



Rapid assessment of dispersal failure and seedling recruitment of large-seeded non-timber forest products trees in a tropical rainforest

Authors: Lermyte, Clément, and Forget, Pierre-Michel

Source: Tropical Conservation Science, 2(4) : 404-424

Published By: SAGE Publishing

URL: <https://doi.org/10.1177/194008290900200403>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Research Article

Rapid assessment of dispersal failure and seedling recruitment of large-seeded non-timber forest products trees in a tropical rainforest

Clément Lermyte^{1*} and Pierre-Michel Forget¹

1 – Muséum national d'Histoire naturelle, UMR 7179 CNRS–MNHN, 1 avenue du Petit-Château, 91800 Brunoy, France.

* Corresponding author email: clementlermyte@hotmail.fr

Abstract

Forest managers and harvesters of non-timber forest products (NTFPs) need a tool for rapid measurement of the impact of their activities on seed dispersal and tree recruitment. Such a tool could be used for a prospective eco-label which would ensure regeneration. We propose, and have used a new rapid assessment protocol to sample and evaluate the impact of any anthropogenic disturbance on seed dispersal and seedling recruitment of hard-tegument fruit species enclosing large seeds. We set up this protocol in French Guiana for a large-seeded scatter-hoarded tree species, *Carapa surinamensis* (andiroba), at three different forest sites affected by a variety of anthropogenic pressures, such as hunting and logging. Over a limited time we assessed: 1) dispersal failure: from late May to mid-June, the proportion of seeds remaining undispersed was estimated by sampling the number of seeds, seedlings and fruit husks in 25-m² subplots under the tree crown; 2) recruitment effectiveness: in September–October, seedlings were sampled on four 100-m² plots located 5–15 m from the tree base around the tree crown. Altogether, 77 trees were sampled, some 1–2 hours being spent beneath each tree, during a total 4–6 weeks in the field for each dispersal and recruitment sampling. We showed that: 1) seed dispersal is affected by hunting, this being significantly marked in the coastal area, which faces major anthropogenic pressures; 2) logging treatments affect seed dispersal and regeneration, on the average. However, canopy gaps due to silvicultural treatments raise the life expectancy of seedlings.

Keywords: Andiroba, seed dispersal, seedling recruitment, rapid assessment, tropical rainforest

Résumé

Les gestionnaires ont besoin d'un outil permettant d'évaluer rapidement l'impact de l'exploitation forestière et de la collecte des produits forestiers non ligneux (PFNL) sur la dispersion des graines et la régénération des arbres. Cet outil permettrait d'établir un futur écolabel garantissant la régénération des espèces. Nous proposons une méthode rapide d'échantillonnage que nous avons utilisée afin d'évaluer l'impact des perturbations humaines sur la dispersion et la régénération des espèces à grosses graines et à coques dures. Nous avons testé ce protocole en Guyane française sur trois sites présentant différentes pressions anthropiques, comme la chasse et l'exploitation forestière, sur une espèce à grosses graines, *Carapa surinamensis* (andiroba). Dans un temps restreint, nous avons mesuré 1) la proportion de graines non dispersées : estimée entre fin mai et mi-juin en échantillonnant les graines et coques restées au sol à l'intérieur de quadrats de 25 m² sous la couronne ; 2) la régénération : en échantillonnant de septembre à octobre les plantules à l'intérieur de quatre quadrats de 100 m², situés à 5-15 m de la base de l'arbre autour de la couronne. En 4 à 6 semaines, 77 arbres ont été échantillonnés pour la dispersion des graines et la régénération, soit 1 à 2 heures par arbre. L'étude montre que 1) la dispersion est affectée par la chasse, particulièrement sur la côte où les pressions anthropiques sont importantes ; 2) les traitements sylviculturaux affectent la dispersion et la régénération, mais la présence d'ouvertures dans la canopée augmente la survie des plantules.

Mots clés : Andiroba, dispersion des graines, régénération, méthode d'inventaire rapide, forêt tropicale humide

Received: 6 September 2009; Accepted: 28 October 2009; Published: 7 December 2009

Copyright: © Clément Lermyte and Pierre-Michel Forget. This is an open access paper. We use the Creative Commons Attribution 3.0 license <http://creativecommons.org/licenses/by/3.0/> - The license permits any user to download, print out, extract, archive, and distribute the article, so long as appropriate credit is given to the authors and source of the work. The license ensures that the published article will be as widely available as possible and that the article can be included in any scientific archive. Open Access authors retain the copyrights of their papers. Open access is a property of individual works, not necessarily journals or publishers.

Cite this paper as: Lermyte, C. and Forget, P. M. 2009. Rapid assessment of dispersal failure and seedling recruitment of large-seeded non-timber forest products trees in a tropical rainforest. *Tropical Conservation Science* Vol. 2 (4):404-424. Available online: www.tropicalconservationscience.org

Introduction

Tropical forests are increasingly threatened by human activities, especially by hunting, logging, and large-scale deforestation. At the same time, the maintenance of ecological services largely relies on the preservation of diversity in tropical ecosystems [1]. This entails the establishment, protection and reinforcement of indigenous reserves and national parks. In order to satisfy the objectives of environmental protection and the utilization claims of the local population, it is necessary to provide tools allowing the sustainable management of forests, especially regarding the use of non-timber forest products (NTFPs). According to the International Centre for Forestry Research (CIFOR) (<http://www.cifor.cgiar.org/Publications/Corporate/FactSheet/ntfp.htm>), NTFPs are any product or service other than timber that is produced in forests. They include fruits and nuts, vegetables, fish and game, medicinal plants, resins, essences, barks, fibres, bamboo, rattans, and a host of other palms and grasses. As an alternative to the unsustainable use of timber, governments, conservation and development agencies and non-government organizations have widely promoted the sustainable harvesting of NTFPs for conservation and development strategy purposes [2, 3]. NTFPs indeed stand as important sources of income for hundreds of millions of people across the globe [4, 5].

Many NTFPs are extracted from species mainly dependent on animals for dispersal and recruitment [6, 7]. Mutualistic interactions between animals and plants in tropical forests are known to have a functional importance that makes this ecosystem highly sensitive to anthropogenic activities, such as hunting and logging [8-12]. In tropical ecosystems, a majority of fruits are consumed, either in the canopy or on the ground [13], by animals that disperse seeds. Primary seed dispersal determines the potential area of plant recruitment and sets the template for subsequent processes, such as predation, germination, competition, and growth [14, 15]. In tropical forests, seed dispersal can enhance local recruitment success by reducing the impact of two types of spatially non-random offspring mortality [16]: first, in accordance with the Janzen-Connell pattern [17, 18] and the “predator escape” hypothesis [19]; second, in accordance with the “colonization” hypothesis [19].

However, the global increase in NTFP demand and their obvious important economic value nowadays result in overexploitation [20-25]. Demographic pressure and social changes are speeding up, and the demand for organic produce for a rapidly developing international market, especially for the cosmetics industry, is increasing. Harvesters need, therefore, to strike a balance between the use and marketing of

natural resources and the maintenance of the environment on which their welfare and culture depend. Moreover, extraction and production of NTFPs are often associated with subsistence hunting [26], and the long-term effects of the so-called sustainable extractivism on ecological processes remain poorly understood and inadequately investigated.

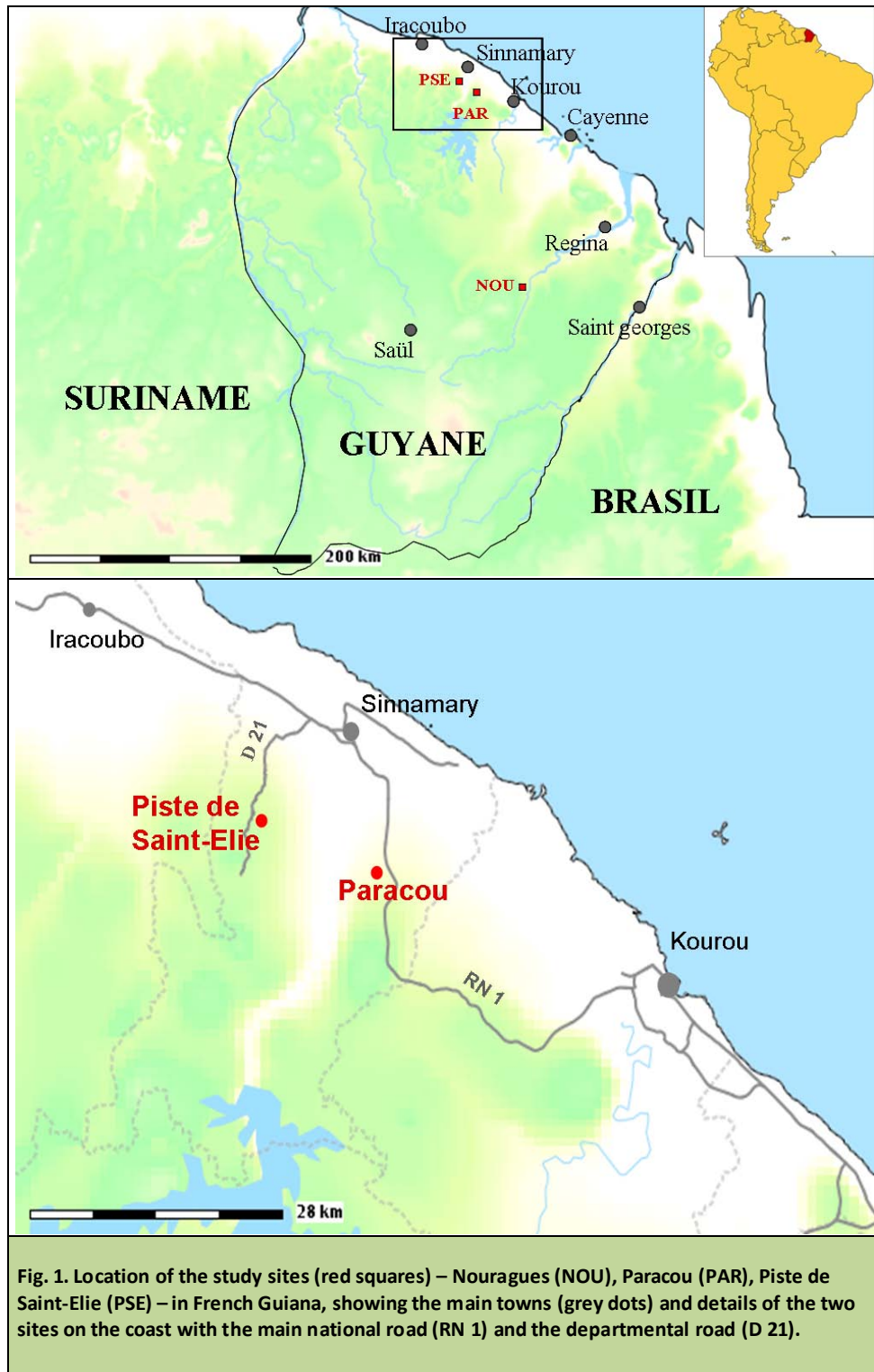
In order to explore how human extractivist activities affect plant communities by limiting seed dispersal and seedling establishment, consequently endangering the sustainable use of NTFPs, different experimental protocols have been used. Generally, seed dispersal is studied by following marked seeds from their sources [27]; thread-marked seeds [28, 29], reviewed by Forget and Wenny [30]; by using genetic markers to establish the sources of seeds retrieved from their post-dispersal locations [31-33], by using seed traps [34-38], crop size measurement to evaluate seed dispersal failure from below parent trees [6], or by documenting the variation in seed deposition or density with distance from sources (for seedling density [39, 40]). Often, field studies are constrained by time and by the number of staff, and generally lack replicates within and across sites. Also, when analyzing seed removal and fate, seedling recruitment is not always documented, owing to the time lag between dispersal and establishment. Finally, studies often fail to be replicated across years, though results may differ depending on crop size which may in turn vary greatly from year to year [6, 39, 41]. There is thus a need for a standardized protocol for rapid assessment of dispersal failure and seedling recruitment, comparable to the methods of rapid biodiversity assessment [42]. Such a tool for hard-tegument fruit species enclosing large seeds, such as are found among key NTFP species in the Amazon, e.g., Andiroba (*Carapa* spp.) and Brazil nut (*Bertholletia excelsa*) [6, 43], could be useful for forest managers as well as harvesters to measure the impact of their activities in extractive reserves (RESEX) [44].

In this paper, we propose and test a new rapid assessment protocol to sample and evaluate the impact of human activities such as logging and hunting on seed dispersal and seedling recruitment for a large-seeded non-timber forest products tree species in French Guiana, *Carapa surinamensis* Miq. (Meliaceae), known as *C. procera* DC. in previous studies, see [45]; hereafter referred to as *Carapa*.

Methods

Study sites

The rapid assessment protocol was tested at the Nouragues Biological Research Station [46], Paracou experimental field station [47], and Piste de Saint-Elie station [also known as ECEREX in the literature] [48, 49], all in French Guiana (Fig. 1). The sites were chosen in the light of the available data (experimental sites), the low heterogeneity of their abiotic factors (pedology, climate), and their contrasting situations: time since occurrence of previous human disturbance, degree of human pressure (exploited/non-exploited, hunting/no hunting), distance from urbanized areas and accessibility [50, 51]. These three mature forests share the same dominant tree families, Caesalpiniaceae, Lecythidaceae, Mimosaceae and Sapotaceae, with average species density values of 150–180 species per hectare. The average canopy height is 25–36 m, with emergent trees reaching 55 m [52, 53]. All sites experience a similar rainfall pattern with peaks in December–January and April–July, and an annual average precipitation of 3,000 mm.



The first site, Nouragues (4° 05' N, 52° 41' W; <http://www.nouragues.cnrs.fr/>), is a lowland rainforest site located 100 km south of Cayenne and 10 km north of the Arataye river [54]. Forest and fauna at the study site may be considered unaffected by humans. All of the extant larger mammal species native to the region—including large predators and two species of peccary (*Tayassu pecari* and *Pecari tajacu*)—are frequently observed. Field work was carried out at the “Grand Plateau,” a relatively flat, homogenous area of ca. 70 ha. Access to the station is restricted to scientists or people involved in scientific projects. Nouragues is only accessible by river or helicopter. Therefore, it is one of the best control sites for ecological studies related to the impact of human pressures in the Guiana Shield [55]. The other sites are affected by humans in different ways and degrees.

The second site, Paracou (5° 15' N, 52° 55' W), has been used for a silvicultural experiment including reduced-impact logging and poisoning (tree poison-girdling included single or double-banded girdling with different concentrations of the herbicide 2,4-D), and is management-oriented [47]. The mammalian fauna is incompletely represented [56], especially primates and other large (> 1 kg) terrestrial vertebrates. Large rodents (> 500 g), such as red acouchi (*Myoprocta exilis*) and especially red-rumped agouti (*Dasyprocta leporina*), are regularly encountered on trails (C. Lermyte and P.-M. Forget, pers. obs.). Tracks and direct observations of deer (*Mazama gouazoubira* and *M. americana*) and peccaries are observed at Paracou but less abundantly than at Nouragues ([6, 56]; C. Lermyte, line transect census, unpublished data). Since the proximity (10 km) of the closest town, Sinnamary, with 3,069 inhabitants (2006 census), the study site being ca. 1–1.5 km distant from the main asphalted road (RN 1), the control and silvicultural plots have been subject to hunting (P. Petronelli, pers. comm.). However, field station policies and procedures have prohibited this activity in the Paracou experimental site since 1989. The silvicultural treatments are extensively described elsewhere [47] and consist of three replicates of four 9-ha plots, each receiving the following treatment: T0 control (untreated) plot; T1 low-intensity logging (10 trees ha⁻¹) of commercial species; T2 low-intensity logging (11 trees ha⁻¹); T3 high-intensity logging (29 trees ha⁻¹) (http://www.cirad.fr/guyane/le_cirad_en_guyane/station_de_paracou).

The third site, Piste de Saint-Elie (5° 17' N, 53° 03' W; http://bft.cirad.fr/cd/BFT_219_79-97.pdf), is a heavily hunted area. It is located 16 km south of the town of Sinnamary, and is easily accessible via a newly asphalted road (D21) linked to the main paved national road (RN1). This forest site has been studied intensively since 1976 [57-59]. Unfortunately there is no information about mammal abundance and diversity. Nonetheless, on the basis of its accessibility, hunting pressure is likely to be intense [60, 61] as observed at other sites along the littoral [62].

Study species

Carapa surinamensis Miq. (Meliaceae) (known as *C. procera* DC. in previous studies, see [45]; hereafter referred to as *Carapa*) is a large-seeded, hard-fruited lower-canopy tree (maximum height 25 m) which is abundant in the Guiana Shield. *Carapa* trees are harvested and traditionally used by local populations for wood. Natural oil is also extracted from *Carapa* seeds (Fig. 2) and is a valued NTFP in the Guiana Shield and Amazonian rainforests [63-65] where it is used as insect repellent, traditional medicine, and cosmetic [66, 67] (<http://www.carapa.org>).

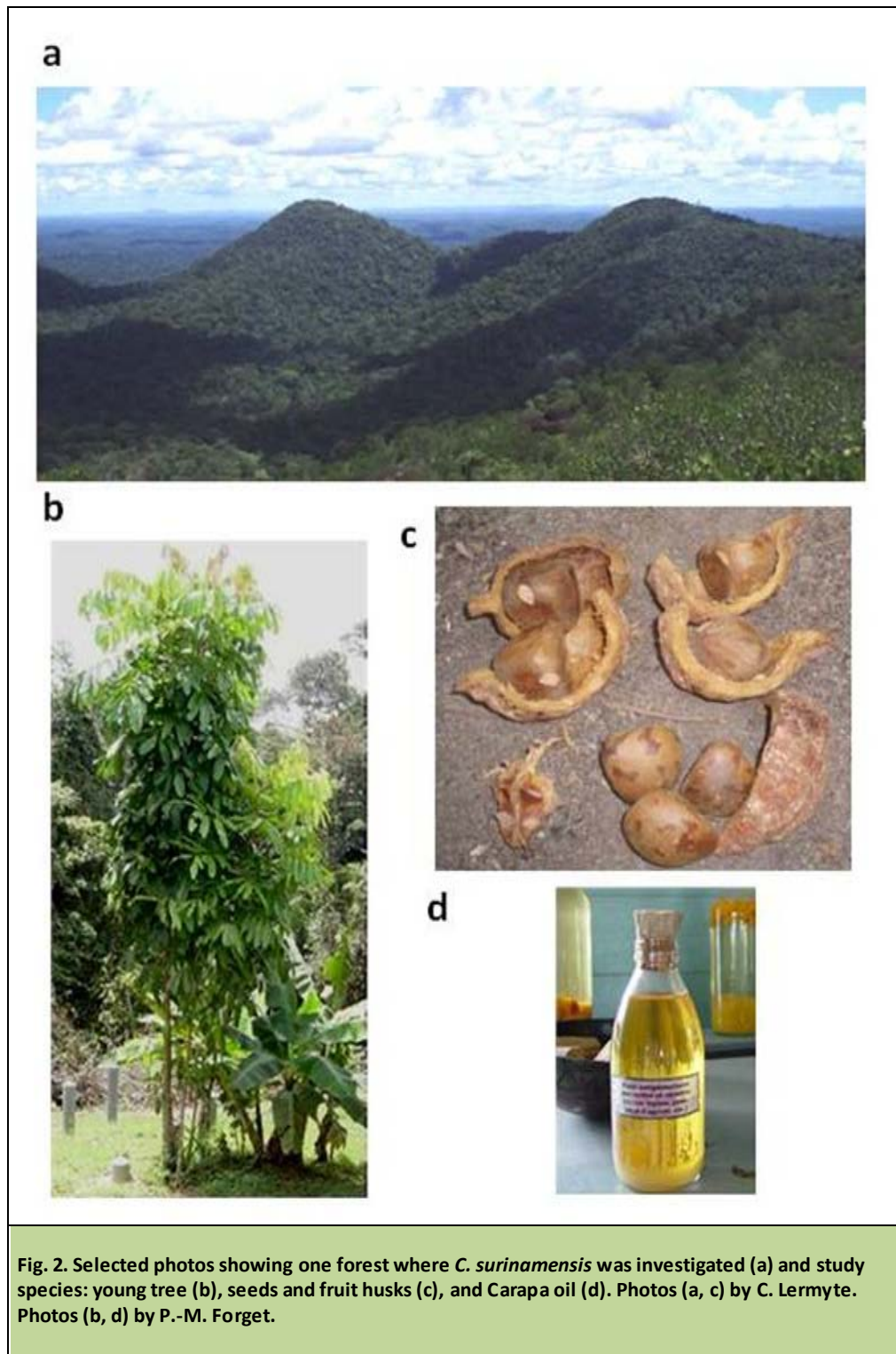


Fig. 2. Selected photos showing one forest where *C. surinamensis* was investigated (a) and study species: young tree (b), seeds and fruit husks (c), and Carapa oil (d). Photos (a, c) by C. Lermyte. Photos (b, d) by P.-M. Forget.

Trees produce up to several hundred large (10 cm in diameter), dry, five-valved fruits (Fig. 2), each containing up to 20 seeds weighing 23 g on average [16]. In the wet season, from February through May and June, *Carapa* fruits drop to the forest floor and burst upon falling. The seed and seedling ecology of *Carapa* has been well documented [16, 29, 41, 68-71]. Seeds are exclusively dispersed by scatter-hoarding rodents, especially acouchi and agouti [72, 73]. The peak season for scatter-hoarding—April to May [73]—coincides with the peak seed crop for several large-seeded tree species, such as *Carapa* [74]. Rodents act as dispersers by removing seeds from below parent trees, and burying the seeds as food reserves in shallow, spatially scattered caches in the topsoil, each cache containing a single seed. A proportion of the hoarded seeds—relatively safe from seed predators—is never recovered by the rodents and can grow into seedlings [29, 41, 75], while unburied seeds face almost certain death, particularly due to granivorous insects, peccaries, and poor rooting. Acouchis, having a small home range, appear to be highly sensitive to forest disturbance, especially hunting [76]. The fact that scatter-hoarding rodents and especially agoutis are important game species is highly relevant [62, 77, 78], and the effects of hunting on pre-dispersal seed predation and seed removal have been ascertained in previous studies [6, 79].

Rapid assessment of dispersal failure and seedling recruitment

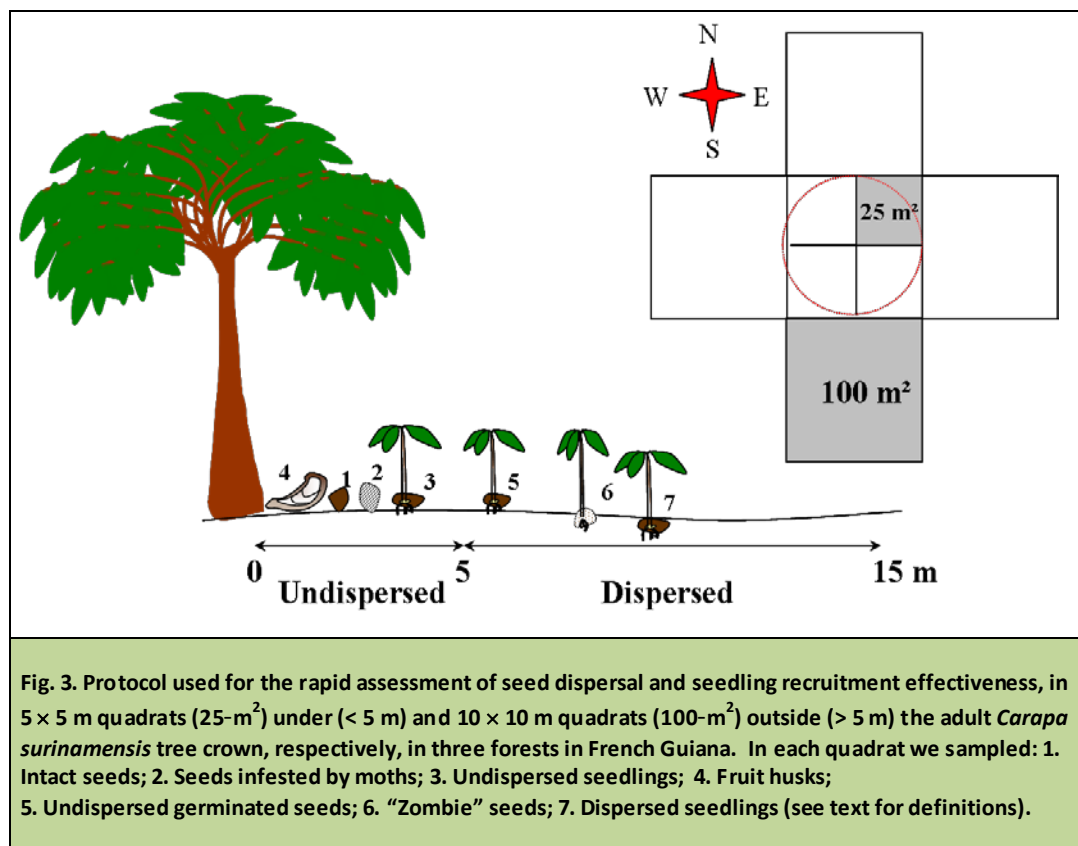
Given the difficulty of measuring the exact number of dispersed seeds, we first estimated seed dispersal by measuring dispersal failure following the methodology used by Forget and Jansen [6]. Dispersal failure is defined as the proportion of unburied seeds and undispersed seedlings, i.e., seedlings with unburied cotyledons remaining on the ground under the tree crown (≤ 5 m).

Between late May and mid-June, i.e., toward the end of the fruiting season, we sampled the number of seeds and fruit husks in four 25-m² (5 × 5-m) subplots under the adult tree crown (Fig. 3). *Carapa* trees have a small crown (5–15 m in diameter, Fig. 4, C. Lermyte and P.-M. Forget, pers. obs.) allowing potentially for the entire crop to be sampled [6]. But, in order to census a large number of trees during the same period of time, the entire crop was not sampled. The number of subplots sampled per tree (1–4) was a function of crop size, the aim being to census at least 50–100 seed-equivalents (e.g., sum of seeds and fruit husks) per tree during each census. All fruit husks and fallen seeds below the crown were counted on the basis of whole seeds and the depression left by seeds (0–4) on the inside of the fruit husk. As rodents rarely remove husks, it is assumed that the estimate of fruit and seed production is accurate [29]. For each seed, we recorded their fate either as intact (1), infested by moths (2), or germinated with visible cotyledons, i.e., undispersed seedlings (3) (Fig. 3). For each site and for each treatment (Paracou), the proportion of dispersal failure is the sum of (1) (2) (3) divided by the seed crop estimated in plots. The proportion of undispersed seedlings is given per plot area (percentage per 25-m²). The missing part of the seed crop was considered removed, either eaten or dispersed by vertebrates [6, 29, 71]. Our estimate of dispersal failure is thus proportional to the number of seeds that were scatter-hoarded (i.e., buried), even though some of the missing seeds were most likely consumed by rodents or peccaries rather than dispersed.

Second, we measured the proportion of dispersed and recruiting seedlings, i.e., yearly seedlings that emerged from scatter-hoarded seeds. Toward the end of the food-limited dry season in September–October, i.e., after the period of post-dispersal predation of cached seeds and seedlings, seedling

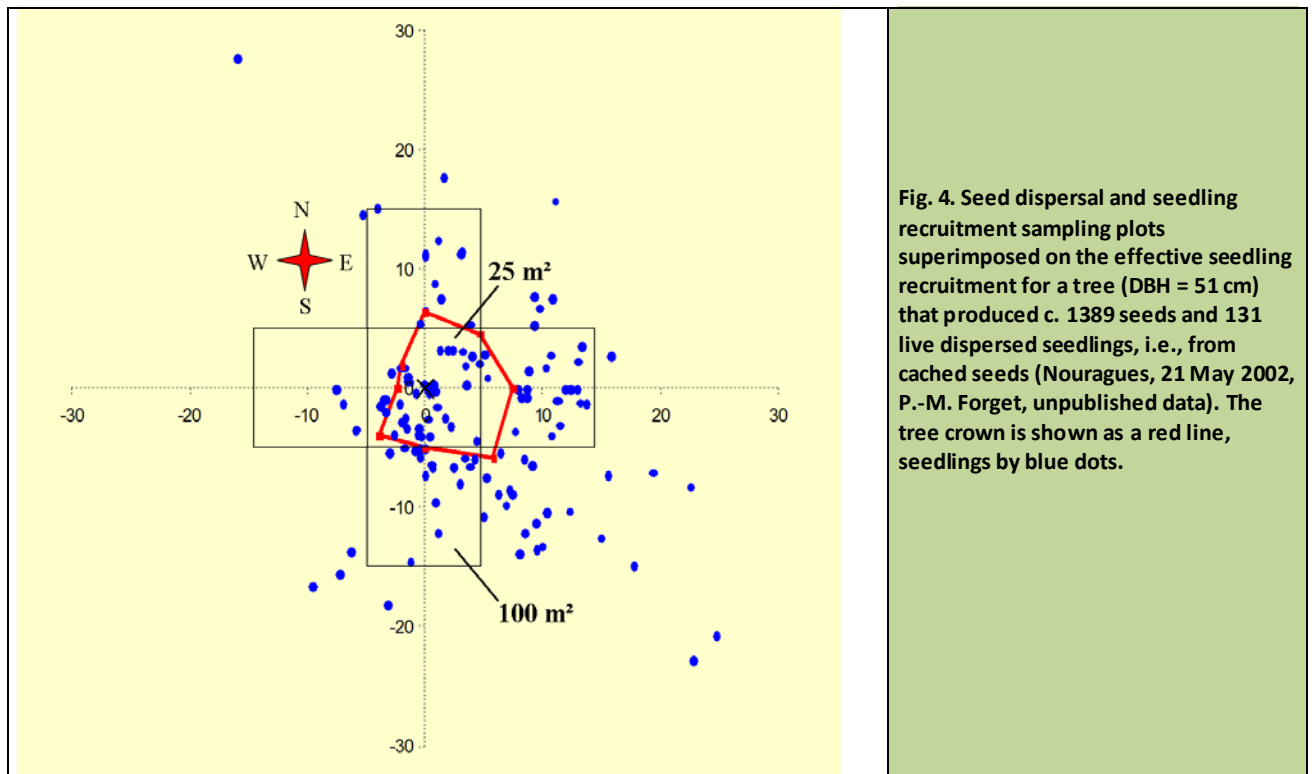
recruitment was sampled on four 100-m² (10 × 10-m) plots located 5–15 m from the tree base around the tree crown (Fig. 3). Jansen *et al.* [41] found that primary caches of *Carapa* seeds were at distances from 0.5 m up to 124 m from the source, the average dispersal distance varying between 12.6 m in rich years and 18.5 m in poor years. So the method allowed the majority of dispersed seedlings to be censused. All seedlings were recorded, as well as zombie seeds, i.e., seeds manipulated by acouchis with slowed germination, still alive but unable to sprout [69], and undispersed germinated seeds (Fig. 3). Indeed, when fruits fall to the ground, seeds are sometimes ejected farther than 5 m, while the crown may also be larger. The proportion of dispersed seedlings per tree was calculated as the number of dispersed seedlings alive versus the overall number of seedlings censused in these plots (zombie seeds, undispersed germinated seeds, dead dispersed seedlings). The proportion of dispersed seedlings is given per plot area (percentage per 100-m²).

Finally we calculated the recruitment effectiveness ratio (RER), defined as the proportion of dispersed seedlings divided by the proportion of undispersed seedlings, the number of seedlings being weighted by the estimated seed crop in both cases. When the RER is under 1, seed dispersal activity is weak; when the RER is equal to 1, seed dispersal activity is moderate; and when the RER is above 1, seed dispersal activity is intense.



Statistical analysis

To analyze the effect of hunting on the four variables measured (proportion of dispersal failure, proportion of undispersed and dispersed seedlings, and RER), we performed one-way ANOVA, testing the effect of sites on each variable using the GLM procedure of SYSTAT 11.0 (Cranes Software International Ltd, 2004). To measure the effect of silvicultural treatment on the factors studied we used nested ANOVAs with plots nested within silvicultural treatment (T0, T1, T2–3). Data were transformed using the angular transformation. When the nested ANOVA was significant for one factor, we used another ANOVA with each treatment to test the homogeneity of the significant measured factor. The Bonferroni adjustment was used to compare means between sites, treatments, and plots. In order to test the robustness of ANOVAs we performed Kruskal-Wallis nonparametric analysis on the factors measured between mature plots across the three different sites (Nouragues, Paracou and Piste de Saint-Elie) and we obtained the same results. Moreover, in order to determine if there is any correlation between dispersal failure and seedling recruitment, correlation tests were run at the three sites between dispersal failure and undispersed seedlings, as well as between dispersal failure and dispersed seedlings. Lastly, the effects on both dispersal failure of seed crop and *Carapa* population densities at Paracou were assessed by two other correlation tests.



Results

Seed dispersal failure

In spite of an estimated low production (548 seeds) at Piste de Saint-Elie, the proportion of infested seeds was highest at this site (Table 1). Dispersal failure differed significantly ($P < 0.001$) among forests; it was the lowest at Nouragues and the highest at Piste de Saint-Elie, see Table 2, Appendix 1, Fig. 5A left. Bonferroni comparisons between pairs of sites yielded significant differences between Nouragues and Piste de Saint-Elie ($P < 0.001$) and between Paracou and Piste de Saint-Elie ($P < 0.001$), but not between Paracou and Nouragues ($P > 0.05$).

Table 1. Raw data estimated by the protocol in *Carapa surinamensis* at the three sites and for silvicultural treatment within Paracou.

Site	Treatment	Seed crop	% Seed entire	% Seed infested	Undispersed seedlings	Dispersed seedlings	Survival rate	No. of Trees
Nouragues	Control	1396	0.00	0.93	2	34	44.8	12
Paracou	Control (T0)	2308	0.48	0.65	34	100	53	18
	T1	1666	1.90	3.73	23	112	70.6	13
	T2–3	2982	6.40	9.17	90	202	73	24
Piste de Saint-Elie	Hunted	548	0.18	4.20	17	26	48.2	10

Regarding the comparisons among the silvicultural treatments at Paracou, the mean percentage of dispersal failure differed significantly among treatments ($P < 0.001$) and there was a significant interaction between plots and treatment ($P < 0.001$). It seems to show a plot effect, so in order to test homogeneity within treatments another ANOVA was performed for each treatment. T1 and T2–3 treatments are heterogeneous (respectively: $P < 0.01$ and $P < 0.001$) as contrasted with control treatment ($P = 0.29$) (Appendix 1). Bonferroni pairwise mean comparison between silvicultural treatments yielded significant differences between T0 and T2–3 ($P < 0.001$) and between T1 and T2–3 ($P = 0.04$) (Fig. 5A right).

Seedling recruitment

The abundance of undispersed seedlings differs significantly between forests and is strongly related to dispersal failure at all sites, except at Paracou. At Paracou an overall low dispersal failure ($2.7\% \pm SE 0.5$) co-occurred with a high proportion of undispersed seedlings ($50.3\% \pm SE 10.2$), with substantial variation across plots (SE 6.3 to 13), see Table 2, Fig. 5B left. Nevertheless, correlation tests between dispersal failure and undispersed seedlings for the three sites were significant ($P < 0.001$; correlation coefficient = 0.61; $N = 40$, $t = 4.78$) and accurate when the Paracou site was excluded ($P < 0.001$; correlation coefficient = 0.79; $N = 22$, $t = 5.48$). Bonferroni post-hoc tests yielded a significant difference in the mean proportion of undispersed seedlings at Nouragues, when compared with Paracou and Piste de Saint-Elie ($P < 0.001$). By contrast, no significant difference ($P = 0.07$) was found between Paracou and Piste de Saint-Elie. The percentage of intact and infested seeds was higher in logged than in unlogged forests in Paracou (Table 1). As in the case of dispersal failure, the fraction of undispersed seedlings

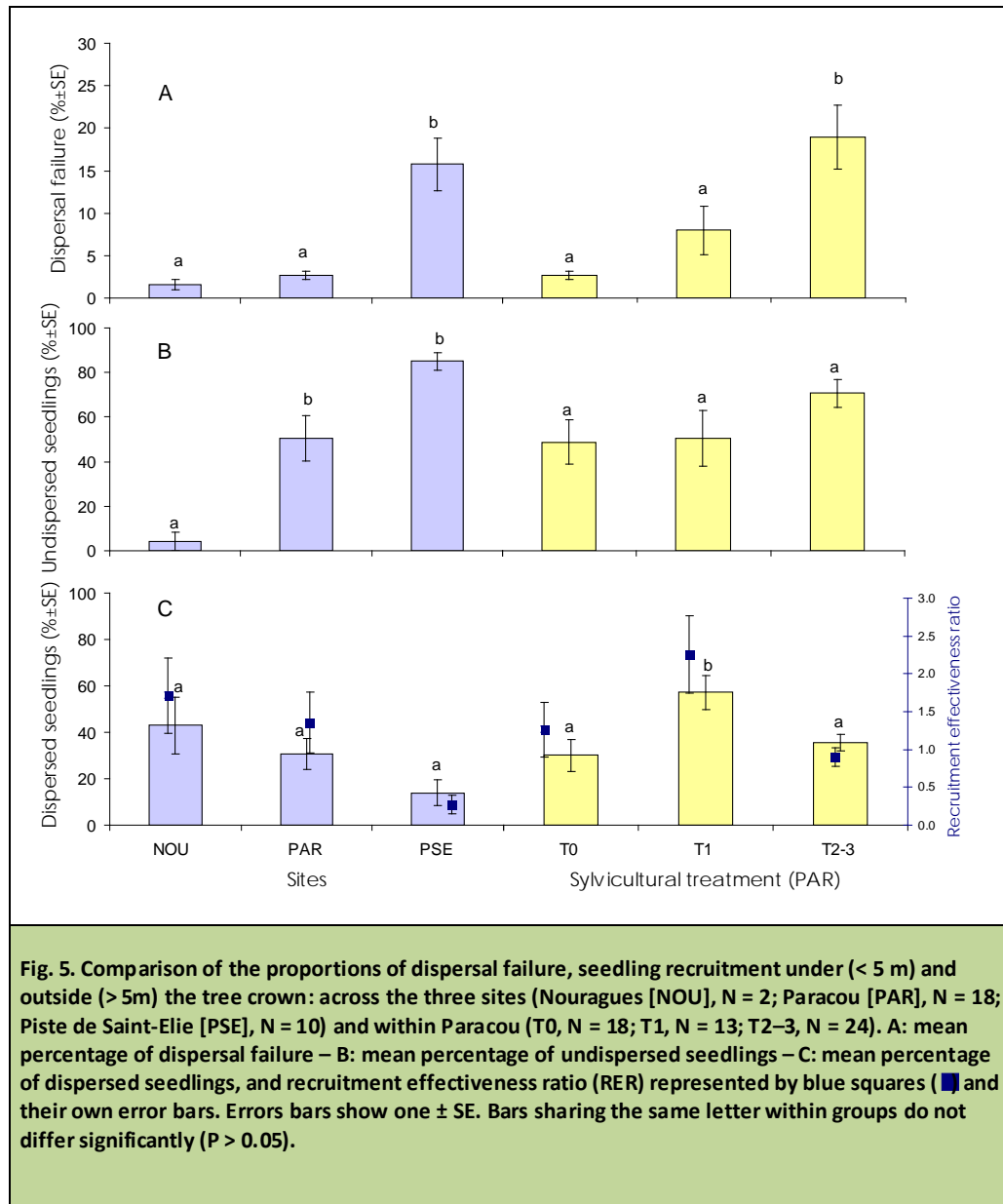
varied among trees, within as well as between plots. Thus, silvicultural treatment did not significantly increase the fraction of undispersed seedlings ($P = 0.19$; Table 2, Appendix 1, Fig. 5B right). However, there is a tendency for the fraction of undispersed seedlings to increase with logging intensity (50.3% at T0 versus 73.1% at T2–3).

Table 2. Mean percentage of seed dispersal, undispersed and dispersed seedlings from adult *Carapa surinamensis* trees and recruitment effectiveness ratio (RER) at controlled forest sites (Nouragues, Paracou and Piste de Saint-Elie) and silvicultural treatments (Paracou).

Site	Treatment	Dispersal failure (Mean % \pm SE)	Undispersed seedlings (Mean % \pm SE)	Dispersed seedlings (Mean % \pm SE)	Recruitment effectiveness ratio (Mean \pm SE)	No. of Trees
Nouragues	Control	1.55 \pm 0.62	4.17 \pm 4.17	42.92 \pm 12.23	1.58 \pm 0.44	12
Paracou	Control (T0)	2.71 \pm 0.5	50.33 \pm 10.25	30.60 \pm 6.74	1.26 \pm 0.36	18
	T1	8.09 \pm 2.85	52.24 \pm 13.03	58.28 \pm 6.94	2.25 \pm 0.51	13
	T2–3	19.25 \pm 3.86	73.06 \pm 6.32	36.02 \pm 3.56	0.90 \pm 0.12	24
Piste de Saint-Elie	Hunted	15.73 \pm 3.1	85.00 \pm 4.1	13.87 \pm 5.51	0.29 \pm 0.12	10

The fraction of dispersed seedlings did not vary significantly across sites (Table 2, Appendix 1, Fig. 5C left). However, the mean fraction of dispersed seedlings differed between Nouragues (42.9% \pm SE 12.2) and Piste de Saint-Elie (13.9% \pm SE 5.5). On the contrary, the fraction of dispersed seedlings varied significantly among silvicultural treatments ($P = 0.024$) and there was a significant interaction between plots and treatment ($P < 0.034$). So in order to test homogeneity within treatments another ANOVA was performed for each treatment. No significant differences were found; silvicultural treatments appeared to be homogeneous (Appendix 1). Bonferroni pairwise mean comparison between silvicultural treatments yielded significant differences between T0 and T1 ($P = 0.002$) and between T1 and T2–3 ($P = 0.03$) (Fig. 5C right). Over the three sites, dispersal failure was inversely correlated with the proportion of dispersed seedlings ($P = 0.008$; correlation coefficient = -0.41 ; $N = 40$, $t = -2.81$).

The RER did not differ significantly ($P = 0.149$) across forests (Appendix 1, Fig. 5C left). The RER was highest at Nouragues (1.6 \pm SE 0.44) and lowest at Piste de Saint-Elie (0.3 \pm SE 0.12) (Table 2). At Paracou, the RER did not differ significantly between silvicultural treatments ($P = 0.132$), but there was significant interaction between plots and silvicultural treatment ($P = 0.002$). So in order to test homogeneity within treatments another ANOVA was performed for each treatment. For T1 and T2–3, plots appeared to be homogeneous (respectively, $P = 0.096$ and $P = 0.37$) (Appendix 1) by contrast to T0 ($P = 0.012$). A Bonferroni pairwise mean comparison yielded significant differences only between T0 and T1 ($P = 0.042$) and between T1 and T2–3 ($P = 0.044$). Despite a significant dispersal failure (8.09 \pm SE 2.85), intermediate silvicultural treatment T1 positively affected the RER (2.3 \pm SE 0.51); on the contrary, heavily-impacted treatment T2–3 negatively affected the RER (0.9 \pm SE 0.12), see Table 2, Fig. 5C right. We observed more live seedlings in logged plots than in unlogged plots (Table 1).



Discussion

Effect of hunting

Paracou and Piste de Saint-Elie sites, situated on a densely populated coastal area, face major anthropogenic pressure from low-income populations [62]. We found that seed dispersal and seedling recruitment at Piste de Saint-Elie were most significantly affected, whereas only the proportion of undispersed seedlings was significantly affected at Paracou. Inter-site differences in the abundance of seed- and seedling predators may account for this result. At Nouragues, with a greater prevalence of

ground-dwelling granivorous/herbivorous vertebrates—especially rodents, peccaries and deer, two species highly valued by hunters [11, 80, 81]—we may assume that postdispersal predation is higher than at the two other sites. A lower hunting pressure may be postulated at Paracou, an experimental field station, although such pressure cannot be excluded. We also observed that the rodent predation index at Piste de Saint-Elie was almost twice as high as at Paracou. This difference can be explained by greater seed predation by small rodents, more frequent in disturbed and/or hunted areas like Piste de Saint-Elie and which seldom disperse seeds [29]. Thus, we may assume that at Piste de Saint-Elie, where hunting pressure is greater, there is a lower density of large rodents than at Paracou. On the other hand, with a recruitment effectiveness ratio under 1, dispersal activity was low at Piste de Saint-Elie. Finally, these findings seem to corroborate our hypothesis according to which hunting is the primary disturbing factor. Furthermore, other studies show that both pre-dispersal seed predation [79] and post-dispersal predation [82, 83] are affected by hunting, as is the case here for *Carapa* seeds.

However, the fraction of dispersed seedlings and the recruitment effectiveness ratio observed at Piste de Saint-Elie did not differ significantly from the two other sites. Other factors may indeed cause the patterns observed. These include community-wide food availability, open to considerable variation depending on the year and forest area, and crop size, which varies from year to year and in different trees. Moreover, the demographic resilience of fauna to hunting pressure is linked to habitat productivity [10, 84]. Lastly, the selectivity of hunters, the intensity of hunting pressure, and the compensatory potential between game and non-game species must be taken into account in order to determine whether disturbance may be ascribed to hunting pressure [83].

Effect of logging

Analysis of the data concerning seed dispersal and seedling recruitment at Paracou showed that logging treatment affected seed dispersal [85]. We observed a higher rate of dispersal failure and undispersed seedlings at the logged plots, on average, especially in heavily logged plots. The high level of insect-infested seeds on the most heavily logged plots confirms this observation. Indeed, as we have pointed out, insect-infested seeds may still be viable but are discriminated against by rodents [41]. Moreover this high rate of insect-infested seeds may be due to lower seed predation by mammals, which are less abundant at Paracou than at Nouragues ([56], C. Lermyte and P.-M. Forget, pers. obs.). On the other hand, contrary to our working hypothesis, logging treatment had no clear negative effect on seedling recruitment. Indeed, the fraction of dispersed seedlings and the recruitment effectiveness ratio were found to be positively affected by logging, especially in moderately logged plots. The reason may be that seedlings are well exposed to light in logged plots, thus surviving better even when seeds were not buried [86]. Indeed, the canopy structure of the logged plots still differs from the control plots more than 20 years after silvicultural treatment [87]. By increasing access to light, the canopy gaps promote the growth of light-demanding woody species and raise the life expectancy of *Carapa* seedlings [72, 88]. Thus, despite fewer dispersed seeds in logged plots, the number of dispersed seedlings remaining alive is the same or even greater than in unlogged plots. Conversely, despite the larger number of seeds dispersed, dispersed seedlings on the control plots may have a higher mortality, and a weaker gap effect in the understory may cause higher *Carapa* seedling mortality [72].

Nevertheless, the heterogeneity between trees sampled in different treatment plots as well as in the same treatment plots was high. This heterogeneity could be accounted for by variable production at the

sampled trees. There was no correlation, however, between the number of estimated seeds during sampling and the percentage of non-dispersed seeds, as well as between the density of *Carapa* and the non-dispersed seed rate. However, two qualitatively and quantitatively different patterns may influence dispersal: the overall seed crop of *Carapa* at the plot level and the community-level availability of resources near sampled trees. Our results do not allow us to disprove any such influence. Indeed, large rodents such as agouti and acouchi rely on many other fruit and seed species such as Myristicaceae [89] and Sapotaceae [39], generally dispersed by monkeys and birds, as well as on large-seeded, bat-dispersed species such as Fabaceae [90].

Towards a standardization of the rapid assessment strategy

Our protocol allowed us rapidly to evidence the perturbation of seed dispersal, and seedling dispersal at the two disturbed sites (Paracou, and Piste de Saint-Elie). It would be useful, however, in order to assess the influence of production, to carry out a long-term monitoring project at one single site, to achieve a better interpretation of the findings. Even though the response variables measured may have been influenced by other factors, as mentioned earlier, it is combinations of such variables that make it possible to identify the perturbations involved. Indeed, we may more precisely refine the finding for dispersal failure—which of itself does not allow discrimination between seeds removed or predated, and seeds dispersed—by way of the recruitment effectiveness ratio, which depends on the abundances of both undispersed and dispersed seedlings, further weighted with regard to estimated seed crop. The recruitment effectiveness ratio is particularly useful, since it yields information both as to seed dispersal and seedling recruitment.

This protocol is singularly suitable for tree species dispersed by scatter-hoarding rodents, and may fairly readily be extended to cover other species exhibiting similar dispersal syndromes, without impairing sampling efficiency. To that end, plot layout, and size will need to be adjusted, to cater for the life-history traits of these tree species, e.g., crown area, seed size, and dispersal range (this being related to seed size). It would be feasible to implement this protocol for two species involving approximately 8–10 m crown area, but larger seed size and dispersal distance: *Vouacapoua americana* (Caesalpiniaceae), and *Licania alba* (Chrysobalanaceae), for instance. *V. americana*, for which maximal dispersal distance is 23 m [28], would require plots located 10–20 m from the tree base.

Implications for conservation

So far, only a handful of studies have been carried out to analyse the demography and population dynamics of these harvested species (*Bertholletia excelsa*, *Carapa procera*). Authors show that populations subject to intensive harvest and hunting pressure on both seed dispersers and large herbivores are threatened. In a harvesting model for the Brazil nut tree (*Bertholletia excelsa*), Peres *et al.* [43] confirmed that intensive exploitation levels over the past century are such that juvenile recruitment is insufficient to maintain populations over the long term. In the same way, Forget and Jansen [6] argued that subsistence hunting, which usually accompanies seed collection, is at the cost of seed dispersal and may contribute to recruitment failure of *Carapa*. In the Atlantic forest (Brazil) palm extraction and hunting pressure have lasting effects on palm regeneration by severely limiting survival of pre-reproductive individuals [91]. As such studies are time consuming, we ultimately often lack a valid estimate of the human impact at a broader scale, that could be readily repeated at different time and spatial scales.

Few studies have simultaneously estimated the proportion of seeds dispersed along with seedling recruitment. The present sampling method afforded, in a limited time, a rapid assessment of dispersal failure and recruitment effectiveness at different areas for a large number of trees. Indeed, overall, 77 trees were sampled, approximately 1–2 hours being spent beneath each tree at three forest sites during a total 4–6 weeks in the field for each dispersal and recruitment sampling, that is to say 30 minutes for 2 persons by tree (N=13). Moreover, without using the time-consuming line transect census method this protocol may rapidly detect the lack of large rodents in forests with contrasting levels of human pressure. This new protocol may be a supplementary tool, especially useful in disturbed areas for taking management decisions, but it is unable to capture all of the complexity of seedling recruitment, or substitute for specific and global studies in the complex process of seed dispersal. One of the main advantages of this approach is that it can be rapidly and easily set up and repeated without sophisticated material and equipment for hard-tegument fruit species enclosing large seeds. It may also be simultaneously duplicated by several persons in various NTFP forests, where there is an urgent need to evaluate the impact of human activities in order to implement natural resource protection and conservation measures. This is particularly true in extractivism reserves where, apart from biological or organic certification or fair trade rules, there is no true ecological certification. Such an eco-label would ensure that development of the NTFP market does not endanger seedling recruitment and tree survival in the short term, thus threatening use of natural resources by the local fauna and native populations in the long term. Thus we can produce indices that may be used to define an ecological “sustainable management” label (or eco-label) for the harvesting of forest products and for fauna management purposes (conservation and protection measures) useful for the regeneration dynamics of commercial large-seeded hard-fruited species harvested for NTFPs.

Acknowledgements

This study was made possible by the following people and funding sources: Lilian Blanc, Cécile Richard-Hansen, for the grant from UMR 7179 CNRS–MNHN and the Programme Pluri Formation; for their welcome Eric Marcon and UMR EcoFoG; for help in field work Ficadici Kago, Etienne Abner, Ngwete Oenofe and Pascal Petronelli, Laure Debeire; for the data analysis Marion Echard and Audrey Jolivot. A draft of this paper was read by Jacqueline Reuss, Helen Arnold and Jean-François Roberts and three anonymous referees who made helpful suggestions.

References cited

- [1] Laurance, W. F., and Peres, C. A. (Eds.). 2006. *Emerging Threats to Tropical Forests.*, Chicago University Press, Chicago, USA.
- [2] Panayotou, T., and Ashton, P. (Eds.). 1992. *Not by Timber Alone: the Case for Multiple Use Management of Tropical Forests*, Island Press, Covelo, CA.
- [3] Nepstad, D. C., and Schwartzman, S. 1992. *Non-Timber Product Extraction from Tropical Forest: Evaluation of a Conservation and Development Strategy*, New York Botanical Garden, Bronx, NY (USA).
- [4] Iqbal, M. 1993. *International Trade in Non-wood Forest Products. An Overview*. FAO, Roma, Italy.
- [5] Walter, S. 2001. *Non-wood Forest Products in Africa. A Regional and National Overview. Les Produits forestiers non ligneux en Afrique. Un aperçu régional et national*. FAO, Forestry Department, Roma, Italy.

- [6] Forget, P.-M., and Jansen, P. A. 2007. Hunting increases dispersal limitation in the tree *Carapa procera*, a nontimber forest product. *Conservation Biology* 21: 106-113.
- [7] Peres, C. A., and Baidier, C. 1997. Seed dispersal, spatial distribution and population structure of Brazilnut trees (*Bertholletia excelsa*) in southeastern Amazonia. *Journal of Tropical Ecology* 13(4): 595-616.
- [8] Peres, C. A., and Palacios, E. 2007. Basin-Wide Effects of Game Harvest on Vertebrate Population Densities in Amazonian Forests: Implications for Animal-Mediated Seed Dispersal. *Biotropica* 39(3): 304-315.
- [9] Hammond, D. (Ed.) 2005. *Tropical Forests of the Guiana Shield*, CABI Publishing, Wallingford, UK.
- [10] Peres, C. A., and Dolman, P. M. 2000. Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* 122(2): 175-189.
- [11] Redford, K. H. 1992. The empty forest. *Bioscience* 2: 412-422.
- [12] Bertault, J.-G. 1986. *Etude de l'effet d'interventions sylvicoles sur la régénération naturelle au sein d'un périmètre expérimental d'aménagement en forêt dense humide de Côte d'Ivoire*. Thèse de sciences naturelles, Nancy I.
- [13] Forget, P.-M., and Hammond, D. S. 2005. Rainforest vertebrates and food plant diversity in the Guiana shield. In: *Tropical Forests of the Guiana Shield: Ancient forests in a modern world*. Hammond, D. S. (Ed.). pp. 233-294, CABI International, Wallington, UK.
- [14] Schupp, E. W., and Fuentes, M. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2(3): 267-275.
- [15] Nathan, R., and MullerLandau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15(7): 278-285.
- [16] Jansen, P. A., Bongers, F., and Van der Meer, J. 2008. Is farther seed dispersal better? Spatial patterns of offspring mortality in three rainforest tree species with different dispersal abilities. *Ecography* 31(1): 43-52.
- [17] Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104: 501-528.
- [18] Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of Populations*. Den Boer, P. J., and Gradwell, G. R. (Eds.). pp. 298-312, Centre for Agricultural Publishing and Documentation, Wageningen, the Netherlands.
- [19] Howe, H. F., and Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.
- [20] Vasquez, R., and Gentry, A. H. 1989. Use and misuse of forest-harvested fruits in the Iquitos area. *Conservation Biology* 3(4): 350-361.
- [21] Cunningham, A. B. 1993. *African medicinal plants. Setting priorities at the interface between conservation and primary healthcare*. UNESCO, Paris, France.
- [22] Clay, J. W. 1997. Harvesting wild species: Implications for biodiversity conservation. In: *The Impact of Palm Heart Harvesting in the Amazon Estuary*. Freese, C. H. (Ed.). pp. 283-314, Johns Hopkins University Press, Baltimore, MD (USA).
- [23] Rawat, G. S. 1997. Conservation status of forest and wildlife in the Eastern Ghats, India. *Environment Conservation* 24(4): 307-315.

- [24] Rebelo, A. G., and Holmes, P. M. 1988. Commercial exploitation of *Brunia albiflora* (Bruniaceae). *Biological Conservation* 45(3): 195-207.
- [25] Tiwari, B. K. 2000. Non-timber forest produce of northeast India. *Journal of Human Ecology* 11(6): 445-455.
- [26] Plowden, C. 2004. The ecology and harvest of andiroba seeds for oil production in the Brazilian Amazon. *Conservation & Society* 2: 251-272.
- [27] Turchin, P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*, Sinauer Associates, Sunderland.
- [28] Forget, P.-M. 1990. Seed-dispersal of *Vouacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. *Journal of Tropical Ecology* 6: 459-468.
- [29] Forget, P.-M. 1996. Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. *Journal of Tropical Ecology* 12(6): 751-761.
- [30] Forget, P.-M., and Wenny, D. 2005. How to elucidate seed fate? A review of marking methods used to study seed removal and secondary seed dispersal. In: *Seed Fate: Predation, Dispersal and Seedling Establishment*. Forget, P.-M., Lambert, J., Hulme, P., and Vander Wall, S. B. (Eds.). pp. 379-393, CABI publishing, Wallingford.
- [31] Ouborg, N. J., Piquot, Y., and VanGroenendael, J. M. 1999. Population genetics, molecular markers and the study of dispersal in plants. *J. Ecol.* 87(4): 551-568.
- [32] Cain, M. L., Milligan, B. G., and Strand, A. E. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* 87(9): 1217-1227.
- [33] Holbrook, K. M., and Smith, T. B. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia* 125(2): 249-257.
- [34] Guariguata, M. R., Adame, J. J. R., and Finegan, B. 2000. Seed removal and fate in two selectively logged lowland forests with contrasting protection levels. *Conservation Biology* 14(4): 1046-1054.
- [35] Hubbell, S. P., Foster, R. B., O'Brien, S. T., Harms, K. E., Condit, R., Wechsler, B., Wright, S. J., and De Lao, S. L. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science (Washington D C)* 283(5401): 554-557.
- [36] Harms, K. E., Wright, S. J., Calderon, O., Hernandez, A., and Herre, E. A. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404: 493-495.
- [37] Dalling, J. W., Muller-Landau, H. C., Wright, S. J., and Hubbell, S. P. 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. *J. Ecol.* 90(4): 714-727.
- [38] Ratiarison, S., and Forget, P.-M. 2005. Frugivores and seed removal at *Tetragastris altissima* (Burseraceae) in a fragmented forested landscape of French Guiana. *Journal of Tropical Ecology* 21(5): 501-508.
- [39] Feer, F., and Forget, P.-M. 2002. Spatio-temporal variation in post-dispersal seed fate. *Biotropica* 34(4): 555-566.
- [40] Wright, I. J., Clifford, H. T., Kidson, R., Reed, M. L., Rice, B. L., and Westoby, M. 2000. A survey of seed and seedling characters in 1744 Australian dicotyledon species: cross-species trait correlations and correlated trait-shifts within evolutionary lineages. *Biological Journal of the Linnean Society* 69(4): 521-547.
- [41] Jansen, P. A., Bongers, F., and Hemerik, L. 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodents. *Ecological Monograph* 74(4): 569-589.

- [42] Bonebrake, T. C., and Sorto, R. 2009. Butterfly (Papilionoidea and Hesperioidea) rapid assessment of a coastal countryside in El Salvador. *Mongabay.com Open Access Journal - Tropical Conservation Science* 2(1): 34-51.
- [43] Peres, C. A., Baider, C., Zuidema, P. A., Wadt, L. H. O., Kainer, K. A., Gomes-Silva, D. A., Salomão, R. P., Simões, L. L., Franciosi, E. R. N., Cornejo Valverde, F., Gribel, R., Shepard, G. H. J., Kanashiro, M., Coventry, P., Yu, D. W., Watkinson, A. R., and Freckleton, R. P. 2003. Demographic threats to the sustainability of Brazil Nut exploitation. *Science* 302: 2112-2114.
- [44] Brasil 2000. *Law No. 9,985, 18th July 2000*. Sistema Nacional de Unidades de Conservação.
- [45] Kenfack, D. 2008. *Systematic and evolution of Carapa (Meliaceae-Swietenioideae)*. University of Missouri, St. Louis.
- [46] Bongers, F., Charles-Dominique, P., Forget, P.-M., and Théry, M. 2001. *Nouragues: dynamics and plant-animal interactions in a neotropical rainforest*, Kluwer Academic Publisher, Dordrecht, The Netherlands.
- [47] Gourlet-Fleury, S., Ferry, B., Molino, J.-F., Petronelli, P., and Schmitt, L. 2004. Experimental Plots: keys features. In: *Ecology and Management of a Neotropical Rainforest: Lessons drawn from Paracou, a long-term experimental research site in French Guiana*. Gourlet-Fleury, S., Guehl, J. M., and Laroussinie, O. (Eds.). pp. 3-60, Elsevier, Paris.
- [48] Sarrailh, J.-M. 1989. L'opération ECEREX. Etudes sur la mise en valeur de l'écosystème forestier guyanais après déboisement. Le point sur les recherches en cours. *Bois et Forêts des Tropiques* 219: 79-97.
- [49] Sarrailh, J.-M. 1990. *Mise en valeur de l'écosystème forestier guyanais. Opération Ecerex Ecologie-Erosion-Expérimentation*, CIRAD-CTFT, Nogent-sur-Marne.
- [50] Laurance, W. F., Bergen, S., Cochran, M. A., Fearnside, P. M., Delamonica, P., D'angelo, S., Barber, C., and Fernandes, T. 2005. The future of the Amazon. In: *Tropical Rainforests: Past, Present, and Future* Birmingham, E., Dick, C. W., and Moritz, C. (Eds.). pp. 583-609, University of Chicago Press, Chicago, U.S.A.
- [51] Laurance, W. F. 2009. Roads are ruining the rainforests. *The New Scientist* 203(2723): 24-25.
- [52] Kohler, P., Chave, J., Riera, B., and Huth, A. 2003. Simulating the long-term response of tropical wet forests to fragmentation. *Ecosystems* 6(2): 114-128.
- [53] Lescure, J. P. 1978. Architectural study of vegetations regeneration in French-Guiana. *Vegetatio* 37(1): 53-60.
- [54] Poncy, O., Sabatier, D., Prévost, M.-F., and Hardy, I. 2001. The lowland high forest: structure and tree species diversity. In: *Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest*. Bongers, F., Charles-Dominique, P., Forget, P.-M., and Théry, M. (Eds.). pp. 31-46, Kluwer Academic Publishers, Dordrechts.
- [55] Hammond, D. S., Gond, V., de Thoisy, B., Forget, P. M., and DeDijn, B. P. E. 2007. Causes and consequences of a tropical forest gold rush in the Guiana Shield, South America. *Ambio* 36(8): 661-670.
- [56] Voss, R. S., Lunde, D. P., and Simmons, N. B. 2001. Mammals of Paracou, French Guiana: a neotropical lowland rainforest fauna. Part 2: Nonvolant species. *Bulletin of the American Museum of Natural History* 263: 1-236.
- [57] Lescure, J.-P., and Boulet, R. 1985. Relationships between soil and vegetation in a tropical rainforest in French Guiana. *Biotropica* 17(2): 155-164.

- [58] Lescure, J. P., Puig, H., Riéra, B., and Sabatier, D. 1990. Une forêt primaire en Guyane française, données botaniques. In: *Mise en valeur de l'écosystème forestier guyanais opération ECEREX*. INRA, CTFT Paris. Sarrailh, J. M. (Ed.). pp. 137-168.
- [59] Puig, H., Riéra, B., and Lescure, J.-P. 1990. Phytomasse et productivité en forêt guyanaise. *Bois et Forêts des Tropiques* 220: 25-32.
- [60] Robinson, J. G., Boundas, E., and Bennett, E. L. 2000. *Hunting for Sustainability in Tropical Forests*, Columbia University Press, New York.
- [61] Peres, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* 14(1): 240-253.
- [62] Richard-Hansen, C., De Thoisy, B., Hansen, E., Catzeflis, F., and Grenand, P. 2003. Conservation et gestion de la faune en Guyane : contexte local, moyens d'actions et études. In: *Revue Forestière Française, numéro spécial*. pp. 306-321, ENGREF, Nancy, France.
- [63] Creveaux, J. 1883. *Voyages dans l'Amérique du Sud*, Hachette, Paris, France.
- [64] Van Andel, T. 2000. *Non-Timber Forest Products of the North West District of Guyana part II: a Field Guide*, Tropenbos Guyana Programme, Georgetown, Guyana.
- [65] Van Andel, T. R., Mackinven, A. V., and Banki, O. S. 2003. *Commercial Non-Timber Forest Products of the Guiana Shield. An inventory of commercial NTFP extraction and possibilities for sustainable harvesting*, Netherland Committee for IUCN.
- [66] Grenand, P., Moretti, C., and Jacquemin, H. 1987. *Pharmacopées traditionnelles en Guyane. Créoles, Palikur, Wayãpi*, ORSTOM, Paris.
- [67] DeFilippis, R. A., Maina, S. L., and Crepin, J. 2004. *Medicinal Plants of the Guianas (Guyana, Surinam, French Guiana)*, Smithsonian Institution, Washington, D.C.
- [68] Jansen, P. A., Bartholomeu, M., Bongers, F., Elzinga, J. A., Den Ouden, J., and Van Wieren, S. E. 2002. The role of seed size in dispersal by a scatter-hoarding rodent. In: *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. Levey, D. J., Silva, W. R., and Galetti, M. (Eds.). pp. 209-225, CABI, Wallingford.
- [69] Jansen, P. A., Bongers, F., and Prins, H. H. T. 2006. Tropical rodents change rapidly germinating seeds into long-term food supplies. *Oikos* 113(3): 449-458.
- [70] Jansen, P. A., and Den Ouden, J. 2005. Observing seed removal: remote video monitoring of seed selection, predation and dispersal. In: *Seed Fate: Predation, Dispersal and Seedling Establishment*. Forget, P.-M., Lambert, J. E., Hulme, P. E., and Vander Wall, S. B. (Eds.). pp. 363-378, CABI Publishing, Wallingford, UK.
- [71] Jansen, P. A., and Forget, P.-M. 2001. Scatterhoarding rodents and tree regeneration. In: *Nouragues : Dynamics and Plant-Animal Interactions in a Neotropical Rainforest*. Bongers, F., Charles-Dominique, P., Forget, P.-M., and Théry, M. (Eds.). pp. 275-288, Kluwer Academic Publishers, Dordrechts.
- [72] Forget, P.-M. 1997. Effect of microhabitat on seed fate and seedling performance in two rodent-dispersed tree species in rain forest in French Guiana. *J. Ecol.* 85: 693-703.
- [73] Forget, P.-M., Hammond, D., Milleron, T., and Thomas, R. 2002. Seasonality of fruiting and food hoarding by rodents in Neotropical forests: consequences for seed dispersal and seedling recruitment. In: *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. Levey, D. J., Silva, W. R., and Galetti, M. (Eds.). pp. 241-253, CABI Publishing, Wallingford.
- [74] Sabatier, D. 1985. Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. *Revue d'Ecologie (Terre et Vie)* 40: 89-320.

- [75] Forget, P.-M. 1994. Regeneration pattern of *Vouacapoua americana* (Caesalpinaceae), a rodent-dispersed tree species in French Guiana. *Biotropica* 26: 420-426.
- [76] Dubost, G. 1988. Ecology and social life of the red acouchy, *Myoprocta exilis*; comparisons with the orange-rumped agouti, *Dasyprocta leporina*. *Journal of Zoology, London* 214: 107-123.
- [77] Peres, C. 1999. Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. In: *Hunting for Sustainability in Tropical Forests*. Robinson, J. G., and Bennett, E. L. (Eds.). pp. 31-56, Columbia University Press, New York.
- [78] De Thoisy, B., Renoux, F., and Julliot, C. 2005. Hunting in northern French Guiana and its impacts on primate communities. *Oryx* 39(2): 1-9.
- [79] Beckman, N., and Muller-Landau, H. C. 2007. Differential effects of hunting on predispersal seed predation and primary and secondary seed removal of two neotropical tree species. *Biotropica* 39(3): 328-339.
- [80] Bodmer, R. E., Fang, T. G., Moya, L., and Gill, R. 1994. Managing wildlife to conserve amazonian forests-population biology and economic-considerations on game hunting. *Biological Conservation* 67(1): 29-35.
- [81] Redford, K. H., and Robinson, J. G. 1987. The game of choice: patterns of Indians and colonist hunting in the Neotropics. *American Anthropologist* 89(3): 650-667.
- [82] Dirzo, R., Mendoza, E., and Ortiz, P. 2007. Size-related differential seed predation in a heavily defaunated neotropical tropical rainforest. *Biotropica* 39(3): 355-362.
- [83] Wright, S. J., Hernandez, A., and Condit, R. 2007. The bushmeat harvest alters seedling banks by favoring lianas, large seeds, and seed dispersal by bats, birds, and wind. *Biotropica* 39(3): 363-371.
- [84] Bodmer, R. E., Puertas, P., Aquino, R., and Reyes, C. J. 2000. Influence of habitats on the sustainability of mammal harvest in the peruvian Amazon. In: *Biological and Cultural Diversity of Amazonia: A world in transformation*. Oren, D. (Ed.), CNPq, Brazilia.
- [85] Forget, P. M., RankinDeMerona, J. M., and Julliot, C. 2001. The effects of forest type, harvesting and stand refinement on early seedling recruitment in a tropical rain forest. *Journal of Tropical Ecology* 17: 593-609.
- [86] Baraloto, C., and Forget, P.-M. 2004. Effects of post-logging microhabitats on regeneration from seed: implications for sustainable forest management. In: *Ecology and Management of a Neotropical Rainforest : Lessons drawn from Paracou, a long-term experimental research site in French Guiana*. Gourlet-Fleury, S., Guehl, J.-M., and Laroussinie, O. (Eds.). pp. 191-203, Elsevier, Paris.
- [87] Flores, O., Gourlet-Fleury, S., and Picard, N. 2006. Local disturbance, forest structure and dispersal effects on sapling distribution of light-demanding and shade-tolerant species in a French Guianian forest. *Acta Oecologica* 29: 141-154.
- [88] Baraloto, C., Forget, P.-M., and Goldberg, D. E. 2005. Seed mass, seedling size and neotropical tree seedling establishment. *J. Ecol.* 93: 1156-1166.
- [89] Forget, P.-M., and Milleron, T. 1991. Evidence for secondary seed dispersal in Panama. *Oecologia* 87: 596-599.
- [90] Forget, P.-M. 1993. Régénération naturelle en forêt guyanaise: un exemple comparatif. *Nature Guyanaise (supplément)*: 111-117.
- [91] Galletti, M., Donnati, C. I., Pires, S. A., Guimaraes JR, P. R., and Jordano, P. 2006. Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. *Botanical Journal of the Linnean Society* 151(1): 141-149.

Appendix 1. Results of ANOVA's with seed dispersal and seedling recruitment for *Carapa surinamensis* trees between controlled forest sites (Nouragues, Paracou and Piste de Saint Elie) and between silvicultural treatments (Paracou). P in bold are significant at $p < 0.05$, and p in bold and italics are significant at $p < 0.001$

Dependent variable	N	F	df	p
<i>Comparison between controlled forest sites :</i>				
<i>Nouragues (N = 12), Paracou (N = 18) and Piste de Saint Elie (N = 10)</i>				
Dispersal failure	40	29.91	2,37	<0.001
Undispersed seedlings	40	16.6	2,37	<0.001
Dispersed seedlings	40	1.85	2,37	0.171
Recruitment effectiveness ratio	40	2.01	2,37	0,149
<i>Comparison between silvicultural treatments (Paracou, N = 55)</i>				
Dispersal failure				
Silvicultural treatment	55	14.15	2,45	<0.001
Plots (Silvicultural treatment)	55	8.64	7,45	<0.001
T0	18	1.35	2,15	0.29
T1	13	13.9	2,10	<0.01
T2-3	24	9.08	3,20	<0.001
Undispersed seedlings				
Silvicultural treatment	55	1.73	2,45	0.189
Plots (Silvicultural treatment)	55	0.7	7,45	0.672
Dispersed seedlings				
Silvicultural treatment	55	4.05	2,45	0.024
Plots (Silvicultural treatment)	55	2.42	7,45	0.034
T0	18	3.25	2,15	0.067
T1	13	2.04	2,10	0.181
T2-3	24	1.29	3,20	0.306
Recruitment effectiveness ratio				
Silvicultural treatment	55	2.11	2,45	0.132
Plots (Silvicultural treatment)	55	3.94	7,45	0.002
T0	18	5.96	2,15	0.012
T1	13	2.98	2,10	0.096
T2-3	24	1.11	3,20	0.367