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SEED DISPERSAL OF A USEFUL PALM (*ASTROCARYUM CHAMBIRA* BURRET) IN THREE AMAZONIAN FORESTS WITH DIFFERENT HUMAN INTERVENTION

*Dispersión de semillas de la palma útil (*Astrocaryum chambira* Burret) en tres bosques amazónicos con diferente grado de intervención humana*

Keywords: Amazon forest, chambira palm, seed predation, insect seed predation, rodents.

Palabras clave: bosque amazónico, depredación de semillas, depredación por insectos, palma de chambira, roedores.

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ABSTRACT

The young leaves of *Astrocaryum chambira* are used by the indigenous people in the Amazon as raw material for handicrafts. However, few studies have been made on the natural history of this palm and on the indirect impact caused by the decrease of its dispersal agents. Considering that the loss of animal dispersal vectors due to hunting and landscape modification can affect seed dispersal processes of tropical forest plants, the goal of this study was to compare seed dispersal of *A. chambira* in three terra firme forests of the Colombian Amazon, with different degrees of human intervention. We censused densities of dispersal agents of *A. chambira*, and characterized the seed shadow. We also marked seeds to estimate dispersal distances, and established density and distance-dependent experimental stations to assess their relevance on seed dispersal. The results showed that seed removal was proportional to dispersal agent densities and forest intervention levels. Insects were the main seed predators in all sites but their effect was less pronounced in the low intervened forest site. Seed density did not show any effect on removal, while a higher probability of survival at intermediate distances from the parent palm (10 m) was found. Future studies should focus on seedling establishment, recruitment rates and the effects of human intervention on subsequent life stages of the palm.

RESUMEN

Las hojas jóvenes de *Astrocaryum chambira* son utilizadas por las comunidades indígenas amazónicas como materia prima para la fabricación de artesanías. Sin embargo, son muy pocos los estudios acerca de su historia de vida y de los impactos indirectos causados por la disminución de sus agentes dispersores. Teniendo en cuenta que la pérdida de animales dispersores de semillas por factores como cacería y modificación de hábitat afecta la dispersión de semillas de las especies de plantas tropicales, el objetivo de este estudio fue comparar la dispersión de semillas de *A. chambira* en tres bosques de tierra firme del Amazonas colombiano sujetos a diferentes niveles de intervención antrópica. Censamos las densidades de los agentes dispersores de *A. chambira* y caracterizamos la sombra de semillas. También marcamos semillas con el fin de estimar las distancias de dispersión y

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establecimos estaciones experimentales de denso-distancio-dependencia para evaluar su relevancia en la dispersión de semillas de esta especie. Los resultados muestran que la remoción de semillas fue proporcional a la densidad de animales y al nivel de intervención del bosque. Los insectos fueron los principales depredadores en todos los sitios pero su efecto fue menos pronunciado en el bosque menos intervenido. La densidad de semillas no generó ningún efecto en la remoción, mientras que encontramos una mayor probabilidad de supervivencia a distancias intermedias de la palma (10 m). Estudios futuros se deberían enfocar en el establecimiento de las plántulas, las tasas de reclutamiento y el efecto de la intervención antrópica en los posteriores estadios de vida de esta palma tropical.

INTRODUCTION

The chambira palm, *Astrocaryum chambira* Burret (1934) (Arecaceae), has been traditionally used by different indigenous communities of Amazonia (Schultes 1977, Jensen & Balslev 1995, Vormisto 2002). They obtain fibers from new leaves to produce nets, hammocks, household and ritual artifacts (Borgoft 1994, Jensen & Balslev 1995, Vormisto 2002). These products also generate economical income due to the interest of tourists in local handi-crafts (Jensen & Balslev 1995). The traditional harvest system consists on the removal of the youngest unfolded leaf, but leaving the next one intact in order to guarantee palm growth (Borgoft 1994, Jensen & Balslev 1995). However, it has been reported that several communities are not using this system anymore, harvesting the whole plant, and therefore affecting the development and growth regeneration dynamics of the species (Coomes 2004). Additionally to these direct stresses, other anthropogenic disturbances can alter the demography of the species. For example, the loss of animal dispersal vectors due to hunting and landscape modification can affect seed dispersal processes of tropical forest plants (Beckman & Muller-Landau 2007, Peres & Palacios 2007), which in turn have an effect on recruitment rates, genetic flux, colonization abilities and patterns of spatial distribution (Nathan & Muller-Landau 2000). Since trade of handicrafts has been increasing, but the exploitation depends exclusively on the natural population of the palm (Coomes 2004), it is unknown whether the natural populations of *A. chambira* will be able to tolerate such demand.

A. chambira is a palm species dispersed mainly by caviomorph rodents such as species of the genera *Agouti, Dasyprocta* and *Myoprocta*. These animals generally act as seed predators as they bury seeds to retrieve and eat them in periods of food scarcity. The successful seed dispersal occurs when the rodents fail to recover the buried seeds (Smythe 1989, Jansen & Forget 2001). The advantage of seed burial is that it reduces seed predation, as insects predate upon unburied seeds, particularly those that are not taken away from the parent palm (Janzen 1971, Forget 1990, Forget & Milleron 1991). The genera *Agouti* and *Dasyprocta,* commonly known as “borugos” and “guaras”, respectively, have been highly targeted by hunters. Additionally, although in several places of the Amazon *Myoprocta* is usually ignored (Carrillo *et al.* 2000, Peres & Palacios 2007), in the Colombian Amazonia they are highly hunted, particularly in intervened forests where they are found by dogs or caught with small traps by any member of an indigenous community working in the community garden (De la Hoz 2007). Thus, human intervention in the forest, generated by both planned and/or sporadic hunting, and proximity to settlements might be related with low animal population densities and affect regeneration dynamics of the species. For instance, Peres & Palacios (2007) have found lower population densities of caviomorph rodents in heavily hunted forests than in lightly hunted forests or non-hunted forests. Also, changes in mammal densities have shown differential effects on seed dispersal and seed predation depending on the traits and dispersal modes of the plant species (Bustamante & Simonetti 2000, Cordeiro & Howe 2001, Beckman & Muller-Landau 2007). In that way, knowledge of the seed dispersal processes of *A. chambira* under different intervention conditions might be very important for management purposes of its natural populations. Since *A. chambira* is one-large-seeded species that depends on secondary seed dispersal, a reduction in seed-disperser populations by hunting or any other form of human disturbance might reduce the proportion of removed seeds, and many of them will remain under the parent plant where the risk of mortality by seed predation is the highest (Forget & Jansen 2007).

In order to contribute to a better understanding of the consequences of changes in disperser populations for regeneration of tropical forest plants, we studied the seed fate of *A. chambira* in three forests subjected to different degree of human intervention, where densities of seed dispersers were supposed to be different. For this purpose, in each forest site we censused the dispersal agents, characterized the seed shadow and evaluated seed predation, seed removal by animals and seed dispersal distances. With lower disperser densities as a consequence of human intervention, we expected less seeds removed and shorter dispersal distances from the parent palm.

METHODS

STUDY AREA

Three Amazonian Tropical Humid Forest sites were selected for this study. The first two sites were located in Macedonia, an indigenous community on the northern margin of the Amazon River, state of Amazonas, Colombia (70° 13' 22.4" W, 3° 49' 01.0" S). Mean annual temperature is 26ºC and mean annual precipitation reaches values of 3200 mm, averaging 270 mm per month (Rudas & Prieto 2004). July and October are the driest months while January and April are the wettest months (UAESPNN 1999). The two sites were selected on the basis of the degree of human intervention according to Pinilla (2004) from high to moderate. The highly intervened forest (HIF) was considered as the forest continuously used by indigenous people for the extraction of both timber and non timber products (Pinilla 2004), including *A. chambira* leaves for craft-making purposes. This forest was located less than 5 km away from the community (modified from Pinilla 2004), where local people have used slash-and-burn cultivation systems, which have turned the forest into a mosaic of different regeneration stages. The moderately intervened forest (MIF) consisted on forests regularly used for hunting and natural resources harvesting (planned journeys), including the extraction of *A. chambira* leaves, neither historic nor current cultivation. For the purposes of this study, this site was located more than 5 km away from the Macedonia settlement (modified from Pinilla 2004).

The third forest was located at the biological station Mosiro Itajura located in the state of Vaupés, Colombia (69°31'2.9''W, 1°04'21.8''S). Mean annual temperature is 25.1° C and mean annual precipitation is between 3000 and 4000 mm (Defler 1996). May is the month with the highest precipitation (384 mm) and September is the driest month (258 mm: Palacios & Rodríguez 1995). The nearest indigenous community is located more than 8 km away in a straight line or more than 5 hours by foot. According to the local indigenous communities this is a sacred site, therefore hunting has always been restricted. Also, the existence since the 1980s of the biological station has entailed additional protection. There is no exploitation of young leaves of *A. chambira* or harvest of any other forest products. This forest was defined as the low intervened forest (LIF).

STUDY SPECIES

Astrocaryum chambira is a palm with a solitary erect trunk up to 22 m tall and 19-35 cm in diameter (Henderson *et al.* 1995). The internodes are covered with black or grey spines of up to 20 cm in length. The leaf rachis is covered densely by yellow or brown flat spines of 3 up to 15 cm in length. Four to six leaves can be produced per year (Coomes 2004). Inflorescences are interfoliary and erect at anthesis, and in fruit. Fruits are obovoid of 5-6 cm in length by 4-4.5 cm in diameter, with yellow-green epicarp and with tiny spinules of white-brown color. The mesocarp is fibrous and yellow when ripe (Stevenson *et al.* 2000a). The endocarp is black, thick and bony with three lateral pores (Henderson *et al.* 1995). Each fruit is single-seeded and according to Bodmer *et al*. (1997) both fruits and seeds of the genus *Astrocaryum* are lipid-rich. Germination of the seeds occurs 8-10 months after they fall to the ground (Coomes 2004).

A. chambira is restricted to the Amazon basin and it can be found in *terra firme*, open vegetation and temporarily flooded forests (Várzea). It can be highly frequent at elevations below 350 m, and it is not categorized as an endangered species (Kahn & Moussa 1994, Henderson 1997, Calderón *et al.* 2005). *A. chambira* is distributed along the Amazon region of Colombia (Amazonas, Caquetá, Guaviare, Meta, Putumayo and Vaupés), Venezuela (Amazonas), Ecuador (Morona-Santiago, Napo), Perú (Amazonas, Loreto) and Brazil (Acre, Amazonas) (Henderson *et al*. 1995).

DATA COLLECTION

Data were collected from January to May 2004 at the HIF and the MIF, and from February to June 2005 at the LIF. In each forest we estimated density of seed dispersal agents, and chose eight fruiting individuals of *A. chambira* to characterize the seed shadow, seed removal and dispersal distances. The minimum distance between individuals was 100 m.

Census of seed dispersal agents

In each forest type, we estimated the density of dispersal agents of *A. chambira, Dasyprocta fuliginosa* (common name guara) and *Myoprocta* sp. (*Myoprocta acouchy - Myoprocta exilis;* common name tintín) by visual censuses on linear transects. The total length covered by the census was 60.6 km at the HIF, 56.7 km at the MIF and 129.4 km at the LIF. The effective transect width was determined by King's method (Giles 1974). Although forests have been subjected to a different disturbance regime, altering both plant and animal species composition, there were not significant more open conditions at the HIF, as well as we did not sample in gardens or barbechs. Additionally, effective transect width was estimated based on the perpendicular distance from the centre of the survey path separately in each forest site, where the largest width was obtained at the LIF site (mean 12.04 m). Thus, animal censuses were not biased in favor of a particular site. The average speed of the census was 2 km/h (SD = 0.3 km/h). Censuses were carried out over 3 months at least once per week, between 6:00 h and 10:00 h. Each time a *D. fuliginosa* or *Myoprocta* sp. was observed, the perpendicular distance to the transect and the number of individuals were recorded. The Kruskall-Wallis analysis was used in order to compare densities of each rodent species between forest types. Also, in order to define the differences between pair of forests Mann-Whitney U-tests were performed.

Seed shadow

Four of the eight adult individuals of *A. chambira* selected per forest were used to characterize the seed shadow created after the fruits fell from the palm. Around the trunk of each individual we established a 78.5 m^2 area (5 m radius). From this 5 m radius we set six transects of 1 m × 50 m every 60°. Every fifteen days, we counted and classified all *A. chambira* seeds found within the 78.5 m^2 area and in each transect. Seeds were classified according to the seed's condition: intact, predated by mammals, or predated by insects. A seed was classified as intact when its endocarp was not perforated or broken. Evidence to classify a seed as predated by mammals consisted of broken seeds or pieces of endocarp found on the ground. When a seed presented holes that passed through the endocarp and reached the endosperm it was classified as predated by insects. In this case, these were classified into subgroups depending on the infesting agent. Samples of the predating insects were identified at the entomological collection of the Amsterdam Zoological Museum.

One-way analysis of variance (ANOVA) was performed to compare the differences between forests in the amount of fruits found in the 5 m radius area around each palm. Change in the percentage of predated seeds along time was obtained for forest site. We compared the proportion of predated seeds per forest at the 45th day after they began to fall to the ground. If there were significant differences we carried out a *post hoc* Tukey HSD test. All analyses were performed using the software SPSS version 14 (SPSS 2005).

Seed removal and dispersal distance

The other four individuals of *A. chambira* per forest site were used to experimentally assess seed removal by animals, dispersal distance and density and distance-dependent effects. In each palm, every 72° we installed five 50 m transects from the trunk. In each transect we placed three stations at 2, 10 and 50 m from the palm. On each station, densities were of one, two and five seeds. Each transect had a different combination of distance and density treatments (Table 1). On a biweekly basis, we counted the number of seeds per station and determined their condition (intact, predated or missing). We never replaced predated or missing seeds.

Table 1. Combination of seed densities along the experimental transects of each palm.

	2 m	10 m	50 m
Transect 1	2	1	5
Transect 2	5	2	1
Transect 3	1	2	5
Transect 4	2	5	1
Transect 5	5	1	2

The Cox proportional hazard analysis (Cox 1972) was used to determine if the forest type, the distance from the parent palm or the seed density significantly affected potential seed survival. It was calculated as those seeds that remained intact in the station and/or those that were missing (assuming that removal enhances seed survival) minus those seeds predated. All variables were treated as categorical values. If differences were significant we showed the Hazard Ratio (HR), which indicates the increase in the probability of a seed to potentially survive when subjected to a particular treatment in comparison to the other one. To test for the proportional hazard assumption we visually examined the Log-Log plots for parallel curves (Kleinbaum 1996). We also estimated the mean removal time of the seeds at each forest type with a Kaplan-Meier removal analysis (Pollock *et al.* 1989). Analyses were made using SPSS version 14 (SPSS 2005).

For determining dispersal distances we marked 50 seeds per palm, all of them with green epicarp and yellow mesocarp. We marked each seed by attaching 50 cm of nylon line with 10 cm of vinyl fluorescent tape (*sensu* Jansen 2003). To tie the seed, we drilled a hole through the tip of the seed without entering the endosperm and passed the nylon line through it. Due to the lack of electricity at the LIF forest, we used glue to attach the nylon thread to the seed. Seeds were placed in ten groups of five seeds at 3 m distance from the parent trunk and checked them every 15 days. If a seed was missing we looked for it along ten transects 50 m long that began from the trunk of the palm every 36°. For each seed found we measured the dispersal distance and depth. We also verified whether removed seeds found on previous revisions were still buried, and their condition was recorded only until the end of this study. Non-recovered seeds were classified as lost.

RESULTS

CENSUSES OF DISPERSAL AGENTS

Mean density of *D. fuliginosa* individuals at the HIF was 7 ind/km^2, and 10 ind/km^2 at the MIF and at the LIF. Mean density of *Myoprocta* sp. at the HIF was 5 ind/km^2, 11 ind/km^2 at the MIF and 16 ind/km^2 at the LIF. Total *D. fuliginosa* and *Myoprocta* sp. sample size were 45 and 54 individuals in all forest sites, respectively. Although the number of individuals observed was small, the analysis showed significant differences in densities of *Myoprocta* sp. and *D. fuliginosa* among forests (*D. fuliginosa*: $\chi -^2_2 = 9.4$, P = 0.009, *Myoprocta* sp.: $\chi -^2_2 = 16.3$, P < 0.001; Figure 1). Differences between the HIF and the MIF were not significant for both rodent species (*D. fuliginosa*: Z = -0.3, P = 0.762, *Myoprocta sp*: Z = -0.5, P = 0.650). In contrast, we found significant differences between the LIF and the MIF for both *D. fuliginosa* and *Myoprocta* sp. (Z = -2.2, P = 0.029 and Z = -3.4, P = 0.001, respectively), and between the LIF and the HIF as well (*D. fuliginosa*: Z = -2.2, P = 0.008, *Myoprocta sp*: Z = -3.0, P = 0.003).

SEED SHADOWS AND SEED PREDATION

Our results showed that all seeds produced by *A. chambira* palms in the three forest sites fell within a radius of 5 m around the parent palm. Two species of beetles were identified as the main seed predators (Table 2). The first was an adult Col.: Curculionidae, Scolytinae (*Coccotrypes* sp.), which drills through the endocarp. Its entrance hole is characterized by white dust around it, a small perforation size and absence of exudates. The second infesting agent was a beetle larva of Curculionidae. Seeds infested by these larvae were characterized by a larger hole of entrance (*ca.* 4 - 5 mm diameter), a foul-smelling brown fluid and yellow or orange exudate outside the fruit or seed, either on the endocarp or the exocarp. The percentage of seeds predated by rodents was very low (Table 2).

The percentage of predated seeds over time per forest showed a tendency to increase (Figure 2). Seeds at the HIF suffered a high predation rate within the first 20 days after they fell to the ground, but afterwards, the predation rate decreased. At the MIF, most of the seeds fell to the ground already infested and the rate of predation, once on the ground, was also high. Predation of seeds at the LIF was low and constant in comparison to the other two forests until the 45th day when the predation rate increased (Figure 2). On the 45th day, there were significant differences in the percentage of predated seeds between forest types ($F_{2,9}$ = 6.4, P = 0.019). The Tukey HSD test showed that LIF had a significant lower percentage of predated seeds than the MIF (mean difference = -55.4, P = 0.015), but between the MIF and the HIF no significant differences were found (mean difference = 30.1, P = 0.19), nor between the LIF and the HIF (mean difference = 25.4, P = 0.28; Figure 2).

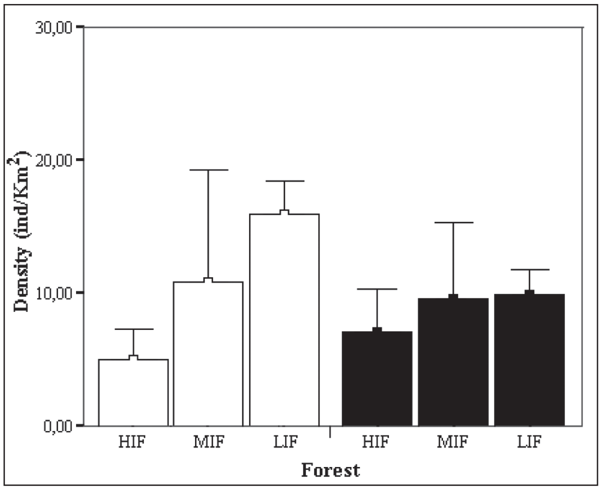

Figure 1. Densities of *Myoprocta* sp. (empty bars) and *D. punctata* (solid bars), at the highly intervened forest (HIF), the moderately intervened forest (MIF) and the low intervened forest (LIF) in the Colombian Amazon. Bars indicate the standard error (*Myoprocta* sp.: HIF n = 4; MIF n = 3; LIF n= 48; *D. punctata*: HIF n = 8; MIF n = 6; LIF n = 31).

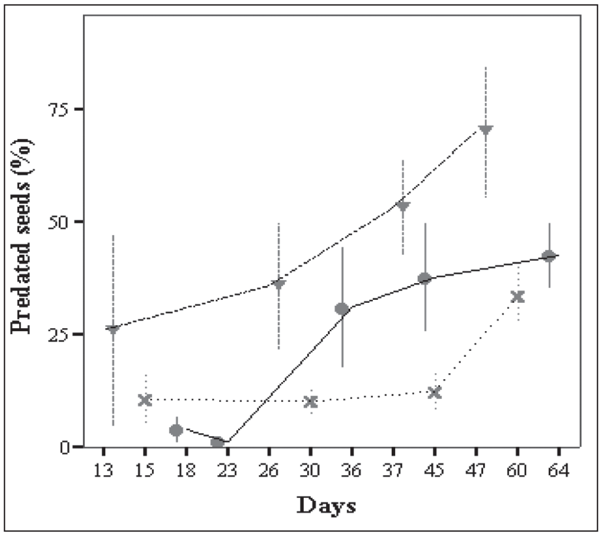

Figure 2. Changes in time (days) of the mean percentage of predated seeds of *Astrocaryum chambira* found in the seed shadow at the highly intervened forest (HIF: solid line), at the moderately intervened forest (MIF: broken line) and at the low intervened forest (LIF: dotted line), in the Colombian Amazon. Bars indicate the standard error.

Table 2. Mean percentage (± standard error) of intact and predated seeds at the end of the study, at the highly intervened forest (HIF), moderately intervened forest (MIF) and low intervened forest (LIF). n = 4 palms per forest site.

Seed condition	**Percentage of seeds (%)**		
	HIF	**MIF**	**LIF**
Intact	57.4 ± 7.3	29.8 ± 14.8	74.7 ± 9.4
Insect damage (Curculionidae larvae)	5.1 ± 4.9	37.5 ± 19.3	15.2 ± 6.7
Insect damage Coccotrypes sp. adult	37.1 ± 7.0	37.5 ± 13.9	10.1 ± 5.0
Rodents	0.4 ± 0.2	0.7 ± 0.4	0.0 ± 0.0

SEED SURVIVAL ANALYSIS

The Cox proportional hazard analysis of the seeds placed at different densities and distances from the parent palm indicated that density does not affect potential survival (five seed-density: $\text{Wald}_2 = 3.3$, $P = 0.20$, two seed-density: $\text{Wald}_1 = 0.2$, $P = 0.65$, one seed-density: $\text{Wald}_1 = 3.3$, $P = 0.71$). Therefore, seed density was excluded from the model. The omnibus test of model coefficients indicated that the model including forest type and distance as categorical values was highly significant $\chi^2_4 = 30.5$, $P < 0.001$). Hence, distance affected seed survival. Seeds at 10 m ($\text{Wald}_2 = 7.8$, $P = 0.02$) showed a significantly higher chance of survival than seeds at 2 m ($\text{Wald}_1 = 7.7$, $P = 0.006$, HR = 1.6) and than seeds at 50 m ($\text{Wald}_1 = 4.1$, $P = 0.044$, HR = 1.5). Seeds at 2 m and at 50 m had no difference in survival chance ($\text{Wald}_1 = 0.3$, $P = 0.59$).

The forest type was significantly associated with seed survival (Figure 3). Seeds at the LIF ($\text{Wald}_2 = 21.9$, $P < 0.001$) had a significant higher probability of survival than seeds at the MIF ($\text{Wald}_1 = 19.8$, $P < 0.001$, HR = 2.4) and at the HIF ($\text{Wald}_1 = 18.6$, $P < 0.001$, HR = 2.3). Seeds at the MIF and at the HIF had no significant difference in survival probability ($\text{Wald}_1 = 0.02$, $P = 0.89$). Mean seed survival time at the three forests, obtained through the Kaplan-Meier removal analysis, was the shortest at the HIF (33.1 days ± 0.99), followed by the MIF (32.5 days ± 1.39), while seeds at the LIF exhibited the longest survival time (43.9 days ± 1.24).

FATE OF MARKED SEEDS

From the four studied palms per forest, seed removal was detected only in one palm of the HIF, two palms of the MIF and three of the LIF. Percentages of seed removal per palm at the HIF was of 26%, at the MIF ranged from 8% to 26%, while at the LIF ranged from 4% to 36%. Dispersal distances were similar between the HIF and the MIF (Table 3). We could not collect data of dispersal distance at the LIF because none of the removed seeds could be recovered as the nylon line was always found cut on the spot.

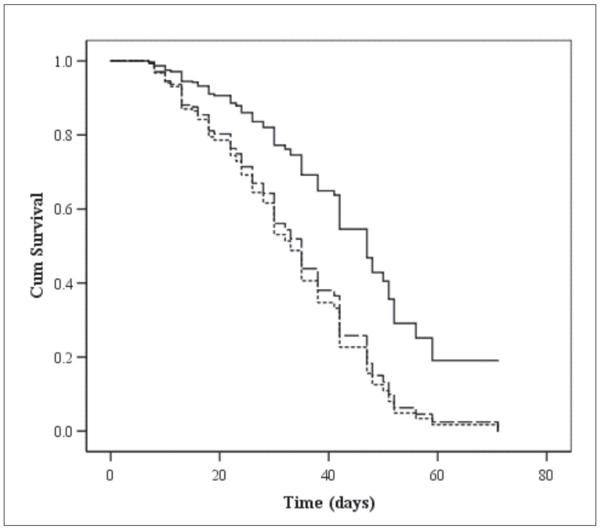

Figure 3. Cumulative removal curves of *Astrocaryum chambira* seeds in three different forest types in the Colombian Amazon. The broken line represents removal at the highly intervened forest (HIF), the dotted line represents removal at the moderately intervened forest (MIF) and the solid line represents removal at the low intervened forest (LIF).

Table 3. Number and percentage of removed, recovered, lost and unburied marked seeds on the palms where removal was observed, at the highly intervened forest (HIF), the moderately intervened forest (MIF) and the low intervened forest (LIF) in the Colombian Amazon. Average of seed dispersal and depth of burial are also included. nda. = no data available.

	HIF	MIF		LIF		
	Palm 1	Palm 1	Palm 2	Palm 1	Palm 2	Palm 4
Removed seeds	13 (26%)	13 (26%)	4 (8%)	5 (10%)	2 (4%)	18 (36%)
Recovered seeds	9 (18%)	9 (18%)	3 (6%)	0	0	0
Lost seeds	4 (8%)	4 (8%)	1 (2%)	5 (10%)	2 (4%)	18 (36%)
Recached seeds	1 (2%)	0	0	0	0	0
Dispersal distance (m)	12.6 ± 7.6	11.2 ± 2.8	6.6 ±2.5	nda.	nda.	nda.

All seeds at the HIF and MIF started to be removed after the second month of being placed, and all of them exhibited *Coccotrypes* holes before being removed. This was not the case at the LIF, where all seeds were removed within the first two months after being placed at the stations, and only two of them had holes of *Coccotrypes* before being removed. In this forest type, we found no evidence of seed predation by rodents such as pieces of seeds that indicated handling. Thus, we assumed all removed seeds were not eaten *in situ*. There was only one case of recaching of seeds by dispersers at the HIF forest (Table 3).

DISCUSSION

This study provides some evidence on the effects of human intervention on the seed dispersal processes of plants, as we found a strong correspondence between seed removal of *Astrocaryum chambira*, seed disperser densities and human intervention. First, despite the very small sample size, density of *A. chambira* seed dispersers such as *Myoprocta* sp. and *D. fuliginosa* corresponded to the level of disturbance. Thus, the lowest density was found at the HIF site, followed by the MIF and LIF. Although these differences can be also a consequence of habitat quality, forest structure and floristic composition, results coincide with other studies that have found significant differences in vertebrate population densities between heavy, light and non hunted (undisturbed) forest sites (Peres & Palacios 2007). Additionally, even if the number of individuals observed were small, these are likely to be higher than several studies focused on densities and movement patterns for any members of genus *Dasyprocta* (e.g. Haugaasen & Peres 2005, Silvius & Fragoso 2003). Since most of the *A. chambira* seeds remain beneath the parent palm, seed dispersal is rather limited and will exclusively depend on secondary seed dispersers to transport the seeds away, our reported differences in disperser densities may have consequences for seed dispersal and seed predation of the palm, as found in other studies (e.g. Beckman & Muller-Landau 2007, Peres & Palacios 2007). Additionally, even if seed predation at the three sites was mainly caused by insects, seed predation increases with intervention, where no burial occurs, and hence, it is not just that few seeds are dispersed, but also that few will survive.

We found that despite the hard woody endocarp of *A. chambira* seeds, main predators are two insect species. One is a species of the Curculionidae beetle family which seems to infest the seeds even before they fall to the ground, indicating pre-dispersal predation. This represents a loss to the palm, independently of the effectiveness or abundance of secondary dispersal agents, unless they predate infested seeds (Sallabanks *et al*. 1992). Unfortunately, as seed predation by rodents was very low in all forest types, we did not obtain evidence of predation of infested seeds by these animals. The second insect predator of the *A. chambira* seeds was another beetle species of the genus *Coccotrypes* (Curculionidae, Scolytinae). It predated seeds found under the parent palm, as well as the seeds placed in the experimental stations at 2, 10 and 50 m from the palm. Although we recorded rodents burring seeds already infested by this beetle, we could not test whether seed burial reduced the insect fitness. Janzen (1972) also reported a species of this genus attacking seeds of *Euterpe globosa*. He stressed there might be an exponential burst of this predator since generation times are too short and only 5% of the progeny was male. Besides these invertebrate predators, monkeys and squirrels have also been seen predating unripe fruits directly removed from the palm (Stevenson *et al.* 2000b, Parrado-Rosselli unpubl. data). Although they can reduce the fitness of the Curculionidae predator, these animals also affect the palm regeneration.

In all forest types, caviomorph rodents predated very few seeds *in situ* (< 1%) while they actively removed and buried *A. chambira* seeds. The preference of rodents to bury seeds instead of eating them under the parent palm and/or in the stations can be due to the morphological and physiological characteristics of the seeds. Mainly, their long dormancy, high fat content and resistance to rotting make them suitable as reserves for lean periods (Xiao *et al.* 2006b). As a contrasting example, Forget (1996) reported a higher percentage of predation (10%-20%) *in situ* by rodents on *Carapa procera,* which is more susceptible to rotting and early germination (Jansen & Forget 2001) than *A. chambira.*

The total percentage of predated seeds in all forests showed that during the first two months among 30-70% of the seeds were predated. Also, seed predation percentages increased throughout time. As seeds of *A. chambira* can stand for almost a year before germinating, they are highly susceptible to reach a 100% of predation if left unburied. Therefore, dispersal and burial by mammals will be very important for the successful regeneration of the palm. Additionally, as predation increases with time, the time frame in which seeds can be removed and buried by rodents before being already infested by insects will vary with human intervention.

Almost every seed of the density and distance experiment was either predated by *Coccotrypes* or removed by rodents. Regarding density we did not find any effect potential seed survival (see Cox proportional hazard analysis). However, we are aware that our densities were low, and perhaps a higher concentration of seeds (> 5) might have a positive effect on attracting rodents. On the other hand, we did find an effect of distance potential seed survival, as seeds placed at 10 m from the parent palm exhibited a higher removal probability than seeds at 2 m and at 50 m. Probably, seeds at shorter distances will be more exposed to predation because of a higher concentration of seed predators beneath the parent palm (Janzen 1971). In contrast, considering that predation by insects increase with time, and that rodents seem to take more time to find seeds placed at the 50 m stations, the low survival probability of seeds placed at long distances can be due to a broader time window for seeds to be attacked by predators before they are removed or buried. The higher probability of survival at intermediate distances from the parent palm (10 m) coincides with the average dispersal distances obtained in our marked seeds experiment (6 m and 12 m). Thus, it is likely that rodents have intense activity at these distances from the parent palm where they can easily find and bury seeds. These patterns of over dispersion have been reported, for other rodent species, to be effective in reducing cache loss (Male & Smulders 2007). Also, this short distance dispersal and its importance in forest structure has been reported for *Dasyprocta leporina* in Brazil (Silvius & Fragoso 2003).

Considering the patterns of seed predation and removal described above we can conclude that caviomorph rodents are playing an important role on seed removal. They are high quality dispersers (*sensu* Jordano & Schupp 2000) of *A. chambira* seeds as they do not predate a significant amount of seeds, and because without their removal and burial, seeds will most likely be predated by insects either beneath the parent palm (Forget & Jansen 2007) or anywhere on the surface of the forest floor. The LIF showed higher seed removal and higher disperser densities than the other two forests (MIF and HIF). Also, there were not significant differences between them both in seed removal and disperser densities. Besides, all marked seeds removed at the HIF and MIF were already infested by

Coccotrypes, while at the LIF most seeds were taken intact. The faster removal at the LIF than at the other two forests gives insects a narrower time window to attack. Although, it has been suggested that seed marking delay seed removal (Xiao *et al*. 2006a); we consider that results are comparable between forests sites.

From a conservation point of view, we conclude that seed removal and consequent burial is crucial for *A. chambira* seed survival, thus the reduction of seed disperser populations might have a negative impact on the fitness of this species. Considering the importance of *A. chambira* for local communities, particularly since exploitation depends exclusively on the natural population of the palm, it would be important to maintain adequate densities of its seeds dispersers in order to have favorable regeneration rates and to avoid significant seed loss in natural stands. Fauna management strategies that do not prohibit hunting but that include sustainable harvest levels will be important for enhancing natural regeneration of the species and to avoid depletion in the proximity of local communities. Additionally, palm cultivation can be a strategy, if predation by *Coccotrypes* is controlled. However, in order to design effective management plans for palm, more information is needed on dispersal distances and its relationship with seedling establishment and recruitment rates. Also, it will be necessary to test whether changes in herbivore populations as a consequence of human disturbance might also affect seedling survival (Terborgh *et al.* 2008), as well as thresholds caused by human extraction of the subsequent life stages.

CONCLUSIONS

- There was a strong correspondence between seed removal of *Astrocaryum chambira*, seed disperser densities and human intervention.
- Most of the *A. chambira* seeds remained beneath the parent palm; thus seed dispersal exclusively depends on secondary dispersers to transport the seeds away. In consequence, changes in disperser densities might affect the regeneration patterns of the species.
- Seed predation increased with intervention, particularly seed predation by *Coccotrypes* sp. In contrast, seed predation by vertebrates was minimum in all forest sites with no particular pattern.
- The importance of caviomorph rodents as seeds dispersers consists on their seed burial. As *A. chambira* seeds can stand for almost a year before germinating, they are highly susceptible to reach a 100% of predation if left unburied. Additionally, as predation increases with time, the time frame in which seeds can be removed and buried by rodents before being already infested by insects will vary with human intervention.
- Fauna management strategies should consider sustainable harvest levels of scatter hoarding rodents, while palm management should consider intermediate establishment distances, as potential seed survival was the highest at 10 m distance from the parent palm. Also *Coccotrypes* seed predation should be controlled.

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