates and the number of seed removers are lower in the more-disturbed habitat (agroforestry system) and that they increase along the continuum of disturbance, and that animal communities are different between habitats. We aim to: (1) describe seed remover communities and their quantitative contribution to seed removal; (2) test if rates of seed removal and richness of

seed removers are lower in more-disturbed habitats than in less-disturbed habitats; (3) test if the communities of seed removers are different between habitats. We then discuss our findings in the context of effective seed dispersal services provided by animal communities that have been observed removing seeds, and how it could influence plant recruitment and regeneration. With this study, we hope to increase our understanding of the seed dispersal dynamics of *P. aequatorialis*, which could help the conservation of this keystone forest resource.

Methods

Study Species

Phytelephas aequatorialis Spruce is a large-seeded palm endemic to western Ecuador, where less than 25% of the natural forests remain (Sierra, 2013). It grows from sea level up to 1600 masl in rain forests and seasonally dry forests on the Pacific coastal plain, and in pre-montane and montane forests in the west Andean foothills (Borchsenius et al., 1998). This palm is common in disturbed non-forest habitats such as agroforestry systems or pastures where it is left standing for its economic value (Borgtoft Pedersen & Skov, 2001). However, populations in these altered habitats lack natural regeneration due to the high mortality of juveniles and sub adults (Brokamp et al., 2014; Velásquez Runk, 1998). The absence of these cohorts may occur by mechanical removal or low tolerance to direct sunlight of the palm seedlings. Therefore, populations of *P. aequatorialis* that grow in disturbed habitats may present altered dispersal dynamics due to changes in the communities of seed dispersers.

Phytelephas aequatorialis is an important Non-Timber Forest Product (NTFP) in western Ecuador where it is commercialized in rural and urban areas. Natural populations are exploited mainly for their seeds, locally known as *tagua*, which are collected from the ground. The seeds of *P. aequatorialis*, like those of other phytelephantoid palms, are the source of vegetable ivory because of their very hard texture and white color. They are used as a raw material in button and handicraft manufacturing, and their commerce has been a profitable industry in the region since the 19th century until today (Barfod et al., 1990; Brokamp et al., 2014; Montúfar et al., 2013). The leaves of this palm, which are locally known as *cade*, are in turn harvested for thatch and are commercialized locally (Borchsenius & Moraes, 2006). The exploitation of *tagua* from natural forests seems to be sustainable, whereas land conversion is a more severe threat to the species (Brokamp et al., 2014) and therefore, to its provisioning of income to the local human population.

In addition to its economic importance, the fruits and seeds of *P. aequatorialis* are an important food resource for many animals in the forest. Female palms carry 10–25 spherical infructescences, which reach up to 30 cm in diameter (Barfod, 1991), each consisting of ~25 obconical fruits (Brokamp et al., 2014). Each fruit produces 4–8 seeds that measure ~5 cm in length and have an average dry weight of 36 g (Brokamp et al., 2014). Ripe fruits detach from the infructescence axis and fall to the base of the palm, opening and exposing the seeds, which are encased in mesocarp that attracts frugivores. Animals such as the Central-American agouti (*Dasyprocta punctata* Gray), the paca (*Cuniculus paca* Linnaeus), the Tomes' spiny rat (*Proechimys semispinosus* Tomes), the red-tailed squirrel (*Sciurus granatensis* Humboldt), among others, feed on the lipid-rich fleshy mesocarp that covers the seeds (Barfod, 1991; Brokamp et al., 2014). Some of them may act as secondary seed dispersers by removing seeds from the ground and transporting them to their burrows or scatter-hoarding them for future consumption (Brokamp et al., 2014). According to a genetic parentage analysis, two-thirds of 92 seed dispersal events measured in established seedlings occurred over 10 m in the less-disturbed forest studied here (see Study Sites), and only a few dispersal events occurred over 100 m (Escobar et al. unpubl. data). Seed predation by insects such as bruchid beetles can be extensive in wild populations of *P. aequatorialis* (Borgtoft Pedersen, 1995), highlighting the importance of seed dispersal for the survival and recruitment of this palm.

Study Sites

We studied seed removal in the palm *P. aequatorialis* in a seasonally dry region between the towns of Pedernales and Jama at ~100 masl, in the coastal plain of Manabí province in northwestern Ecuador (Figure 1). Over the past 30 years, half of this area has been deforested (Haro-Carrión & Southworth, 2018). The temperature fluctuates from 13–36°C, with a mean around 25°C. Precipitation is seasonal with a humid season from January to April with 100–400 mm of rain every month, and a dry season between May and December with up to 20 mm of rain per month (Instituto Nacional de Meteorología e Hidrología, 2014, 2015, 2017). Part of the vegetation is deciduous (Clark et al., 2006).

We conducted our experiments within three habitats that represent a continuum of disturbance (agroforestry system, disturbed forest, less-disturbed forest). The agroforestry system (0°5'2" S, 80°7'35" W) was in an area where natural forests have been turned into farms and crops. We worked in a private farm of six hectares where natural vegetation had been replaced with banana, cocoa, and coffee plantings. Most of the trees had

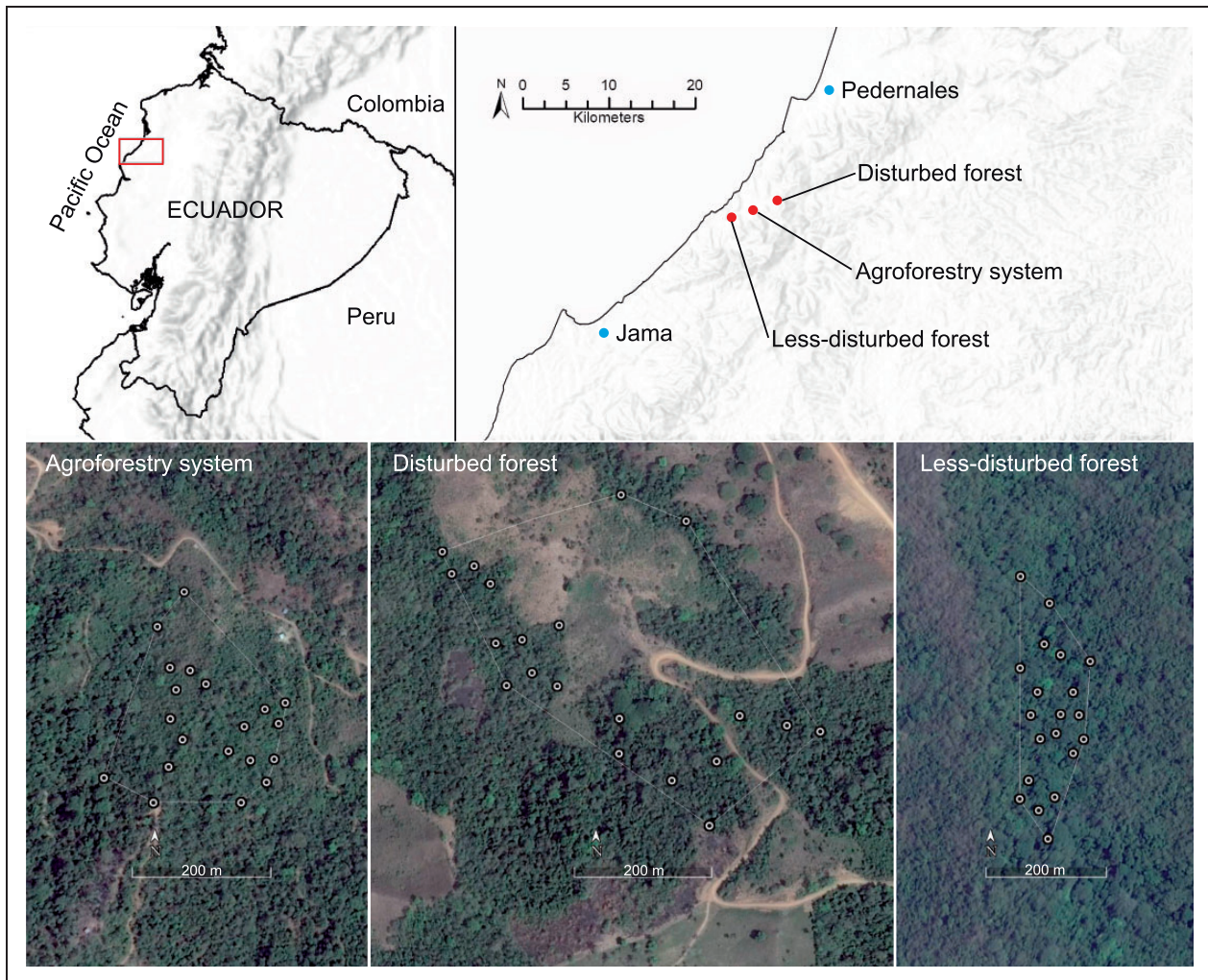


Figure 1. Study Sites. Maps and locations of the three habitats studied in western Ecuador. The dotted circles show the 20 experimental stations placed within each habitat, and the white line represents the perimeter used to calculate the work area within each habitat type. Landsat images from 2013 obtained from Google Earth Pro.

been cut but *P. aequatorialis* palms were left standing for harvesting seeds and to provide shade. Farmers clear the ground vegetation regularly as part of the agroforestry's maintenance, usually also removing palm seedlings. The disturbed forest ($0^{\circ}4'16''$ S, $80^{\circ}6'23''$ W) was located 2.6 km from the agroforestry system. The landscape here consists of smaller unprotected forest fragments ranging from 5–80 hectares in a mosaic with pastures of similar extent, where some individuals of *P. aequatorialis* are left standing. We worked in a private property of 17 hectares, where a pasture of around nine hectares was surrounded by forest fragments, including the largest fragment of 80 hectares. We worked only in the forest fragments and avoided palms left in the pastures so as not to expose the camera traps used. The less-disturbed forest ($0^{\circ}5'12''$ S, $80^{\circ}9'$ W) was located at 2.5 km away from the agroforestry system, but in the opposite direction of the disturbed forest. The less-

disturbed forest was placed within a protected fragment of mature forest. This fragment has an extension of 200 hectares and is part of the privately owned reserve Lalo Loor. Our study plot in the less-disturbed forest covered four hectares and was located in an area that was apparently more humid than the rest of the fragment, where *P. aequatorialis* is present. The density of female palms here was 20 individuals per hectare (Escobar et al., unpubl. data).

Seed Removal Experiments and Camera Trapping

Seed removal experiments were conducted from July to August 2018, during the dry season. The experiments were done consecutively in the three habitats for logistic reasons. We located 20 adult female palms with mature and immature fruits in each of the three habitats ($n = 60$). The maternal palms were selected as far from

each other as possible, separated by at least 30 m distance, which ensures independent seed removal observations (DeMattia et al., 2004). For each of the 60 palms, we collected all seeds remaining enclosed in the mesocarp of the mature fruits because the mesocarp attracts frugivores and promotes the removal of seeds. We removed mature seeds from nearby fruiting palms to reduce the bias that could be generated if there would be different densities of female palms between habitats. At the base of each maternal palm, we cleared an area of 3–4 m² of leaf litter to enhance the visibility of the seeds during the experiments. This litter clearing process can attract some mammals such as rodents, because the clearing makes it easier for the animals to find the seeds. Since rodents were supposed to be the main consumers of fruits and seeds of this palm, and therefore its dispersers (Brokamp et al., 2014), we did not consider this process as a bias against other animal groups. In the cleared area, we set up an experimental station with 20 seeds (total number of seeds = 1200), arranged in a circle with a radius of 0.5 m. When less than 20 seeds were available below a focal palm individual, we used seeds from other nearby palms. We visited the experimental stations daily for seven days to count the seeds remaining. We did not continue the experiment beyond seven days because at that time the mesocarp attached to the seeds had decomposed and was unattractive to seed removers (see Results). We checked for seeds with intact mesocarp in a radius of 2 m around each station, assuming that an animal could have accidentally moved it while passing or removing other seeds. In this case, we

placed the seed again at the station assuming that the seed had not been moved deliberately. We confirmed this assumption at the end of the first day of the experiments (24 hours after placing the stations), and therefore we maintained the procedure. If a seed with the mesocarp eaten was found within the 2 m radius, it was considered as deliberately removed and displaced by an animal.

We placed one camera trap (Bushnell Trophy Cam HD model 119537C; Bushnell Corporation, Overland, Kansas, USA) at each experimental station to identify the animal species and quantify their contribution to seed removal. We placed the camera 2–3 m from the station on available trunks (or stakes), and 0.5–1 m from the ground pointing to the seeds. Cameras were programmed to take three color photographs followed by a color video of one minute (max length) when the movement of a passing animal triggered their sensor; the same procedure was repeated after one second if the sensor was still detecting movement. We set the sensors to the highest possible sensitivity. Photographs and videos were used to count the number of seeds that each animal species removed. Based on the daily amounts of removed seeds per station, we classified as “unknown” the animals that we could not identify due to camera failing (see Results). A seed was considered as removed when an animal took it with its mouth or front legs and moved it out of the vision range of the camera (Figure 2). We used The Field Guide of the Mammals of Ecuador (Tirira, 2007) for animal identification. We did not consider a seed as removed when an animal ate



Figure 2. Seed Removal by a Coati. Sequence of images of a white-nosed coati *Nasua narica* removing a seed of *Phytelephas aequatorialis* in western Ecuador. (A) Coati arriving at the experimental station attracted by the fragrance of the seeds; (B) Coati taking the seed in its mouth; (C) Coati leaving the experimental station with a seed in its mouth; (D) Coati moving away from the vision range of the camera. Note that there are eight seeds in the station at the beginning of the sequence and there are seven seeds at the end.

only the mesocarp without moving the seed out of the station.

Data Analysis

We conducted statistical analyses in R 3.3.3 (R Core Team). To examine how the rates of seed removal varied between the three habitats, we conducted a linear mixed-effects (LME) regression model using the R-package *nlme* (Pinheiro et al., 2018). We used the number of seeds removed from each experimental station as a response variable and the type of habitat as a fixed factor, and accounted for spatial autocorrelations by incorporating latitude and longitude of each station in the model. Even though we could not identify the seed removers for all removal events (see Results), we compared their richness and composition as an approximation of the actual variation of these parameters in the studied habitats. For this purpose, we compared these measures using only the removal events where we identified the responsible animal species. We conducted the same analysis to see how the three habitats varied in the

richness of observed seed removers. We used the animal species richness observed in each experimental station as a response variable and the type of habitat as a fixed factor. We examined differences in the frugivore community composition among the three habitats using a nonparametric permutational multivariate analysis (PERMNOVA) with the R-package *vegan* (Oksanen et al., 2018) based on Bray-Curtis similarity metrics (Anderson, 2001; McArdle & Anderson, 2001) with 9999 permutations.

Results

Seed Removal Rates

After seven days of observations in each habitat, a total of 1048 seeds (87%) had been removed in the three habitats. Animals removed 305 seeds (76%) in the agroforestry system, 358 (89%) in the disturbed forest, and 385 seeds (96%) in the less-disturbed forest (Table 1). The most intense seed removal occurred within the first two days of observation in the less-disturbed forest, and

Table 1. Summary of Seed Removal Experiments and Camera Trapping in *Phytelephas aequatorialis* in western Ecuador.

Habitat	Total seeds removed	Seeds removed per station	Seeds with known remover	Remover richness per station
Agroforestry system	305 (76%)	15 (SD \pm 5.57)*	86 (28%)	1 (SD \pm 0.5) *
Disturbed forest	358 (89%)	18 (SD \pm 3.01)	162 (45%)	2 (SD \pm 1.3)
Less-disturbed forest	385 (96%)	19 (SD \pm 1.68)	158 (41%)	2 (SD \pm 1.3)

Note. Mean numbers of seeds removed and remover richness are averaged over 20 stations. Percentages of seeds with known remover are calculated from the total of seeds removed. * shows significant differences with the other two habitats ($P < 0.05$; Linear mixed-effects (LME) regression model).

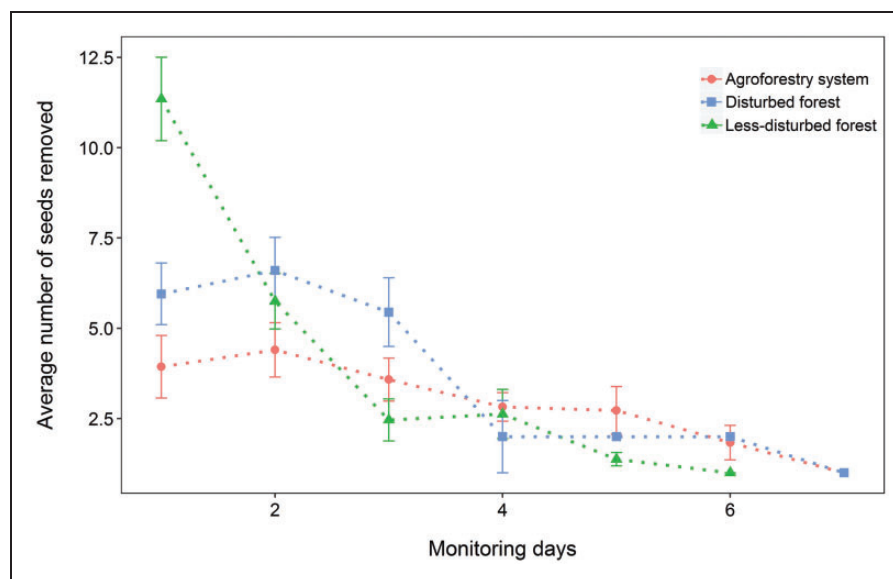


Figure 3. Daily Seed Removal. Mean number of seeds of *Phytelephas aequatorialis* removed each day among three habitats studied in western Ecuador. Vertical lines represent the standard error (S.E.) of the means.

within the first three days in the other two more disturbed habitats (Figure 3). Removal within the less-disturbed forest extended up to the sixth day, whereas one dispersal event occurred on the seventh day in both the agroforestry system and the disturbed forest. The mean number of removed seeds per experimental station in the agroforestry system was 15 ($SD \pm 5.57$), whereas in the disturbed forest it was 18 ($SD \pm 3.01$), and in the less-disturbed forest, it was 19 ($SD \pm 1.68$). The agroforestry system had significantly lower rates of seed removal than the disturbed forest ($P = 0.03$, $\beta = 2.65$, $t = 2.22$, $DF = 57$) and the less-disturbed forest ($P < 0.01$, $\beta = 4$, $t = 3.35$, $DF = 57$). No significant differences in seed removal were found between the disturbed forest and the less-disturbed forest.

Richness and Composition of Seed Removers

Based on the pictures and videos, we identified the seed removers in 28% of the removal events in the agroforestry system, in 45% in the disturbed forest, and in 41% in the less-disturbed forest (Table 1). We identified five

mammal species that removed seeds in the agroforestry system, and seven in both the disturbed forest and the less-disturbed forest (Table 2). The percentage of seeds removed by each animal species varied among the three habitats (Figure 4). We could not identify the animals in all the removal events because the cameras failed in their activation or were not fast enough to capture the moving animals. Thus, the results obtained from camera traps are preliminary and may not be fully representative of the actual richness and composition of seed remover communities. The medium-sized Tomes' spiny rat (*Proechimys semispinosus*) was the main seed remover in the agroforestry system, whereas large-sized rodents such as the Central-American agouti (*Dasyprocta punctata*) and the paca (*Cuniculus paca*) were less important for seed removal. Rodents of all sizes removed seeds in the disturbed forest, including agoutis, spiny rats the Talamanca trans-Andean mouse (*Transandinomys talamancae* Allen), and the Ecuadorian spiny pocket mouse (*Heteromys teleus* Anderson, R. P. y Jarrín-V, P.). In the less-disturbed forest, large-sized mammals such as pacas,

Table 2. Animal Seed Removers. Mammal species identified as removers of the large seeds of *Phytelephas aequatorialis* in three habitats in western Ecuador.

Order	Species	Common name	Habitat type	Weight (kg)*
Carnivora	<i>Nasua narica</i>	White-nosed coati	DF, L-DF	3.5–5.9
Didelphimorphia	<i>Didelphis marsupialis</i>	Common opossum	DF, L-DF	0.75–2.5
Rodentia	<i>Cuniculus paca</i>	Paca	AS, L-DF	5–13
Rodentia	<i>Dasyprocta punctata</i>	Central-American agouti	AS, DF, L-DF	3–5
Rodentia	<i>Heteromys teleus</i>	Ecuadorian spiny pocket mouse	DF	0.01
Rodentia	<i>Sciurus granatensis</i>	Red-tailed squirrel	AS, DF, L-DF	0.21–0.53
Rodentia	<i>Proechimys semispinosus</i>	Tomes' spiny rat	AS, DF, L-DF	0.32–0.53
Rodentia	<i>Transandinomys talamancae</i>	Talamanca trans-Andean mouse	AS, DF, L-DF	0.05–0.07

Note. AS = agroforestry system, DF = disturbed forest, L-DF = less-disturbed forest.

*See Tirira (2007).

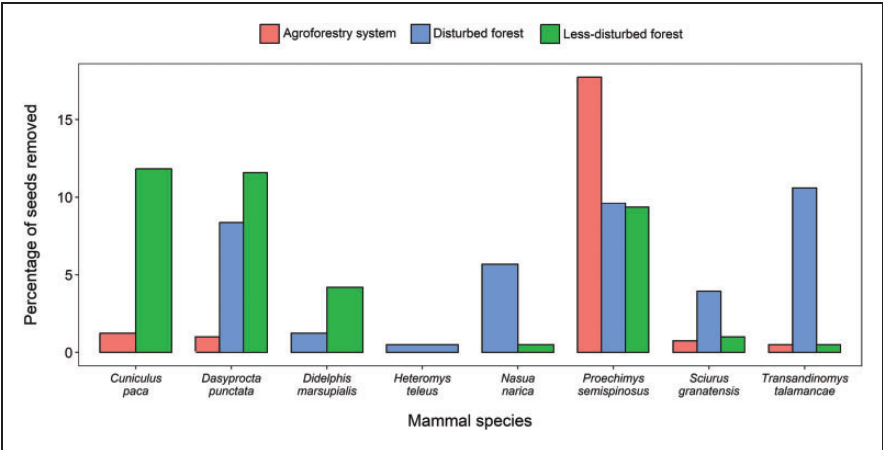


Figure 4. Contribution to Seed Removal. Total contribution of each mammal species to the removal of the large seeds of *Phytelephas aequatorialis* among three habitats studied in western Ecuador. Removal events with an unknown animal seed remover are not shown.

agoutis and common opossums (*Didelphis marsupialis* Linnaeus) as well as spiny rats contributed the most to seed removal. The actual contribution of small-sized rodents may be higher in the three habitats because they were not detected by the cameras due to their size and rapid movement.

Based on the events where we were able to identify the animals, we found, on average, one species ($SD \pm 0.5$) of seed remover per station in the agroforestry system and two species per station in both the disturbed forest ($SD \pm 1.3$) and the less-disturbed forest ($SD \pm 1.3$; Table 1). The number of species of seed removers was significantly lower in the agroforestry system than in the disturbed forest ($P < 0.01$, $\beta = 1.5$, $t = 4.19$, $DF = 57$) and in the less-disturbed forest ($P < 0.01$, $\beta = 1.45$, $t = 4.06$, $DF = 57$). No significant differences were found between the disturbed forest and the less-disturbed forest. Frugivore community composition significantly differed among the three habitats ($P < 0.01$), although there is an overlap in species between the agroforestry system and the disturbed forest (Figure 5).

Discussion

We studied post-dispersal seed removal patterns in the large-seeded palm *Phytelephas aequatorialis* within three habitats with different degrees of disturbance. Even though we could not determine all the frugivore species removing seeds in our experiments, camera trapping proved useful to describe the fauna associated with seed dispersal in *P. aequatorialis*. The Tomes' spiny rat (*Proechimys semispinosus*) and the Central-American

agouti (*Dasyprocta punctata*) stand out as effective seed removers and are potential seed dispersers over short and long distances, respectively. We detected significantly lower seed removal rates and richness of animal seed removers in the agroforestry system compared to the two forest habitats, indicating a negative effect of habitat disturbance in the seed dispersal dynamics of *P. aequatorialis*. The population growing in the agroforestry system presented altered seed dispersal dynamics; however, it could still maintain effective seed dispersal over short distances because of the high contribution of spiny rats to seed removal. Thus, the future of this population depends on the maintenance of its already reduced frugivore community.

Seed removal in *P. aequatorialis* is done by a variety of frugivore mammals whose potential contribution to effective seed dispersal depends on their size and behavior (Howe, 2016). For instance, non-granivore animals, such as the common opossum (*Didelphis marsupialis*) and the white-nosed coati (*Nasua narica* Linnaeus), may act as generalist dispersers for *P. aequatorialis* seeds that only feed on the fruit mesocarp, leaving the seeds near the removal site. Even though seed removal by these generalist dispersers could help seeds to escape density- and distance-dependent mortality (Comita et al., 2010, 2014; Johnson et al., 2014), they may not survive if they are not cached to reduce predation. The small sizes of the Talamanca trans-Andean mouse (*Transandinomys talamancae*) and the Ecuadorian spiny pocket mouse (*Heteromys teleus*) probably prevent the seeds removed by them from escaping the surroundings of parental plants where mortality is high. Thus,

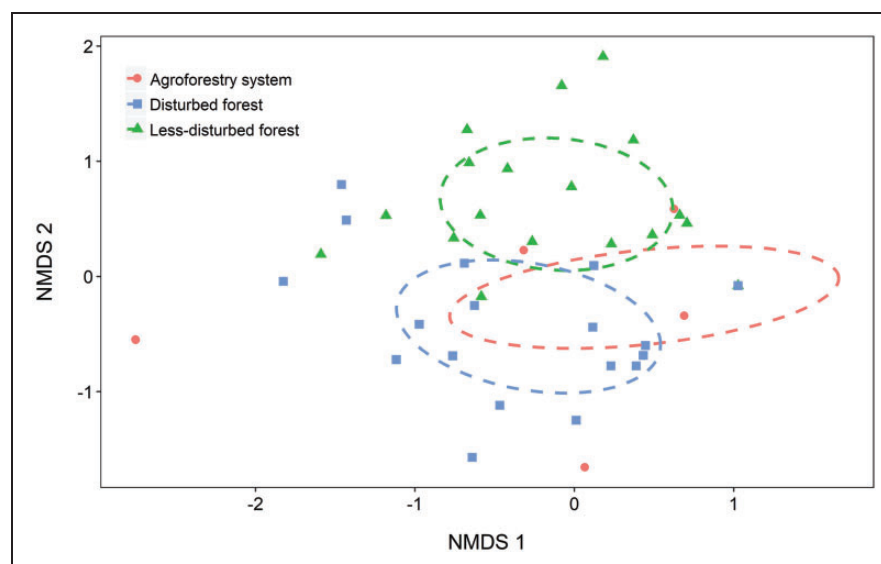


Figure 5. Ordination of Seed Removers. Ordination of the animal communities that remove the large seeds of *Phytelephas aequatorialis* in three habitats studied in western Ecuador in terms of species composition as represented by two axes of non-metric multidimensional scaling (NMDS).

their contribution to effective seed dispersal may be even lower than that of the generalist dispersers. On the other side, removal by larger rodents such as agoutis, spiny rats, pacas (*Cuniculus paca*), and red-tailed squirrels (*Sciurus granatensis*) could enhance effective seed dispersal because rodents cache seeds in microsites where they have higher chances of being recruited to become reproductive adults (Choo et al., 2012; Dunham, 2011). In addition, agoutis, spiny rats, and squirrels scatter-hoard seeds, which increases seed dispersal distances through time (Brodin, 2010; Carvajal & Adler, 2008; Dittel et al., 2015; Jansen et al., 2012; Kuprewicz & García-Robledo, 2019; Wright & Duber, 2001).

Regarding the relative contribution, spiny rats stand out as effective removers of the large seeds of *P. aequatorialis*, particularly in the agroforestry system where they removed most of the seeds that we could link to an animal species. This rodent species is abundant in tropical regions and common in disturbed habitats (Carvajal & Adler, 2008; Rojas-Robles et al., 2012), and extensively removes seeds of other large-seeded palms (Carvajal & Adler, 2008; Dittel et al., 2015; Hoch & Adler, 1997). Spiny rats can disperse large seeds for distances larger than 10 m (Dittel et al., 2015), potentially enhancing seed survival and establishment outside the surroundings of parental plants. The relatively high rates of seed removal by spiny rats observed in the agroforestry system suggest that this rodent could play an important role in the recruitment of *P. aequatorialis* in this habitat. Thus, spiny rats could be key elements for the regeneration of *P. aequatorialis* in disturbed habitats such as agroforestry systems because they are the main contributors to seed removal.

The limited seed removal by larger rodents such as agoutis and pacas in the agroforestry system suggests that dispersal occurs mostly over short distances in this habitat. Agoutis are the only rodents that are capable of dispersing large seeds over long-distances through scatter-hoarding (Jansen et al., 2012; Kuprewicz & García-Robledo, 2019). For instance, a single large seed of the Neotropical palm *Astrocaryum standleyanum* can be buried and re-cached up to 36 times by agoutis, and in this way, become dispersed more than 100 m away from the parental palm (Jansen et al., 2012). Apparently, pacas do not scatter hoard seeds (Meritt, 1989); however, these rodents occupy large home ranges of up to 212 hectares (Gutierrez et al., 2016), which makes them able to occasionally disperse seeds over long distances. Since these two large rodents are commonly hunted for their meat (Galetti et al., 2006; Gallina et al., 2012; Jones et al., 2019; Valsecchi et al., 2014), they may avoid non-forest habitats where they are exposed to hunters and predators (Gutierrez et al., 2016; Jax et al., 2015). For this reason, seed dispersal over long-distances must be rare in the agroforestry system.

On the other side, agoutis and pacas are among the main seed removers in the two forests, which is a habitat where their populations are abundant (Aliaga-Rossel et al., 2008; Beck-King et al., 1999; Kuprewicz & García-Robledo, 2019). Agoutis could be responsible for long-distance dispersal events for more than 100 m which were previously estimated in the less-disturbed forest through a genetic parentage analysis in established seedlings (Escobar et al. unpubl. data). Long-distance dispersal may also occur in the disturbed forest where agoutis removed a high amount of seeds.

Seed removal rates and richness of seed removers seem to be negatively influenced by habitat disturbance. Based on our camera trap results, removal rates and richness of animal seed removers were lower in the agroforestry system, which is the most disturbed habitat analyzed here. These results agree with previous research in which lower seed removal occurred in disturbed habitats due to lower richness of seed removers compared to less-disturbed habitats (Blackham & Corlett, 2015; Galetti et al., 2006; Lehouck et al., 2009; Ramírez et al., 2009; Wright et al., 2000; Wright & Duber, 2001). Additional studies have described lower rates of seed removal in disturbed habitats compared to less-disturbed habitats without accounting for the richness of seed removers (Brum et al., 2010; Iob & Vieira, 2008; Razafindratsima, 2017; Sánchez-Cordero & Martínez-Gallardo, 1998). These two parameters were statistically similar between the two forest habitats, suggesting that the loss of forest cover could lower animal species richness (Martensen et al., 2012) and subsequent reduction in seed removal. In this perspective, populations of *P. aequatorialis* that grow in non-forest habitats could present altered seed dispersal dynamics because of lower seed removal rates and lower number of frugivore species that remove their seeds.

Relative high removal rates of *P. aequatorialis* seeds occur in the three habitats studied even if the composition of seed remover communities was different between the habitats. Although fewer seeds were removed in the agroforestry system compared to the two forest habitats, the percentage of removal in the agroforestry system could be considered high when compared to the removal rates of other large-seeded palms in well-preserved Neotropical forests. For instance, 55% of the 1400 seeds of *Astrocaryum standleyanum* in 15 forested islands in Panama were removed by spiny rats (Hoch & Adler, 1997). Nearby, on Barro Colorado Island, agoutis and spiny rats removed 72% of 589 seeds from the same species (Jansen et al., 2012). Spiny rats and squirrels also removed 20% of 1500 seeds of the palm *Attalea butyracea* and the tree *Dipteryx oleifera* on the same island (Carvajal & Adler, 2008). Additionally, most of the seeds of *P. aequatorialis* were removed during the first four days of observation in the agroforestry

system, similar to what we found in the disturbed forest. Relatively high removal rates in the agroforestry system suggest that different animal communities can maintain functional roles such as seed removal to some extent in disturbed habitats (Dehling et al., 2020; Farwig et al., 2017; Neuschulz et al., 2011).

Identifying animal seed removers using camera traps is a common practice in ecological research on seed dispersal (Blackham & Corlett, 2015; Campos et al., 2018; Christianini & Galetti, 2007; Cramer et al., 2007; da Silva et al., 2011; Dai et al., 2018; Galetti et al., 2015; Iob & Vieira, 2008; Razafindratsima, 2017; Seufert et al., 2010; Ssali et al., 2018). Several studies have used camera traps to attribute single events of seed removal to particular animal species (Brown et al., 2016; Jansen et al., 2012; White et al., 2017). Our study used this same method to identify animal seed removers and to quantify their contribution to seed removal within a continuum of habitat disturbance, although we could not determine the animals responsible for all removal events due to camera failing. Even if camera failing can occur during seed removal experiments (Brown et al., 2016; Razafindratsima, 2017; Seufert et al., 2010), we did show that camera trapping is a useful tool for describing the mammalian fauna associated with seed removal processes and that it has the potential for evaluating the contribution of single mammal species to seed removal.

Continued field observations may provide a deeper understanding of the seed dispersal dynamics of *P. aequatorialis*. First, identifying the animal species responsible for all removal events would provide more reliable conclusions on the relationship between seed removal and the richness of animal seed removers. This can be achieved by using cameras with greater sensitivity and faster activation, or by placing more than one camera at each experimental station. That could also help to determine animal abundance, which can influence seed removal (Galetti et al., 2006; Ramírez et al., 2009), by recognizing different individuals for each animal species. Alternatively, camera trapping can be complemented with surveys to obtain better estimates of animal abundance. Seed fate experiments should be added to determine the mortality rates of seeds and the actual contribution of scatter-hoarding rodents to the dispersal of *P. aequatorialis* seeds. Furthermore, replicating the experiments performed in the three different habitats will provide more reliable conclusions about the effects of habitat disturbance on the seed removal of *P. aequatorialis* and other large-seeded plants. Such follow-up research could enhance our understanding of the seed dispersal dynamics of this palm, which would make possible the development of conservation programs and politics that aim to keep *P. aequatorialis* as a sustainable NTFP resource.

Implications for Conservation

Frugivore communities studied in the three habitats have the potential to ensure effective dispersal of large seeds away from maternal palms, allowing the regeneration of populations (Comita et al., 2014). Spiny rats are particularly important for recruitment in the agroforestry system, where the contribution of larger animals to seed removal was low. Thus, the future permanence of *P. aequatorialis* populations in non-forest habitats might depend on the presence of this rodent. In spite of that, dispersal over long distances could be limited in the agroforestry system because spiny rats tend to disperse seeds over short distances (Dittel et al., 2015), which is not enough for connecting populations. Long-distance seed dispersal over distances larger than 100 m occurs in the less-disturbed forest, as estimated by a genetic parentage analysis (Escobar et al. unpubl. data), probably because of the high rates of seed removal performed by agoutis. Long-distance dispersal could also occur in the disturbed forest because agoutis showed a significant contribution to seed removal in this habitat. Therefore, forest habitats could be connected by the seed dispersal services provided by agoutis, but non-forest habitats may be isolated from other populations.

The absence of effective seed dispersal could endanger the long-term persistence of local populations of *P. aequatorialis* due to alterations in their demographic and genetic patterns (Comita et al., 2014; Wotton & Kelly, 2011; Young et al., 1996). The potential future loss of populations growing in non-forest habitats such as agroforestry systems or pastures could be caused by the absence of medium- and large-sized rodents and their seed dispersal services. This may not affect the conservation of *P. aequatorialis* as a species; nevertheless, it could reduce the connectivity between “healthy” populations growing in the few remaining forests of the region. The loss of populations could also reduce the species’ genetic diversity and its consequent capacity to face future environmental changes (Nutt et al., 2016; Wernberg et al., 2018). Considering that more than 75% of the natural forests in western Ecuador have already been cleared or disturbed (Sierra, 2013), a large proportion of *P. aequatorialis* populations would be threatened under this scenario. Other large-seeded plants distributed in the region could face a similar situation. To counteract that, plant-frugivore interactions should be restored through forest regeneration and forest conservation programs. Additionally, the conservation of effective seed dispersers such as agoutis and spiny rats could make a difference in the long-term presence of local populations of *P. aequatorialis* and other large-seeded plants.

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References

- Aliaga-Rossel, E., Kays, R. W., & Fragoso, J. M. V. (2008). Home-range use by the Central American agouti (*Dasyprocta punctata*) on Barro Colorado Island, Panama. *Journal of Tropical Ecology*, 24(4), 367–374. <https://doi.org/10.1017/S0266467408005129>
- Alroy, J. (2017). Effects of habitat disturbance on tropical forest biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 114(23), 6056–6061. <https://doi.org/10.1073/pnas.1611855114>
- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32–46.
- Barfod, A. S. (1991). A monographic study of the subfamily Phytelephantoideae (Arecaceae). *Opera Botanica*, 105, 1–73.
- Barfod, A. S., Bergmann, B., & Pedersen, H. B. (1990). The vegetable ivory industry: Surviving and doing well in Ecuador. *Economic Botany*, 44(3), 293–300. <https://doi.org/10.1007/BF03183910>
- Beck-King, H., Helversen, O. v., & Beck-King, R. (1999). Home range, population density, and food resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: A study using alternative methods 1. *Biotropica*, 31(4), 675–685. <https://doi.org/10.1111/j.1744-7429.1999.tb00417.x>
- Blackham, G. V., & Corlett, R. T. (2015). Post-dispersal seed removal by ground-feeding rodents in tropical peatlands, Central Kalimantan, Indonesia. *Scientific Reports*, 5, 14152. <https://doi.org/10.1038/srep14152>
- Borchsenius, F., Borgtoft Pedersen, H., & Balslev, H. (1998). *Manual to the palms of Ecuador*. AAU Reports 37.
- Borchsenius, F., & Moraes, M. R. (2006). Diversidad y usos de palmeras andinas (Arecaceae) [Diversity and uses of Andean palms (Arecaceae)]. In M. R. Moraes, B. Øllgaard, L. P. Kvist, F. Borchsenius, & H. Balslev (Eds.), *Botánica Económica de los Andes Centrales* (Vol. 2, pp. 412–433). Universidad Mayor de San Andrés.
- Borgtoft Pedersen, H. (1995). Predation of *Phytelephas aequatorialis* seeds (“vegetable ivory”) by the bruchid beetle *Caryoborus chiriquensis*. *Principes*, 39, 89–94.
- Borgtoft Pedersen, H., & Skov, F. (2001). Mapping palm extractivism in Ecuador using pair-wise comparison and bioclimatic modeling. *Economic Botany*, 55(1), 63–71. <https://doi.org/10.1007/BF02864546>
- Brodin, A. (2010). The history of scatter hoarding studies. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1542), 869–881. <https://doi.org/10.1098/rstb.2009.0217>
- Brokamp, G., Borgtoft Pedersen, H., Montúfar, R., Jácome, J., Weigend, M., & Balslev, H. (2014). Productivity and management of *Phytelephas aequatorialis* (Arecaceae) in Ecuador. *Annals of Applied Biology*, 164(2), 257–269. <https://doi.org/10.1111/aab.12098>
- Brown, A. J., Deutschman, D. H., Braswell, J., & McLaughlin, D. (2016). Remote cameras reveal experimental artifact in a study of seed predation in a semi-arid shrubland. *PLoS One*, 11(10), e0165024. <https://doi.org/10.1371/journal.pone.0165024>
- Brum, F., Duarte, L., & Hartz, S. (2010). Seed removal patterns by vertebrates in different successional stages of *Araucaria* forest advancing over Southern Brazilian grasslands. *Community Ecology*, 11(1), 35–40. <https://doi.org/10.1556/ComEc.11.2010.1.6>
- Campos, C. M., Campos, V. E., Giannoni, S. M., Rodríguez, D., Albanese, S., & Cona, M. I. (2017). Role of small rodents in the seed dispersal process: *Microcavia australis* consuming *Prosopis flexuosa* fruits. *Austral Ecology*, 42(1), 113–119. <https://doi.org/10.1111/aec.12406>
- Campos, C. M., Velez, S., Miguel, M. F., Papú, S., & Cona, M. I. (2018). Studying the quantity component of seed dispersal effectiveness from exclosure treatments and camera trapping. *Ecology and Evolution*, 8(11), 5470–5479. <https://doi.org/10.1002/ece3.4068>
- Carvajal, A., & Adler, G. H. (2008). Seed dispersal and predation by *Proechimys semispinosus* and *Sciurus granatensis* in gaps and understorey in central Panama. *Journal of Tropical Ecology*, 24(5), 485–492. <https://doi.org/10.1017/S0266467408005270>
- Caughlin, T. T., Ferguson, J. M., Lichstein, J. W., Zuidema, P. A., Bunyavejchewin, S., & Levey, D. J. (2015). Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proceedings of the Royal Society B: Biological Sciences*, 282(1798), 20142095. <https://doi.org/10.1098/rspb.2014.2095>

- Choo, J., Juenger, T. E., & Simpson, B. B. (2012). Consequences of frugivore-mediated seed dispersal for the spatial and genetic structures of a neotropical palm. *Molecular Ecology*, 21(4), 1019–1031. <https://doi.org/10.1111/j.1365-294X.2011.05425.x>
- Christianini, A. V., & Galetti, M. (2007). Spatial variation in post-dispersal seed removal in an Atlantic Forest: Effects of habitat, location and guilds of seed predators. *Acta Oecologica*, 32(3), 328–336. <https://doi.org/10.1016/j.actao.2007.06.004>
- Clark, J. L., Neill, D. A., & Asanza, M. (2006). *Floristic checklist of the Mache-Chindul mountains of northwestern Ecuador*. Department of Botany, National Museum of Natural History.
- Comita, L. S., Muller-Landau, H. C., Aguilar, S., & Hubbell, S. P. (2010). Asymmetric density dependence shapes species abundances in a tropical tree community. *Science*, 329(5989), 330–332. <https://doi.org/10.1126/science.1190772>
- Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., Beckman, N., Zhu, Y., & Gómez-Aparicio, L. (2014). Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *The Journal of Ecology*, 102(4), 845–856. <https://doi.org/10.1111/1365-2745.12232>
- Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In P. J. den Boer & G. R. Gradwell (Eds.), *Dynamics of populations* (pp. 298–312). Centre for Agricultural Publishing and Documentation.
- Cramer, J. M., Mesquita, R. C. G., & Williamson, G. B. (2007). Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation*, 137(3), 415–423. <https://doi.org/10.1016/j.biocon.2007.02.019>
- Crawley, M. J., & Long, C. R. (1995). Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. *The Journal of Ecology*, 83(4), 683–696. <https://doi.org/10.2307/2261636>
- da Silva, F. R., Begnini, R. M., Lopes, B. C., & Castellani, T. T. (2011). Seed dispersal and predation in the palm *Syagrus romanzoffiana* on two islands with different faunal richness, southern Brazil. *Studies on Neotropical Fauna and Environment*, 46(3), 163–171. <https://doi.org/10.1080/01650521.2011.617065>
- Dai, R., Ngoprasert, D., Gale, G. A., & Savini, T. (2018). Secondary removal of seeds dispersed by gibbons (*Hylobates lar*) in a tropical dry forest in Thailand. *Raffles Bulletin of Zoology*, 66, 517–527.
- Dehling, D. M., Peralta, G., Bender, I. M. A., Blendinger, P. G., Böhning-Gaese, K., Muñoz, M. C., Neuschulz, E. L., Quitián, M., Saavedra, F., Santillán, V., Schleuning, M., & Stouffer, D. B. (2020). Similar composition of functional roles in Andean seed-dispersal networks, despite high species and interaction turnover. *Ecology*, 101(7), e03028. <https://doi.org/10.1002/ecy.3028>
- DeMattia, E. A., Curran, L. M., & Rathcke, B. J. (2004). Effects of small rodents and large mammals on neotropical seeds. *Ecology*, 85(8), 2161–2170. <https://doi.org/10.1890/03-0254>
- Dittel, J. W., Lambert, T. D., & Adler, G. H. (2015). Seed dispersal by rodents in a lowland forest in central Panama. *Journal of Tropical Ecology*, 31(5), 403–412. <https://doi.org/10.1017/S0266467415000280>
- Dunham, A. E. (2011). Soil disturbance by vertebrates alters seed predation, movement and germination in an African rain forest. *Journal of Tropical Ecology*, 27(6), 581–589. <https://doi.org/10.1017/S0266467411000344>
- Escobar, S., Couvreur, T. L. P., Montúfar, R., & Balslev, H. (2019). The ivory palm *Phytelephas aequatorialis* in western Ecuador. *Palms*, 63(2), 69–79.
- Farwig, N., Schabo, D. G., & Albrecht, J. (2017). Trait-associated loss of frugivores in fragmented forest does not affect seed removal rates. *Journal of Ecology*, 105(1), 20–28. <https://doi.org/10.1111/1365-2745.12669>
- Forget, P.-M., Munoz, E., & Leigh, E. G., Jr. (1994). Predation by rodents and bruchid beetles on seeds of *Scheelea* palms on Barro Colorado Island, Panama. *Biotropica*, 26(4), 420–426.
- Galetti, M., Bovendorp, R. S., & Guevara, R. (2015). Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. *Global Ecology and Conservation*, 3, 824–830. <https://doi.org/10.1016/j.gecco.2015.04.008>
- Galetti, M., Donatti, C. I., Pires, A. S., Guimarães, P. R., & Jordano, P. (2006). Seed survival and dispersal of an endemic Atlantic forest palm: The combined effects of defaunation and forest fragmentation. *Botanical Journal of the Linnean Society*, 151(1), 141–149. <https://doi.org/10.1111/j.1095-8339.2006.00529.x>
- Gallina, S., Pérez-Torres, J., & Guzmán-Aguirre, C. C. (2012). Use of the paca, *Cuniculus paca* (Rodentia: Agoutidae) in the sierra de Tabasco State Park, Mexico. *Revista de Biología Tropical*, 60(3), 1345–1355. <https://doi.org/10.15517/rbt.v60i3.1812>
- González-Varo, J. P. (2010). Fragmentation, habitat composition and the dispersal/predation balance in interactions between the mediterranean myrtle and avian frugivores. *Ecography*, 33(1), 185–197. <https://doi.org/10.1111/j.1600-0587.2009.06021.x>
- Gutierrez, S. M., Harmsen, B. J., Doncaster, C. P., Kay, E., & Foster, R. J. (2016). Ranging behavior and habitat selection of pacas (*Cuniculus paca*) in central Belize. *Journal of Mammalogy*, 98(2), 542–550. <https://doi.org/10.1093/jmammal/gyw179>
- Hardesty, B. D., Hubbell, S. P., & Bermingham, E. (2006). Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. *Ecology Letters*, 9(5), 516–525. <https://doi.org/10.1111/j.1461-0248.2006.00897.x>
- Harms, K. E., Wright, S. J., Calderón, O., Hernández, A., & Herre, E. A. (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, 404(6777), 493–495. <https://doi.org/10.1038/35006630>
- Haro-Carrión, X., & Southworth, J. (2018). Understanding land cover change in a fragmented forest landscape in a

- biodiversity hotspot of coastal Ecuador. *Remote Sensing*, 10(12), 1–21. <https://doi.org/10.3390/rs10121980>
- Haugaasen, J. M. T., Haugaasen, T., Peres, C. A., Gribel, R., & Wegge, P. (2010). Seed dispersal of the Brazil nut tree (*Bertholletia excelsa*) by scatter-hoarding rodents in a central Amazonian forest. *Journal of Tropical Ecology*, 26(3), 251–262. <https://doi.org/10.1017/S0266467410000027>
- Hoch, G. A., & Adler, G. H. (1997). Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). *Journal of Tropical Ecology*, 13(1), 51–58. <https://doi.org/10.1017/S0266467400010245>
- Howe, H. F. (1984). Implications of seed dispersal by animals for tropical reserve management. *Biological Conservation*, 30(3), 261–281. [https://doi.org/10.1016/0006-3207\(84\)90087-9](https://doi.org/10.1016/0006-3207(84)90087-9)
- Howe, H. F. (2016). Making dispersal syndromes and networks useful in tropical conservation and restoration. *Global Ecology and Conservation*, 6, 152–178. <https://doi.org/10.1016/j.gecco.2016.03.002>
- Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13(1), 201–228.
- Instituto Nacional de Meteorología e Hidrología. (2014). *Anuario Meteorológico* [Meteorological yearbook] (Vol. 51–2011). <http://www.serviciometeorologico.gob.ec/wp-content/uploads/anuarios/meteorologicos/Am2011.pdf>
- Instituto Nacional de Meteorología e Hidrología. (2015). *Anuario Meteorológico* [Meteorological yearbook] (Vol. 52–2012). <http://www.serviciometeorologico.gob.ec/wp-content/uploads/anuarios/meteorologicos/Am2012.pdf>
- Instituto Nacional de Meteorología e Hidrología. (2017). *Anuario Meteorológico* [Meteorological yearbook]. http://www.serviciometeorologico.gob.ec/docum_institucion/anuarios/meteorologicos/Am_2013.pdf
- Iob, G., & Vieira, E. M. (2008). Seed predation of *Araucaria angustifolia* (Araucariaceae) in the Brazilian Araucaria Forest: Influence of deposition site and comparative role of small and 'large' mammals. *Plant Ecology*, 198(2), 185–196. <https://doi.org/10.1007/s11258-007-9394-6>
- Jansen, P. A., Hirsch, B. T., Emsens, W.-J., Zamora-Gutiérrez, V., Wikelski, M., & Kays, R. (2012). Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences of the United States of America*, 109(31), 12610–12615. <https://doi.org/10.5441/001/1.9t0m888q>
- Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104(940), 501–528. <https://doi.org/10.1086/282687>
- Jax, E., Marin, S., Rodríguez-Ferraro, A., & Isasi-Catalá, E. (2015). Habitat use and relative abundance of the spotted paca *Cuniculus paca* (Linnaeus, 1766) (Rodentia: Cuniculidae) and the red-rumped agouti *Dasyprocta leporina* (Linnaeus, 1758) (Rodentia: Dasyproctidae) in Guatopo National Park, Venezuela. *Journal of Threatened Taxa*, 7(1), 6739–6749. <https://doi.org/10.11609/JoTT.o3915.6739-49>
- Johnson, D. J., Bourg, N. A., Howe, R., McShea, W. J., Wolf, A., & Clay, K. (2014). Conspecific negative density-dependent mortality and the structure of temperate forests. *Ecology*, 95(9), 2493–2503. <https://doi.org/10.1890/13-2098.1>
- Jones, K. R., Lall, K. R., & Garcia, G. W. (2019). Omnivorous behaviour of the agouti (*Dasyprocta leporina*): A neotropical rodent with the potential for domestication. *Scientifica*, 2019, 3759783. <https://doi.org/10.1155/2019/3759783>
- Jordano, P. (1995). Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaptation and constraints in plant-animal interactions. *The American Naturalist*, 145(2), 163–191.
- Kuprewicz, E. K., & García-Robledo, C. (2019). Deciphering seed dispersal decisions: Size, not tannin content, drives seed fate and survival in a tropical forest. *Ecosphere*, 10(1), e02551.
- Lehouck, V., Spanhove, T., Colson, L., Adringa-Davis, A., Cordeiro, N. J., & Lens, L. (2009). Habitat disturbance reduces seed dispersal of a forest interior tree in a fragmented African cloud forest. *Oikos*, 118(7), 1023–1034.
- Martensen, A. C., Ribeiro, M. C., Banks-Leite, C., Prado, P. I., & Metzger, J. P. (2012). Associations of forest cover, fragment area, and connectivity with neotropical understory bird species richness and abundance. *Conservation Biology*, 26(6), 1100–1111. <https://doi.org/10.1111/j.1523-1739.2012.01940.x>
- McArdle, B. H., & Anderson, M. J. (2001). Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology*, 82(1), 290–297.
- Meritt, D. (1989). The husbandry and management of the Paca *Cuniculus paca* at Lincoln Park Zoo, Chicago. *International Zoo Yearbook*, 28(1), 264–267. <https://doi.org/10.1111/j.1748-1090.1989.tb03297.x>
- Montúfar, R., Brokamp, G., & Jácome, J. (2013). Tagua: *Phytelephas aequatorialis*. In R. Valencia, R. Montúfar, H. Navarrete, & H. Balslev (Eds.), *Palmeras ecuatorianas: Biología y uso sostenible* (pp. 165–173). Herbario QCA de la Pontificia Universidad Católica del Ecuador.
- Morris, R. J. (2010). Anthropogenic impacts on tropical Forest biodiversity: A network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1558), 3709–3718. <https://doi.org/10.1098/rstb.2010.0273>
- Nathan, R. (2006). Long-distance dispersal of plants. *Science*, 313(5788), 786–788. <https://doi.org/10.1126/science.1124975>
- Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., & Tsoar, A. (2008). Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution*, 23(11), 638–647. <https://doi.org/10.1016/j.tree.2008.08.003>
- Neuschulz, E. L., Botzat, A., & Farwig, N. (2011). Effects of forest modification on bird community composition and seed removal in a heterogeneous landscape in South Africa. *Oikos*, 120(9), 1371–1379. <https://doi.org/10.1111/j.1600-0706.2011.19097.x>
- Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverría-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., ... Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520(7545), 45–50. <https://doi.org/10.1038/nature14324>

- Nutt, K. S., Burslem, D. F. R. P., Maycock, C. R., Ghazoul, J., Khoo, E., Hastie, A. Y. L., & Kettle, C. J. (2016). Genetic diversity affects seedling survival but not growth or seed germination in the Bornean endemic dipterocarp *Parashorea tomentella*. *Plant Ecology & Diversity*, 9(5–6), 471–481. <https://doi.org/10.1080/17550874.2016.1262923>
- Oksanen, A. 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. (2018). *vegan: Community ecology package*. R package version 2.5-1.
- Peters, H. A. (2003). Neighbour-regulated mortality: The influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters*, 6(8), 757–765. <https://doi.org/10.1046/j.1461-0248.2003.00492.x>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team (2018). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-137.
- Ramírez, B., Parrado-Rosselli, Á., & Stevenson, P. (2009). Seed dispersal of a useful palm (*Astrocaryum chambira* burret) in three Amazonian forests with different human intervention. *Colombia Forestal*, 12(1), 5–16.
- Razafindratsima, O. H. (2017). Post-dispersal seed removal by rodents in Ranomafana rain forest, Madagascar. *Journal of Tropical Ecology*, 33(3), 232–236. <https://doi.org/10.1017/S0266467417000104>
- Rojas-Robles, R., Gary Stiles, F., & Muñoz-Saba, Y. (2012). Frugivoría y dispersión de semillas de la palma *Oenocarpus bataua* (Arecaceae) en un bosque de los Andes colombianos [Frugivory and seed dispersal of the palm *Oenocarpus bataua* (Arecaceae) in a forest in the Colombian Andes]. *Revista de Biología Tropical*, 60(4), 1445–1461. <https://doi.org/10.15517/rbt.v60i4.2054>
- Sánchez-Cordero, V., & Martínez-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>
- Schupp, E. W., Jordano, P., & Gómez, J. M. (2010). Seed dispersal effectiveness revisited: A conceptual review. *The New Phytologist*, 188(2), 333–353. <https://doi.org/10.1111/j.1469-8137.2010.03402.x>
- Seufert, V., Linden, B., & Fischer, F. (2010). Revealing secondary seed removers: Results from camera trapping. *African Journal of Ecology*, 48(4), 914–922. <https://doi.org/10.1111/j.1365-2028.2009.01192.x>
- Sezen, U. U., Chazdon, R. L., & Holsinger, K. E. (2009). Proximity is not a proxy for parentage in an animal-dispersed neotropical canopy palm. *Proceedings of the Royal Society B: Biological Sciences*, 276(1664), 2037–2044. <https://doi.org/10.1098/rspb.2008.1793>
- Sierra, R. (2013). *Patrones y factores de deforestación en el Ecuador continental, 1990-2010. Y un acercamiento a los próximos 10 años* [Deforestation patterns and factors in continental Ecuador, 1990–2010. And an approach to the next 10 years]. Conservación Internacional y Forest Trends.
- Ssali, F., Moe, S. R., & Sheil, D. (2018). Tree seed rain and seed removal, but not the seed bank, impede forest recovery in bracken (*Pteridium aquilinum* (L.) Kuhn)-dominated clearings in the African highlands. *Ecology and Evolution*, 8(8), 4224–4236. <https://doi.org/10.1002/ece3.3944>
- Sunyer, P., Muñoz, A., Bonal, R., & Espelta, J. M. (2013). The ecology of seed dispersal by small rodents: A role for predator and conspecific scents. *Functional Ecology*, 27(6), 1313–1321. <https://doi.org/10.1111/1365-2435.12143>
- Tirira, D. (2007). *Guía de campo de los mamíferos del Ecuador [Field guide to the mammals of Ecuador]*. Ediciones Murciélagos Blanco. Publicación especial sobre los mamíferos del Ecuador 6.
- Valsecchi, J., El Bizri, H., & Figueira, J. (2014). Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. *Brazilian Journal of Biology*, 74(3), 560–568. <https://doi.org/10.1590/bjb.2014.0098>
- Vander Wall, S. B. (2001). The evolutionary ecology of nut dispersal. *The Botanical Review*, 67(1), 74–117. <https://doi.org/10.1007/BF02857850>
- Vander Wall, S. B., Kuhn, K. M., & Beck, M. J. (2005). Seed removal, seed predation, and secondary dispersal. *Ecology*, 86(3), 801–806. <https://doi.org/10.1890/04-0847>
- Velásquez Runk, J. (1998). Productivity and sustainability of a vegetable ivory palm (*Phytelephas aequatorialis*, Arecaceae) under three management regimes in northwestern Ecuador. *Economic Botany*, 52(2), 168–182. <https://doi.org/10.1007/BF02861205>
- Wandrag, E. M., Dunham, A. E., Duncan, R. P., & Rogers, H. S. (2017). Seed dispersal increases local species richness and reduces spatial turnover of tropical tree seedlings. *Proceedings of the National Academy of Sciences of the United States of America*, 114(40), 10689–10694. <https://doi.org/10.1073/pnas.1709584114>
- Wernberg, T., Coleman, M. A., Bennett, S., Thomsen, M. S., Tuya, F., & Kelaher, B. P. (2018). Genetic diversity and kelp forest vulnerability to climatic stress. *Scientific Reports*, 8(1), 1–8. <https://doi.org/10.1038/s41598-018-20009-9>
- White, J. D., Bronner, G. N., & Midgley, J. J. (2017). Camera-trapping and seed-labelling reveals widespread granivory and scatter-hoarding of nuts by rodents in the Fynbos Biome. *African Zoology*, 52(1), 31–41. <https://doi.org/10.1080/15627020.2017.1292861>
- Wotton, D. M., & Kelly, D. (2011). Frugivore loss limits recruitment of large-seeded trees. *Proceedings of the Royal Society B: Biological Sciences*, 278(1723), 3345–3354. <https://doi.org/10.1098/rspb.2011.0185>
- Wright, S. J., & Duber, H. C. (2001). Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica*, 33(4), 583–595. [https://doi.org/10.1646/0006-3606\(2001\)033\[0583:paffas\]2.0.co;2](https://doi.org/10.1646/0006-3606(2001)033[0583:paffas]2.0.co;2)
- Wright, S. J., Zeballos, H., Dominguez, I., Gallardo, M. M., Moreno, M. C., & Ibáñez, R. (2000). Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology*, 14(1), 227–239. <https://doi.org/10.1046/j.1523-1739.2000.98333.x>
- Young, A., Boyle, T., & Brown, T. (1996). The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology & Evolution*, 11(10), 413–418.