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Modifications of the rain forest frugivore community are associated with reduced seed removal at the community level

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Abstract. Tropical rain forests 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 that 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 1-m² 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: French Guiana; frugivory; hunting; logging; seed dispersal; seed removal; tropical rain forest.

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

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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.

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.

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 3-h 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 northeast 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 a 1-h 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, *personal observation*). Hunting is both recreational and commercial (C. Richard-Hansen, *personal communication*). 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, *personal communication*). 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, *personal communication*). Commercial selective logging occurs within a logging concession where 2,000 m³ of timber are taken annually.

METHODS

Study sites

The protected forest site is located at Nouragues Research Station (4°05' N, 52°40' W), in the 105,800-ha

Tree families

Although the whole community of fruiting endozoochorous tree species was sampled, four families were eventually selected on the basis of their abundance, sample size, and significance to frugivores: Burseraceae,

Myristicaceae, Sapotaceae, and Fabaceae. These families accounted for 88% of all fruiting endozoochorous trees encountered and sampled ($n = 82$) and thus represent the vast majority of the fruit resource available to frugivores during the study. The sampled species of Burseraceae and Myristicaceae are dispersed by both mammals and birds, whereas Sapotaceae and Fabaceae are dispersed by mammals only. The fruits of these families (Fig. 1) all contain hard outer parts that are left uneaten and dropped to the ground by frugivores (Sabatier 1983, van Roosmalen 1985b), which allows counts of fallen fruits to be made, contrary to some other animal-dispersed families whose soft fruits are entirely consumed by frugivores (Boissier et al. 2014).

Burseraceae and Myristicaceae are canopy trees. Burseraceae fruit annually, from February to June in French Guiana (Ratiarison 2003, Ratiarison and Forget 2005). They produce green to bright purple-red pseudocapsules containing one to six locules closed by valves that dehisce at maturity, revealing white, medium-sized, arillate seeds (one per locule; length 16–22 mm). Myristicaceae fruit earlier than Burseraceae, between October and April in French Guiana (Sabatier 1983, 1997). Like Burseraceae, they produce dehiscent fruits (capsules). These open into two valves that expose a single arillate seed (length: 19–28 mm). The bright red, netlike aril is very nutritious, containing over 50% lipids (Howe 1981,

Howe and Kerckhove 1981). Seeds of both families are dispersed by primates (*Ateles paniscus*, *Alouatta macconnelli*, *Sapajus apella*, and *Cebus olivaceus*), Kinkajou (*Potos flavus*), Toucans (Ramphastidae), Trogons (Trogonidae), Guans (Cracidae), and Motmots (Mototidae). In addition, Burseraceae are dispersed by Midas tamarin (*Saguinus midas*) and a wide range of other avian dispersers such as Cotingas (Cotingidae), Parrots (Psittacidae), and Squirrels (Sciuridae) predate the seeds of both families (Howe 1980, 1981, Howe and Kerckhove 1981, Simmen and Sabatier 1996, Sabatier 1997, Kays 1999, Pack et al. 1999, Oliveira and Ferrari 2000, Julien-Laferrrière 2001, Ratiarison 2003, Ratiarison and Forget 2005, 2013, Holbrook and Loiselle 2009).

Unlike Burseraceae and Myristicaceae, Sapotaceae produce indehiscent fruits (berries) that cannot be opened by birds, except parrots (Ratiarison 2003, Ratiarison and Forget 2011). These canopy trees fruit from January to June, some on a yearly basis (e.g., *Chrysophyllum*), some on mast fruiting events (e.g., *Manilkara*; Norden et al. 2007, Mendoza et al. 2015). Berries display a fibrous pericarp that contains 1–10 seeds (length 13–25 mm) surrounded by sweet-tasting pulp (van Roosmalen 1985a). Sapotaceae fruits are a primate favorite: red-faced black spider monkey (*Ateles paniscus*), Guianan red howler (*Alouatta macconnelli*), and Guianan brown capuchin (*Sapajus apella*) all disperse their seeds



FIG. 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 Charley.

(van Roosmalen 1985b, Julliot and Sabatier 1993, Simmen and Sabatier 1996, Ratiarison 2003, Ratiarison and Forget 2011), as well as Kinkajou (*Potos flavus*) (Kays 1999, Julien-Laferrière 2001), while Parrots (Psittacidae) and squirrels (Sciuridae) predate the seeds (Ratiarison 2003, Ratiarison and Forget 2011). Finally, Fabaceae were represented by the genus *Inga*. In March–April, these trees produce pods whose medium-sized seeds (length 12–18 mm) are surrounded by a sugar-rich pulp (Sabatier 1983, van Roosmalen 1985a). These attract primates (*A. paniscus*, *S. apella*, *S. midas*, but not *A. macconnelli*) and *P. flavus*, which disperse the seeds (van Roosmalen 1985b, Julliot and Sabatier 1993, Simmen and Sabatier 1996, Kays 1999, Pack et al. 1999, Oliveira and Ferrari 2000, Julien-Laferrière 2001), that are also predated by parrots (Psittacidae) (Galetti and Rodrigues 1992).

Abundance of frugivorous mammals and birds

We performed line transect censuses (Bibby et al. 2000) to estimate the density of frugivores at each site, focusing on confirmed and potential seed dispersers and predators of our four tree families. Three transects were used at Nouragues (control site) and four at Montagne de Kaw, two of which were in the logging concession (hunting and logging) and two outside (hunting alone). Given the great number of mammalian and avian species to be censused (around 60), which translated into high contact frequency along transects, we established transects that were shorter than those in similar studies (Wright et al. 2000, Lamertink 2004, Nuñez-Iturri and Howe 2007, Terborgh et al. 2008). Transect length was 2,000 m at Nouragues. Transects at Montagne de Kaw were 1,600, 1,900, 2,000, and 2,100 m in length. Surveys were performed during the wet season (late January–early May) in 2010 and 2011. All surveys were conducted by the same observer (O. Boissier). Transects at one site were walked every day in turns, with each site being alternately censused for three weeks so as to minimize any seasonal effects. Transects were walked 10 times each over the 2 yr of the study, four times in 2010 and six times in 2011. Total distance walked was 136 km (60 km at Nouragues and 76 km at Montagne de Kaw). No survey was conducted on rainy days. If rain started during a transect walk, the census was suspended and resumed if rain stopped within 30 min, and aborted otherwise. Censuses started at 07:00. Transects were walked at an average speed of 800 m/h, with markers every 100 m for calibration. All seed dispersers and predators of the study families were recorded. Not included were nocturnal frugivores, most notably Kinkajou (*Potos flavus*), nocturnal rodents such as Lowland Paca (*Cuniculus paca*) and spiny rats (*Proechimys* spp.), and bats. For each contact, the observer recorded the species, number of individuals, type of detection (visual or auditory), time, position along the transect, and estimated the perpendicular distance from the transect line to the animal or the center of the group for

gregarious species. Distance was estimated in 5-m classes for visual contacts and, in 2011 only, in five distance intervals for acoustic contacts (0–20 m, 20–50 m, 50–100 m, 100–200 m, and beyond 200 m). Birds flushed by the observer were recorded, but not those seen or heard flying past. This led to an underestimation of species that call mostly in flight and remain silent when perched, such as some Psittacidae species (e.g., *Pionus* spp.). Small, solitary, terrestrial animals and quiet and secretive bird species that do not flush easily also tend to be underestimated, as in most survey methods (Bibby et al. 2000, Denis et al. 2017).

Fruit consumption and seed removal of fruiting trees

Between March and May 2010 and February and April 2011, during the fruiting season of most tree families (Sabatier 1985, Mendoza et al. 2018), we assessed fruit consumption and seed removal by counting fallen fruits and seeds beneath the crowns of fruiting trees. We located fruiting trees of endozoochorous families along the same transects as those used for frugivore censuses, and up to 50 m away from the transect line. Underneath each tree, we placed a single 1-m² quadrat where fruit density on the ground was maximal (Boissier et al. 2014). Trees with fewer than 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 χ^2 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 data set (e.g., outliers) was tested using a bootstrap in which the model was repeatedly run over a random sampling with replacement of the original data set (1,000 runs, resampling units were individual trees, sample size of trees was kept the same as in the initial data set for each site).

RESULTS

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*), Amazonian Motmot (*Momotus momota*), Purple-throated Fruitcrow (*Querula purpurata*), and Slate-colored Grosbeak (*Salinator grossus*). In addition, Guianan red howler (*Alouatta macconnelli*) was 12 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

TABLE 1. Animal densities and 95% confidence intervals (in parentheses) estimated with DISTANCE 6.0 (2011 data).

Taxon	Seed disperser or predator	Density (individuals/km ²)		Density difference (%)
		Nouragues	Kaw	
Mammals				
Primates				
<i>Alouatta macconnelli</i> †	SD	1.89 (0.63–5.69)	0.16 (0.03–0.77)	–92
<i>Ateles paniscus</i> †	SD	5.41 (2.57–11.36)	0.00	–100
<i>Pithecia pithecia</i> †	SP	0	0.01	NA
<i>Saguinus midas</i> †	SD	2.58 (1.31–5.05)	3.05 (1.17–7.92)	+18
<i>Saimiri sciureus</i> †	SD/SP	0	0.01	NA
<i>Sapajus apella</i> and <i>Cebus olivaceus</i> †	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				
<i>Ungulates spp.</i>	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> †	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> †	SD	1.75 (1.00–3.07)	0.61 (0.26–1.46)	–65
<i>Pteroglossus viridis</i> †	SD	0.02	0.01	–50
<i>Ramphastos tucanus</i> †	SD	1.46 (1.25–1.70)	1.54 (0.80–2.95)	+5
<i>Ramphastos vitellinus</i>†	SD	0.69 (0.51–0.94)	3.51 (2.26–5.46)	+409
<i>Ramphastos spp.</i>†	SD	2.15 (1.87–2.48)	5.40 (3.86–7.55)	+151
<i>Selenidera piperivora</i> †	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> †	?	0.30	0.26	–13
Psittacidae				
<i>Amazona spp.</i> †	SP	5.39 (3.44–8.45)	4.61 (2.61–8.16)	–14
<i>Ara spp.</i> †	SP	0.17	0.03	–82

TABLE 1. (Continued)

Taxon	Seed disperser or predator	Density (individuals/km ²)		Density difference (%)
		Nouragues	Kaw	
<i>Brotogeris chrysoptera</i> †	SP	3.24 (1.26–8.36)	0.93 (0.29–3.00)	–71
<i>Deropterus accipitrinus</i> †	SP	0.56 (0.34–0.90)	0.16 (0.06–0.48)	–71
<i>Pionites melanocephalus</i> †	SP	1.43 (0.47–4.34)	4.34 (2.09–9.04)	+203
<i>Pionus</i> spp.†	SP	1.59 (0.77–3.30)	1.26 (0.43–3.66)	–21
<i>Pyrrhura caica</i> †	SP	<i>0.02</i>	<i>0</i>	–100
<i>Pyrrhura picta</i> †	SP	<i>0.10</i>	<i>0.08</i>	–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	<i>0.13</i>	<i>0.03</i>	–77
<i>Phoenicircus carnifex</i>	SD	3.01 (1.36–6.66)	0.89 (0.24–3.38)	–70
<i>Querula purpurata</i> †	SD	0.69 (0.47–1.02)	0.05 (0.01–0.26)	–93
<i>Rupicola rupicola</i>	SD	<i>0.18</i>	<i>0.01</i>	–94
<i>Xipholena punicea</i>	SD	<i>0.02</i>	<i>0.03</i>	+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> †	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

Notes: *Alouatta macconnelli*, *Sapajus apella*, *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 boldface type. Densities of some species could not be estimated with Distance. In these cases, mean encounter rate in individuals or groups per km² 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).

†Gregarious species counted in groups per km².

Nouragues. Taken as a group, *Ramphastos* Toucans (*R. vitellinus* and *R. tucanus*) were significantly more abundant at Montagne de Kaw.

Fruit consumption and seed removal

A total of 72 trees of the four focal families was sampled over the 2 yr 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* (Bursaceae, three species), *Inga* (Fabaceae, six species), *Iryanthera*, *Osteophloeum*, and *Virola* (Myristicaceae, five species), and *Chrysophyllum*, *Manilkara*, and *Micropholis* (Sapotaceae, six 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, 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, 5). The overall community level seed removal rate was 77% at Nouragues (protected) and 47% at

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

Taxon	Nouragues			Kaw		
	Removal rate (%)	Sample size (no. fruits/m ²)	No. trees sampled	Removal rate (%)	Sample size (no. fruits/m ²)	No. trees sampled
Burseraceae						
<i>Tetragastris panamensis</i>	56.65	49.2 \pm 39.3	5	35.26	72.5 \pm 50.1	4
<i>Tetragastris</i> sp2	15.15	77	1	–	–	
<i>Protium sagotianum</i>	67.42	18	1	68.00	15	1
Total	52.26	48.7 \pm 36.3	7	41.81	61.0 \pm 50.4	5
Myristicaceae						
<i>Virola michelii</i>	79.10	23.0 \pm 6.2	3	36.59	205	1
<i>Virola kwatae</i>	91.67	24	1	–	–	
<i>Iryanthera sagotiana</i>	93.23	45.0 \pm 1.4	2	80.24	49.2 \pm 33.5	6
<i>Iryanthera hostmannii</i>	–	–		96.00	25	1
<i>Osteophloeum platyspermum</i>	–	–		50.00	16	1
Total	85.91	30.5 \pm 11.9	6	73.78	60.1 \pm 61.8	9
Sapotaceae						
<i>Chrysophyllum lucentifolium</i>	74.90	18.8 \pm 6.8	4	–	–	
<i>Manilkara huberi</i>	78.29	41.7 \pm 26.7	3	31.99	53.8 \pm 45.8	5
<i>Manilkara bidentata</i>	69.00	37.5 \pm 2.1	2	–	–	
<i>Micropholis guyanensis</i>	32.14	140	1	42.57	251.0 \pm 285.7	2
<i>Micropholis</i> sp1	–	–		12.73	958	1
<i>Micropholis</i> sp2	–	–		26.71	161	1
Total	70.46	41.5 \pm 38.5	10	31.61	210.0 \pm 311.7	9
Fabaceae						
<i>Inga leiocalycina</i>	53.87	20.0 \pm 11.3	2	–	–	
<i>Inga thibaudiana</i>	91.89	8	1	–	–	
<i>Inga alba</i>	–	–		79.07	26.5 \pm 4.4	4
<i>Inga rubiginosa</i>	–	–		81.48	18.0 \pm 1.4	2
<i>Inga paraensis</i>	–	–		8.33	17	1
<i>Inga huberi</i>	–	–		57.89	26	1
Total	66.54	16.0 \pm 10.6	3	68.18	23.1 \pm 5.4	8
Total	68.67	38.0 \pm 31.6	26	54.94	94.2 \pm 182.1	31

Montagne de Kaw (hunted and logged; Fig. 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 data set, since the effect was significant in most data sets resampled by bootstrap (95.5% of data sets by t test and 89.7% by likelihood ratio test; Tables 3, 5).

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

Abundance of frugivores

In the frugivore community, the most notable difference between the two sites was the probable extinction of the red-faced black spider monkey (*Ateles paniscus*) at Montagne de Kaw. The species was never contacted during the study. This was consistent with the findings of other studies (Bodmer et al. 1997, de Thoisy et al. 2005,

Nuñez-Iturri and Howe 2007). *Ateles* spp. are reputedly very sensitive to hunting (Peres 1990) due to their large size, conspicuous behavior and low reproductive rate (Bodmer et al. 1997). Although they are legally protected in French Guiana, they are one of the most sought-after game species (C. Richard-Hansen, *personal communication*) and the first to disappear with hunting (de Thoisy et al. 2005). Although less sensitive to hunting (Peres and Palacios 2007, Boubli et al. 2008), the Guianan red howler (*Alouatta macconnelli*) was apparently greatly reduced in Kaw. It is also a preferred target

of hunters (C. Richard-Hansen, *personal communication*). In Guyana, Bicknell and Peres (2010) found that *A. paniscus* was significantly reduced by reduced-impact logging, but not driven to extinction, and found *A. macconnelli* to be unaffected. In our study, these species are respectively extinct and reduced on all transects at Montagne de Kaw, not specifically the logged ones. This suggests that hunting, and not logging, is responsible for their demise and scarcity at our hunted site. However, these species are the two major seed dispersers in the primate community of the Guianas (Mittermeier and van Roosmalen 1981). They are especially important dispersers of families such as Sapotaceae (van Roosmalen 1985b, Julliot 1996). Among our study families, Fabaceae, Myristicaceae, and Sapotaceae were the top three families eaten by *A. paniscus* in Voltzberg, Suriname, while Burseraceae ranked sixth (van Roosmalen 1985b).

We found no significant difference in densities of capuchin monkeys (*Sapajus apella* and *Cebus olivaceus*) between Nouragues and Montagne de Kaw, in contrast with Nuñez-Iturri and Howe (2007), who found an 80% reduction of capuchin densities at their heavily hunted site, but in accordance with Peres and Palacios (2007), who found no significant density reduction for *S. apella* in lightly to moderately hunted sites. Midas tamarin (*Saguinus midas*), the smallest species in the Guianese primate assemblage, was present at similar densities at the two sites, in congruence with Peres and Dolman (2000). Ungulates (*Mazama americana*, *M. nemorivaga*, *Pecari tajacu*, and *Tapirus terrestris*) as a group were typically affected by hunting. But although highly frugivorous, they are not very efficient seed dispersers, with the

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.

Response variable, data set, and 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; 7.39 (1.42–15.98)	1	<0.001; 0.007 (<i><0.0001–0.23</i>)
Family	8.186	3	0.042
Site x Family	3.159	3	0.368

Notes: Significant P values are shown in boldface type. Median bootstrap values of bootstrapped parameters appear in italics along with their 95% confidence intervals.

TABLE 4. Generalized linear mixed model results: fixed effects of site and species on fruit consumption for Sapotaceae, tested by t test.

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

Notes: Intercepts are Montagne de Kaw (site effect) and Sapotaceae sp1 (species effect). Significant P values are shown in boldface type.

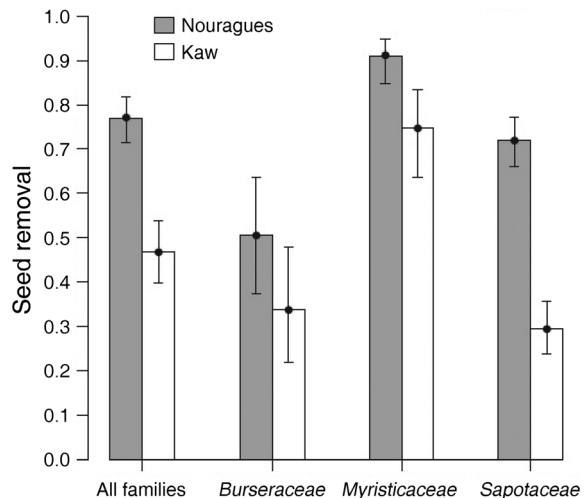


FIG. 2. Seed removal rate (mean ± SE) of all families pooled together, and family-level rates of Burseraceae, Myristicaceae, and Sapotaceae, at Nouragues (protected site) and Montagne de Kaw (hunted and partly logged site). Estimates of the final model are shown (site and family as fixed effects, no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

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.

Parameter	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

Notes: Intercepts are Montagne de Kaw (site effect) and Burseraceae (family effect). Significant *P* values are shown in boldface type. Median bootstrap values of bootstrapped parameters appear in italics along their 95% confidence intervals.

exception of *T. terrestris*; *P. tajacu* and *Mazama* spp. destroy seeds (Bodmer 1991). However, the densities of some important seed dispersers, Common Red-rumped Agouti (*Dasyprocta leporina*), Gray-winged Trumpeter (*Psophia crepitans*), and Cracidae (Erard et al. 1991, Emmons and Feer 1997, Larue 1999), which are all hunted species, seemed to be typically reduced at Montagne de Kaw compared to Nouragues (more than halved for *D. leporina* and *P. crepitans*).

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

However, it is difficult to attribute the changes of abundance of some other, non-hunted species to hunting or logging alone. Specific habitat preferences or subtle biogeographical differences could explain these differences as much as hunting or logging (Richard-Hansen et al. 2015), and our 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 parsimonious 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.

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

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

Seed removal is the quotient of the number of removed seeds over the number of produced 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 rain forests. 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 klaineamum* (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.

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. This means that the animals that eat Sapotaceae fruits at Montagne de Kaw consume them but do not take away their seeds. We interpret this difference in terms of seed size. A good example is given by *Manilkara huberi* and *M. bidentata*. These two Sapotaceae species produce 2.5–3.0 cm fruits that are mostly dispersed by large-bodied primates but also eaten by tamarins (Ratiarison and Forget 2011). At Montagne de Kaw, many eaten fruits found on the ground were barely open by a narrow slit, with all seeds in place (O. Boissier, *personal observation*). We hypothesize that those were squeezed open by tamarins to suck in the pulp without swallowing the seeds (P.-M. Forget, *personal observation*). *Manilkara* seeds are approximately 2.4 cm in length and 1.3 cm in width (Ratiarison and Forget 2011). Oliveira and Ferrari (2000) noted for the now split *Saguinus niger* (formerly *S. midas niger*) that seeds with diameter >1 cm or length >2 cm were discarded. While tamarins might offset the absence of large-bodied primates in terms of fruit consumption, they are unable to replace them in terms of seed dispersal. There is no compensation possible for Sapotaceae, neither by birds, which do not eat their fruits, nor by small-bodied primates, which cannot swallow their seeds.

However, Burseraceae and Myristicaceae did not show such a marked decrease in seed removal. Unlike

Sapotaceae, both families are also dispersed by birds. For example, the genus *Virola* (Myristicaceae) is the genus whose fruits are most frequently consumed by *A. paniscus* (van Roosmalen 1985b). However, at Nouragues, Toucans (Ramphastidae) also account for 60.8% and 51.9% of consumer visits at *Virola kwatae* and *V. michelii* trees, respectively (Ratiarison and Forget 2013). With *Ramphastos* Toucans significantly more abundant at Montagne de Kaw, one can imagine that the overall number of their visits will be greater and may offset the absence of spider monkeys. Moreira et al. (2017) found that toucans visited all *Virola surinamensis* trees equally across a human-modified landscape in southern Costa Rica, at rates similar to those observed in a protected forest, and could thus provide resilience against seed dispersal limitation. Holbrook and Loiselle (2009), however, observed fewer visits by Toucans at *Virola flexuosa* trees at their hunted site in Ecuador relative to their protected site, which suggests that these birds might be less hunted at our site than theirs. Burseraceae have a more generalist seed dispersal strategy than Myristicaceae (Howe 1982), with various bird species visiting fruiting trees in addition to *A. paniscus*, *A. macconnelli*, and Ramphastidae (Ratiarison and Forget 2005), which suggests that frugivore compensation would be even more likely. However, Howe (1980) noted that birds only represented 25% of the potential seed dispersal of *Tetragastris panamensis* in years of heavy fruit fall. In more heavily defaunated contexts than Montagne de Kaw, it is unlikely that birds would completely offset the absence of mammals, especially since dispersers of *T. panamensis* use many other food resources. As Wright (2003) noted, the likelihood of compensation decreases as hunting pressure increases and depletes more species. Moreover, birds are also affected by hunting and logging. Two avian dispersers of Burseraceae also had significantly reduced abundances at Montagne de Kaw (*Momotus momota* and *Querula purpurata*). Finally, the uncensused nocturnal Kinkajou (*Potos flavus*) may play an additional potential role in compensation, as this species disperses the seeds of both families (Julien-Laferrrière 2001). The use of arboreal camera trapping could prove ideal to fill this knowledge gap, as well as to generally monitor fruit consumption in tree canopies (Gregory et al. 2014). Poulsen et al. (2002) showed that in-depth studies are required to ascertain the potential for compensation in seed dispersal services between different groups of frugivores. While our study suggests that some compensation may occur for Burseraceae and Myristicaceae, further studies would be needed to confirm this.

Implications for the management of tropical forests

Our method of fruit and seed counts allows us to estimate proportions of fruit consumption and seed removal, which directly takes into account potential differences in crop size between trees and facilitates

comparisons. This method is also relatively rapid and allows a great number of different trees across different species and families to be sampled without much prior knowledge of their specific biology. It confirms the possibility to generalize the method originally tested by Boissier et al. (2014) on a single genus to any zoochorous tree species whose fruits contain hard outer parts uneaten by frugivores. The facility, rapidity and ease of implementation of this method thus make it an ideal monitoring tool for protected area managers and other field practitioners who desire to go beyond wildlife censuses and monitor the health of ecological processes in a forest. It can be used to monitor seed dispersal processes both over time, for example to monitor the potential ecological impacts of poaching in a protected area or to assess the impacts of a new logging operation, and space, to compare different sites. It is also very cost-effective, as field data collection requires very little gear and limited manpower and experience. It could thus be used at a country scale by a ministry of the environment or department of forestry to get a nation-wide picture of the state of ecological processes in a country's protected area network. Implementation of the method requires choosing species whose fruits contain hard outer parts that are left uneaten by frugivores, such as capsules, pods or berries and drupes with a fibrous pericarp; it cannot be applied to fleshy fruits that are swallowed whole by frugivores. Besides, species such as Sapotaceae whose seed number prior to fruit consumption cannot be counted require prior knowledge of the mean number of seeds per fruit. However, this figure can be relatively easily evaluated in the field by opening a number of intact fruits and counting their seeds to average them.

As seed removal limitation occurs at a community scale and threatens the forest as a whole, it is crucial to protect the most important seed dispersers. *Ateles paniscus* and *Alouatta macconnelli* are two of the most important seed dispersers in the Guianas (Mittermeier and van Roosmalen 1981). Their extinction and greatly reduced density at Montagne de Kaw, respectively, is one of the most remarkable results of the first part of this study and is likely to be responsible for a significant proportion of the observed collapse in seed removal at this site. However, this is far from being an isolated case, and Atelid monkeys are threatened by local and global extinctions across the Neotropics. More than 70% of species (18 out of 25) are globally threatened, making Atelidae the most threatened monkey family in the world (Estrada et al. 2017). This is especially true of the seven species of spider monkeys (*Ateles*), of which two are Critically Endangered, four Endangered, and one Vulnerable (IUCN 2019). Atelids are the most important primate seed dispersers of the Neotropics (Mittermeier and van Roosmalen 1981, Bufalo et al. 2016) and are of great importance for plant regeneration. High abundances of Atelids are directly associated with a greater diversity of regenerating plants (Stevenson 2010). A recent study by Genes et al. (2019) showed that the

successful reintroduction of howler monkeys to a defaunated site of the Atlantic Forest of Brazil restored ecological interactions between howler monkeys and the plants that they consume, as well as secondary seed dispersal by dung beetles, a group commonly affected by hunting through the loss of mammals whose feces they rely on (Culot et al. 2013, Feer and Boissier 2015). Primate translocation (Beck 2016) is a promising conservation tool and has already been successfully implemented with howler monkeys in French Guiana, Belize, and Brazil (Richard-Hansen et al. 2000, Beck 2016, Genes 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.

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.

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DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.tmpg4f4vc>