

Frugivores and seed removal at *Tetragastris altissima* (Burseraceae) in a fragmented forested landscape of French Guiana

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Abstract: We aimed at (1) determining how community-wide disruptions affect visitation by frugivores at trees and (2) estimating the impact of visitation shifts on seed fate following fruit consumption, especially seed removal. We compared the seed fate of a frugivore-dispersed tree species (*Tetragastris altissima*, Burseraceae) in four forested islands with that for a mainland continuous forest at Saint-Eugène, French Guiana. *Tetragastris* trees attracted opportunistic frugivore species available in the area, the most productive trees attracting more consumer species. Only primates, which are more susceptible to forest disturbances than birds and have low abilities to cross a non-forested matrix, were more frequent at *Tetragastris* on the mainland than on islands. Only opportunistic frugivorous primate species acting as low-efficiency seed dispersers were recorded. As a result, seed removal was equally low among habitats (nearly 26%), high percentages of seeds dropping below tree crowns. The scarcity of large-bodied specialist frugivorous primates throughout the landscape probably explained this low removal. Our results underline how difficult it is to generalize the cascading effects of disruptions in a frugivore community on tree seed fate, these effects likely varying according to the tree species and animal community involved.

Key Words: Forest fragmentation, French Guiana, frugivores, seed removal, *Tetragastris altissima*

INTRODUCTION

In tropical forests, anthropogenic activities such as agriculture, logging, road building and flooding due to dam construction lead to fragmentation and degradation of forested habitats (Laurance *et al.* 2000, Whitmore 1997). In addition, human intrusion in forest remnants increases hunting pressure (Robinson 1996, Thiollay 1999). Following fragmentation, animal communities are immediately affected, while plant communities appear (often deceptively) unchanged for a long time (Corlett & Turner 1997, Phillips 1997). Disruptions in animal community composition particularly affect frugivore and granivore species, which play important roles in seed fate (Dirzo & Miranda 1990, Graham *et al.* 1998), seed dispersal (Pizo 1997, Santos *et al.* 1999) and seedling recruitment (Benítez-Malvido 1998, Chapman & Onderdonk 1998, Cordeiro & Howe 2001, Marsh & Loiselle 2003)

of tropical trees. In order to predict long-term changes in diversity and integrity of the remaining fragmented habitats, it is of particular interest to know how seed dispersal is altered by changes in animal communities.

Disruptions in frugivore communities vary according to the susceptibility of animal species to habitat fragmentation. Large, rare and/or specialized species (*sensu* McKey 1975, i.e. strongly dependent on fruit resources for at least part of their life) are more prone to extinction than small, abundant and/or opportunistic ones (i.e. species with mixed diet or irregular frugivory) (Cosson *et al.* 1999, Estrada *et al.* 1993, Thiollay 1999, Turner 1996). Species with limited abilities to move among isolated habitat patches are particularly affected (Chiarello 1999, Estrada *et al.* 1994, Kattan *et al.* 1994). Furthermore, hunting probably exacerbates fragmentation effects as species preferred by hunters are often those which are the most sensitive to fragmentation, especially primates (Chiarello 1999, Laurance *et al.* 2000, Peres 1997). Consequences to seed dispersal may then vary according to the frugivore species involved and the degree of

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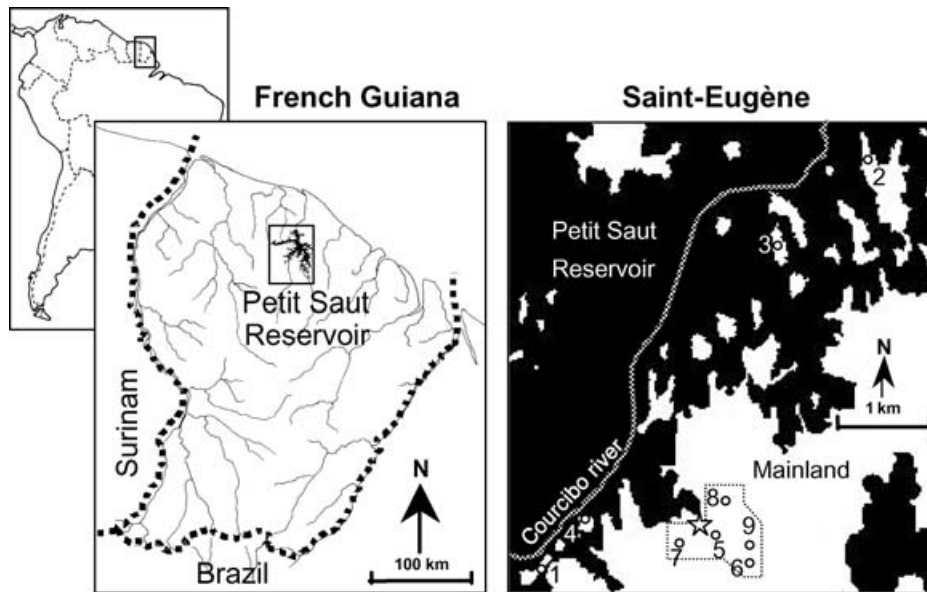


Figure 1. The Saint-Eugène Field Station, French Guiana. *Tetragastris altissima* focal trees (numbered dots) and the camp (star) are indicated. A dotted frame delimits the 60-ha plot on the mainland. Areas of study islands are (in ha): 1: 3.4, 2: 2.2, 3: 2.9 and 4: 0.4.

specialization of a given plant species towards its consumers (Graham *et al.* 2002, Peres & van Roosmalen 2002).

The aim of this study is to determine the impact of forest disturbances on the primary seed dispersal system of *Tetragastris altissima* (Aublet) Swart (Burseraceae) in a forest suffering from fragmentation by inundation and hunting. *Tetragastris altissima* is similar to the closely related species *T. panamensis*, both usually coexisting in French Guiana and being equally exploited for fruits by frugivores, at least by primates (Guillotin *et al.* 1994, van Roosmalen 1985a, Zhang 1994). At tree crown level, *Tetragastris* seed fate depends on a wide array of both specialized and opportunistic frugivores (Howe 1980). As *Tetragastris* seems almost impervious to density-dependent factors of mortality in the vicinity of the parent tree (De Steven & Wright 2002, Howe 1993), seed removal probably provides few advantages to *Tetragastris* seed survival on the ground. But, it might increase the number of seeds that establish in sites more favourable to seedling growth and survival, such as gaps (Fraver *et al.* 1998).

Here, we compare the visitation by frugivores–granivores at *T. altissima* in two habitats: a mainland continuous forest and a set of forested islands. In addition, *Tetragastris* fruits display useful morphological features to survey fruit and seed fall following fruit consumption and the different fates of seeds, notably seed removal, in both habitats. Results are discussed in the light of studies of *Tetragastris* conducted at other forest sites and using similar field methods.

MATERIAL AND METHODS

Study site

Research was carried out in 1999 at the Saint-Eugène Biological Station (4°51'N; 53°04'W, maximum altitude 170 m), French Guiana (Claessens *et al.* 2002). The study site includes: (1) a set of forested islands isolated by the inundation of the reservoir of the Petit Saut dam in 1994–1995 and (2) a 1000-ha area of continuous forest forming a large peninsula connected with the rest of the mainland by a 700-m isthmus (Figure 1). Vegetation is tall mature lowland rain forest (Larue *et al.* 2002). Mean annual rainfall is 2750 mm, with a rainy season from November to July. Data were gathered within a 60-ha plot on the mainland and on four islands numbered 1 to 4 (Figure 1).

At Saint-Eugène, past human activities were mostly concentrated near the river banks until the beginning of the 20th century (Forget 2002) and probably weakly affected the mainland (Dalecky *et al.* 2002). In 1999, the site was legally protected from hunting, logging and gold-mining. However, recent evidence of casual poaching has been found during the study period, on islands as well as on the mainland. The vertebrate fauna, representative of a Guianan mature forest, remains almost complete (320 bird and 99 mammal species), but islands and mainland support different species. On the mainland, species richness and composition of bird and mammal communities are unaffected by human disturbances. In contrast, the overall species richness on islands has rapidly declined after flooding (Claessens 2000, Cosson

et al. 1999, Dalecky *et al.* 2002, Larue 1999). Among frugivores, six species of primate are present on the mainland: *Alouatta seniculus*, *Cebus olivaceus*, *Cebus apella*, *Saguinus midas*, *Ateles paniscus* and *Pithecia pithecia*. *Alouatta seniculus* and *C. apella* are the only species present on study islands 2 and 3, while islands 1 and 4 do not support any primates (Dalecky *et al.* 2002). Compared with the mainland, toucans and canopy omnivore birds are under-represented in the fragmented area, while parrot populations remain undisturbed so far (Claessens 2000, Larue 1999).

Study species and focal trees

Tetragastris altissima (Burseraceae) is a dioecious canopy tree of about 30 m in height, occurring from Central America to northern South America and in the West Indies (van Roosmalen 1985b). Fruiting is annual from February to May in French Guiana, but fruiting intensity is likely to vary between years (De Steven & Wright 2002). Fruits are dehiscent capsules that consist of a red central core with one to six locules; each locule contains one arillate seed protected by a reddish-purple valve. At maturity, valves fall and arillate seeds hang from the core. The pure white aril is rich in sugars and tightly adherent to the seed. Of 19 *T. altissima* adult trees located in the mainland plot and 22 trees on 17 islands (representing approximately 68 ha), only nine trees fruited on the mainland and eight on six islands in 1999, suggesting a poor fruiting year, as observed at Nouragues in French Guiana (Jansen 2003). We selected nine focal trees: one each on four islands and five on the mainland (Figure 1). Focal trees were those that started to fruit during the study period and had crowns separated from each other and from other conspecific trees. Mean trunk diameter at breast height (dbh) of focal trees was 66.5 ± 7.2 cm (\pm SE hereafter). Fruits averaged 2.7 ± 0.09 seeds per fruit ($n = 83$); seed size averaged 1.6 ± 0.02 cm \times 0.8 ± 0.01 cm ($n = 212$); mean fresh masses of seed and aril were 0.8 ± 0.01 g and 1.9 ± 0.07 g, respectively.

Seed collection and analysis

Following Howe (1980), seed crop size, i.e. the original number of arillate seeds in all fruits dropped beneath trees, and seed fate, including seed removal, pre-dispersal predation by vertebrates and seed fall beneath trees, were estimated weekly at each focal tree ($n = 9$) from 12 March to 21 May 1999. For this purpose, trees were equipped with fruit traps as soon as mature fruits were observed falling and fruit collection lasted 7–10 wk per tree. Traps consisted of 1-m² nets (1.5-mm-wide mesh)

hung about 1.5 m above ground and placed at random within the horizontal projection area of each focal tree crown. This area was calculated from a circular projection based on the mean of two crown diameters measured along N–S and E–W axes. The relation: number of traps = $2 \times \log$ (crown area) was used to assign adequate sampling pressures for both small and large trees. Sampling effort ranged from 4–16% of the crown area ($7 \pm 1\%$), representing 9–11 traps per tree (9 ± 1 traps).

Traps collected seeds, entire valves and pieces of valves chewed by animals. Valve pieces were converted to an equivalent number of entire valves by dividing the total biomass of chewed valves by the mean mass of an entire valve. The total number of valves estimated the seed crop size. The number of seeds truly removed away from focal trees (seed removal) was assessed by subtracting the number of seeds collected from the seed crop size. Traps collected seeds that were crushed by parrots, which dropped two half endocarps after aril and embryo were eaten (seed predation). Predation was probably underestimated since predation by animals consuming seeds out of the parent tree crowns and/or leaving no seed residue could not be quantified and then was included in seed removal. However, since parrots appeared as the main *Tetragastris* seed predators (Howe 1980, Ratiarison 2001), the error was probably minimal. Entire seeds fallen in traps (seed fall) were also counted, distinguishing between (1) single seeds, either still embedded in aril or naked after regurgitation or defecation by animals foraging in tree crowns, and (2) seeds in unopened fruits fallen because of animal movements or wind. At each focal tree, seed crop size was calculated in relation to the proportion of the crown area sampled and each seed fate was expressed as a percentage of seed crop size.

Diurnal consumers

Concurrently with fruit collection, diurnal consumers were recorded at each focal tree. Two–three days per week, three census sets per day were conducted by a single observer (S. Ratiarison) in the morning (07h00–09h00), at midday (11h30–13h30) and late in the afternoon (16h00–18h00), in all weather conditions but rain. During each census set, either trees on the mainland or trees on islands were considered. Ordering trees randomly within each census set, each tree crown was scanned from the ground using binoculars (7×40) for 15 min, once per census set. All sightings of animals eating arils and/or seeds were recorded. Consumer species were classified within three types: (1) potential seed dispersers when they swallowed arillate seeds or had a large enough gape width to do so, (2) non-dispersers when they pecked at arils and dropped seeds beneath trees or had too small a gape width to swallow seeds and (3) seed predators. Given

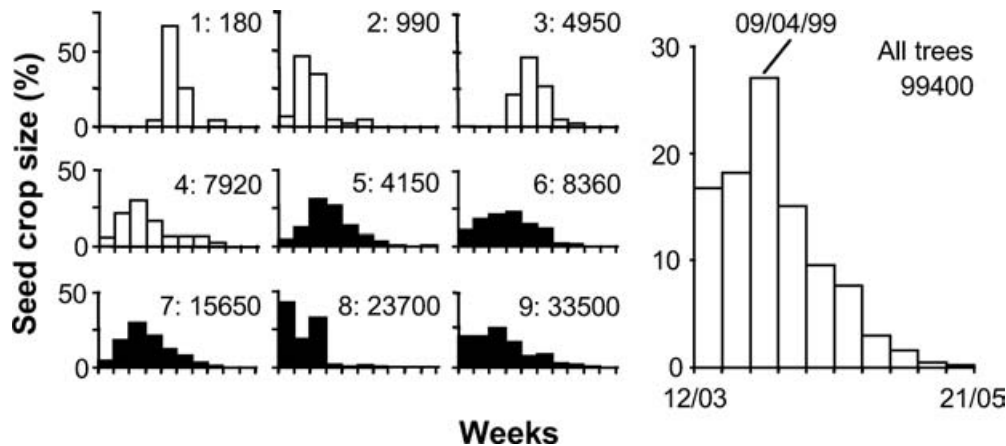


Figure 2. Weekly individual and total (all trees pooled) seed crop sizes of *Tetragastris altissima* at Saint-Eugène. Values are percentages of the seed crop sizes estimated during the whole study period (indicated in the upper part of graphs with tree numbers). Island (hollow bars) and mainland (solid bars) trees are distinguished.

that *Tetragastris* spp. contribute little to the diet of the nocturnal *Potos flavus*, another potential seed disperser (Julien-Laferriere 2001, Kays 1999), and since nocturnal visitation seems far less frequent than diurnal (Howe 1980), no observation was conducted after dark. We carried out a total of 272 censuses, with 21–35 censuses per tree (30 ± 2 censuses). To mitigate differences of census effort among trees, consumer visitation at each tree was calculated as the number of sightings per census (i.e. divided by the number of censuses performed at each tree).

Data analysis

Percentages related to seed fate were arcsine-square-root-transformed, and seed crop sizes and data related to consumer visitation were square-root-transformed $[(x + 1)^{1/2}]$ for normalization (Sokal & Rohlf 1981). Relationships between seed crop size, consumer visitation and seed fate were analysed using linear regressions. One-way ANOVA and ANCOVA with seed crop size as covariate were used to compare mainland vs. island data ('habitat' effect). In ANCOVA, the interaction term (covariate \times habitat) tested for homogeneity of slopes. All statistics were performed with the statistical software SPSS 9.0 for Windows.

RESULTS

Seed crop size

The estimated seed crop size ranged from 200–33 500 seeds per tree (Figure 2). The study period included the last two-thirds of the entire *T. altissima* fruiting season. However, the total seed crop size estimated during this

period represented 98.9% of the entire seed production (S. Chauvet, pers. comm.). Seven trees showed a distinct fruiting peak (Kurtosis > 0), the overall fruiting pattern showing a weak peak (Kurtosis = -0.56) in early April (Figure 2). Mean seed crop size was significantly greater on the mainland ($17\,100 \pm 5300$ seeds) than on islands (3500 ± 1800 seeds) (ANOVA, $F_{1,7} = 6.5$; $P = 0.038$). This difference probably did not reflect tree size differences as there was no significant relationship between seed crop size and trunk dbh ($P = 0.23$), and no difference in trunk dbh between mainland and island trees ($F_{1,7} = 2.8$; $P = 0.14$).

Consumer assemblage and visitation

A total of 164 consumer sightings were recorded in focal trees, comprising 22 species in 12 families (Table 1). The number of consumer species per census significantly increased with seed crop size on the mainland (Linear regression: $y = 0.0005x + 1.02$; $R^2 = 0.96$; $df = 1, 3$; $P = 0.003$), but not on islands ($P = 0.06$) (Table 2). On average, it did not differ significantly among habitats (ANCOVA, habitat: $F_{1,5} = 5.0$; $P = 0.08$ – seed crop size: $F_{1,5} = 42.6$; $P = 0.001$). But, the interaction term in the ANCOVA was significant ($F_{1,5} = 13.4$; $P = 0.015$) showing that, at equal seed crop size, trees on islands tended to attract more consumer species, i.e. birds, than trees on the mainland.

Among birds, Cracidae, Ramphastidae, Cotingidae, Trogonidae, *Cacicus* sp. and the unidentified species with large gape width acted as seed dispersers. The small-bodied omnivorous species *Thraupis* sp. and *Icterus* sp. and the unidentified species with small gape width were classified as non-dispersers. Psittacidae were the main seed predators observed. Disperser, non-disperser and predator bird sightings represented 31.7, 28.7 and 17.7%

Table 1. *Tetragastris altissima* consumer assemblage in tree crowns at Saint-Eugène. The total number of sightings of each consumer species recorded from March–May 1999 is presented. Nomenclature follows Tostain *et al.* (1992) for birds, Fleagle (1999) for primates and Wilson & Reeder (1993) for other mammals.

Family	Species	Type ¹	Islands (101) ²	Mainland (171) ²
All birds			57	71
Columbidae	<i>Columba plumbea</i>	P		1
Cotingidae	<i>Perissocephalus tricolor</i>	D	6	
	<i>Querula purpurata</i>	D		1
Cracidae	<i>Penelope marail</i>	D		9
Emberezidae	<i>Thraupis episcopus</i>	ND	10	
Icteridae	<i>Cacicus cela</i>	D	1	
	<i>Icterus sp.</i>	ND	15	
Psittacidae	<i>Amazona amazonica</i>	P	2	
	<i>Amazona sp.</i>	P		2
	<i>Deroptylus accipitrinus</i>	P	1	
	<i>Pionites melanocephala</i>	P	3	
	<i>Pionus fuscus</i>	P	1	
	<i>Pionus menstruus</i>	P	1	
	Unidentified parrots	P		2
	Unidentified parakeets	P		16
Ramphastidae	<i>Ramphastos tucanus</i>	D	4	
	<i>Ramphastos vitellinus</i>	D	3	
Trogonidae	<i>Trogon collaris</i>	D		1
	<i>Trogon melanurus</i>	D		2
	<i>Trogon rufus</i>	D	2	
Unidentified	<i>Trogon viridis</i>	D	1	
	Large species ³	D	3	19
	Small species ³	ND	4	18
All mammals			1	35
Atelidae	<i>Alouatta seniculus</i>	D	1	7
Callitrichidae	<i>Saguinus midas</i>	D		12
Cebidae	<i>Cebus apella</i>	D		14
Sciuridae	<i>Sciurus aestuans</i>	P		2
Total			58	106

¹ D: disperser; ND: non-disperser; P: predator.

² Total number of censuses.

³ Sizes of unidentified species refer to their potential ability to swallow (large species) or not (small species) *Tetragastris* seeds.

of all sightings, respectively (Table 1). On the mainland as well as on islands, there were no significant relationships between seed crop size and visitation by disperser ($P = 0.11$ and $P = 0.19$, respectively), non-disperser

($P = 0.51$ and $P = 0.27$) and predator birds ($P = 0.50$ and $P = 0.08$) (Table 2). Mean visitation of each bird type did not differ significantly among habitats (ANOVA, dispersers: $F_{1,7} = 0.6$, $P = 0.47$; non-dispersers: $F_{1,7} = 0.1$, $P = 0.76$; predators: $F_{1,7} = 1.0$, $P = 0.35$).

Primates were the only diurnal mammalian dispersers recorded, representing 20.7% of sightings. On the mainland, opportunistic frugivorous primates such as small and medium-sized omnivores (*S. midas* and *C. apella*) were regularly observed, in addition to the large folivore-frugivore *A. seniculus*. The frugivore specialist *A. paniscus* was seen only once feeding at a non-studied *Tetragastris* tree. Disperser mammal visitation was not significantly correlated to seed crop size ($P = 0.29$) on the mainland (Table 2). Only one individual *A. seniculus* was observed on island 3. Mean disperser mammal visitation was significantly greater on the mainland than on islands (ANOVA, $F_{1,7} = 24.7$, $P = 0.002$). *Sciurus aestuans* was infrequent as a seed predator (1.2% of sightings).

Seed fate in tree crown

In total, 90.9% of the seed crop size corresponded to fruit consumption and 9.1% to unopened fruit fall due to animal movements or wind. Of the former, 26.0% of seeds were removed from trees, 10.6% were preyed on by parrots and 54.3% were dropped singly. None of the percentages related to the different seed fate was significantly correlated to seed crop size on the mainland (all $P > 0.54$) or on islands ($P > 0.70$). There were no significant differences between habitats in the mean percentage of seeds removed (ANOVA, $F_{1,7} = 0.4$, $P = 0.56$), preyed on ($F_{1,7} = 1.6$, $P = 0.25$) and fallen singly ($F_{1,7} = 0.6$, $P = 0.48$) or in unopened fruits ($F_{1,7} = 0.1$, $P = 0.83$) (Table 3). The percentage of seeds removed or preyed on was not significantly correlated to disperser visitation ($P = 0.95$) or predator visitation ($P = 0.99$), respectively. There was also no significant correlation between the percentage of seeds fallen singly or in unopened fruits and visitation by all consumers combined ($P = 0.99$ and $P = 0.57$, respectively).

Table 2. Individual seed crop size and consumer visitation (numbers of consumer species and sightings per census) at *Tetragastris altissima* from March–May 1999 at Saint-Eugène.

Trees	Islands				Mainland				
	1	2	3	4	5	6	7	8	9
Seed crop size	180	990	4950	7920	4150	8360	15650	23700	33500
Consumer species	0	0	0.12	0.28	0.11	0.15	0.17	0.19	0.24
Consumer sightings									
Disperser birds	0	0	0.06	0.45	0.05	0.23	0.14	0.19	0.48
Non-disperser birds	0	0	0	0.73	0.11	0.08	0.11	0	0.28
Predator birds	0	0	0.12	0.10	0.16	0.08	0.05	0	0.40
Disperser mammals	0	0	0.03	0	0.05	0.33	0.14	0.29	0.28
Predator mammals	0	0	0	0	0	0.05	0	0	0

Table 3. Percentages related to seed fate in *Tetragastris altissima* tree crowns over March–May 1999 at Saint-Eugène (mean \pm SE).

	Mainland (n = 5) ¹	Islands (n = 4) ¹	Total (n = 9) ¹
Removal	27.3 \pm 5.3	22.1 \pm 3.9	25.0 \pm 3.4
Predation	9.9 \pm 3.2	5.4 \pm 2.3	7.9 \pm 2.1
Single-seed fall	53.1 \pm 4.4	60.2 \pm 9.4	56.3 \pm 4.7
Seed fall in unopened fruits	9.6 \pm 1.9	12.3 \pm 6.6	10.8 \pm 2.9

¹ Number of focal trees.

DISCUSSION

Effects of forest disturbances on frugivore visitation

In 1999, *Tetragastris altissima* represented an attractive fruit resource for numerous frugivore species at Saint Eugène, in the continuous forest zone as well as in the fragmented zone. This confirmed the low level of specialization by this species to its consumers (Howe 1980): *T. altissima* attracted the opportunistic as well as specialist frugivore species available in the habitats, the most productive trees tending to attract more consumer species. As a result, this study demonstrated clear effects of forest disturbances only on visitation by frugivorous mammals at *T. altissima*, especially primates, which show stronger susceptibilities to forest disturbances than birds due to their poor abilities to cross over the aquatic matrix (Estrada *et al.* 1994).

Birds were the main consumers of *T. altissima* throughout the landscape. Despite lower bird species richness and abundance, especially of canopy specialist frugivore and omnivore species (Claessens 2000, Larue 1999), and less-attractive trees in terms of fruit abundance in the fragmented habitat, bird visitation patterns in *T. altissima* were similar on the mainland and on islands. These patterns were also similar to those recorded at *T. panamensis* trees at BCI (Howe 1980) and Nouragues (Ratiarison 2001). Our results suggest that the scarcity of frugivorous birds on islands was probably compensated for by an increased attractiveness of trees near edges: at equal seed crop size, island trees tended to attract more bird species than mainland trees, especially when located close to the mainland.

The opportunistic frugivorous primate species *Cebus apella*, *Saguinus midas* and *Alouatta seniculus* visited *T. altissima* trees where they were present, i.e. mostly on the mainland, while the specialist frugivorous species *A. paniscus* was almost absent in the whole area. This primate assemblage strongly differed from those recorded at *Tetragastris* at other forest sites. At Nouragues, a pristine Guianan forest (Ratiarison 2001), the only primate species observed dispersing *T. panamensis* seeds were *A. paniscus* (25.8% of sightings) and *A. seniculus* (10.2%). Primate visits were disproportionate to their related densities: *A. seniculus* (19.9 ind. km⁻²), *C. apella*

(12.9 ind. km⁻²) and *A. paniscus* (8.4 ind. km⁻²) (Simmen *et al.* 1998), and then likely reflected the first-choice preference of *A. paniscus* for *Tetragastris* spp. fruits (Guillotin *et al.* 1994, van Roosmalen 1985a). Conversely, at Barro Colorado Island, Panama, primate visits at *T. panamensis* trees reflected the composition of the primate community: *Alouatta palliata*: 49.1% of sightings; *Cebus capucinus*: 6.8%; *Ateles geoffroyi*: not recorded (Howe 1980). These data suggest that the lack of *A. paniscus* at *T. altissima* might result from its low local abundance at Saint-Eugène, this species being very sensitive to forest disturbances and hunting (Robinson 1996, Sussman & Phillips-Conroy 1995). However, further replications in time and space are necessary to conclude if this pattern really reflected forest disturbances or simply variations in primate densities in relation with natural environmental conditions (Kay *et al.* 1997, Peres 1994, Peres & Dolman 2000, van Schaik *et al.* 1993).

Consequences to seed fate

Tetragastris altissima seed fate following fruit consumption did not differ between habitats at Saint-Eugène, indicating the difficulty of generalizing the cascading effects of disruptions in a frugivore community on seed fate. Pre-dispersal seed predation was similar on the mainland and on islands at Saint-Eugène, and was also similar to those recorded at BCI (6.4%, Howe 1980) and Nouragues (12.6%, Ratiarison 2001). This probably reflected the low impact of short-term disturbances on parrot populations at Saint-Eugène (Claessens 2000). We also found no significant differences in the percentage of *T. altissima* seeds removed between habitats, although primate visitation at *T. altissima* varied throughout the landscape. This weak contrast between the patterns of seed removal in both habitats mostly resulted from the low efficiency of the recorded consumer assemblage at removing seeds, high proportions of seeds dropping beneath tree crowns both on the mainland (62.7% on average) and on islands (72.5%). On the mainland, the observed primate species probably caused substantial seed fall by moving in tree crowns or spitting seeds beneath trees after aril consumption (see Howe 1980). While on islands, wind probably exacerbated seed fall near edges (Leigh *et al.* 1993).

Although there was no difference in seed removal patterns between habitats at Saint-Eugène, comparisons of our results with studies of *Tetragastris* at other forest sites suggest that consequences of forest disturbances on the frugivore community (see de Thoisy *et al.* 2005) might affect *Tetragastris* seed removal. *Tetragastris* seed removal greatly varied between sites in relation to the consumer species involved, especially primates. Seed removal was lower where the large specialist frugivores *Ateles* spp. were lacking in the consumer assemblage, i.e. at Saint-Eugène

(26%) and Barro Colorado Island (27.8%, vs. 43.9% at Nouragues). *Ateles* spp. then might be effective dispersers of *Tetragastris* seeds, their disappearance likely affecting *Tetragastris* seed removal and regeneration in the long term.

To conclude, this study failed to provide any direct evidence of the cascading effects of disruptions in a frugivore community on primary seed removal at *T. altissima*. The flexibility of its consumer assemblage allows *Tetragastris* to maintain seed removal in a variety of places, with a variable efficiency according to the disperser species involved. However, the small sample size makes our conclusions only suggestive. Further investigation, with larger sample sizes, would be required to verify the observed patterns. In addition, as the susceptibility of trees to disturbances may vary between tree species according to their pattern of seed consumption (Graham *et al.* 2002, Guariguata *et al.* 2002), future research should include similar studies at specialist tree species relying on a small number of frugivore species for dispersal. Finally, this study only focused on the impact of forest disturbances on the first stages of *Tetragastris* seed dispersal process. But, consequences of low seed removal on *Tetragastris* regeneration are difficult to predict since all stages, such as secondary dispersal and predation, may also be affected by forest fragmentation (Guariguata *et al.* 2002, Pizo 1997).

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