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6 Article type : Articles

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9 Running Head: Frugivore communities and seed removal

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11 Modifications of the rainforest frugivore community are associated
12 with reduced seed removal at the community level

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This article has been accepted for publication and undergone full peer review but has not been
through the copyediting, typesetting, pagination and proofreading process, which may lead to
differences between this version and the [Version of Record](#). Please cite this article as [doi:
10.1002/eap.2086](#)

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20 Manuscript received 30 September 2019; accepted 2 December 2019; final version received 29
21 January 2020.

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Abstract

Tropical rainforests worldwide are under increasing pressure from human activities, which are altering key ecosystem processes such as plant-animal interactions. However, while the direct impact of anthropogenic disturbance on animal communities has been well studied, the consequences of such defaunation for mutualistic interactions such as seed dispersal remains chiefly understood at the plant species level. We asked whether communities of endozoochorous tree species had altered seed removal in forests affected by hunting and logging and if this could be related to modifications of the frugivore community. At two contrasting forest sites in French Guiana, Nouragues (protected) and Montagne de Kaw (hunted and partly logged), we focused on four families of animal-dispersed trees (Sapotaceae, Myristicaceae, Burseraceae and Fabaceae) which represent 88 % of all endozoochorous trees which were fruiting at the time and location of the study. We assessed the abundance of the seed dispersers and predators of these four focal families by conducting diurnal distance sampling along line transects. Densities of several key seed dispersers such as large-bodied primates were greatly reduced at Montagne de Kaw, where the specialist frugivore *Ateles paniscus* is probably extinct. In parallel, we estimated seed removal rates from fruit and seed counts conducted in one-square-meter quadrats placed on the ground beneath fruiting trees. Seed removal rates dropped from 77 % at Nouragues to 47 % at Montagne de Kaw, confirming that the loss of frugivores associated with human disturbance impacts seed removal at the community level. In contrast to Sapotaceae, whose seeds are dispersed by mammals only, weaker declines in seed removal for Burseraceae and Myristicaceae suggest that some compensation may occur for these bird- and mammal-dispersed families, possibly because of the high abundance of toucans at the disturbed site. The defaunation process currently occurring across many tropical forests could dramatically reduce the diversity of entire communities of animal-dispersed trees through seed removal limitation.

Key words: seed dispersal; seed removal; frugivory; hunting; logging; tropical rain forest; French Guiana.

Introduction

Large vertebrates in tropical forests are under major threat from overhunting across all continents (Corlett 2007, Peres and Palacios 2007, Fa and Brown 2009, Cuthbert 2010). Harvest rates often prove unsustainable (Fa et al. 2002, Robinson and Bennett 2004), and hunting pressure on game species is sometimes compounded by other forms of human disturbance such as logging (Robinson et al. 1999). Together with habitat loss, these pressures have combined to bring species such as primates, tapirs, hornbills and cracids to the brink of extinction (Estrada et al. 2017, IUCN 2019). But beyond the issue of local or global extinctions, many of the species targeted by hunters are involved in key ecological interactions with plants that profoundly influence plant regeneration and forest dynamics (Dirzo 2001, Wright 2003, Dirzo et al. 2014).

Previous studies have shown frugivores to be more sensitive than other trophic guilds to overhunting (Peres and Palacios 2007) or other forms of forest disturbance (Gray et al. 2007). But as seed dispersers, these animals play a key role in plant regeneration. They ensure the survival of seeds away from parent trees (Janzen 1970, Connell 1971, Chapman and Chapman 1995), shape the spatial pattern of trees in the forest (Howe 1989, Julliot 1997, Fragoso et al. 2003, Russo and Augspurger 2004, Trolliet et al. 2017) and facilitate establishment in new territories (Howe and Smallwood 1982, Galindo-González et al. 2000, Carlo and Morales 2016). Moreover, a majority of woody plants in tropical forests rely on vertebrates for seed dispersal (Forget et al. 2007). The possibility that overhunting may indirectly impact seed dispersal was first highlighted by Janzen (1986) and Redford (1992), who argued that an otherwise intact forest depleted of its seed dispersers would have many of its ecological processes stalled.

At the recruitment stage, hunting has been shown to reduce the density and species richness of saplings of tree species dispersed by game animals (Nuñez-Iturri and Howe 2007, Terborgh et al. 2008, Vanthomme et al. 2010). Sapling recruitment of species with animal-dispersed seeds declines compared to those that are abiotically dispersed, and large-seeded species are affected to an even greater extent (Harrison et al. 2013). These observed differences in sapling recruitment can be explained by hunting-induced seed dispersal limitation. Fewer frugivores visit fruiting trees in hunted forests, which translates into reduced seed removal in the canopy (Holbrook and Loiselle 2009). Consequently, many more fallen seeds are to be found underneath trees (Wang et al. 2007, Brodie et

al. 2009), the vast majority of which are undispersed and come from the same mother tree (Wang et al. 2007). Fewer seeds are scatter-hoarded by rodents (Forget and Jansen 2007), and a much lower proportion of dispersed seeds are found in the forest away from beneath fruiting conspecifics (Wright et al. 2000, Brodie et al. 2009). This in turn translates into reduced recruitment and sapling density. However, all studies investigating the impact of hunting on seed dispersal so far have chosen to focus on one or two species of animal-dispersed trees (Wright et al. 2000, Beckman and Muller-Landau 2007, Forget and Jansen 2007, Wang et al. 2007, Brodie et al. 2009, Holbrook and Loiselle 2009). Whether these results can be extrapolated at the community level remains to be confirmed.

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In this paper, we compare levels of seed removal beneath parent trees of four widespread endozoochorous tree families with different life histories and representing the majority of the fruiting endozoochorous tree community (Burseraceae, Myristicaceae, Sapotaceae and Fabaceae) in relation to the abundance of their mammalian and avian seed dispersers and predators. Two rain forest sites are compared in French Guiana, one with hunting and logging and one protected from human activities. First, we assess the impact of hunting and logging on the community of diurnal mammals and birds that either disperse or predate the seeds of these families. Then, we compare fruit consumption and seed removal ratios calculated from quadrats placed underneath the crowns of fruiting trees at the two sites, in an attempt to establish a link between modifications of the frugivore community and patterns of seed removal. We hypothesize that population reductions of key frugivores at the hunted and logged site will be associated with reductions in seed removal of the tree families that they disperse.

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100 Methods

101 Study sites

The protected forest site is located at Nouragues Research Station (4°05' N, 52°40' W), in the 105,800 ha Nouragues National Nature Reserve in central French Guiana. The climate is of equatorial

type and is characterized by one dry (August – November) and one wet season (December – July), with a slight decrease in precipitation around March. The average annual rainfall is 2,990 mm, and the mean annual temperature 26°C (Grimaldi and Riéra 2001). The elevation ranges from 80 to 200 m above sea level. The habitat is mature lowland evergreen rain forest, dominated by a 420 m high granite inselberg. The site is located 100 km upriver from the nearest settlement, the town of Régina. Access is by river only, coupled with a three-hour walk. Although some poaching occurs in other parts of the reserve in relation to illegal gold mining (Laurance et al. 2012), the site is effectively protected from hunting due to permanent presence of researchers and/or staff. Logging does not occur inside the reserve.

The hunted and logged forest is situated on Montagne de Kaw (4°33' N, 52°12' W), 70 km north-east of Nouragues Research Station. The climate is the same as at Nouragues, but for a higher mean annual rainfall of 4,099 mm, with important local variations. Montagne de Kaw is a 40 km long, elongated hill, reaching 333 m above sea level (study locations from 20 to 290 m in elevation). Montagne de Kaw and Nouragues are part of the same forest landscape (Guitet et al. 2015). The site is adjacent to the town of Roura, population 2,600, and an hour's drive from Cayenne, the territory's capital. A road that runs along the ridge was opened in 1980 and paved in 1991. Both local and urban populations hunt along the road and on the tracks that go into the forest, using shotguns, motorized vehicles, and, for some of them, dogs and spotlights (O. Boissier, pers. obs.). Hunting is both recreational and commercial (C. Richard-Hansen, pers. comm.). Although parts of Montagne de Kaw are protected as Kaw-Roura National Nature Reserve and Trésor Regional Nature Reserve, the forest is not effectively protected from hunting, which occurs within reserve boundaries (C. Richard-Hansen, pers. comm.). The most sought-after species include peccaries (Tayassuidae), deer (*Mazama* spp.), lowland tapir (*Tapirus terrestris*), atelid and capuchin monkeys (*Ateles paniscus*, *Alouatta macconnelli*, *Sapajus apella* and *Cebus olivaceus*), armadillos (Dasypodidae and Chlamyphoridae), lowland paca (*Cuniculus paca*), common red-rumped agouti (*Dasyprocta leporina*), Cracidae, gray-winged trumpeter (*Psophia crepitans*) and toucans (Ramphastidae) (C. Richard-Hansen, pers. comm.). Commercial selective logging occurs within a logging concession where 2000 m³ of timber are taken annually.

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133 Tree families

134 Although the whole community of fruiting endozoochorous tree species was sampled, four
135 families were eventually selected on the basis of their abundance, sample size and significance to
136 frugivores: Burseraceae, Myristicaceae, Sapotaceae and Fabaceae. These families accounted for 88%
137 of all fruiting endozoochorous trees encountered and sampled (n=82) and thus represent the vast
138 majority of the fruit resource available to frugivores during the study. The sampled species of
139 Burseraceae and Myristicaceae are dispersed by both mammals and birds, whereas Sapotaceae and
140 Fabaceae are dispersed by mammals only. The fruits of these families (Figure 1) all contain hard outer
141 parts that are left uneaten and dropped to the ground by frugivores (Sabatier 1983, van Roosmalen
142 1985b), which allows counts of fallen fruits to be made, contrary to some other animal-dispersed
143 families whose soft fruits are entirely consumed by frugivores (Boissier et al. 2014).

144 Burseraceae and Myristicaceae are canopy trees. Burseraceae fruit annually, from February to
145 June in French Guiana (Ratiarison 2003, Ratiarison and Forget 2005). They produce green to bright
146 purple-red pseudocapsules containing one to six locules closed by valves that dehisce at maturity,
147 revealing white, medium-sized arillate seeds (one per locule; length: 16-22 mm). Myristicaceae fruit
148 earlier than Burseraceae, between October and April in French Guiana (Sabatier 1983, 1997). Like
149 Burseraceae, they produce dehiscent fruits (capsules). These open into two valves that expose a single
150 arillate seed (length: 19-28 mm). The bright red, netlike aril is very nutritious, containing over 50 %
151 lipids (Howe 1981, Howe and Kerckhove 1981). Seeds of both families are dispersed by primates
152 (*Ateles paniscus*, *Alouatta macconnelli*, *Sapajus apella* and *Cebus olivaceus*), kinkajou (*Potos flavus*),
153 toucans (Ramphastidae), trogons (Trogonidae), guans (Cracidae) and motmots (Momotidae). In
154 addition, Burseraceae are dispersed by Midas tamarin (*Saguinus midas*) and a wide range of other
155 avian dispersers such as cotingas (Cotingidae). Parrots (Psittacidae) and squirrels (Sciuridae) predate
156 the seeds of both families (Howe 1980, 1981, Howe and Kerckhove 1981, Simmen and Sabatier 1996,
157 Sabatier 1997, Kays 1999, Pack et al. 1999, Oliveira and Ferrari 2000, Julien-Laferrière 2001,
158 Ratiarison 2003, Ratiarison and Forget 2005, Holbrook and Loiselle 2009, Ratiarison and Forget
159 2013).

160 Unlike Burseraceae and Myristicaceae, Sapotaceae produce indehiscent fruits (berries) that
161 cannot be opened by birds (except parrots) (Ratiarison 2003, Ratiarison and Forget 2011). These
162 canopy trees fruit from January to June, some on a yearly basis (e.g. *Chrysophyllum*), some on mast
163 fruiting events (e.g. *Manilkara*) (Norden et al. 2007, Mendoza et al. 2015). Berries display a fibrous
164 pericarp that contains one to ten seeds (length: 13-25 mm) surrounded by sweet-tasting pulp (van
165 Roosmalen 1985a). Sapotaceae fruits are a primate favorite: red-faced black spider monkey (*Ateles*
166 *paniscus*), Guianan red howler (*Alouatta macconnelli*) and Guianan brown capuchin (*Sapajus apella*)
167 all disperse their seeds (van Roosmalen 1985b, Julliot and Sabatier 1993, Simmen and Sabatier 1996,
168 Ratiarison 2003, Ratiarison and Forget 2011), as well as kinkajou (*Potos flavus*) (Kays 1999, Julien-
169 Laferrière 2001), while parrots (Psittacidae) and squirrels (Sciuridae) predate the seeds (Ratiarison
170 2003, Ratiarison and Forget 2011). Finally, Fabaceae were represented by the genus *Inga*. In March-
171 April, these trees produce pods whose medium-sized seeds (length: 12-18 mm) are surrounded by a
172 sugar-rich pulp (Sabatier 1983, van Roosmalen 1985a). These attract primates (*A. paniscus*, *S. apella*,
173 *S. midas*, but not *A. macconnelli*) and *P. flavus*, which disperse the seeds (van Roosmalen 1985b,
174 Julliot and Sabatier 1993, Simmen and Sabatier 1996, Kays 1999, Pack et al. 1999, Oliveira and
175 Ferrari 2000, Julien-Laferrière 2001), that are also predated by parrots (Psittacidae) (Galetti and
176 Rodrigues 1992).

177

178 Abundance of frugivorous mammals and birds

179 We performed line transect censuses (Bibby et al. 2000) to estimate the density of frugivores
180 at each site, focusing on confirmed and potential seed dispersers and predators of our four tree
181 families. Three transects were used at Nouragues (control site) and four at Montagne de Kaw, two of
182 which were in the logging concession (hunting and logging) and two outside (hunting alone). Given
183 the great number of mammalian and avian species to be censused (around 60), which translated into
184 high contact frequency along transects, we established transects that were shorter than those in similar
185 studies (Wright et al. 2000, Lammertink 2004, Nuñez-Iturri and Howe 2007, Terborgh et al. 2008).
186 Transect length was 2000 m at Nouragues. Transects at Montagne de Kaw were 1600, 1900, 2000 and
187 2100 m in length. Surveys were performed during the wet season (late January – early May) in 2010

188 and 2011. All surveys were conducted by the same observer (OB). Transects at one site were walked
189 every day in turns, with each site being alternately censused for three weeks so as to minimize any
190 seasonal effects. Transects were walked 10 times each over the two years of the study, four times in
191 2010 and six times in 2011. Total distance walked was 136 km (60 km at Nouragues and 76 km at
192 Montagne de Kaw). No survey was conducted on rainy days. If rain started during a transect walk, the
193 census was suspended and resumed if rain stopped within 30 minutes, and aborted otherwise.
194 Censuses started at 0700 h. Transects were walked at an average speed of 800 m.h⁻¹, with markers
195 every 100 m for calibration. All seed dispersers and predators of the study families were recorded.
196 Not included were nocturnal frugivores, most notably kinkajou (*Potos flavus*), nocturnal rodents such
197 as lowland paca (*Cuniculus paca*) and spiny rats (*Proechimys* spp.), and bats. For each contact, the
198 observer recorded the species, number of individuals, type of detection (visual or auditory), time,
199 position along the transect, and estimated the perpendicular distance from the transect line to the
200 animal or the center of the group for gregarious species. Distance was estimated in 5 m classes for
201 visual contacts and, in 2011 only, in five distance intervals for acoustic contacts (0 – 20 m, 20 – 50 m,
202 50 – 100 m, 100 – 200 m and beyond 200 m). Birds flushed by the observer were recorded, but not
203 those seen or heard flying past. This lead to an underestimation of species that call mostly in flight
204 and remain silent when perched, such as some Psittacidae species (e.g. *Pionus* spp.). Small, solitary,
205 terrestrial animals and quiet and secretive bird species that do not flush easily also tend to be
206 underestimated, as in most survey methods (Bibby et al. 2000, Denis et al. 2017).

207

208 Fruit consumption and seed removal of fruiting trees

209 Between March and May 2010 and February and April 2011, during the fruiting season of
210 most tree families (Sabatier 1985, Mendoza et al. 2018), we assessed fruit consumption and seed
211 removal by counting fallen fruits and seeds beneath the crowns of fruiting trees. We located fruiting
212 trees of endozoochorous families along the same transects as those used for frugivore censuses, and
213 up to 50 m away from the transect line. Underneath each tree, we placed a single one-square-meter
214 quadrat where fruit density on the ground was maximal (Boissier et al. 2014). Trees with fewer than
215 10 fruits per quadrat were not sampled, although a value of eight was allowed on one instance to

reach a minimum number of *Inga* trees at Nouragues. Within each quadrat, we counted all conspecific fruits and seeds, which were classified as (1) intact fruit, (2) eaten fruit, (3) open fruit (in the case of families with dehiscent fruits), and (4) seed. Fruits were photographed, sampled and dried to confirm identification at the laboratory's reference collection.

For each sampled tree, two proportions were calculated from these figures (Ratiarison and Forget 2005, Lermyte and Forget 2009, Boissier et al. 2014). In the case of Sapotaceae and Fabaceae, the fruit consumption rate was calculated as the number of eaten fruits divided by the total number of fruits. This ratio cannot be calculated for Burseraceae and Myristicaceae, whose fruits dehisce, whether eaten or not (fruits are either intact or open).

For all families, the seed removal rate for each sampled tree was calculated as:

$$R = 1 - \frac{S_g + S_f}{S_F},$$

where S_g is the number of loose seeds counted on the ground, S_f is the number of seeds contained in all intact fruits, and S_F is the number of seeds originally contained in all fruits, whether intact, eaten or open, prior to consumption by frugivores. In other words, $S_g + S_f$ is the number of seeds that remain within the quadrat, and S_F is the number of seeds one would expect to find in the quadrat given the number of fruits present if no fruit at all had been consumed by frugivores.

S_g is always counted. However, the way to determine S_f and S_F varies between families. In Burseraceae and Fabaceae, the exact number of seeds per fruit can easily be counted, since each seed leaves a characteristic mark on the fruit (a notch and a bulge on the pod, respectively). Thus S_f is the number of seed marks summed over all intact fruits, and S_F is the number of seed marks summed over all fruits, whether intact, eaten or open. Myristicaceae and some Sapotaceae species only have one seed per fruit. Then S_f is the number of intact fruits and S_F is the total number of fruits (Boissier et al. 2014). However, the number of seeds originally contained in a multiple-seeded Sapotaceae fruit cannot be counted once the fruit has been eaten and all or some of the seeds swallowed. For these species, we had to rely on a mean number of seeds per fruit n taken from the literature for each

species (Ratiarison 2003, Ratiarison and Forget 2011). S_f and S_F are obtained by multiplying n by the number of intact fruits and the total number of fruits, respectively.

Discovering fruiting trees is a serendipitous process: trees of focal families must be present in the vicinity of transects, they must be fruiting at the time of study and they must be found. Our tree sampling thus depended entirely on the availability of fruiting trees. Consequently, Burseraceae and Sapotaceae were represented by only two trees each along the two hunted transects at Montagne de Kaw, and no fruiting Myristicaceae were to be found along the two hunted and logged transects. Sample size was thus too small at this level, and we had to pool all four transects at Montagne de Kaw to consider the site as a whole. With these data, we thus tested for a difference in fruit consumption and seed removal rates between the protected site (Nouragues) and the hunted and logged site (Montagne de Kaw).

Data analysis

We used DISTANCE 6.0 software (Thomas et al. 2009) to estimate animal densities. Visual and acoustic detections were truncated to an effective strip width of 200 m on either side of the transect. Each species was analyzed separately. We fit detection functions to the data, using uniform and half-normal key functions with or without adjustment terms. Whenever possible, separate detection functions were fit for Nouragues and Montagne de Kaw, to account for potential differences in detection probability between the two sites. The best model was selected on the basis of the lowest Akaike Information Criterion (Buckland et al. 2001). Model fit was examined with chi-square goodness-of-fit tests. Since distances were estimated by the same observer but not accurately measured with a rangefinder, the densities calculated are suitable for comparisons between sites and between species within this study, but their absolute value should be used with caution for comparisons with other studies. For each animal species, density was considered significantly different between the two sites when 95 % confidence intervals did not overlap.

All statistical analyses were performed with R 2.14.1 (R Development Core Team 2011). In order to assess if fruit consumption and seed removal rates differed between the two sites, we fit

generalized linear mixed models with function lmer of package lme4 (Bates et al. 2011). Since the response variables were proportion data, we used a binomial error distribution with a logit link, adjusted for overdispersion (Bolker et al. 2009). Fruit consumption was analyzed separately for Sapotaceae and Fabaceae, with site and species as fixed effects and transect and year as random effects. Seed removal was analyzed at the community level, with all four families pooled together, with site and family as fixed effects and an interaction term allowing for the effect of site to differ between families. Transect, year and species nested within family were included as random effects. The statistical significance of fixed effects and their interaction was assessed by likelihood ratio tests between nested models fit by maximum likelihood. The robustness of the statistical significance of the site effect to specificities of the available dataset (e.g. outliers) was tested using a bootstrap in which the model was repeatedly run over a random sampling with replacement of the original dataset (1000 runs, resampling units were individual trees, sample size of trees was kept the same as in the initial dataset for each site).

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283 Results

284 Abundance of frugivores

Densities could be estimated for 41 out of the 58 species that we censused (Table 1). Five species or groups of species were significantly less abundant at Montagne de Kaw (hunted and logged) compared to Nouragues (protected): red-faced black spider monkey (*Ateles paniscus*), which was never observed at Montagne de Kaw during the study and is probably locally extinct, ungulates (*Mazama americana*, *M. nemorivaga*, *Pecari tajacu* and *Tapirus terrestris*), blue-crowned motmot (*Momotus momota*), purple-throated fruitcrow (*Querula purpurata*) and slate-colored grosbeak (*Saltator grossus*). In addition, Guianan red howler (*Alouatta macconnelli*) was twelve times more abundant at Nouragues than Montagne de Kaw, although sample size at Montagne de Kaw was probably too small for the difference to be significant (only one contact). All mammalian species

recorded at Nouragues had lower densities at Montagne de Kaw, except the smaller Midas tamarin (*Saguinus midas*) and Guianan squirrel (*Sciurus aestuans*). Notable bird families with reduced densities at Montagne de Kaw include Cracidae, gray-winged trumpeter *Psophia crepitans* (Psophiidae), trogons (Trogonidae) and all species of parrots (Psittacidae) but one. Conversely, only one species was significantly more abundant at Montagne de Kaw: channel-billed toucan (*Ramphastos vitellinus*), which was five times more abundant at Montagne de Kaw compared to Nouragues. Taken as a group, *Ramphastos* toucans (*R. vitellinus* and *R. tucanus*) were significantly more abundant at Montagne de Kaw.

302

303 Fruit consumption and seed removal

A total of 72 trees of the four focal families was sampled over the two years of the study. As some trees could not be identified to species level or mean number of seeds per fruit was not available in the literature for some species, seed removal rate could be calculated for 57 trees: 26 trees of 12 species at the protected site of Nouragues (987 fruits), and 31 trees of 14 species at the hunted and logged site of Montagne de Kaw (2921 fruits); 7 out of 9 genera and 6 out of 20 species were sampled at both sites. Genera sampled included *Protium* and *Tetragastris* (Burseraceae, 3 species), *Inga* (Fabaceae, 6 species), *Iryanthera*, *Osteophloeum* and *Virola* (Myristicaceae, 5 species), and *Chrysophyllum*, *Manilkara* and *Micropholis* (Sapotaceae, 6 species) (Table 2). The disproportionately large number of fruits sampled at Montagne de Kaw was due to the presence of several individuals of the genus *Micropholis*, which are characterized by very large crops, whereas this genus was represented by just one individual at Nouragues. Analyses were thus also conducted after removing this genus from the data set, to insure that any site effect was not due to a possible saturation of seed dispersers and predators at *Micropholis* trees at Montagne de Kaw.

Fruit consumption in Sapotaceae was estimated on an additional 11 trees of 7 species for which no data on mean number of seeds per fruit were available. These trees consequently could not be included in the seed removal analysis, but could be used to calculate a fruit consumption rate. The total of Sapotaceae trees used for the fruit consumption analysis thus amounted to 13 trees of 7

species at Nouragues and 17 of 10 species at Kaw, for a total of 13 species of genera *Chrysophyllum*,
Manilkara, *Micropholis* and *Pouteria*.

Fruit consumption of Sapotaceae did not significantly differ between the protected site (77 %) and the hunted and logged site (67 %; $\chi^2 = 1.595$, $df = 1$, $P = 0.207$) (Tables 3 and 4). Fabaceae could not be compared between sites since only three trees were sampled at Nouragues. Seed removal differed significantly between Nouragues and Montagne de Kaw ($\chi^2 = 12.497$, $df = 1$, $P < 0.001$) (Tables 3 and 5). The overall community level seed removal rate was 77 % at Nouragues (protected) and 47 % at Montagne de Kaw (hunted and logged) (Figure 2). Seed removal also differed among families ($\chi^2 = 8.186$, $df = 3$, $P = 0.042$), but there was no significant site-by-family interaction ($\chi^2 = 3.159$, $df = 3$, $P = 0.368$). Seed removal rate at Nouragues and Montagne de Kaw was 50 % and 34 % for Burseraceae, 91 % and 75 % for Myristicaceae, and 72 % and 29 % for Sapotaceae, respectively. The site effect was robust to the omission of genus *Micropholis* from the data set ($\chi^2 = 9.063$, $df = 1$, $P = 0.003$), whereas in this case there was no significant family effect ($\chi^2 = 6.867$, $df = 3$, $P = 0.076$). The statistical difference in seed removal between sites was relatively robust to potential specificities of the initial dataset, since the effect was significant in most datasets resampled by bootstrap (95.5 % of datasets by t-test and 89.7 % by likelihood ratio test; Tables 3 and 5).

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339

340 Discussion

Modifications in the frugivore community at Montagne de Kaw, some of them linked to hunting and logging activities, were associated with a profound disruption of the seed removal process at the community scale. Populations of several key seed dispersers were severely depleted. But although some other species did not seem to be affected or even were present at higher densities, widespread reductions in seed removal were observed at the community scale. This suggests that dispersal failure is occurring to a greater extent at the hunted and logged site. However, some families

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347 seemed to be less affected than others, with Sapotaceae exhibiting a stronger reduction in seed
348 removal than Burseraceae and Myristicaceae, suggesting that some level of compensation might be
349 taking place for the latter two families.

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351 Abundance of frugivores

352 In the frugivore community, the most notable difference between the two sites was the
353 probable extinction of the red-faced black spider monkey (*Ateles paniscus*) at Montagne de Kaw. The
354 species was never contacted during the study. This was consistent with the findings of other studies
355 (Bodmer et al. 1997, de Thoisy et al. 2005, Nuñez-Iturri and Howe 2007). *Ateles* spp. are reputedly
356 very sensitive to hunting (Peres 1990) due to their large size, conspicuous behavior and low
357 reproductive rate (Bodmer et al. 1997). Although they are legally protected in French Guiana, they are
358 one of the most sought-after game species (C. Richard-Hansen, pers. comm.) and the first to disappear
359 with hunting (de Thoisy et al. 2005). Although less sensitive to hunting (Peres and Palacios 2007,
360 Boubli et al. 2008), the Guianan red howler (*Alouatta macconnelli*) was apparently greatly reduced in
361 Kaw. It is also a preferred target of hunters (C. Richard-Hansen, pers. comm.). In Guyana, Bicknell
362 and Peres (2010) found that *A. paniscus* was significantly reduced by reduced-impact logging, but not
363 driven to extinction, and found *A. macconnelli* to be unaffected. In our study, these species are
364 respectively extinct and reduced on all transects at Montagne de Kaw, not specifically the logged
365 ones. This suggests that hunting, and not logging, is responsible for their demise and scarcity at our
366 hunted site. However, these species are the two major seed dispersers in the primate community of
367 the Guianas (Mittermeier and van Roosmalen 1981). They are especially important dispersers of
368 families such as Sapotaceae (van Roosmalen 1985b, Julliot 1996). Among our study families,
369 Fabaceae, Myristicaceae and Sapotaceae were the top three families eaten by *A. paniscus* in
370 Voltzberg, Suriname, while Burseraceae ranked sixth (van Roosmalen 1985b).

371 We found no significant difference in densities of capuchin monkeys (*Sapajus apella* and
372 *Cebus olivaceus*) between Nouragues and Montagne de Kaw, in contrast with Nuñez-Iturri and Howe
373 (2007), who found an 80 % reduction of capuchin densities at their heavily hunted site, but in

374 accordance with Peres and Palacios (2007), who found no significant density reduction for *S. apella*
375 in lightly to moderately hunted sites. Midas tamarin (*Saguinus midas*), the smallest species in the
376 Guianese primate assemblage, was present at similar densities at the two sites, in congruence with
377 Peres and Dolman (2000). Ungulates (*Mazama americana*, *M. nemorivaga*, *Pecari tajacu* and *Tapirus*
378 *terrestris*) as a group were typically affected by hunting. But although highly frugivorous, they are not
379 very efficient seed dispersers, with the exception of *T. terrestris*; *P. tajacu* and *Mazama* spp. destroy
380 seeds (Bodmer 1991). However, the densities of some important seed dispersers, common red-rumped
381 agouti (*Dasyprocta leporina*), gray-winged trumpeter (*Psophia crepitans*) and Cracidae (Erard et al.
382 1991, Larue 1999, Emmons and Feer 2007), which are all hunted species, seemed to be typically
383 reduced at Montagne de Kaw compared to Nouragues (more than halved for *D. leporina* and *P.*
384 *crepitans*).

385 Among the seed dispersers of our focal families, channel-billed toucan (*Ramphastos vitellinus*)
386 stood out as the only species to be significantly more abundant at Montagne de Kaw. With red-billed
387 toucan (*R. tucanus*) present at the same densities on both sites, the large toucans (*Ramphastos* spp.)
388 were significantly more abundant at Montagne de Kaw. With their large gape size, these birds are key
389 seed dispersers for a number of families, including Myristicaceae (Howe 1981, Howe and Kerckhove
390 1981, Holbrook and Loiselle 2009, Ratiarison and Forget 2013) and, to a lesser extent, Burseraceae
391 (Ratiarison and Forget 2005). They potentially disperse seeds over several hundred meters (Holbrook
392 2011). However, Ramphastidae, and especially *Ramphastos* spp., are the most targeted group by
393 hunters in French Guiana, accounting for 12 % of all catches (C. Richard-Hansen, pers. comm.). The
394 resilience of *Ramphastos* toucans at Montagne de Kaw indicates that levels of hunting at the site are
395 intermediate, with enough hunting to drive spider monkeys to local extinction, but not to affect toucan
396 densities. With the persistence of howler monkeys (at low densities), medium-sized primates and
397 brocket deer, Montagne de Kaw is not at the end of the defaunation spectrum.

398 However, it is difficult to attribute the changes of abundance of some other, non-hunted
399 species to hunting or logging alone. Specific habitat preferences or subtle biogeographical differences
400 could explain these differences as much as hunting or logging (Richard-Hansen et al. 2015), and our
401 study design does not allow us to discriminate between these factors. As often in this kind of study

(e.g. Wang et al. 2007, Terborgh et al. 2008, Holbrook and Loiselle 2009), the time-consuming character of single observer line transect surveys, along with cost and logistic constraints, limited the span of our study to a single control and impacted site and precluded site replication. This is a frequently encountered situation in field ecological research (Davies and Gray 2015). Nevertheless, our results are consistent with those of other studies that show a decline of large game species due to hunting (Peres and Palacios 2007) along with a significant decrease in seed removal (Wright et al. 2000, Forget and Jansen 2007, Wang et al. 2007, Brodie et al. 2009, Holbrook and Loiselle 2009, Lermyte and Forget 2009). While the fact that hunting is responsible for the decline of large hunted species such as *Ateles paniscus*, *Alouatta macconnelli* and ungulates is the most parcimonious conclusion, we remain cautious regarding the factors leading to abundance changes in other, non-hunted species. Also, since we only practiced daytime censuses, we missed a few seed dispersers of our focal families, most notably kinkajou (*Potos flavus*) and lowland paca (*Cuniculus paca*).

Seed removal limitation

Combined with the loss or decline of seed dispersers, we found a significant reduction in seed removal at the community level, from 77 % at Nouragues (protected) to 47 % at Montagne de Kaw (hunted and logged). This decrease was also observed for all three families for which sample size allowed family-level comparisons to be made (Burseraceae, Myristicaceae and Sapotaceae). This confirms that limitation of seed removal under hunting is not just the fact of a few case species (Wright et al. 2000, Forget and Jansen 2007, Wang et al. 2007, Brodie et al. 2009, Holbrook and Loiselle 2009, Lermyte and Forget 2009), but happens at the community level. At Nouragues, Burseraceae, Myristicaceae, Sapotaceae and Fabaceae (*Inga* spp.) represent 24.3 % of the trees of a 12 ha study plot (5.1, 1.9, 13.1 and 4.2 %, respectively) (Allié 2012). On the mere basis of our four study families, the regeneration of 24.3 % of the forest would thus be jeopardized by seed removal limitation, were Nouragues to be subjected to the same pressures as Montagne de Kaw. We suppose that the results that we obtained from these four major families would apply to other families whose fruits are dispersed totally or partially by hunted animal species and that an even greater proportion of the forest would be threatened by seed removal limitation.

430 A slightly significant family effect was noted in addition to this site effect. Families had
431 different baseline seed removal rates at Nouragues, where 91 % of Myristicaceae seeds were
432 removed, but only 50 % of Burseraceae seeds. Even with an intact frugivore community, half of a
433 Burseraceae crop is left undispersed under the crown of the parent tree, where the seeds will likely die
434 of density-dependent competition and increased predation (Janzen 1970, Connell 1971). This is
435 consistent with the findings of Howe (1980), who showed that *Tetragastris panamensis* (Burseraceae)
436 had a generalized seed dispersal strategy, characterized by fruit superabundance, low investment and
437 considerable waste of seeds, with 66 % of seeds falling under parent trees. In another study, the mean
438 removal rate of *T. panamensis* was 23 %, while it was 62 % for *Virola surinamensis* (Myristicaceae)
439 (Howe 1982). The seed removal rates that we observe for Myristicaceae (91 % and 75 % at
440 Nouragues and Montagne de Kaw, respectively) are comparable to those found by Holbrook and
441 Loiselle (2009) for *Virola flexuosa* in Ecuador (89 % and 67 % at a non-hunted and hunted site,
442 respectively). However, these data are derived from seed traps placed above the ground under fruiting
443 trees; while these record arboreal seed dispersal and predation, they do not account for terrestrial
444 predation and secondary dispersal.

445 Our method of seed removal estimation is based on the proportion of seeds that remain on the
446 ground beneath parent trees (Boissier et al. 2014). It is not associated with direct observations of seed
447 removal by visiting frugivores in fruiting trees (Holbrook and Loiselle 2009). Thus missing seeds may
448 have been either removed and dispersed by arboreal frugivores, predated by arboreal granivores
449 (Psittacidae, Sciuridae, white-faced saki *Pithecia pithecia*), secondarily dispersed by terrestrial
450 frugivores (lowland tapir *Tapirus terrestris*, black curassow *Crax alector*, gray-winged trumpeter
451 *Psophia crepitans*) or scatter-hoarding rodents, or destroyed by terrestrial seed predators (peccaries,
452 scatter-hoarding rodents, *Proechimys* spp.). The proportion that we calculate is the resultant of all
453 these processes and should on no account be interpreted as a seed dispersal rate. Nonetheless, while
454 we cannot discriminate between these seed dispersal and predation processes, it is a strong cumulative
455 indicator of their overall health.

456 Seed removal is the quotient of the number of removed seeds over the number of produced
457 seeds. Hence a lower seed removal rate could theoretically be caused as much by a higher absolute

seed production as by a lower absolute seed removal. If trees consistently produce more fruits at Montagne de Kaw than at Nouragues, frugivores may not be able to eat as many fruits in proportion, not because there are fewer frugivores but because there are more fruits (frugivore saturation). Higher annual rainfall is among the environmental factors that may be considered to lead to a higher fruit production at Kaw, as it may influence tree size or fructification. However, the links between rainfall and fruit biomass production are unresolved. Wet and cloudy conditions may even reduce fruit production (Wright et al. 1999). Long-term studies in Uganda showed that relationships between rainfall and fruiting are complex and vary among sites and species, with some species exhibiting reduced fruit production with increased rainfall (Chapman et al. 2005). Likewise, links between rainfall and tree size are not strongly established in tropical rainforests. Another factor that may change between sites is the density of trees themselves. Some specific species may be found at higher densities, or even be dominant, in some local patches following past historical events, whether climatic (e.g. storms provoking treefalls and thence favoring light-demanding species) or anthropic (e.g. past forest uses by Amerindians, Levis et al. 2017). If many conspecific trees are present at the same site, they will produce too many fruits for the frugivores interacting with this species to eat, and frugivore saturation could likewise be expected (Moreira et al. 2017). However, these potential phenomena are species-specific and would be a concern for studies focusing on one tree species only. Looking at the community scale as we did averages any such potential differences in tree species density over many different species. Hence no environmental factor potentially diverging between the two sites could be definitely considered to let us think that the lower seed removal rate observed at Montagne de Kaw could be explained by a higher fruit production at this site. Conversely, the strong negative changes observed in the frugivore community composition strongly corroborate a lower seed removal.

Frugivores eating fruits in a tree may also defecate and disperse both hetero- and conspecific seeds underneath that tree (Clark et al. 2004). Consequently, a certain proportion of the seeds that we counted in our quadrats to calculate seed removal rates could have come from other conspecific trees and biased our estimate. Wang et al. (2007) similarly counted diaspores underneath fruiting trees of *Antrocaryon klaineianum* (Anacardiaceae) in Central Africa. The genetic parentage analysis that they conducted to estimate the proportion of dispersed diaspores within their quadrats revealed that 42 %

of diaspores found underneath trees in their protected forest actually came from a different “mother” tree, while this proportion was only 2 % at their hunted site. If we extrapolate these results to our study and postulate that the proportion of dispersed diaspores is always higher at a protected site compared to a hunted site, this means that there are even fewer seeds at Nouragues (the protected site) that actually come from the tree above, since some of the seeds that we count have been dispersed and come from other conspecific trees. Consequently, we overestimate the number of remaining seeds and underestimate seed removal rates at Nouragues. Thus the between-site difference in seed removal is probably even greater than our estimates suggest.

495

496 Compensation between frugivore species

There has been a long-standing debate about the possibility of compensation in dispersal services by remaining frugivores when other guild members have been extirpated (Gautier-Hion et al. 1985, Poulsen et al. 2002, Jansen et al. 2012). In our study, generalist families that rely on both mammals and birds for seed dispersal (Burseraceae and Myristicaceae) faced smoother declines in seed removal than specialist families that depend entirely on mammals (Sapotaceae). This suggests that some compensation by birds may occur for the more generalist families.

Consumption rates of Sapotaceae fruits were not significantly different between Nouragues and Montagne de Kaw, while Sapotaceae are the first-ranking family in the fruit diet of *Ateles paniscus*, *Alouatta macconnelli* and *Sapajus apella* during fruit peak at Nouragues (Simmen and Sabatier 1996). A possible explanation to the similar consumption rates is that smaller primates (*Saguinus midas*, *S. apella* and *Cebus olivaceus*) and seed predators such as Psittacidae take advantage of the absence of *A. paniscus* and scarcity of *A. macconnelli* (which are especially important dispersers of this family, Julliot 1996) to eat more Sapotaceae fruits or seeds at Montagne de Kaw. Midas tamarins (*S. midas*) are two to three times more abundant than capuchins (*S. apella* and *C. olivaceus*) at Montagne de Kaw and could be responsible for a large part of this ‘compensation’ in fruit consumption. However, this does not translate into compensation in terms of seed removal, which barely reaches 29 % at Montagne de Kaw, compared with 72 % at Nouragues.

514 This means that the animals that eat Sapotaceae fruits at Montagne de Kaw consume them but do not
515 take away their seeds. We interpret this difference in terms of seed size. A good example is given by
516 *Manilkara huberi* and *M. bidentata*. These two Sapotaceae species produce 2.5 – 3 cm fruits that are
517 mostly dispersed by large-bodied primates but also eaten by tamarins (Ratiarison and Forget 2011).
518 At Montagne de Kaw, many eaten fruits found on the ground were barely open by a narrow slit, with
519 all seeds in place (O. Boissier, pers. obs.). We hypothesize that those were squeezed open by tamarins
520 to suck in the pulp without swallowing the seeds (P.-M. Forget, pers. obs.). *Manilkara* seeds are
521 approximately 2.4 cm in length and 1.3 cm in width (Ratiarison and Forget 2011). Oliveira and
522 Ferrari (2000) noted for the now split *Saguinus niger* (formerly *S. midas niger*) that seeds with
523 diameter > 1 cm or length > 2 cm were discarded. While tamarins might offset the absence of large-
524 bodied primates in terms of fruit consumption, they are unable to replace them in terms of seed
525 dispersal. There is no compensation possible for Sapotaceae, neither by birds, which do not eat their
526 fruits, nor by small-bodied primates, which cannot swallow their seeds.

527 However, Burseraceae and Myristicaceae did not show such a marked decrease in seed
528 removal. Unlike Sapotaceae, both families are also dispersed by birds. For example, the genus *Virola*
529 (Myristicaceae) is the genus whose fruits are most frequently consumed by *A. paniscus* (van
530 Roosmalen 1985b). However, at Nouragues, toucans (Ramphastidae) also account for 60.8 % and
531 51.9 % of consumer visits at *Virola kwatae* and *V. michelii* trees, respectively (Ratiarison and Forget
532 2013). With *Ramphastos* toucans significantly more abundant at Montagne de Kaw, one can imagine
533 that the overall number of their visits will be greater and may offset the absence of spider monkeys.
534 Moreira et al. (2017) found that toucans visited all *Virola surinamensis* trees equally across a human-
535 modified landscape in southern Costa Rica, at rates similar to those observed in a protected forest, and
536 could thus provide resilience against seed dispersal limitation. Holbrook and Loiselle (2009),
537 however, observed fewer visits by toucans at *Virola flexuosa* trees at their hunted site in Ecuador
538 relative to their protected site, which suggests that these birds might be less hunted at our site than
539 theirs. Burseraceae have a more generalist seed dispersal strategy than Myristicaceae (Howe 1982),
540 with various bird species visiting fruiting trees in addition to *A. paniscus*, *A. macconnelli* and
541 Ramphastidae (Ratiarison and Forget 2005), which suggests that frugivore compensation would be
542 even more likely. However, Howe (1980) noted that birds only represented 25 % of the potential seed

543 dispersal of *Tetragastris panamensis* in years of heavy fruit fall. In more heavily defaunated contexts
544 than Montagne de Kaw, it is unlikely that birds would completely offset the absence of mammals,
545 especially since dispersers of *T. panamensis* use many other food resources. As Wright (2003) noted,
546 the likelihood of compensation decreases as hunting pressure increases and depletes more species.
547 Moreover, birds are also affected by hunting and logging. Two avian dispersers of Burseraceae also
548 had significantly reduced abundances at Montagne de Kaw (*Momotus momota* and *Querula*
549 *purpurata*). Finally, the uncensused nocturnal kinkajou (*Potos flavus*) may play an additional
550 potential role in compensation, as this species disperses the seeds of both families (Julien-Laferrière
551 2001). The use of arboreal camera trapping could prove ideal to fill this knowledge gap, as well as to
552 generally monitor fruit consumption in tree canopies (Gregory et al 2014). Poulsen et al. (2002)
553 showed that in-depth studies are required to ascertain the potential for compensation in seed dispersal
554 services between different groups of frugivores. While our study suggests that some compensation
555 may occur for Burseraceae and Myristicaceae, further studies would be needed to confirm this.

556

557 Implications for the management of tropical forests

558 Our method of fruit and seed counts allows to estimate proportions of fruit consumption and
559 seed removal, which directly takes into account potential differences in crop size between trees and
560 facilitates comparisons. This method is also relatively rapid and allows a great number of different
561 trees across different species and families to be sampled without much prior knowledge of their
562 specific biology. It confirms the possibility to generalize the method originally tested by Boissier et
563 al. (2014) on a single genus to any zoochorous tree species whose fruits contain hard outer parts
564 uneaten by frugivores. The facility, rapidity and ease of implementation of this method thus make it
565 an ideal monitoring tool for protected area managers and other field practitioners who desire to go
566 beyond wildlife censuses and monitor the health of ecological processes in a forest. It can be used to
567 monitor seed dispersal processes both over time, for example to monitor the potential ecological
568 impacts of poaching in a protected area or to assess the impacts of a new logging operation, and
569 space, to compare different sites. It is also very cost-effective, as field data collection requires very
570 little gear and limited manpower and experience. It could thus be used at a country scale by a ministry

571 of the environment or department of forestry to get a nation-wide picture of the state of ecological
572 processes in a country's protected area network. Implementation of the method requires choosing
573 species whose fruits contain hard outer parts that are left uneaten by frugivores, such as capsules, pods
574 or berries and drupes with a fibrous pericarp; it cannot be applied to fleshy fruits that are swallowed
575 whole by frugivores. Besides, species such as Sapotaceae whose seed number prior to fruit
576 consumption cannot be counted require prior knowledge of the mean number of seeds per fruit.
577 However, this figure can be relatively easily evaluated in the field by opening a number of intact fruits
578 and counting their seeds to average them.

579 As seed removal limitation occurs at a community scale and threatens the forest as a whole, it
580 is crucial to protect the most important seed dispersers. *Ateles paniscus* and *Alouatta macconnelli* are
581 two of the most important seed dispersers in the Guianas (Mittermeier and van Roosmalen 1981).
582 Their extinction and greatly reduced density at Montagne de Kaw, respectively, is one of the most
583 remarkable results of the first part of this study and is likely to be responsible for a significant
584 proportion of the observed collapse in seed removal at this site. However, this is far from being an
585 isolated case, and Atelid monkeys are threatened by local and global extinctions across the
586 Neotropics. More than 70 % of species (18 out of 25) are globally threatened, making Atelidae the
587 most threatened monkey family in the world (Estrada et al. 2017). This is especially true of the seven
588 species of spider monkeys (*Ateles*), of which two are Critically Endangered, four Endangered and one
589 Vulnerable (IUCN 2019). Atelids are the most important primate seed dispersers of the Neotropics
590 (Mittermeier and van Roosmalen 1981, Bufalo et al. 2016) and are of great importance for plant
591 regeneration. High abundances of Atelids are directly associated with a greater diversity of
592 regenerating plants (Stevenson 2010). A recent study by Genes et al. (2019) showed that the
593 successful reintroduction of howler monkeys to a defaunated site of the Atlantic Forest of Brazil
594 restored ecological interactions between howler monkeys and the plants that they consume, as well as
595 secondary seed dispersal by dung beetles, a group commonly affected by hunting through the loss of
596 mammals whose feces they rely on (Culot et al. 2013, Feer and Boissier 2015). Primate translocation
597 (Beck 2016) is a promising conservation tool and has already been successfully implemented with
598 howler monkeys in French Guiana, Belize and Brazil (Richard-Hansen et al. 2000, Beck 2016, Genes
599 et al. 2019). We thus highly encourage similar attempts to reintroduce Atelids to sites from where

they have been extirpated. In the case of Montagne de Kaw, it would be interesting to see if a reintroduction of *Ateles paniscus* increases seed removal, and if so, to what extent. Naturally, such projects can only be viable if accompanied by a strict control of hunting. The active protection of Atelidae should thus be a top conservation priority, with global and country-scale action plans, both to prevent species extinctions and their manifold consequences on Neotropical forest communities and ecological processes. This is also true for other large and highly threatened primate families elsewhere in the tropics, such as gibbons (Hylobatidae) and great apes (Hominidae). Nonetheless, while these species should be of top conservation concern, the great number of species whose populations are affected by hunting, as exemplified by this and other studies, calls for holistic solutions to be found in order to control hunting in tropical forests and insure that it becomes sustainable.

610

611 Conclusion

Focal observations of visiting frugivores (Holbrook and Loiselle 2009), quantification of seed removal and dispersal (Wright et al. 2000, Forget and Jansen 2007, Wang et al. 2007, Brodie et al. 2009, Holbrook and Loiselle 2009) and recruitment (Nuñez-Iturri and Howe 2007, Terborgh et al. 2008, Vanthomme et al. 2010) all come to the same conclusions: hunting leads to dispersal limitation of tree species dispersed by game animals and threatens to impoverish tropical tree communities, with potentially negative feedbacks on both animals and plants (McConkey et al. 2012). Our study showed that hunting and logging were associated with reduced densities of large, key frugivores and reduced seed removal at the tree community level. We urge that sustainable alternatives be found to commercial hunting in tropical forests before large-scale changes in their community composition dramatically reduce their exceptional richness.

622

623 Acknowledgments

624

O. Boissier, F. Feer and P.-M. Forget conceived the study. O. Boissier collected all field data, performed statistical analyses and wrote the manuscript, with contributions from F. Feer, P.-Y Henry and P.-M. Forget. We thank Marie Charlery and Mélanie Congretel for their assistance in the field, as well as Philippe Gaucher, Patrick Châtelet and Wemo Betian of Nouragues Research Station and Benoît Villette and Jean-François Szpigel of Trésor Regional Nature Reserve. Bernard Perrin (ONF) provided field advice at Montagne de Kaw, and Christian Zwahlen granted us access to the logging concession. Cécile Richard-Hansen (ONCFS) shared with us her experience of hunting in French Guiana. We are especially indebted to Adeline Caubère and Odile Poncy for their assistance with the identification of fruit samples. We are grateful to Jean-Yves Barnagaud, Simon Ducatez, Irene Mendoza and François Mallard for their help with data analysis. Finally, we wish to thank two anonymous reviewers for constructive comments on the original manuscript. Funding for this research was provided by UMR 7179 CNRS-MNHN and Ecole Normale Supérieure.

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896 **Data Availability**

897 Data are available from the Dryad Digital Repository:

898 <https://doi.org/10.5061/dryad.tmpg4f4vc>

899

Table 1: Animal densities and 95 % confidence intervals estimated with DISTANCE 6.0, in individuals per km² (2011 data). Gregarious species (indicated with an ^a) are counted in groups per km². *Alouatta macconnelli*, *Sapajus apella* and *Cebus olivaceus*, *Dasyprocta leporina* and *Psophia crepitans* density estimates are based on 2010 and 2011 visual data. Species with significant differences in density between the two sites (non-overlapping 95% confidence intervals) appear in bold. Densities of some species could not be estimated with Distance. In these cases, mean encounter rate in individuals or groups per km is given in italics. Density difference from Nouragues to Kaw is calculated as: (Density[Kaw] - Density[Nouragues]) / Density[Nouragues]. Each species or species group is specified as being predominantly a seed disperser (SD), seed predator (SP) or both (SD/SP, e.g. the scatter-hoarding *Dasyprocta leporina* eats and destroys seeds but also forgets some of the seeds it caches away from the parent tree).

	Seed disperser/ predator	Nouragues	Kaw	Density difference
MAMMALS				
Primates				
<i>Alouatta macconnelli</i> ^a	SD	1.89 (0.63 - 5.69)	0.16 (0.03 - 0.77)	-92%
<i>Ateles paniscus</i> ^a	SD	5.41 (2.57 - 11.36)	0.00	-100%
<i>Pithecia pithecia</i> ^a	SP	0	0.01	NA
<i>Saguinus midas</i> ^a	SD	2.58 (1.31 - 5.05)	3.05 (1.17 - 7.92)	+18%
<i>Saimiri sciureus</i> ^a	SD/SP	0	0.01	NA
<i>Sapajus apella</i> and <i>Cebus olivaceus</i> ^a	SD/SP	1.63 (0.53 - 5.03)	1.39 (0.67 - 2.87)	-15%
Rodents				

<i>Dasyprocta leporina</i>	SD/SP	3.53 (1.14 - 10.99)	1.50 (0.42 - 5.35)	-58%
<i>Myoprocta acouchy</i>	SD/SP	7.61 (3.69 - 15.66)	6.26 (2.25 - 17.38)	-18%
<i>Sciurillus pusillus</i>	?	0.03	0	-100%
<i>Sciurus aestuans</i>	SD/SP	6.93 (2.42 - 19.82)	11.26 (5.38 - 23.57)	+62%
Ungulates				
Ungulates spp.	SD/SP	5.48 (2.70 - 11.12)	0.41 (0.07 - 2.48)	-93%
Carnivores				
<i>Eira barbara</i>	?	0	0.01	NA
BIRDS				
Tinamidae				
<i>Crypturellus cinereus</i>	SP	0.02	0.03	+50%
<i>Crypturellus variegatus</i>	SP	0.76 (0.41 - 1.43)	1.64 (1.07 - 2.53)	+116%
<i>Tinamus major</i>	SP	0.14 (0.03 - 0.71)	0.44 (0.14 - 1.33)	+214%
Cracidae				
<i>Cracidae spp.</i>	SD/SP	4.05 (1.11 - 14.77)	2.74 (1.21 - 6.23)	-32%
Columbidae				
<i>Geotrygon montana</i>	SP	0.13	0.43	+231%
<i>Leptotila rufaxilla</i>	SP	0.97 (0.43 - 2.20)	4.65 (1.76 - 12.30)	+379%
<i>Patagioenas plumbea</i>	SP	1.67	1.95	+17%
<i>Patagioenas speciosa</i>	SP	0.08	0	-100%

<i>Patagioenas subvinacea</i>	SP	1.18 (0.33 - 4.21)	0.66 (0.21 - 2.04)	-44%
Psophiidae				
<i>Psophia crepitans</i> ^a	SD	1.77 (0.83 - 3.75)	0.86 (0.41 - 1.81)	-51%
Trogonidae				
<i>Trogon collaris</i>	SD	0.12	0.01	-92%
<i>Trogon melanurus</i>	SD	0.97 (0.43 - 2.20)	0.27 (0.12 - 0.64)	-72%
<i>Trogon rufus</i>	SD	2.73 (0.64 - 11.68)	1.52 (0.61 - 3.77)	-44%
<i>Trogon violaceus</i>	SD	0.32	0.12	-63%
<i>Trogon viridis</i>	SD	1.56 (0.44 - 5.50)	1.13 (0.63 - 2.04)	-28%
Momotidae				
<i>Momotus momota</i>	SD	3.25 (1.13 - 9.35)	0.29 (0.09 - 0.94)	-91%
Ramphastidae				
<i>Pteroglossus aracari</i> ^a	SD	1.75 (1.00 - 3.07)	0.61 (0.26 - 1.46)	-65%
<i>Pteroglossus viridis</i> ^a	SD	0.02	0.01	-50%
<i>Ramphastos tucanus</i> ^a	SD	1.46 (1.25 - 1.70)	1.54 (0.80 - 2.95)	+5%
<i>Ramphastos vitellinus</i> ^a	SD	0.69 (0.51 - 0.94)	3.51 (2.26 - 5.46)	+409%
<i>Ramphastos spp.</i> ^a	SD	2.15 (1.87 - 2.48)	5.40 (3.86 - 7.55)	+151%
<i>Selenidera piperivora</i> ^a	SD	4.95 (3.76 - 6.51)	5.21 (2.34 - 11.61)	+5%
Capitonidae				
<i>Capito niger</i>	SD	1.63 (0.60 - 4.47)	1.29 (0.40 - 4.17)	-21%

Falconidae					
<i>Ibycter americanus</i> ^a	?	0.30	0.26	-13%	
Psittacidae					
<i>Amazona</i> spp. ^a	SP	5.39 (3.44 - 8.45)	4.61 (2.61 - 8.16)	-14%	
<i>Ara</i> spp. ^a	SP	0.17	0.03	-82%	
<i>Brotoyeris chrysoptera</i> ^a	SP	3.24 (1.26 - 8.36)	0.93 (0.29 - 3.00)	-71%	
<i>Deroptryus accipitrinus</i> ^a	SP	0.56 (0.34 - 0.90)	0.16 (0.06 - 0.48)	-71%	
<i>Pionites melanocephalus</i> ^a	SP	1.43 (0.47 - 4.34)	4.34 (2.09 - 9.04)	+203%	
<i>Pionus</i> spp. ^a	SP	1.59 (0.77 - 3.30)	1.26 (0.43 - 3.66)	-21%	
<i>Pyrilia caica</i> ^a	SP	0.02	0	-100%	
<i>Pyrrhura picta</i> ^a	SP	0.10	0.08	-20%	
Cotingidae					
<i>Lipaugus vociferans</i>	SD	28.61 (23.28 - 35.16)	42.51 (31.25 - 57.82)	+49%	
<i>Perissocephalus tricolor</i>	SD	0.13	0.03	-77%	
<i>Phoenicircus carnifex</i>	SD	3.01 (1.36 - 6.66)	0.89 (0.24 - 3.38)	-70%	
<i>Querula purpurata</i> ^a	SD	0.69 (0.47 - 1.02)	0.05 (0.01 - 0.26)	-93%	
<i>Rupicola rupicola</i>	SD	0.18	0.01	-94%	
<i>Xipholena punicea</i>	SD	0.02	0.03	+50%	
Turdidae					

<i>Turdus albicollis</i>	SD	7.86 (5.35 - 11.53)	5.72 (3.74 - 8.74)	-27%
Icteridae				
<i>Psarocolius viridis</i>	SD ?	4.30 (2.27 - 8.16)	6.80 (4.26 - 10.84)	+58%
Cardinalidae				
<i>Caryothraustes canadensis</i> ^a	SD ?	4.48 (1.99 - 10.11)	1.77 (0.57 - 5.45)	-60%
Thraupidae				
<i>Saltator grossus</i>	SP	1.53 (0.82 - 2.86)	0.11 (0.04 - 0.31)	-93%

Table 2: Mean removal rate, mean sample size and number of trees sampled for each family and species at Nouragues and Montagne de Kaw (raw data).

	Nouragues		Kaw	
	Mean removal rate (%)	Mean number of fruits per m ² ± SD (number of trees sampled)	Mean removal rate (%)	Mean number of fruits per m ² ± SD (number of trees sampled)
Burseraceae				
<i>Tetragastris</i>	56.65	49.2 ± 39.3 (5)	35.26	72.5 ± 50.1 (4)
<i>panamensis</i>				
<i>Tetragastris</i> sp2	15.15	77 (1)	-	-
<i>Protium</i>	67.42	18 (1)	68.00	15 (1)
<i>sagotianum</i>				
Total	52.26	48.7 ± 36.3 (7)	41.81	61.0 ± 50.4 (5)
Myristicaceae				
<i>Virola michelii</i>	79.10	23.0 ± 6.2 (3)	36.59	205 (1)
<i>Virola kwatae</i>	91.67	24 (1)	-	-
<i>Iryanthera</i>	93.23	45.0 ± 1.4 (2)	80.24	49.2 ± 33.5 (6)
<i>sagotiana</i>				
<i>Iryanthera</i>	-	-	96.00	25 (1)
<i>hostmannii</i>				
<i>Osteophloeum</i>	-	-	50.00	16 (1)
<i>platyspermum</i>				
Total	85.91	30.5 ± 11.9 (6)	73.78	60.1 ± 61.8 (9)
Sapotaceae				
<i>Chrysophyllum</i>	74.90	18.8 ± 6.8 (4)	-	-
<i>lucentifolium</i>				
<i>Manilkara huberi</i>	78.29	41.7 ± 26.7 (3)	31.99	53.8 ± 45.8 (5)
<i>Manilkara</i>	69.00	37.5 ± 2.1 (2)	-	-
<i>bidentata</i>				

<i>Micropholis</i>	32.14	140 (1)	42.57	251.0 ± 285.7 (2)
<i>guyanensis</i>				
<i>Micropholis</i> sp1	-	-	12.73	958 (1)
<i>Micropholis</i> sp2	-	-	26.71	161 (1)
Total	70.46	41.5 ± 38.5 (10)	31.61	210.0 ± 311.7 (9)
Fabaceae				
<i>Inga leiocalycina</i>	53.87	20.0 ± 11.3 (2)	-	-
<i>Inga thibaudiana</i>	91.89	8 (1)	-	-
<i>Inga alba</i>	-	-	79.07	26.5 ± 4.4 (4)
<i>Inga rubiginosa</i>	-	-	81.48	18.0 ± 1.4 (2)
<i>Inga paraensis</i>	-	-	8.33	17 (1)
<i>Inga huberi</i>	-	-	57.89	26 (1)
Total	66.54	16.0 ± 10.6 (3)	68.18	23.1 ± 5.4 (8)
Total	68.67	38.0 ± 31.6 (26)	54.94	94.2 ± 182.1 (31)

Table 3: Generalized linear mixed model results: fixed effects for fruit consumption of Sapotaceae and for seed removal across all families, assessed by likelihood ratio tests. Significant P-values are shown in bold. Median bootstrap values of bootstrapped parameters appear in italics along their 95 % confidence intervals.

Response variable	Dataset	Fixed effects	χ^2	Df	P
Fruit consumption	Family level (Sapotaceae)	Site	1.595	1	0.207
		Species	24.994	13	0.023
Seed removal	Community level	Site	12.497	1	< 0.001
			7.39		0.007
			(1.42; 15.98)		(< 0.0001; 0.23)
		Family	8.186	3	0.042
		Site x Family	3.159	3	0.368

Table 4: Generalized linear mixed model results: fixed effects of site and species on fruit consumption for Sapotaceae, tested by t-test. Intercepts are Montagne de Kaw (site effect) and Sapotaceae sp1 (species effect). Significant P-values are shown in bold.

	Estimate	Standard Error	Z value	<i>P</i>
Intercept	-0.76	0.74	-1.02	0.309
Site Nouragues	0.54	0.42	1.28	0.201
Species Chrysophyllum cuneifolium cf	4.07	1.45	2.80	0.005
Chrysophyllum lucentifolium	2.83	1.02	2.78	0.005
Chrysophyllum sp1	2.03	1.20	1.69	0.092
Manilkara bidentata	1.43	1.01	1.42	0.157
Manilkara huberi	1.59	0.80	1.98	0.048
Manilkara sp	0.45	0.91	0.49	0.623
Micropholis cayennensis	1.84	0.87	2.12	0.034
Micropholis guyanensis	0.97	0.85	1.14	0.254
Micropholis sp1	0.24	0.99	0.24	0.812
Micropholis sp2	0.77	1.00	0.77	0.441
Micropholis sp3	-0.01	1.06	-0.01	0.991
Pouteria egregia	2.84	1.04	2.75	0.006
Pouteria filipes	1.23	1.17	1.05	0.294

Table 5: Generalized linear mixed model results: fixed effects of site and family on seed removal across all families (community level), tested by t-test. Intercepts are Montagne de Kaw (site effect) and Burseraceae (family effect). Significant P-values are shown in bold. Median bootstrap values of bootstrapped parameters appear in italics along their 95 % confidence intervals.

	Estimate	Standard Error	Z value	<i>P</i>
Intercept	-0.91	0.31	-2.96	0.003
Site Nouragues	1.27	0.28	4.50	< 0.00001
	<i>1.35</i>	<i>0.34</i>	<i>3.85</i>	<i>0.0001</i>
	<i>(0.66; 2.01)</i>	<i>(0.21; 0.58)</i>	<i>(1.59; 8.00)</i>	<i>(<0.0001; 0.11)</i>
Family Fabaceae	1.14	0.64	1.78	0.076
Myristicaceae	1.99	0.54	3.66	< 0.001
Sapotaceae	0.32	0.34	0.95	0.34

Figure 1: Representative fruits of the studied tree families. (A) *Tetragastris panamensis* (Burseraceae); (B) *Iryanthera sagotiana* (Myristicaceae); (C) *Manilkara bidentata* (Sapotaceae); (D) *Inga leiocalycina* (Fabaceae). Photographs: Olivier Boissier and Marie Charlery.

Figure 2: Seed removal rate (\pm S.E.) of all families pooled together, and family-level rates of Burseraceae, Myristicaceae and Sapotaceae, at Nouragues (protected site) and Montagne de Kaw (hunted and partly logged site). Estimates of the final model are shown (site and family as fixed effects, no interaction; transect, year and species nested within family as random effects).

A



B



C



D



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