

Influence of conspecific negative distance-dependence and fire events on recruitment of Brazil nut (Bertholletia excelsa) in the Peruvian Amazon

Vincent Porcher

► To cite this version:

Vincent Porcher. Influence of conspecific negative distance-dependence and fire events on recruitment of Brazil nut (Bertholletia excelsa) in the Peruvian Amazon. Life Sciences [q-bio]. 2017. dumas-01650803

HAL Id: dumas-01650803 https://dumas.ccsd.cnrs.fr/dumas-01650803

Submitted on 28 Nov 2017

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.









Master thesis

Presented by Vincent PORCHER

To obtain the national grade of master

in Biodiversity, ecology, evolution

specified in tropical plant biodiversity and tropical ecosystems management (BioGET)

Title:

Influence of conspecific negative distance-dependence and fire events on recruitment of Brazil nut (Bertholletia excelsa) in the Peruvian Amazon.

Tutor: Dr Evert Thomas

Publicly defended 11 september 2017

in Montpellier

in front of the jury:

Dr Plinio SIST Dr Yves CARAGLIO Dr Doyle McKey Dr Raphaël MANLAY Rapporteur Examiner Examiner Academic supervisor

ACKNOWLEDGEMENTS

I would especially like to thank Evert Thomas who welcomed me to Bioversity and who has been an exemplary supervisor, who has helped me and provided me good advice throughout this internship. His passion, his critical eye, his rigor and his good humor have made this internship, exciting, professional an enriching experience, both at personal and intellectual level. I learned a lot and it enabled me to fill many gaps. I will always retain a great memory of this experience, even if our collaboration is just beginning. I would like to thank Ricardo Bardales Lozano, Engineer and Director of the Brazil nut program at the Peruvian Amazon Research Institute (IIAP), without whose collaboration this study would not have been possible. His enthusiasm, his interest in my work and the logistical means he has provided made possible to carry out the work within a constrained time period. My thoughts are with his daughter and I hope for her good recovery. I also thank Fidel Ernesto Chiriboga Arroyo for our many exchanges and our common interests, and Ériks Arroyo and Aron for their invaluable help in the field. I thank David Lefebvre, first of all an excellent friend and of course Eloise Ponzi. Finally, I thank all the people who helped me or with whom I shared the sweet life of Puerto Maldonado.

RESUME

La faible régénération naturelle de la noix du Brésil (Bertholletia excelsa) dans la région de Madre de Dios au Pérou est une préoccupation majeure pour la conservation et l'utilisation durable de cette espèce qui soutient l'une des économies de produits forestiers non ligneuses les plus importantes en Amazonie. La noix du Brésil est une espèce pionnière à longue durée de vie dépendante des chablis et qui, il a été monté, se régénérait plus efficacement dans les jachères que dans les forêts matures. Outre la disponibilité de la lumière et des nutriments, le succès du recrutement de l'espèce pourrait également être conditionné par des processus conspécifiques dépendant de la distance, comme cela a été démontré pour de nombreuses espèces d'arbres tropicaux, mais à ce jour n'a pas été étudié pour la noix du Brésil. Nous avons mesuré le recrutement de la noix du Brésil avec un total de guarante transects de 150x10m (totalisant 6 ha) disposés dans des forêts matures et des jachères. Nous avons trouvé une probabilité beaucoup plus élevée de régénération en jachère que dans les forêts matures, principalement en raison de la transition plus réussie du semis aux jeunes arbres dans les jachères. Les taux de recrutement en jachère semblent augmenter avec le nombre passager du feu survenu au cours des 12 dernières années, mais cette corrélation positive n'a été observée que jusqu'à trois cycles de brûlis. Nous avons observé une distance-dépendance négative pour le recrutement conspécifique (CNDD) en jachère, mais pas en forêt mature. L'absence de ce modèle dans la forêt mature peut être due à la faible disponibilité de la lumière, combinée à des niveaux d'humidité plus élevés et moins variables dans les forêts matures par rapport aux jachères, entravant la transition du semis aux jeunes arbres en raison des pressions plus fortes des herbivores, d'insectes et des agents pathogènes dans ces conditions. En outre, la stérilisation partielle et temporelle du feu dans les jachères pourrait être un facteur supplémentaire favorisant la régénération de la noix du Brésil. Nos résultats suggèrent qu'une meilleure gestion des jachères et une utilisation plus contrôlée du feu dans les peuplements des noyers du Brésil voisins pourraient être rentables pour augmenter les taux de recrutement.

ABSTRACT

The low natural regeneration of Brazil nut (Bertholletia excelsa) in the Madre de Dios region of Peru is a major concern for the conservation and sustainable use of this species which sustains one of the cornerstone non-timber forest product economies in Amazonia. Brazil nut is a gap-dependent long-lived pioneer species and has been shown previously to regenerate more effectively in fallows than in the mature forest. Aside from light and nutrient availability, recruitment success of the species might also be conditioned by negative conspecific distancedependent processes as has been shown for a myriad of tropical tree species, but to date has not been studied in Brazil nut We measured Brazil nut recruitment in forty 150x10m2 transects (totaling 6 ha), proportionally laid out in mature forest and fallow land. We found a much higher likelihood of regeneration in fallow than in the mature forest, which was mainly due to more successful transitioning from seedling to sapling in fallows. Recruitment rates in fallow increased with the number of fire events occurred over the past 12 years, but this positive correlation was only observed up to three fire events. We observed conspecific negative distance-dependent recruitment of Brazil nut in the fallow but not mature forest. The absence of this pattern in the mature forest may be due to the lower light availability, combined with higher and more stable humidity levels in the mature forest compared to fallows, hampering the transition from seedling to sapling owing to pest and disease-driven mortality under these conditions. Furthermore, the sterilizing effect of fire in fallows might be an additional factor promoting the establishment of the relatively fire-resistant Brazil nut seedlings and saplings. Our findings suggest that a better management of fallow land and more controlled use of fire in land uses neighboring Brazil nut stands could be a cost-effective manner to increase recruitment rates.

Keywords: conspecific negative distance-dependence, Brazil nut recruitment.

TABLE DES MATIÈRES

ACKNOWLEDGEMENTS	1
RESUME	3
Abstract	3
TABLE DES MATIÈRES	5
1. INTRODUCTION	7
2. MATERIALS AND METHODS	9
2.1. Sudy area	9
2.2. Plot design and data collection	9
2.3. Data analysis	11
3. Results	13
4. DISCUSSION	17
5. CONCLUSION	19
6. References	21
7. ABREVIATIONS LIST	25
8. TABLE OF FIGURES	27
9. APPENDICES	29
APPENDICES TABLE	29
Appendice 1. Seedling protection device.	30
Appendice 2. Proof of seedling predation of Bertholletia excelsa by agouti.	31
Appendice 3. Trace of predation by an unidentified rodent, probably a rat.	32
Appendice 4. Cache of agouti in an empty dead trunk.	33

Vincent PORCHER Mémoire de stage de Master 2 mention BEE parcours BioGET 2016-2017 Influence of conspecific negative distance-dependence on recruitment of Brazil nut (*Bertholletia exelsa*) in the Peruvian Amazon

1. INTRODUCTION

Brazil nut (*Bertholletia excelsa* Humb. and Bonpl.: Lecythidaceae) seed is one of the cornerstone non-timber forest products (NTFPs) in Amazonia, sustaining substantial extractive economies in Bolivia, Brazil and Peru (Guariguata et al., 2017). However, concern has been raised about low levels of juvenile recruitment putting at risk the maintenance of populations over the long term. Peres et al (2003) attributed the recruitment bottlenecks observed in Brazil nut trees with diameter at breast height (DBH) \geq 10cm and <60cm in study sites across the Amazon to intensive exploitation levels over extended periods of time. This viewpoint has since been contested by a growing number of studies which also looked at regenerating Brazil nut trees with DBH<10cm and found no negative effect of harvesting intensity on recruitment rates (Bertwell et al., 2017; Ribeiro et al., 2014; Scoles and Gribel, 2012; Wadt et al., 2008). In fact, there are increasing indications that extractive activities in natural Brazil nut stands may actually promote natural regeneration, possibly through modifications of the understory resulting in increased light regimes, along with other favorable side-effects of human disturbance (Scoles and Gribel, 2015, 2011).

Brazil nut is a gap-dependent, long-lived pioneer species, implying that its natural regeneration is strongly favored by the availability of light through natural or anthropogenic gap creation (Moll-Rocek et al., 2014; Myers et al., 2000; Peña-Claros et al., 2002). Brazil nut is known to regenerate much more effectively in swiddens and fallows than under natural forest conditions (higher survival rates, stronger growth and higher densities) (Cotta et al., 2008; Guedes et al., 2014; Kainer et al., 1998; Paiva et al., 2011; Scoles et al., 2011). This finding has been attributed to a combination of (i) the preferential dispersion activities in swiddens and fallows of the tree's principal dispersal agent, the agouti (Dasyprocta spp), (ii) the more favorable growth conditions in cultivated fields (light and soil fertility) and (iii) the species' capacity to re-sprout after cutting (Cotta et al., 2008; Guedes et al., 2014; Kainer et al., 1998; Paiva et al., 2011; Scoles et al., 2011). Seedling recruitment is likely to be additionally promoted by hunting of agoutis in swiddens and fallows, thus freeing more abandoned scatter hoards for germination (Ribeiro et al., 2014; Shepard and Ramirez, 2011). Interestingly, Paiva et al. (2011) showed that the positive effects of repeated slash-and-burn events on Brazil nut regeneration seem to be cumulative. In a study in Amapa, eastern Amazonia, they found that Brazil nut densities increased from 9 to 14 and 27 trees ha-1 after one, two and three or more shifting cultivation cycles, respectively.

The positive effect on Brazil nut recruitment of longstanding practices of swidden agriculture since pre-Columbian times is believed to explain, at least partly, the aggregated distribution pattern of Brazil nut observed in many areas across the species' distribution range (Thomas et al., 2015). Especially in central and eastern Amazonia Brazil nut tends to occur in high-density groves, commonly referred to as 'manchales', 'castanhais' or 'bolas', with densities ranging from 10 to 20 trees (\geq 10 cm DBH) per hectare, interspersed with vast areas of forest (literally up to thousands of hectares) with little to no Brazil nut trees (Mori and Prance, 1990; Peres and Baider, 1997; Salomão, 2009). By contrast, in Southwestern Amazonia Brazil nut has a more continuous occurrence in the forest and tree densities are much lower (~1-2 trees ≥ 10 cm DBH per hectare). Thomas et al. (2015) hypothesized that the absence, or much reduced salience, of high-density brazil nut groves in Southwestern Amazonia might be partly due to different ecological conditions in this region compared to central and eastern Amazonia. Notably, differences in the incidence of pests and diseases might influence Brazil nut recruitment rates. For example, Shepard and Ramirez (2011) found exceptionally high brazil nut densities (50 individuals/ha, mostly in the size class of 10-60 cm DBH) in a small fire-impacted grove in Alter do Chão, Pará, with most of the trees being multi-trunked. They attributed these observations to the combination of positive influences on recruitment from anthropogenic disturbance and the site's drier climate, resulting in lower rates of Brazil nut recruits succumbing to fungus.

Negative impacts of pests and diseases on tree recruitment rates are well known in the tropics. Seeding mortality in tropical trees in shaded areas has been shown to be mainly due to the higher

> Vincent PORCHER Mémoire de stage de Master 2 mention BEE parcours BioGET 2016-2017

Influence of conspecific negative distance-dependence on recruitment of Brazil nut (Bertholletia exelsa) in the Peruvian Amazon

presence of undergrowth pests and pathogens in conspecific aggregates (Augspurger, 1984), generating conspecific distance- and/or density-dependent mortality. This process is known as the Janzen (1970) - Connell (1971) hypothesis according to which mortality of seedlings and saplings will be larger closer to conspecific adults that attract predators, herbivores and host-specific pathogens. Conspecific negative distance or density-dependent recruitment is responsible for distribution patterns in many tropical trees (Comita et al., 2014, Queenborough et al. 2007; Jansen et al., 2014, LaManna et al 2017). However, to the best of our knowledge no study had yet investigated to role of negative distance and density dependence recruitment in Brazil nut.

Our objective here is threefold. First we test whether Brazil nut recruitment in Madre de Dios, Peru, is higher in fallows than in high forest as found by Paiva et al (2011) in eastern Brazil and whether recruitment levels in fallows are lower in Peru than eastern Brazil as hypothesized by Thomas et al (2015). Second, we assess if Brazil nut recruitment is conditioned by conspecific negative distance-dependent patterns, and if their manifestation differs between fallows and mature forest. Third, we investigate the impact of the number of fire events occurred over a period of 12 years on recruitment success and size in fallows. We end by discussing the management implications of our findings.

2. MATERIALS AND METHODS

2.1. STUDY AREA

We carried out fieldwork in Tambopata province, Madre de Dios, Peru, at three sites within a radius of 20km around Puerto Maldonado: (1) two mature forest concessions of the IIAP (Instituto de Investigation de la Amazonia Peruana) called *Castanal* (site A: 12°38'S, 69°19'O) and *Fitzearrald* (site B: 12°39'S, 69°19'O) (300 and 181 hectares respectively); and (2) fallow lands in the buffer zone of the Tambopata national park (site C: 12°38'S, 69°08'O) (250 to 990ha) The three sites correspond with *terra firme* forests located on deposits of ancient alluvium.



Figure 1. Map of study sites, Puerto Maldonado, Madre de Dios, Peru, QGIS 2.18 Vincent Porcher

2.2. PLOT DESIGN AND DATA COLLECTION

We measured Brazil nut recruitment in a total of forty 150x10m transects equally distributed over mature forest and fallow lands, representing a total sample area of 6ha. Each transect was constructed starting at the foot of an adult Brazil nut tree (>40cm DBH) and oriented in a direction so as to maximize the distance to transect line of neighboring adult trees. We avoided the inclusion of canopy gaps in mature forest transects as this would bias distance-dependent recruitment rates. The twenty fallow transects were laid out in thirteen locations with different fire histories and secondary vegetation in different stages of development. Vegetation disturbance in fallows was a combination of abandonment after swidden cultivation of mainly cassava and the escape of fire from vegetation burning practices in neighboring land uses, mainly pastures. Fallow transects were sampled at the beginning of the dry season (July) before the initiation of the yearly cycle of vegetation burning in the region.

Vincent PORCHER Mémoire de stage de Master 2 mention BEE parcours BioGET 2016-2017

Influence of conspecific negative distance-dependence on recruitment of Brazil nut (Bertholletia exelsa) in the Peruvian Amazon

The transect length of 150m was chosen to allow assessing both the potential occurrence of negative distance-dependent recruitment and seed dispersal processes. In a previous study in eastern Brazil, the highest regeneration frequency observed was found in the distance class to the nearest adult tree conspecific seed producer of 40-60m (Paiva et al., 2011). Brazil nut's main disperser, the agoutis, have generally short dispersion distance of about 35m (Jorge and Peres, 2005; Peres and Baider, 1997). However, recent work shows seed dispersal is not as far as inefficient, owing to the intraspecific competition for resources which can engender an accumulation of thieving between agoutis. The seeds stolen from initial caches are buried a few tens of meters further and this process can be repeated up to 36 times, resulting in record dispersal distances of 300m from the mother tree (Jansen et al., 2014, Jansen et al., 2012). Considering a mean adult tree density in the Madre de Dios region of 0.5 ± 1.5 individual ha-1 (Moll-Rocek et al., 2014), we can estimate a theoretical nearest neighbor distance (Not taking into account aggregation) between mature trees (Distance to nearest neighbor with $1/(2\sqrt{d})$ length unit (Morisita, 1962)) of 40-70 m. Finally, we chose the arbitrary distance of 150m long for the transect, in order to consider the possible large distance caused by the cumulative seed robbery by the agoutis and also study the effect of the CNDD over a distance exceeding 60m.

To choose the location and direction of our transects insites A (15 transects) and B (5 transects) where we already knew the UTM coordinates of adult trees (Thomas, 2017), we constructed 150m wide internal buffer zones along the study area margins using QuantumGIS (QGIS 2.18) to exclude the potential influence of adult Brazil nut trees located outside the study areas. Next we constructed circular buffer zones with 150m radius around all adult trees to determine the true nearest neighborhood distances between each regenerating brazil nut plant found and its closest adult neighbor. This is importance as at larger distances from the transect starting point is becomes increasingly likely that other adult trees. Due to the excessive GPS accuracy errors, related with multitrack and DOP (Dilution of precision) due to dense forest cover including fallow (Lejeune and Hellemans 2000, Freycon and Fauvet, 1998), we re-verified the UTM coordinates of each tree already georeferenced. Owing to the dense canopy cover in mature forest we recorded the GPS points of each individual several times, respecting a time interval of five minutes between each data take to optimize the satellite constellation (Lejeune and Hellemans 2000).

We recorded the number of regenerating individuals in each plot and measured the height (axis 1) and, where relevant (i.e. when >10cm dbh) the diameter of all individuales .We classified all individuals inheight and diameter classes following (Zuidema and Boot, 2002): seedlings depending on the albumen of \leq 50 cm high (A); seedlings independent of albumin stock of >50 cm and \leq 150 cm high (B); Saplings \geq 150 cm and <10 cm dbh (C); Juvenile (or non-mature adult) > 10 cm dbh and \leq 40 cm dbh (D) and mature adults (breeder) \geq 40 cm dbh (E). Here we define recruitment as the number of individuals reaching a well-defined size but not yet reproductive. In the case where the exact stage is not specified, the term recruitment will refer mainly to any germinated individuals belonging to the size class A (seedlings <50 cm) corresponding to the first stage of development, the establishment of Axis 1 (without branching).

To compare the effect of distance and density on the relative height of each individual (ia) and the probability of encountering seeds for each distance class (ib), we used a spatial analysis tool (Matrix of distance) from QuantumGIS to calculate the minimum Euclidean distance to the nearest productive Brazil nut (BN) trees. We used the nearest neighbor method based on a linear distance matrix (N*k x 3). First we calculated the distance between each regenerating individual and the nearest mature tree (ia). In a second step (ib), fifteen 100 m2 cells were constructed from the field data along each transect in order to then calculate the minimum Euclidean distance from the center of each cell and the nearest adult BN tree. The construction of these cells allows us both to relate to a surface and thus to calculate the density of the regeneration (including zero densities).

Vincent PORCHER Mémoire de stage de Master 2 mention BEE parcours BioGET 2016-2017 Influence of conspecific negative distance-dependence on recruitment of Brazil nut (*Bertholletia exelsa*) in the Peruvian Amazon. For each individual, we verified whether they were sowing or sprouting. Individuals from seeds have the particularity of keeping the nut almost intact until several years in the first centimeters in the soil (field observations). This could be observed in saplings of 3 years. For sprouting individuals we measured the highest stem even if it is dry when it is still standing. We consider that this stem although dead is representative of the potential height of the individuals at a certain distance from the nearest mature tree. In order to know the fire disturbance history of each growth site (i.e. the number of slash and burn cycles and the number of years past since the last burning), we crossed the data collected from the owners and that obtained with the imagery satellite. We used the Landsat data from Global Forest Watch and Terra-i Peru from 2005 to 2017.

2.3. DATA ANALYSIS

To compare the number of individuals in the two types of vegetation studied, we used non-parametric Wilcoxon tests due to violation of the homoscedasticity assumption for the vast majority of comparisons, ruling out the use of t-tests.

To calculate the probability of occurrence of regeneration at different distance classes, we generated Bootstrap values to balance sampling deviations. Our methodology did not allow to sample the same number of 10x10m cells for each distance class. The final number of these cells was dependent on the density of BN around the transects, but in general disadvantaged cells at larger distance classes. We made 10,000 random selections of ten 10x10m cell for each class of distances in mature forest and fallow. We tested for significant differences between distance classes within both vegetation types by means of a Kruskal-Wallis test and used a non-parametric post-hoc multiple comparison test (threshold at p = 0.05) to distinguish differences between distance classes. This post-hoc test is based on (Siegel and Castellan, 1988) implemented in the "*kruskalme*" function of *pgirmess* package from R. We used the same tests to evaluate the significance between the numbers of fire event. To demonstrate the effect of negative distance-dependence on plant height, we used the correlation coefficients of linear regression lines. Statistical analyzes were performed with R 3.3.3 and the graphs were constructed with the ggplot2 package for R.

3. RESULTS

In all of the 40 transects sampled, representing a surface area of 6 ha, all vegetation combined (fallow and mature forest) we identified and georeferenced 147 regenerating individuals of Bertholletia excelsa. We found a significantly higher number of regenerating individuals (including seedlings, saplings and juvenile trees) per transect in fallow than in mature forest (w = 346, p << 0.001), (Fig.2all). We recorded 110 individuals in fallow for 37 in mature forest with 122 mature trees as potential seed origin. The vegetation type had no effect on the number of seedlings less than 50 cm high (SizeClass A). Both in fallow and mature forest the mean number of individuals per transect of class A did not exceed 3 individuals. On the other hand, for individuals exceeding 50cm (Sizes Class B and C + D), the effect of vegetation was very marked with significantly higher numbers in fallow (p <0.001), respectively w = 335 and w = 1129 (Fig.2).



Figure 2. Boxplots of number of regenerating Brazil nut individuals per transect and height class according to vegetation. In fallow, the number of individuals with all heights included (all), as well as the number of individuals exceeding 50 cm in height (B) and (C + D) is significantly different from the number of individuals encountered in mature forest (p << 0.001) with high Wilcoxon values. Respectively w = 335

and w = 1129. The black dots indicate the means.

Regenerating individuals in larger size classes were almost completely absent in mature forest. In fallow, the tallest individuals only appeared beyond 30m. We found the majority of individuals in the first six distance classes (10-60m). The pattern of negative distance-dependence is only apparent up to 50m, after which the effects of decreasing seed dispersal appear to become more important (Fig.3). For this reason, and the fact that the last distance classes were relatively undersampled, we focused on the first 80 meters of the transect line for bootstrap comparisons of the probability to encounter regenerating Brazil nut trees per distance class. When all heights classes are taken into account, the probability of occurrence of regeneration linearly increased over the first 30 meters in fallow, confirming there is a significant effect of distance-dependent recruitment in fallows (p < 0.001), but this is non-existent in mature forest (Fig. 4A). Both in fallows and mature forest, this pattern was absent in seedlings less than 50 cm (Fig.4B). On the other hand, when we exclude this last class of size (A) we again observed the fallow pattern in saplings (B) and juveniles (C + D). The probability of encountering regeneration is more significant (p < 0.05) in the larger individuals (Fig. 4C and 4D). The highest probabilities are found at increasing distances as we consider the size of individuals, which suggests an effect of negative distance dependence on the size of individuals (Fig. 4C and 4D). The correlations coefficients of linear regressions between the size of the plants and the distance to the nearest adult show that there is a significant effect (R2 = 0.11, p < 0.001) of the negative distance-dependence (NDD) on

Vincent PORCHER Mémoire de stage de Master 2 mention BEE parcours BioGET 2016-2017

the size of the individuals (Fig.5). This effect was already predicted with the probability of occurrence (Fig. 4C and 4D).



Number of individuals per vegetation, distance classes and sizes classes

Figure 3. Distribution of the regenerating individuals encountered by vegetation, distance classes and size classes. For each size class, a greater number of regenerations are observed, which increases with the distance over the first 40 meters in fallow. The number of individuals falls from 70 to 120m in fallow. The number of individuals in mature forest is increases only marginally with distance.



Figure 4. Probability of encountering regeneration as a function of distance to the nearest adult by vegetation and height classes (A all individuals (all), B seedlings <50cm, C saplings 50-150cm, D saplings and juvenile> 150cm-40cm DBH). The probability is significantly different in fallow at different distance from the nearest adult tree (p < 0.001) unlike in mature forest (Kruskal-Wallis, chi-squared = 22768). The

effect of distance on the probability for seedlings in fallow and mature forest is virtually non-existent, unlike larger individuals where the effect is particularly significant in fallow (p < 0.05). The boxplots were constructed based on 10.000 random selection of ten 10x10m plots for each distance class. Letters indicate the distance classes to which the probability is similar based on a post-hoc multiple comparison test (threshold at p = 0.05).



Height regenerating plant vs distance to closest adult

Figure 5. Relations between nearest distance to adult Brazil nut tree and the height of regenerating individuals. For each height class, the correlation coefficients of the respective linear regressions show a significant relationship (p < 0.05) between the size of the plants and the distance they are from the nearest adult. Black points represent all individuals ($R^2 = 0.11$, p < 0.001), the red circled points represent individuals measuring more than 50cm ($R^2 = 0.23$, p < 0.001); and green circled points represent individuals measuring more than 300cm ($R^2 = 0.29$, p < 0.05).

The Landsat images from 2005 to 2017 of the two study sites allowed us to evaluate the effect of the number of fire events on the population of regenerating Bertholletia excelsa. Here the fallow time (between two burns) has not been taken into account. We have considered only the number of fire passes in the fallows studied since 2005. We observe an increase in the total number of individuals (all) with the number of fire events until the 3rd fire events before falling again in transects which experienced 4 fire events (Fig.6). The number of individuals per fire event is significantly different (Kruskal-Wallis chis-squared = 10.472, p = 0.01) (Fig.6all). When separating the individuals into size classes (A, B and C + D), the results are not significant. However, there is a similar trend. Individuals of the highest sizes classes (B, C and D) disappear after a 4th fire passage. On the contrary, the seedling population (A) seems to be maintained even after a 4th cycle. The significance between each fire events indicated by the letters is based on a post-hoc comparison test (threshold at p = 0.05) (A and B). We also examined whether the average size of plants and the number of sprouts varied with the number of fire events (Fig. 7). In both cases, we found significant correlations (p < 0.05). The height of the individuals increased with the number of fire events until the 3rd and then falls to the 4th fire event (p < 0.05) (A). We found that the number of sprouts after 1 and 2 fire event did not vary. From the 3rd it increased significantly and decreased again at 4 fire events (p < 0.05) (B). For the first three fire events (1-3), the number of individuals, sprouts and average plant size follows the same trend as Paiva had described (2011) (Fig.6 and Fig.7)



Figure 6. Fire events and number of individuals for different size classes. The total number of individuals per transect (all) varies significantly (p = 0.01) with the number of fire passages (Kruskal-Wallis chissquared = 10,472). The number of individuals increases until the 3rd fire event and then falls to the 4th. For distinct size classes (A, B and C + D) the results are not significant, but there is a similar trend. However, it is noted that the seedling numbers (A) are maintain at the 4th fire event. The letters indicate the significance between each fire events based on a post-hoc comparison test (threshold at p = 0.05).



Figure 7. Mean height and number of sprouts per transect as a function of the number of fire events. The mean height of plants at each fire event is significantly different (Kruskal-Wallis chis-squared = 8.4232, p <0.05). The height of the individuals increases with the number of fire events until the 3rd and then falls to the 4th passage of the fire (Wilcoxon (1,2,3 and 4) w> 20, p <0.01) (A). Average height and number of sprouts per transect as a function of the number of fire events. The mean height of plants at each fire event is significantly different (Kruskal-Wallis chis-squared = 8.4232, p <0.05). The height of the individuals increases with the number of fire events. The mean height of plants at each fire event is significantly different (Kruskal-Wallis chis-squared = 8.4232, p <0.05). The height of the individuals increases with the number of fire events until the 3rd and then falls to the 4th passage of the fire (p <0.05) (A). The number of sprouts after a 1 and 2 fire event does not vary. From the 3rd it increases significantly decreases then to the 4th (p <0.05) (B). The letters indicate the significance between each fire event based on a post-hoc comparison test (threshold at p = 0.05) (A and B).

Vincent PORCHER Mémoire de stage de Master 2 mention BEE parcours BioGET 2016-2017 Influence of conspecific negative distance-dependence on recruitment of Brazil nut (*Bertholletia exelsa*) in the Peruvian Amazon.

4. DISCUSSION

We found three times as many regenerating Brazil nut trees in fallows, where the passage of fire is a constant of disturbance, than in mature forest where the disturbances are more punctual, corresponding to respectively 36.6 and 12.3 individuals per hectare, i.e. more than what Paiva found (Fig.2). Many factors have already explained a greater Brazil nut regeneration in open environments, owing to better access to soil resources (Ceccon et al., 2003) and presence of a favourable microclimate (Mori et al., 1990, Myers et al., 2000, Cotta et al., 2008, Rockwell et al., 2015) for its, presence of his dispersal and predator (Peres and Baider, 1997, Forget, 1994, Hirsch et al., 2012, Jansen et al., 2012), human intervention (Paiva et al., 2011, Shepard and Ramirez, 2011), and also the proximity and density of seed sources (Janzen, 1970, Cintra and Horna, 1997). Our study shows that there is an effect of negative distance dependence on regeneration in fallow (p < 0.001), but not in the forest (Fig. 3). Brazil nut is a canopy-gap species and this canopy openings are expressed more in disturbed environments than mature forest. The openings in mature forest might be too random to allow us to see the effect of the distance dependence negative in our study, because we sampled in forest continuums. Moreover, the generally small size of canopy openings in mature forest might prevent the negative distance dependence phenomenon to be expressed in that vegetation type.

The agouti is a predator and dispersal agent specific to BN whose population is contextdependent of the distribution Bertholletia excelsa (Jorge and Peres, 2005). The animal is the only one capable of opening the pyxidia to access the seeds, which it can transport over several tens of meters before hiding or consuming it (Peres and Baider, 1997). The observation in the forest of several empty dead trunks used as a cache for agoutis and filled with more than sixty empty Brazilian nut capsules (of the same year) indicates that some of the nuts collected by the animal are consumed directly (Annex 4). Moreover, the unfavorable conditions of this cache do not allow germination in case of nuts being left behind by the agoutis. This behavior may have a significant negative effect on recruitment. Although the abundance of agouti has been shown to be a factor important in the structure and size of the population BN (Wadt et al., 2005) we do not know how the population dynamics of this rodent can influence its ability to disperse Brazil nut seeds. The agoutis regularly steal the seeds they have hidden from one another. In order to limit intraspecific agouti's competition, it tends to hide seeds in places where Brazil nut tree density is lowest (Hirsch et al., 2012) (Forget et al., 2000).

While there is evidences of the presence of agoutis in all types of disturbed environments, the low, dense, regenerating vegetation of fallows appear to be more protective of agoutis from potential predators than mature forests where the undergrowth is more open (Cintra and Horna, 1997, Silvius and Fragoso, 2003), This increased activity in an open environment can help to establish a larger seed bank in this environment and increase the likelihood of recruitment. The light conditions of this microhabitat, similar to those encountered in canopy-gap (Cotta et al., 2008), are favorable for Brazil nut recruitment (Peña-Claros et al., 2002). In addition, exposure to full sunlight enhances the growth of young plants that can withstand moderate water stress (Azevedo, 2014).

Despite the many reserves in its seeds that allow a prolonged life of the seedlings in low light conditions (Zuidema and Boot, 2002), the nut itself is the target of many predators, herbivores as pathogens. First, the empirical data from the experiments we conducted confirmed the presence of strong herbivory pressure on seedling survival of Bertholletia excelsa beyond our expectations. 100% of the unprotected seedlings were eaten or stolen by the Agoutis and another unidentified rodent. Second, specific pathogens are crucial for recruitment. The latter are particularly present in undergrowth in wet and shady conditions, causing higher seedling mortality in tropical trees in conspecific aggregates (Augspurger, 1984a, Augspurger, 1984b). This fungal pressure could explain the low number of individuals encountered in mature forest and the almost nonexistence of individuals exceeding 50 cm in height. Empirical data and field observations suggest strong pressure from specific predators and give meaning to the Janzen hypothesis (1970) - Connel

Vincent PORCHER Mémoire de stage de Master 2 mention BEE parcours BioGET 2016-2017

Influence of conspecific negative distance-dependence on recruitment of Brazil nut (Bertholletia exelsa) in the Peruvian Amazon

(1971). This last hypothesis could explain the strong negative distance-dependence observed on the first 30 meters in fallow (p <0.05) (Fig. 4A). The plots B, C and D in Figure 4 and the Figure 5 show that the pattern of negative distance-dependence expresses itself exclusively on the height classes of the individuals encountered (p <0.05). This suggests herbivore and pathogen pressures might prevent significant portions of seedlings to transition to larger size classes. Older individuals with greater development are more capable to survive herbivor or pathogen attacka and can compete better for resources.

As Paiva (2011) has already shown, the results from this study showed a tendency to increase the number of individuals with the number of fire cycles (Fig.6all), but also a capacity to resprout after the disappearance of the main stem. Rapidly producing a first straight axis is a priority for emerging trees growing in disturbed environments. Brazil nut has this strange ability to produce a new stem to replace a damaged first stem, directly from the seed and not derived from a branch of the first stem in its early years of life. This characteristic confers a great capacity of vegetative regeneration to the young trees. In addition, the Brazil nut has the peculiarity of keeping its nuts almost intact for many years; it can be found in trees already measuring several meters. Brazil nut contains among the highest levels of lipid and protein in its hypocotyl that most other seed oil (Trelease and Doman, 1984). The particular management of its albumen reserves and the conservation of the nut for so long could be a strategy to limit the risks adapted to the canopygap disturbance regime. The delayed mobilization of its oil and wax reserves would allow rapid growth at the right time. Brazil nut tree seems to behave like a "strugglers" or "struggling gamblers" vis-a-vis the light (Oldeman and Van Dijk, 1991). The objective is therefore for the tree to penetrate the first stages of the canopy (young arrow-shaped crown) before establishing its large crown once protected from competition for light.

The passage of fire seems to play a decisive role in the recruitment and survival of regeneration. After the 4th fire passage, the seedling population, contrary to saplings and juveniles, appears to be maintained and even to increase in some cases (Fig.6). These results (Fig. 6 and Fig. 7) suggest that the population of individuals increases by accumulation of sprouts (p <0.05) for the oldest individuals (Fig. 6B and 6C + D), but also by accumulation of new seedling generation (Fig.6A). Moreover, the increase in the number of seedlings seems to show that the cumulative passage of fire has a positive effect on germination and survival of seedlings. The passage of repeated fire on the same area has the effect of changing the microclimate (reducing humidity and increasing the entry of light) by destroying vegetation and litter in place, but also causes temporary and partial sterilization of the soil (Raison, 1979, Cerdà and Robichaud, 2009). Fungi that are more sensitive than bacteria and actinomycetes first disappear with fire (Cerdà and Robichaud, 2009) thus reducing the pressure of pathogens on seedlings. We also found that the total population (all) drops after 4 fire events (p < 0.01) (Fig.6all, Fig.7A and 7B). This might suggest a significant mortality of saplings and juveniles as of four fire events (p < 0.05) (Fig.6). This mortality suggests the existence of a limit to the capacity of vegetative regeneration and endurance to fire. If our hypothesis that part of the reserves of the hypocotile is preserved in order to anticipate possible stress (destruction of the main stem) is verified, then the disappearance of most individuals after a 4th fire events could correspond to the depletion of reserves or at least the regenerative potential of the plant.

5. CONCLUSION

This regenerative capacity of Brazil nut and barriers to recruitment successseem to be an important points to be addressed in future land use management and planning of. A better management of fallows through a limitation of the number of burning cycles and a increasing the time between fire events would enhance Brazil nut recruitment rates and hence allow to revalorize traditional agricultural techniques to the benefit of the conservation and sustainable use of the Brazil nut. Slash-and-burn agriculture can be a sustainable technique based on a fragile equilibrium (Carrière et al., 2002; Carrière, 2003; Bahuchet and Betsch, 2012), but the role of fallows is crucial in the conservation and dynamics of biodiversity (Angelsen, 1995, Dounias and Hladik, 1996, Barrau, 1971, Miller and Kauffman, 1998, Bahuchet and Betsch, 2012). To quote Serge Bahuchet "Slash-and-burn agriculture is part of the forest dynamics and its cycle is part of the history of forests (1997)." The positive effect of shifting agriculture on the population dynamics of Brazil nut, have shaped its current distribution across the Amazon basin and patterns therein since pre-Columbian times (Shepard and Ramirez, 2011, Thomas et al., 2015, Balée, 1993, Clement Et al., 2015). Moreover, we have shown that Brazil nut recruitment is subject to negative distance-dependent processes, which are known to promote interspecific coexistence through spacing mechanisms, resulting in a higher diversity levels (Metz et al., 2010). We therefore believe that a better management of Bertholletia excelsa through concessions and practices of slash-andburn agriculture (Riera et al., 1990) will simultaneously lead to increased conservation of other species in the forest matrix. .

The majority of studies on the distance and / or conspecific negative density-dependence of tropical trees does not mention the effect of the ecosystem in the expression of this ecological process. Our study shows a significant effect of the type of vegetation on the appearance of this mechanism. Many canopy-gap-dependent species to regenerate and / or carry out an important mass seed like Brazil nut seem to be tolerant to the CNDD (Lebrija-Trejos et al., 2016). Consideration of this factor as the type of ecosystem could reveal in other species this mechanism that has been discarded until now.

6. REFERENCES

- Angelsen A., 1995. Shifting cultivation and « deforestation »: A study from Indonesia. World Development, 23 (10), pp. 1713-1729.
- Augspurger C.K., 1984a. Light Requirements of Neotropical Tree Seedlings: A Comparative Study of Growth and Survival. *The Journal of Ecology*, 72 (3), p. 777.
- Augspurger C.K., 1984b. Seedling Survival of Tropical Tree Species: Interactions of Dispersal Distance, Light-Gaps, and Pathogens. *Ecology*, 65 (6), pp. 1705-1712.
- Azevedo G.F. da C., 2014. Photosynthetic parameters and growth in seedlings of *Bertholletia excelsa* and *Carapa guianensis* in response to pre-acclimation to full sunlight and mild water stress. *Acta Amazonica*, 44 (1), pp. 67–77.
- Bahuchet S., 1997. Un style de vie en voie de mutation : Considérations sur les peuples des forêts denses humides. *Civilisations*, 44 (1/2), pp. 16-31.
- Bahuchet S., Betsch J.-M., 2012. L'agriculture itinérante sur brûlis, une menace sur la forêt tropicale humide ?: Savoirs et savoir-faire des Amérindiens en Guyane française. *Revue d'ethnoécologie*, (1).
- Balée W., 1993. Indigenous Transformation of Amazonian Forests: An Example from Maranhão, Brazil. *L'Homme*, 33 (126/128), pp. 231-254.
- Barrau J., 1971. La culture itinérante, longtemps mal comprise et encore mal nommée! *Journal d'agriculture tropicale et de botanique appliquée*, 18 (1), pp. 100-103.
- Carrière S., 2003. Les orphelins de la forêt : pratiques paysannes et écologie forestière (Ntumu, Sud-Cameroun). IRD Editions
- Carrière S.M., Letourmy P., McKey D.B., 2002. Effects of remnant trees in fallows on diversity and structure of forest regrowth in a slash-and-burn agricultural system in southern Cameroon. *Journal of Tropical Ecology*, 18 (3), pp. 375-396.
- Ceccon E., Huante P., Campo J., 2003. Effects of nitrogen and phosphorus fertilization on the survival and recruitment of seedlings of dominant tree species in two abandoned tropical dry forests in Yucatán, Mexico. *Forest Ecology and Management*, 182 (1-3), pp. 387-402.
- Cerdà A., Robichaud P., 2009. Fire Effects on Soils and Restoration Strategies. Science Publishers.
- Clement C.R., Denevan W.M., Heckenberger M.J., Junqueira A.B., Neves E.G., Teixeira W.G., Woods W.I., 2015. The domestication of Amazonia before European conquest. *Proceedings of the Royal Society B: Biological Sciences*, 282 (1812), p. 20150813.
- Comita L.S., Queenborough S.A., Murphy S.J., Eck J.L., Xu K., Krishnadas M., Beckman N., Zhu Y., 2014. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology*, 102 (4), pp. 845-856.
- Connell JH, 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics of Populations: Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations. *Center of Agricultural Publishing and Documentation, Wageningen*, pp. 289-310.
- Cotta J.N., Kainer K.A., Wadt L.H.O., Staudhammer C.L., 2008. Shifting cultivation effects on Brazil nut (*Bertholletia excelsa*) regeneration. *Forest Ecology and Management*, 256 (1-2), pp. 28-35.
- Dounias E., Hladik C.M., 1996. Les agroforêts Mvae et Yassa du Cameroun littoral : fonctions socioculturelles, structure et composition floristique. *L'alimentation en forêt tropicale : interactions bioculturelles et perspectives de développement. Paris: UNESCO*, pp. 1103–1126.
- Espírito-Santo F.D.B., Keller M., Braswell B., Nelson B.W., Frolking S., Vicente G., 2010. Storm intensity and old-growth forest disturbances in the Amazon region: LARGE FOREST DISTURBANCES IN THE AMAZON. *Geophysical Research Letters*, 37 (11), p. n/a-n/a.

Vincent PORCHER Mémoire de stage de Master 2 mention BEE parcours BioGET 2016-2017 Influence of conspecific negative distance-dependence on recruitment of Brazil nut (*Bertholletia exelsa*) in the Peruvian Amazon

- Forget P.-M., 1994. Recruitment Pattern of *Vouacapoua americana* (Caesalpiniaceae), a Rodent-Dispersed Tree Species in French Guiana. *Biotropica*, 26 (4), p. 408.
- Forget P.-M., Milleron T., Feer F., Henry O., Dubost G., 2000. Effects of Dispersal Pattern and Mammalian Herbivores on Seedling Recruitment for Virola michelii (Myristicaceae) in French Guiana1. BIOTROPICA, 32 (3), p. 452.
- Freycon V., Fauvet N., 1998. Les GPS. De l'acquisition des données à leur intégration dans un SIG Série FORAFRI, Document, (10), p. 53.
- Guedes, M.C., Neves, E., Rodrigues, E.G., Paiva, P., Costa, J.B.P., Freitas, M.F. & Lemos, L.M., 2014. "Castanha na roca": increasing yields and renewing Brazil nut stands through shifting cultivation in Amapa State, Brazil ». *Ciências Naturais*, Bole-tim do Museu Paraense Em Ilio Goeldi (419), pp. 381-398.
- Hirsch B.T., Kays R., Pereira V.E., Jansen P.A., 2012. Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. *Ecology Letters*, 15 (12), pp. 1423-1429.
- Holdridge L.R., 1967. Life zone ecology. Rev. ed. San Jose, Costa Rica, Tropical Science Center, 206 p.
- Jansen P.A., Hirsch B.T., Emsens W.-J., Zamora-Gutierrez V., Wikelski M., Kays R., 2012. Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences*, 109 (31), pp. 12610–12615.
- Jansen P.A., Visser M.D., Joseph Wright S., Rutten G., Muller-Landau H.C., 2014. Negative density dependence of seed dispersal and seedling recruitment in a Neotropical palm. *Ecology Letters*, 17 (9), pp. 1111-1120.
- Janzen DH, 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist*, (104), pp. 501-528.
- Jorge M.S.P., Peres C.A., 2005. Population Density and Home Range Size of Red-Rumped Agoutis (*Dasyprocta leporina*) Within and Outside a Natural Brazil Nut Stand in Southeastern Amazonia1. *Biotropica*, 37 (2), pp. 317-321.
- Kainer K.A., Duryea M.L., Costa de Macêdo N., Williams K., 1998. Brazil nut seedling establishment and autecology in extractive reserves of Acre, Brazil. *Ecological Applications*, 8 (2), pp. 397–410.
- Lebrija-Trejos E., Reich P.B., Hernández A., Wright S.J., 2016. Species with greater seed mass are more tolerant of conspecific neighbours: a key driver of early survival and future abundances in a tropical forest. *Ecology Letters*, 19 (9), pp. 1071-1080.
- Lejeune P., Hellemans P., 2000. Effet du couvert forestier sur la précision d'un système de positionnement global différentiel (dGPS). Biotechnologie, Agronomie, Société et Environnement, 4 (1), pp. 41–49.
- Mann C.C., 2008. Ancient earthmovers of the Amazon. Science, 321 (5893), pp. 1148–1152.
- Miller P.M., Kauffman J.B., 1998. Effects of slash and burn agriculture on species abundance and composition of a tropical deciduous forest. *Forest Ecology and Management*, 103 (2-3), pp. 191-201.
- Moll-Rocek J., Gilbert M.E., Broadbent E.N., 2014. Brazil Nut (Bertholletia excelsa, Lecythidaceae) Regeneration in Logging Gaps in the Peruvian Amazon. International Journal of Forestry Research, 2014, pp. 1-8.
- Mori S.A., Prance G.T., others, 1990. Taxonomy, ecology, and economic botany of the Brazil nut (Bertholletia excelsa Humb. and Bonpl.: Lecythidaceae). Advances in Economic Botany, 8, pp. 130–150.
- Morisita M., 1962. I σ-Index, a measure of dispersion of individuals. *Researches on Population Ecology*, 4 (1), pp. 1-7.
- Myers G.P., Newton A.C., Melgarejo O., 2000. The influence of canopy gap size on natural regeneration of Brazil nut (*Bertholletia excelsa*) in Bolivia. *Forest Ecology and Management*, 127 (1–3), pp. 119-128.
- Nelson B.W., Kapos V., Adams J.B., Oliveira W.J., Braun O.P.G., 1994. Forest Disturbance by Large Blowdowns in the Brazilian Amazon. *Ecology*, 75 (3), pp. 853-858.

Vincent PORCHER Mémoire de stage de Master 2 mention BEE parcours BioGET 2016-2017

Influence of conspecific negative distance-dependence on recruitment of Brazil nut (Bertholletia exelsa) in the Peruvian Amazon.

- Osher L., Buol S., 1998. Relationship of soil properties to parent material and landscape position in eastern Madre de Dios, Peru. *Geoderma*, 83 (1-2), pp. 143-166.
- Paiva P.M., Guedes M.C., Funi C., 2011. Brazil nut conservation through shifting cultivation. *Forest Ecology and Management*, 261 (3), pp. 508-514.
- Peña-Claros M., Boot R.G., Dorado-Lora J., Zonta A., 2002. Enrichment planting of *Bertholletia excelsa* in secondary forest in the Bolivian Amazon: effect of cutting line width on survival, growth and crown traits. *Forest Ecology and Management*, 161 (1), pp. 159–168.
- Peres C.A., Baider C., 1997. Seed dispersal, spatial distribution and population structure of Brazilnut trees (*Bertholletia excelsa*) in southeastern Amazonia. *Journal of Tropical Ecology*, 13 (4), pp. 595-616.
- Piao T., Chun J.H., Yang H.M., Cheon K., 2014. Negative Density Dependence Regulates Two Tree Species at Later Life Stage in a Temperate Forest. *PLoS ONE*, 9 (7), p. e103344.
- Queenborough S.A., Burslem D.F., Garwood N.C., Valencia R., 2007. Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. *Ecology*, 88 (9), pp. 2248–2258.
- R Development Core Team, 2011. R: a language and environment for statistical computing. Vienna, Austria.
- Raison R.J., 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: A review. *Plant and Soil*, 51 (1), pp. 73-108.
- Ribeiro M.B.N., Jerozolimski A., de Robert P., Salles N.V., Kayapó B., Pimentel T.P., Magnusson W.E., 2014. Anthropogenic Landscape in Southeastern Amazonia: Contemporary Impacts of Low-Intensity Harvesting and Dispersal of Brazil Nuts by the Kayapó Indigenous People. *PLoS ONE*, 9 (7), p. e102187.
- Riera B., Puig H., Lescure J.-P., 1990. La dynamique de la forêt naturelle. *Bois et forêts des tropiques*, 219, pp. 69–78.
- Salomão, R, 2009. Densidade, estrutura e distribuição espacial de castanheira-do-brasil (*Bertholletia* excelsa H. & B.) em dois platôs de floresta ombro fila densa na Amazônia setentrional brasileira. Boletim do Museu Paraense Em Ilio Goeldi. *Ciências Naturais*, (4), pp. 11-25.
- Schaan D., Pärssinen M., Saunaluoma S., Ranzi A., Bueno M., Barbosa A., 2012. New radiometric dates for precolumbian (2000–700 b.p.) earthworks in western Amazonia, Brazil. *Journal of Field Archaeology*, 37 (2), pp. 132-142.
- Schoener T.W., 1974. Resource partitioning in ecological communities. Science, 185 (4145), pp. 27-39.
- Scoles, R, 2011. Do rio Madeira ao rio Trombetas: novas evidências ecologicas e historicas da origem antro pica dos castanhais amazônicos. *Novos cadernos*, (14), pp. 265-282.
- Scoles R., Gribel R., 2015. Human Influence on the Regeneration of the Brazil Nut Tree (*Bertholletia excelsa* Bonpl., Lecythidaceae) at Capanã Grande Lake, Manicoré, Amazonas, Brazil. *Human Ecology*, 43 (6), pp. 843-854.
- Scoles R., Gribel R., 2011. Population Structure of Brazil Nut (*Bertholletia excelsa*, Lecythidaceae) Stands in Two Areas with Different Occupation Histories in the Brazilian Amazon. *Human Ecology*, 39 (4), pp. 455-464.
- Scoles R., Gribel R., 2012. The regeneration of Brazil nut trees in relation to nut harvest intensity in the Trombetas River valley of Northern Amazonia, Brazil. Forest Ecology and Management, 265, pp. 71-81.
- Shepard G.H., Ramirez H., 2011. « Made in Brazil »: Human Dispersal of the Brazil Nut (*Bertholletia excelsa*, Lecythidaceae) in Ancient Amazonia1. *Economic Botany*, 65 (1), pp. 44–65.
- Siegel, Castellan, 1988. Non-parametric statistics for the behavioural sciences. MacGraw Hill Int, pp. 213-214.
- Silvius K.M., Fragoso J.M.V., 2003. Red-rumped Agouti (Dasyprocta leporina) Home Range Use in an Amazonian Forest: Implications for the Aggregated Distribution of Forest Trees1. *BIOTROPICA*, 35 (1), p. 74.

- Thomas E., Alcázar Caicedo C., McMichael C.H., Corvera R., Loo J., 2015. Uncovering spatial patterns in the natural and human history of Brazil nut (*Bertholletia excelsa*) across the Amazon Basin. *Journal of Biogeography*, 42 (8), pp. 1367-1382.
- Trelease R.N., Doman D.C., 1984. Mobilization of Oil and Wax Reserves. In: Germination and Reserve Mobilization. Elsevier, pp. 201-245.
- Wadt L.H.O., Kainer K.A., Staudhammer C.L., Serrano R.O.P., 2008. Sustainable forest use in Brazilian extractive reserves: Natural regeneration of Brazil nut in exploited populations. *Biological Conservation*, 141 (1), pp. 332-346.
- Zuidema P.A., Boot R.G.A., 2002. Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics. *Journal of Tropical Ecology*, 18 (1), pp. 1-31.

7. ABREVIATIONS LIST

BN: Brazil nut
CNDD: Conspecific negative distance-dependence
DBH: Diameter at breast height
DOP: Dilution of precision
GPS: Global Positioning System
IIAP: Instituto de Inverstigation de la Amazonia Peruana
NDD: Negative distance-dependence
NTFP: Non-timber forest products
QGIS: QantumGIS a geographic information system software
R: Statistical analysis software R
SC: Sizes Classes
UTM: Universal Transverse Mercator, type of cartographic projection

8. TABLE OF FIGURES

9. APPENDICES

APPENDICES TABLE

APPENDICE 1. SEEDLING PROTECTION DEVICE	30
Appendice 2. Proof of seedling predation of Bertholletia excelsa e agouti.	BY 31
Appendice 3. Trace of predation by an unidentified rodent, probably rat	а 32
APPENDICE 4. CACHE OF AGOUTI IN AN EMPTY DEAD TRUNK	33



APPENDICE 1. SEEDLING PROTECTION DEVICE.

Metal cage. Source Vincent Porcher.



APPENDICE 2. PROOF OF SEEDLING PREDATION OF BERTHOLLETIA EXCELSA BY AGOUTI.

Photos taken with an automatic camera trap. The seedlings were installed on 28/06/2017 at 10: 21am. The first visit of the site by an agouti (*Dasyprocta sp*) was at 13: 11pm then the second at 4: 43pm (A) and the seedling consumption was at 4: 52pm (B) the same day. These images show strong predation pressure for regeneration. Image (C) Agouti side view. Picture (D) Paca (*Cuniculus paca*) side view, another consumer of brazil nut seed. Source Vincent Porcher.



APPENDICE 3. TRACE OF PREDATION BY AN UNIDENTIFIED RODENT, PROBABLY A RAT.

The stem was cut and the nut removed leaving the seed hole (A and B). Source Vincent Porcher.



APPENDICE 4. CACHE OF AGOUTI IN AN EMPTY DEAD TRUNK.

The observation of more than sixty capsules (pyxidia) in an empty trunk indicates the agoutis accumulate the fruits before consuming the nuts at the shelter. This behavior could have a negative effect on the recruitment of Brazil nut seedlings. Source Vincent Porcher.