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## **Modifications of the rainforest frugivore community are associated with reduced seed removal at the community level**

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22

Accepted Article

## 23 Abstract

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

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

48

## 49 Introduction



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

59 Previous studies have shown frugivores to be more sensitive than other trophic guilds to  
60 overhunting (Peres and Palacios 2007) or other forms of forest disturbance (Gray et al. 2007). But as  
61 seed dispersers, these animals play a key role in plant regeneration. They ensure the survival of seeds  
62 away from parent trees (Janzen 1970, Connell 1971, Chapman and Chapman 1995), shape the spatial  
63 pattern of trees in the forest (Howe 1989, Julliot 1997, Fragoso et al. 2003, Russo and Augspurger  
64 2004, Trolliet et al. 2017) and facilitate establishment in new territories (Howe and Smallwood 1982,  
65 Galindo-González et al. 2000, Carlo and Morales 2016). Moreover, a majority of woody plants in  
66 tropical forests rely on vertebrates for seed dispersal (Forget et al. 2007). The possibility that  
67 overhunting may indirectly impact seed dispersal was first highlighted by Janzen (1986) and Redford  
68 (1992), who argued that an otherwise intact forest depleted of its seed dispersers would have many of  
69 its ecological processes stalled.

70 At the recruitment stage, hunting has been shown to reduce the density and species richness of  
71 saplings of tree species dispersed by game animals (Nuñez-Iturri and Howe 2007, Terborgh et al.  
72 2008, Vanthomme et al. 2010). Sapling recruitment of species with animal-dispersed seeds declines  
73 compared to those that are abiotically dispersed, and large-seeded species are affected to an even  
74 greater extent (Harrison et al. 2013). These observed differences in sapling recruitment can be  
75 explained by hunting-induced seed dispersal limitation. Fewer frugivores visit fruiting trees in hunted  
76 forests, which translates into reduced seed removal in the canopy (Holbrook and Loiselle 2009).  
77 Consequently, many more fallen seeds are to be found underneath trees (Wang et al. 2007, Brodie et

78 al. 2009), the vast majority of which are undispersed and come from the same mother tree (Wang et  
79 al. 2007). Fewer seeds are scatter-hoarded by rodents (Forget and Jansen 2007), and a much lower  
80 proportion of dispersed seeds are found in the forest away from beneath fruiting conspecifics (Wright  
81 et al. 2000, Brodie et al. 2009). This in turn translates into reduced recruitment and sapling density.  
82 However, all studies investigating the impact of hunting on seed dispersal so far have chosen to focus  
83 on one or two species of animal-dispersed trees (Wright et al. 2000, Beckman and Muller-Landau  
84 2007, Forget and Jansen 2007, Wang et al. 2007, Brodie et al. 2009, Holbrook and Loiselle 2009).  
85 Whether these results can be extrapolated at the community level remains to be confirmed.

86

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

99

## 100 Methods

### 101 Study sites

102 The protected forest site is located at Nouragues Research Station (4°05' N, 52°40' W), in the  
103 105,800 ha Nouragues National Nature Reserve in central French Guiana. The climate is of equatorial

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

113 The hunted and logged forest is situated on Montagne de Kaw (4°33' N, 52°12' W), 70 km  
114 north-east of Nouragues Research Station. The climate is the same as at Nouragues, but for a higher  
115 mean annual rainfall of 4,099 mm, with important local variations. Montagne de Kaw is a 40 km long,  
116 elongated hill, reaching 333 m above sea level (study locations from 20 to 290 m in elevation).  
117 Montagne de Kaw and Nouragues are part of the same forest landscape (Guitet et al. 2015). The site is  
118 adjacent to the town of Roura, population 2,600, and an hour's drive from Cayenne, the territory's  
119 capital. A road that runs along the ridge was opened in 1980 and paved in 1991. Both local and urban  
120 populations hunt along the road and on the tracks that go into the forest, using shotguns, motorized  
121 vehicles, and, for some of them, dogs and spotlights (O. Boissier, pers. obs.). Hunting is both  
122 recreational and commercial (C. Richard-Hansen, pers. comm.). Although parts of Montagne de Kaw  
123 are protected as Kaw-Roura National Nature Reserve and Trésor Regional Nature Reserve, the forest  
124 is not effectively protected from hunting, which occurs within reserve boundaries (C. Richard-  
125 Hansen, pers. comm.). The most sought-after species include peccaries (Tayassuidae), deer (*Mazama*  
126 spp.), lowland tapir (*Tapirus terrestris*), atelid and capuchin monkeys (*Ateles paniscus*, *Alouatta*  
127 *macconnelli*, *Sapajus apella* and *Cebus olivaceus*), armadillos (Dasypodidae and Chlamyphoridae),  
128 lowland paca (*Cuniculus paca*), common red-rumped agouti (*Dasyprocta leporina*), Cracidae, gray-  
129 winged trumpeter (*Psophia crepitans*) and toucans (Ramphastidae) (C. Richard-Hansen, pers.  
130 comm.). Commercial selective logging occurs within a logging concession where 2000 m<sup>3</sup> of timber  
131 are taken annually.

## 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<sup>-1</sup>, 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

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

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

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

226 
$$R = 1 - \frac{S_g + S_f}{S_F},$$

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

232  $S_g$  is always counted. However, the way to determine  $S_f$  and  $S_F$  varies between families. In  
233 Burseraceae and Fabaceae, the exact number of seeds per fruit can easily be counted, since each seed  
234 leaves a characteristic mark on the fruit (a notch and a bulge on the pod, respectively). Thus  $S_f$  is the  
235 number of seed marks summed over all intact fruits, and  $S_F$  is the number of seed marks summed over  
236 all fruits, whether intact, eaten or open. Myristicaceae and some Sapotaceae species only have one  
237 seed per fruit. Then  $S_f$  is the number of intact fruits and  $S_F$  is the total number of fruits (Boissier et al.  
238 2014). However, the number of seeds originally contained in a multiple-seeded Sapotaceae fruit  
239 cannot be counted once the fruit has been eaten and all or some of the seeds swallowed. For these  
240 species, we had to rely on a mean number of seeds per fruit  $n$  taken from the literature for each

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

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

252

## 253 Data analysis

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

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



268 generalized linear mixed models with function lmer of package lme4 (Bates et al. 2011). Since the  
269 response variables were proportion data, we used a binomial error distribution with a logit link,  
270 adjusted for overdispersion (Bolker et al. 2009). Fruit consumption was analyzed separately for  
271 Sapotaceae and Fabaceae, with site and species as fixed effects and transect and year as random  
272 effects. Seed removal was analyzed at the community level, with all four families pooled together,  
273 with site and family as fixed effects and an interaction term allowing for the effect of site to differ  
274 between families. Transect, year and species nested within family were included as random effects.  
275 The statistical significance of fixed effects and their interaction was assessed by likelihood ratio tests  
276 between nested models fit by maximum likelihood. The robustness of the statistical significance of  
277 the site effect to specificities of the available dataset (e.g. outliers) was tested using a bootstrap in  
278 which the model was repeatedly run over a random sampling with replacement of the original dataset  
279 (1000 runs, resampling units were individual trees, sample size of trees was kept the same as in the  
280 initial dataset for each site).

281

282

## 283 Results

### 284 Abundance of frugivores

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

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

302

### 303 Fruit consumption and seed removal

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

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

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

323 Fruit consumption of Sapotaceae did not significantly differ between the protected site (77 %)  
324 and the hunted and logged site (67 %;  $\chi^2 = 1.595$ ,  $df = 1$ ,  $P = 0.207$ ) (Tables 3 and 4). Fabaceae could  
325 not be compared between sites since only three trees were sampled at Nouragues. Seed removal  
326 differed significantly between Nouragues and Montagne de Kaw ( $\chi^2 = 12.497$ ,  $df = 1$ ,  $P < 0.001$ )  
327 (Tables 3 and 5). The overall community level seed removal rate was 77 % at Nouragues (protected)  
328 and 47 % at Montagne de Kaw (hunted and logged) (Figure 2). Seed removal also differed among  
329 families ( $\chi^2 = 8.186$ ,  $df = 3$ ,  $P = 0.042$ ), but there was no significant site-by-family interaction ( $\chi^2 =$   
330  $3.159$ ,  $df = 3$ ,  $P = 0.368$ ). Seed removal rate at Nouragues and Montagne de Kaw was 50 % and 34 %  
331 for Burseraceae, 91 % and 75 % for Myristicaceae, and 72 % and 29 % for Sapotaceae, respectively.  
332 The site effect was robust to the omission of genus *Micropholis* from the data set ( $\chi^2 = 9.063$ ,  $df = 1$ ,  
333  $P = 0.003$ ), whereas in this case there was no significant family effect ( $\chi^2 = 6.867$ ,  $df = 3$ ,  $P = 0.076$ ).  
334 The statistical difference in seed removal between sites was relatively robust to potential specificities  
335 of the initial dataset, since the effect was significant in most datasets resampled by bootstrap (95.5 %  
336 of datasets by t-test and 89.7 % by likelihood ratio test; Tables 3 and 5).

337

338

339

## 340 Discussion

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

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.

350

### 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

402 (e.g. Wang et al. 2007, Terborgh et al. 2008, Holbrook and Loiselle 2009), the time-consuming  
403 character of single observer line transect surveys, along with cost and logistic constraints, limited the  
404 span of our study to a single control and impacted site and precluded site replication. This is a  
405 frequently encountered situation in field ecological research (Davies and Gray 2015). Nevertheless,  
406 our results are consistent with those of other studies that show a decline of large game species due to  
407 hunting (Peres and Palacios 2007) along with a significant decrease in seed removal (Wright et al.  
408 2000, Forget and Jansen 2007, Wang et al. 2007, Brodie et al. 2009, Holbrook and Loiselle 2009,  
409 Lermyte and Forget 2009). While the fact that hunting is responsible for the decline of large hunted  
410 species such as *Ateles paniscus*, *Alouatta macconnelli* and ungulates is the most parcimonious  
411 conclusion, we remain cautious regarding the factors leading to abundance changes in other, non-  
412 hunted species. Also, since we only practiced daytime censuses, we missed a few seed dispersers of  
413 our focal families, most notably kinkajou (*Potos flavus*) and lowland paca (*Cuniculus paca*).

414

#### 415 Seed removal limitation

416 Combined with the loss or decline of seed dispersers, we found a significant reduction in  
417 seed removal at the community level, from 77 % at Nouragues (protected) to 47 % at Montagne de  
418 Kaw (hunted and logged). This decrease was also observed for all three families for which sample  
419 size allowed family-level comparisons to be made (Burseraceae, Myristicaceae and Sapotaceae). This  
420 confirms that limitation of seed removal under hunting is not just the fact of a few case species  
421 (Wright et al. 2000, Forget and Jansen 2007, Wang et al. 2007, Brodie et al. 2009, Holbrook and  
422 Loiselle 2009, Lermyte and Forget 2009), but happens at the community level. At Nouragues,  
423 Burseraceae, Myristicaceae, Sapotaceae and Fabaceae (*Inga* spp.) represent 24.3 % of the trees of a  
424 12 ha study plot (5.1, 1.9, 13.1 and 4.2 %, respectively) (Allié 2012). On the mere basis of our four  
425 study families, the regeneration of 24.3 % of the forest would thus be jeopardized by seed removal  
426 limitation, were Nouragues to be subjected to the same pressures as Montagne de Kaw. We suppose  
427 that the results that we obtained from these four major families would apply to other families whose  
428 fruits are dispersed totally or partially by hunted animal species and that an even greater proportion of  
429 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 *Viola 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 *Viola 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

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

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



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

495

## 496 Compensation between frugivore species

497 There has been a long-standing debate about the possibility of compensation in dispersal  
498 services by remaining frugivores when other guild members have been extirpated (Gautier-Hion et al.  
499 1985, Poulsen et al. 2002, Jansen et al. 2012). In our study, generalist families that rely on both  
500 mammals and birds for seed dispersal (Burseraceae and Myristicaceae) faced smoother declines in  
501 seed removal than specialist families that depend entirely on mammals (Sapotaceae). This suggests  
502 that some compensation by birds may occur for the more generalist families.

503 Consumption rates of Sapotaceae fruits were not significantly different between Nouragues  
504 and Montagne de Kaw, while Sapotaceae are the first-ranking family in the fruit diet of *Ateles*  
505 *paniscus*, *Alouatta macconnelli* and *Sapajus apella* during fruit peak at Nouragues (Simmen and  
506 Sabatier 1996). A possible explanation to the similar consumption rates is that smaller primates  
507 (*Saguinus midas*, *S. apella* and *Cebus olivaceus*) and seed predators such as Psittacidae take  
508 advantage of the absence of *A. paniscus* and scarcity of *A. macconnelli* (which are especially  
509 important dispersers of this family, Julliot 1996) to eat more Sapotaceae fruits or seeds at Montagne  
510 de Kaw. Midas tamarins (*S. midas*) are two to three times more abundant than capuchins (*S. apella*  
511 and *C. olivaceus*) at Montagne de Kaw and could be responsible for a large part of this  
512 ‘compensation’ in fruit consumption. However, this does not translate into compensation in terms of  
513 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

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

610

## 611 Conclusion

612 Focal observations of visiting frugivores (Holbrook and Loiselle 2009), quantification of seed  
613 removal and dispersal (Wright et al. 2000, Forget and Jansen 2007, Wang et al. 2007, Brodie et al.  
614 2009, Holbrook and Loiselle 2009) and recruitment (Nuñez-Iturri and Howe 2007, Terborgh et al.  
615 2008, Vanthomme et al. 2010) all come to the same conclusions: hunting leads to dispersal limitation  
616 of tree species dispersed by game animals and threatens to impoverish tropical tree communities, with  
617 potentially negative feedbacks on both animals and plants (McConkey et al. 2012). Our study showed  
618 that hunting and logging were associated with reduced densities of large, key frugivores and reduced  
619 seed removal at the tree community level. We urge that sustainable alternatives be found to  
620 commercial hunting in tropical forests before large-scale changes in their community composition  
621 dramatically reduce their exceptional richness.

622

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624

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637

638

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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

Accepted Article



**Table 1:** Animal densities and 95 % confidence intervals estimated with DISTANCE 6.0, in individuals per km<sup>2</sup> (2011 data). Gregarious species (indicated with an <sup>a</sup>) are counted in groups per km<sup>2</sup>. *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
<b>MAMMALS</b>				
Primates				
<i>Alouatta macconnelli</i> <sup>a</sup>	SD	1.89 (0.63 - 5.69)	0.16 (0.03 - 0.77)	-92%
<b><i>Ateles paniscus</i></b> <sup>a</sup>	SD	5.41 (2.57 - 11.36)	0.00	-100%
<i>Pithecia pithecia</i> <sup>a</sup>	SP	<i>0</i>	<i>0.01</i>	NA
<i>Saguinus midas</i> <sup>a</sup>	SD	2.58 (1.31 - 5.05)	3.05 (1.17 - 7.92)	+18%
<i>Saimiri sciureus</i> <sup>a</sup>	SD/SP	<i>0</i>	<i>0.01</i>	NA
<i>Sapajus apella</i> and <i>Cebus olivaceus</i> <sup>a</sup>	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				
<b>Ungulates spp.</b>	SD/SP	5.48 (2.70 - 11.12)	0.41 (0.07 - 2.48)	-93%
Carnivores				
<i>Eira barbara</i>	?	0	0.01	NA
<b>BIRDS</b>				
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> <sup>a</sup>	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				
<b><i>Momotus momota</i></b>	SD	3.25 (1.13 - 9.35)	0.29 (0.09 - 0.94)	-91%
Ramphastidae				
<i>Pteroglossus aracari</i> <sup>a</sup>	SD	1.75 (1.00 - 3.07)	0.61 (0.26 - 1.46)	-65%
<i>Pteroglossus viridis</i> <sup>a</sup>	SD	0.02	0.01	-50%
<i>Ramphastos tucanus</i> <sup>a</sup>	SD	1.46 (1.25 - 1.70)	1.54 (0.80 - 2.95)	+5%
<b><i>Ramphastos vitellinus</i></b> <sup>a</sup>	SD	0.69 (0.51 - 0.94)	3.51 (2.26 - 5.46)	+409%
<b><i>Ramphastos spp.</i></b> <sup>a</sup>	SD	2.15 (1.87 - 2.48)	5.40 (3.86 - 7.55)	+151%
<i>Selenidera piperivora</i> <sup>a</sup>	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%

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Falconidae

*Ibycter americanus*<sup>a</sup> ? 0.30 0.26 -13%

Psittacidae

*Amazona* spp.<sup>a</sup> SP 5.39 (3.44 - 8.45) 4.61 (2.61 - 8.16) -14%

*Ara* spp.<sup>a</sup> SP 0.17 0.03 -82%

*Brotogeris chrysoptera*<sup>a</sup> SP 3.24 (1.26 - 8.36) 0.93 (0.29 - 3.00) -71%

*Deropterus accipitrinus*<sup>a</sup> SP 0.56 (0.34 - 0.90) 0.16 (0.06 - 0.48) -71%

*Pionites melanocephalus*<sup>a</sup> SP 1.43 (0.47 - 4.34) 4.34 (2.09 - 9.04) +203%

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*Pionus* spp.<sup>a</sup> SP 1.59 (0.77 - 3.30) 1.26 (0.43 - 3.66) -21%

*Pyrilia caica*<sup>a</sup> SP 0.02 0 -100%

*Pyrrhura picta*<sup>a</sup> SP 0.10 0.08 -20%

Cotingidae

*Lipaugus vociferans* SD 28.61 (23.28 - 35.16) 42.51 (31.25 - 57.82) +49%

*Perissocephalus tricolor* SD 0.13 0.03 -77%

*Phoenicircus carnifex* SD 3.01 (1.36 - 6.66) 0.89 (0.24 - 3.38) -70%

***Querula purpurata***<sup>a</sup> SD 0.69 (0.47 - 1.02) 0.05 (0.01 - 0.26) -93%

*Rupicola rupicola* SD 0.18 0.01 -94%

*Xipholena punicea* SD 0.02 0.03 +50%

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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> <sup>a</sup>	SD ?	4.48 (1.99 - 10.11)	1.77 (0.57 - 5.45)	-60%
Thraupidae				
<b><i>Saltator grossus</i></b>	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).

	<b>Nouragues</b>		<b>Kaw</b>	
	Mean removal rate (%)	Mean number of fruits per m <sup>2</sup> ± SD (number of trees sampled)	Mean removal rate (%)	Mean number of fruits per m <sup>2</sup> ± SD (number of trees sampled)
<b>Burseraceae</b>				
<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)
<b>Myristicaceae</b>				
<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)
<b>Sapotaceae</b>				
<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)
<b>Fabaceae</b>				
<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)
<b>Total</b>	<b>68.67</b>	<b>38.0 ± 31.6 (26)</b>	<b>54.94</b>	<b>94.2 ± 182.1 (31)</b>

**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	$\chi^2$	Df	<i>P</i>
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	<b>&lt; 0.001</b>
			<i>7.39</i>		<i>0.007</i>
			<i>(1.42; 15.98)</i>		<i>(&lt; 0.0001; 0.23)</i>
		Family	8.186	3	<b>0.042</b>
	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	<b>0.005</b>
Chrysophyllum lucentifolium	2.83	1.02	2.78	<b>0.005</b>
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	<b>0.048</b>
Manilkara sp	0.45	0.91	0.49	0.623
Micropholis cayennensis	1.84	0.87	2.12	<b>0.034</b>
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	<b>0.006</b>
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	<b>0.003</b>
Site Nouragues	1.27	0.28	4.50	<b>&lt; 0.00001</b>
	<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>(&lt;0.0001; 0.11)</i>
Family Fabaceae	1.14	0.64	1.78	0.076
Myristicaceae	1.99	0.54	3.66	<b>&lt; 0.001</b>
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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