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

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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 Forget[1]
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-m^2 subplots under the tree crown; 2) recruitment effectiveness: in September–October, seedlings were sampled on four 100-m^2 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 sylvicultural 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 m^2 sous la couronne ; 2) la régénération : en échantillonnant de septembre à octobre les plantules à l'intérieur de quatre quadrats de 100 m^2, 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

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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.htmare), 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.

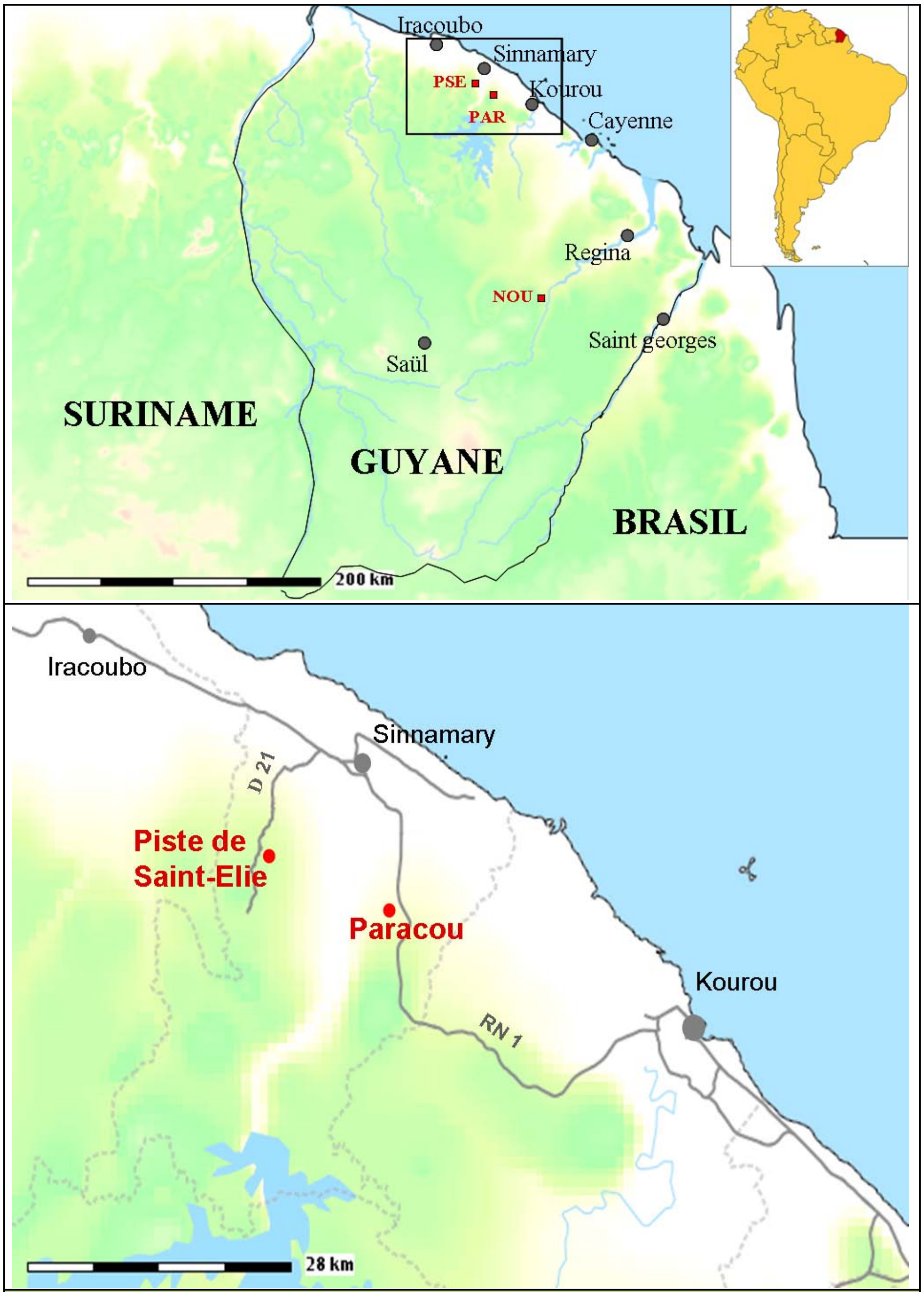

Fig. 1. Location of the study sites (red squares) – Nouragues (NOU), Paracou (PAR), Piste de Saint-Elie (PSE) – in French Guiana, showing the main towns (grey dots) and details of the two sites on the coast with the main national road (RN 1) and the departmental road (D 21).

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 sylvicultural 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 sylvicultural 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 sylvicultural 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).

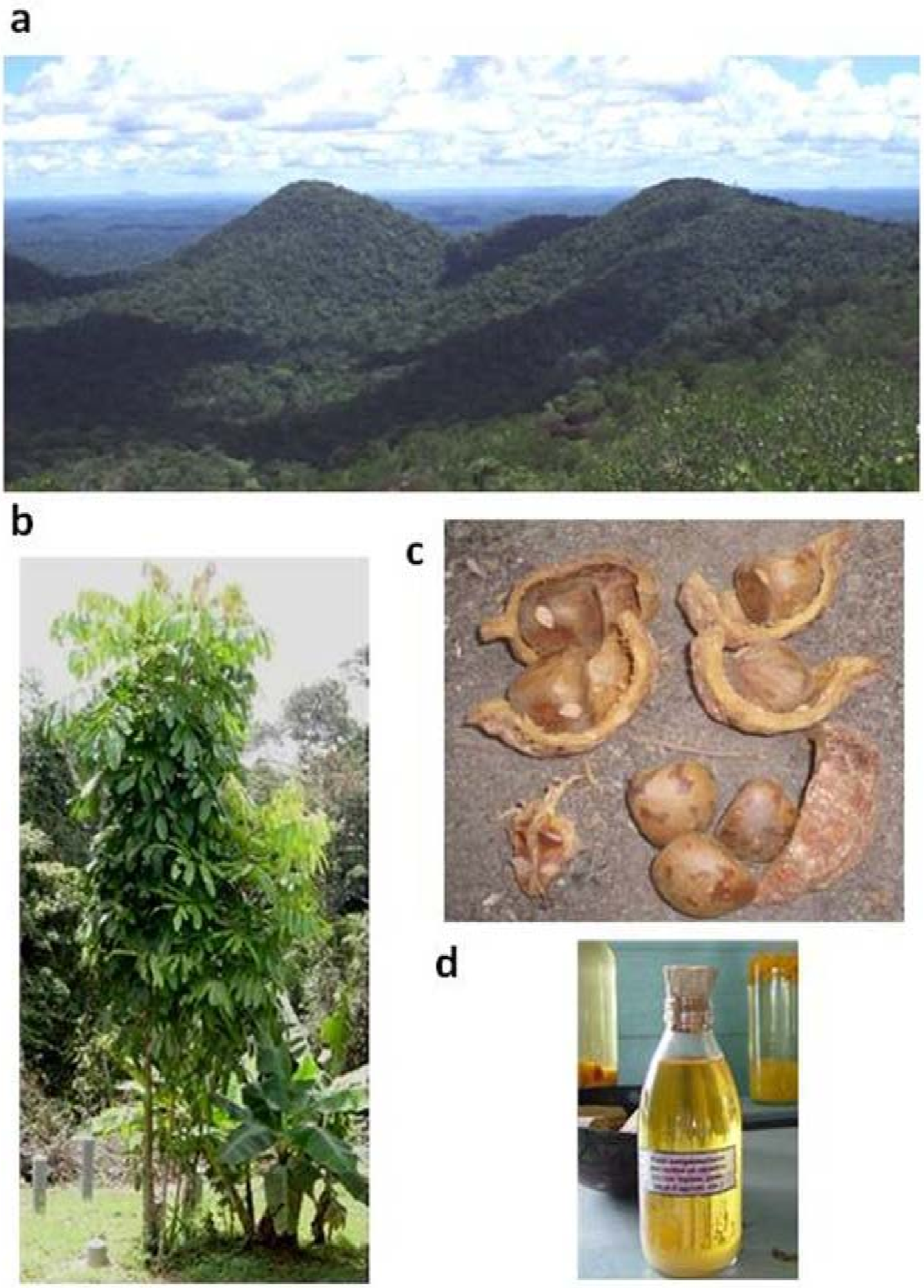

Fig. 2. Selected photos showing one forest where *C. surinamensis* was investigated (a) and study species: young tree (b), seeds and fruit husks (c), and Carapa oil (d). Photos (a, c) by C. Lermyte. Photos (b, d) by P.-M. Forget.

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 *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-m^2 (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-m^2). 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-m^2 (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-m^2).

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.

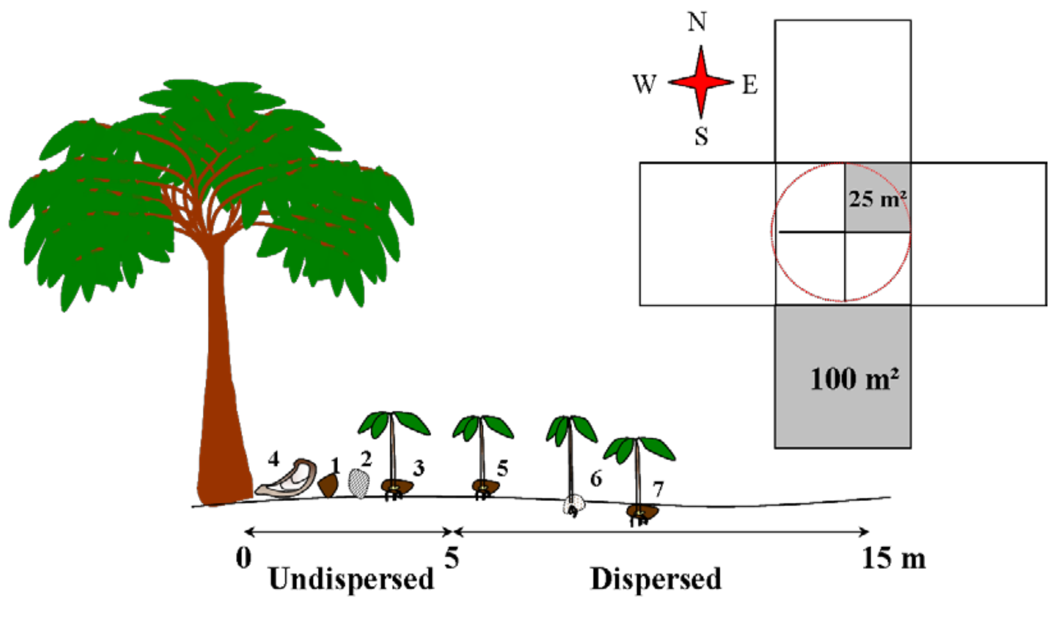

Fig. 3. Protocol used for the rapid assessment of seed dispersal and seedling recruitment effectiveness, in 5 × 5 m quadrats (25-m^2) under (< 5 m) and 10 × 10 m quadrats (100-m^2) outside (> 5 m) the adult *Carapa surinamensis* tree crown, respectively, in three forests in French Guiana. In each quadrat we sampled: 1. Intact seeds; 2. Seeds infested by moths; 3. Undispersed seedlings; 4. Fruit husks; 5. Undispersed germinated seeds; 6. "Zombie" seeds; 7. Dispersed seedlings (see text for definitions).

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 sylvicultural treatment on the factors studied we used nested ANOVAs with plots nested within sylvicultural 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.

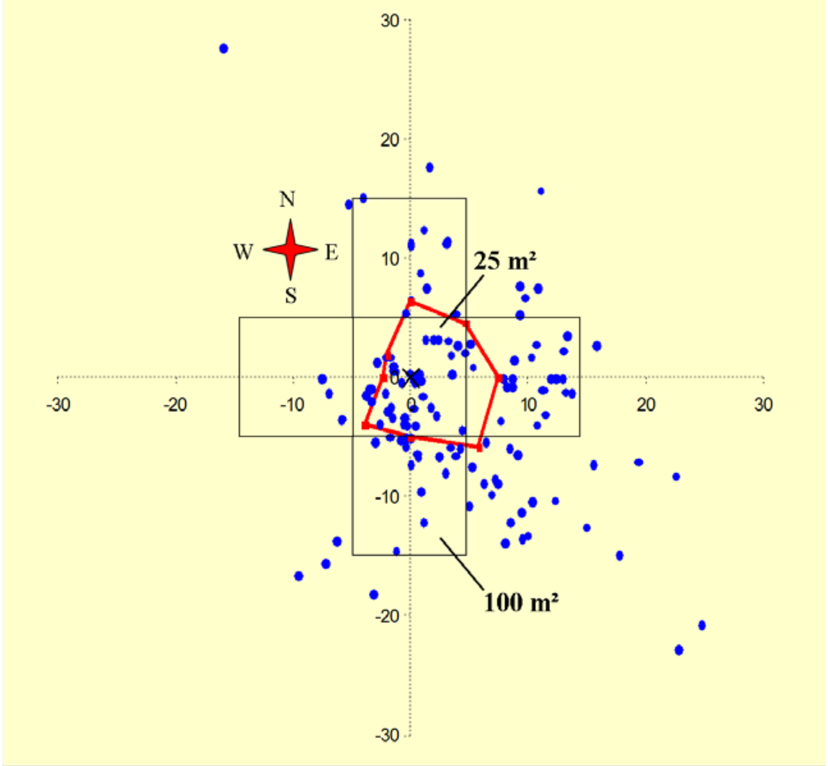

Fig. 4. Seed dispersal and seedling recruitment sampling plots superimposed on the effective seedling recruitment for a tree (DBH = 51 cm) that produced c. 1389 seeds and 131 live dispersed seedlings, i.e., from cached seeds (Nouragues, 21 May 2002, P.-M. Forget, unpublished data). The tree crown is shown as a red line, seedlings by blue dots.

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 sylvicultural 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 sylvicultural 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 sylvicultural 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% ± SE 0.5) co-occurred with a high proportion of undispersed seedlings (50.3% ± 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, sylvicultural 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 sylvicultural treatments (Paracou).

Site	Treatment	Dispersal failure (Mean % ± SE)	Undispersed seedlings (Mean % ± SE)	Dispersed seedlings (Mean % ± SE)	Recruitment effectiveness ratio (Mean ± SE)	No. of Trees
Nouragues	Control	1.55 ± 0.62	4.17 ± 4.17	42.92 ± 12.23	1.58 ± 0.44	12
Paracou	Control (T0)	2.71 ± 0.5	50.33 ± 10.25	30.60 ± 6.74	1.26 ± 0.36	18
	T1	8.09 ± 2.85	52.24 ± 13.03	58.28 ± 6.94	2.25 ± 0.51	13
	T2–3	19.25 ± 3.86	73.06 ± 6.32	36.02 ± 3.56	0.90 ± 0.12	24
Piste de Saint-Elie	Hunted	15.73 ± 3.1	85.00 ± 4.1	13.87 ± 5.51	0.29 ± 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% ± SE 12.2) and Piste de Saint-Elie (13.9% ± SE 5.5). On the contrary, the fraction of dispersed seedlings varied significantly among sylvicultural 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; sylvicultural treatments appeared to be homogeneous (Appendix 1). Bonferroni pairwise mean comparison between sylvicultural 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 ± SE 0.44) and lowest at Piste de Saint-Elie (0.3 ± SE 0.12) (Table 2). At Paracou, the RER did not differ significantly between sylvicultural treatments (P = 0.132), but there was significant interaction between plots and sylvicultural 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 ± SE 2.85), intermediate sylvicultural treatment T1 positively affected the RER (2.3 ± SE 0.51); on the contrary, heavily-impacted treatment T2–3 negatively affected the RER (0.9 ± SE 0.12), see Table 2, Fig. 5C right. We observed more live seedlings in logged plots than in unlogged plots (Table 1).

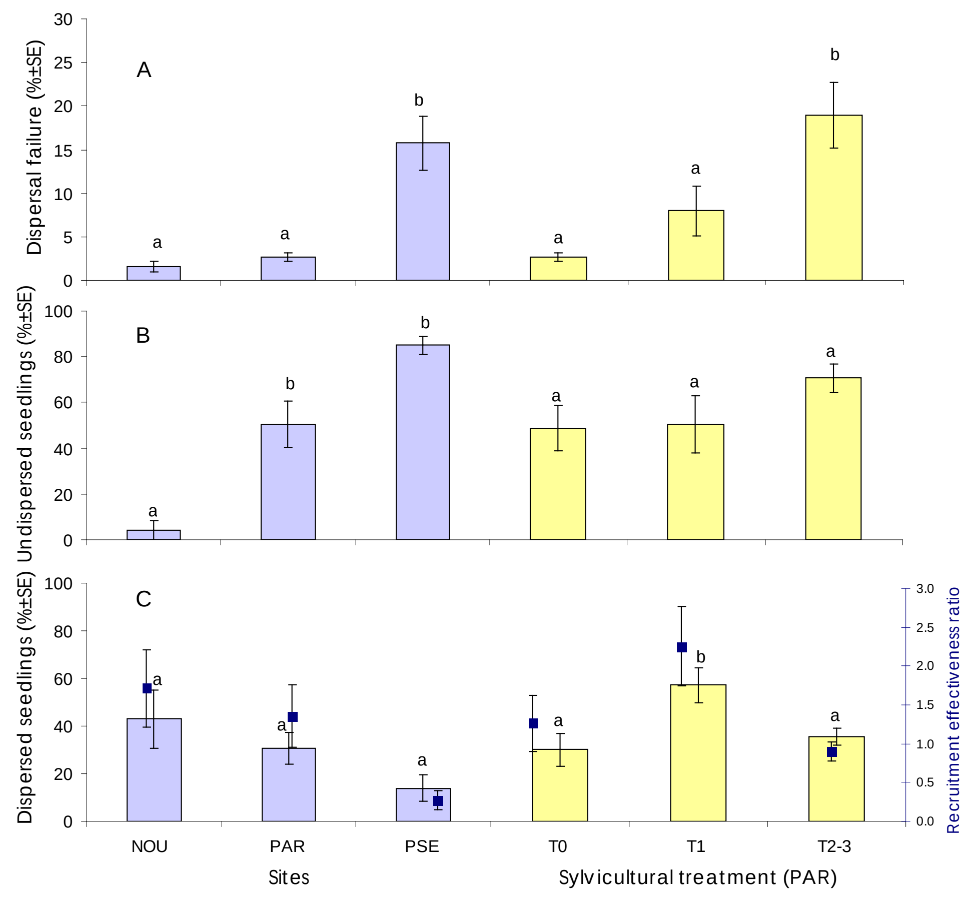

Fig. 5. Comparison of the proportions of dispersal failure, seedling recruitment under (< 5 m) and outside (> 5m) the tree crown: across the three sites (Nouragues [NOU], N = 2; Paracou [PAR], N = 18; Piste de Saint-Elie [PSE], N = 10) and within Paracou (T0, N = 18; T1, N = 13; T2–3, N = 24). A: mean percentage of dispersal failure – B: mean percentage of undispersed seedlings – C: mean percentage of dispersed seedlings, and recruitment effectiveness ratio (RER) represented by blue squares (■) and their own error bars. Errors bars show one ± SE. Bars sharing the same letter within groups do not differ significantly (P > 0.05).

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 sylvicultural 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.

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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 sylvicultural 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**
Comparison between controlled forest sites : *Nouragues (N = 12), Paracou (N = 18) and Piste de Saint Elie (N = 10)*				
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
Comparison between sylvicultural treatments (Paracou, N = 55)				
Dispersal failure				
Sylvicultural treatment	55	14.15	2,45	***<0.001***
Plots (Sylvicultural 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				
Sylvicultural treatment	55	1.73	2,45	0.189
Plots (Sylvicultural treatment)	55	0.7	7,45	0.672
Dispersed seedlings				
Sylvicultural treatment	55	4.05	2,45	**0.024**
Plots (Sylvicultural 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				
Sylvicultural treatment	55	2.11	2,45	0.132
Plots (Sylvicultural 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