

SHORT COMMUNICATION

Does masting result in frugivore satiation? A test with *Manilkara* trees in French Guiana

Irene Mendoza^{*,†,1}, Gabrielle Martin^{*,1}, Adeline Caubère^{*}, Patrick Châtelet[‡], Isabelle Hardy^{*}, Sylvie Jouard^{*} and Pierre-Michel Forget^{*,2}

* UMR 7179 CNRS-MNHN, Muséum National d'Histoire Naturelle, Département d'Écologie et Gestion de la Biodiversité, 1 Av. du Petit Château, 91800 Brunoy, France

† Departamento de Botânica, Plant Phenology and Seed Dispersal Research Group, Universidade Estadual Paulista (UNESP), Avenida 24-A no. 1515 – CEP 13506–900, Rio Claro (São Paulo), Brazil

‡ CNRS Guyane - USR 3456, 2 rue Gustave Charlery, 97300, Cayenne, French Guiana

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Abstract: Species showing mast seeding synchronously produce large amounts of fruits during some scattered years. This massive crop has been hypothesized to improve dispersal effectiveness by a satiation of seed predators, but the consequences for seed dispersers have barely been studied in the tropics. We tested the hypothesis that masting resulted in satiation of frugivorous dispersers using the study case of two *Manilkara* species growing in an Amazonian forest in French Guiana. Seed dispersal was estimated by means of seed traps in two forest types during a 10-y monitoring. *Manilkara huberi* and *M. bidentata* showed three fruiting events in a time span of 10 y (in 2001, 2006 and 2010). Estimates of seed dispersal from 2001 and 2010 showed that satiation of frugivores only occurred in the year with the largest crop of *Manilkara* (2010) and in the habitat where the diversity of primate-dispersed species retrieved in seed traps was the highest (Grand Plateau, with clay soils), while fruit consumers did not seem to be satiated in other instances. Spatio-temporal variability of seed production and the community-crop context are therefore affecting satiation of frugivores during masting events.

Key Words: frugivory, mass fruiting, *Manilkara huberi*, *Manilkara bidentata*, primates, predator satiation hypothesis, seed dispersal, spatio-temporal variation

Mast seeding is the synchronous and massive crop production by some plant species at supra-annual intervals which can result in a significant increase in seedling establishment probability (Kelly & Sork 2002). The proposed mechanism for the selective advantage of masting is the predation satiation hypothesis (Janzen 1971, Kelly & Sork 2002). It posits that seed predators (both invertebrate and vertebrate species) are unable to eat all the produced seeds during the fruit peak, seeds therefore escaping the predator pressure and having increased chances of establishment (Kelly & Sork 2002).

Not only seed predators but also seed dispersers could be satiated with abundant seed crops, consequently dispersing only a part of the available seed pool (Hampe 2008, Kelly & Sork 2002, van Schaik *et al.* 1993). This

would imply that negative density-dependent processes associated with large seed crops would limit dispersal by frugivores (Wright *et al.* 2005). According to this hypothesis, Herrera *et al.* (1998) found that plants dispersed by frugivore mutualists were less variable in inter-annual seed production than plants dispersed by other means. However, the majority of evidence of a negative effect of masting for animal seed dispersal comes from temperate ecosystems (Kelly & Sork 2002) or for dry-fruited species (Levey & Benkman 1999). Albeit masting is a well-known phenomenon in some tropical cases such as Dipterocarpaceae forests in South-East Asia (Sakai 2002) or in Amazonian forest of French Guiana (Norden *et al.* 2007), there is very little knowledge of the interaction between massive crops of fleshy-fruited species and seed dispersal by frugivores in the tropics.

Satiation of seed dispersers might be highly dependent on the community-wide fruiting context (Ratiarison

¹ Contributed equally

² Corresponding author. Email: pierre-michel.forget@mnhn.fr

& Forget 2011). Fruit availability is determined by the phenological patterns and floristic composition of the community, which can vary in time and space (Polansky & Boesch 2013, Sabatier 1985). In addition, habitat characteristics are influencing the spatio-temporal variation of the community of frugivores and their diet (Peres 1994, Stevenson *et al.* 2000). Although spatio-temporal variability in fruit production and habitat characteristics might be affecting satiation of consuming animals, previous studies have addressed them separately, and mainly from the viewpoint of seed-predator satiation (Ratiarison & Forget 2011). Considering the working hypothesis that masting results in satiation of seed dispersers, the aim of this study was to establish the influence of spatio-temporal variability of fruit production on disperser satiation. We thus compared seed dispersal rates of two species of the genus *Manilkara* among different masting events, taking into account the variability of habitats and the diversity of fruiting crop at the community level.

We chose the tree species *Manilkara bidentata* (DC.) A. Chev. and *M. huberi* (Ducke) Standl. (Sapotaceae) as study case given their known masting behaviour, fleshy fruit and frugivore coterie (Norden *et al.* 2007, Ratiarison & Forget 2011). The study area was the Nouragues Biological Station (French Guiana; 4°05'N, 52°40'W), where a phenology monitoring programme has been conducted between February 2001 and February 2011.

Sampling protocol consisted in 160 litter traps (0.5 m² each) hung at 1.5 m above the ground and composed of a nylon mesh (Norden *et al.* 2007, Mendoza *et al.* unpubl. data). Traps were set in two forests differing in soil composition and tree community structure: Petit Plateau (PP), with sandy granitic-derived soil, and Grand Plateau (GP), with clay soil on metamorphic substrate and a higher cover percentage of lianas (Norden *et al.* 2007, Poncy *et al.* 2001). We set 100 seed traps in GP and 60 in PP. Traps were established randomly along parallel trails (five in GP and four in PP), with a minimum distance between neighbours of 15 m. Trap content was emptied every 2 wk, sieved and dried. All the collected seeds, fruits and fragments > 5 mm were determined to species or morphospecies by a skilled assistant (A. Caubère). The two species of *Manilkara* have an uneven adult distribution between the two plateaux (Ratiarison & Forget 2011): *M. huberi* and *M. bidentata* grow in relatively high density at PP (3 indiv. ha⁻¹), whereas the density at GP is much lower (0.65 indiv. ha⁻¹), and is mostly composed of *M. bidentata* (Ratiarison & Forget 2011).

Fifty-eight out of the total 160 traps collected fruits and/or seeds of *Manilkara* during the 10-y census. This reproductive material was used to test a satiation effect of seed dispersers (literally, how many of the available fruits were not eaten by frugivores). Fruits are drupes containing up to five seeds (mean number of seeds per fruit

is 1.1 ± 0.1 for *M. bidentata* and 1.6 ± 0.1 for *M. huberi*, n = 107 and 93 fresh fruits, respectively; Ratiarison 2003) embedded in a fleshy pulp rich in sugar and latex. Fruits are mainly dispersed by primates that swallow the fruit content but do not consume the pericarp, which falls to the ground after being opened with teeth and emptied (Ratiarison 2003, Ratiarison & Forget 2011). Each sample collected per census and seed trap could contain a different combination of entire fruits, entire free seeds, and remains of fruit as debris or pedicels of *Manilkara* spp. We calculated first the actual number of collected (non-dispersed) seeds as the sum of the free seeds and the entire fruits multiplied by the mean number of seeds per fruit (1.1 or 1.6). Secondly, we conservatively estimated the original number of seeds using fruit debris and the number of pedicels. This was achieved dividing the weight of debris found in the traps by the mean dry fruit biomass per species (*M. huberi*: 5.23 ± 2.18 g, n = 129 dry fruits; *M. bidentata*: 3.39 ± 0.76 g, n = 80 dry fruits). We are aware that this measure might be under-estimating the original number of fruits, given that not all the debris was collected in the traps beneath adult trees and that debris could belong to different fruits. For this reason, when the number of free fruit pedicels found in traps was higher than the estimates of fruit based on debris, we also included this difference as fruit estimates. Fruit estimates were then converted to seed estimates using the mean values of seeds per fruit. We calculated the proportion of seeds dispersed (Ds) per each trap and census combination using the following formula:

$$\left\{ \begin{array}{l} \text{if estimated seeds} > \text{collected seeds}, \\ Ds = \frac{\text{estimated seeds} - \text{collected seeds}}{\text{estimated seeds}} \times 100 \\ \text{if estimated seeds} \leq \text{collected seeds}, Ds = 0 \end{array} \right.$$

Counts of estimated seeds were analysed with a Chi-square test that predicts a theoretical homogeneous distribution between habitats and years. The proportion of seeds dispersed was analysed with a logistic regression model (generalized linear model with a binomial distribution) with a logit link function, because the individual probability of each collected seed being dispersed was binary. We tested the null hypothesis of homogeneous distribution between habitats and years. We constructed first a full model (including an interaction between habitat and year) using Ds as dependent variable and compared it with alternative models with less predictor variables, retaining the one with the lowest value of AIC (Zuur *et al.* 2009). Data of both species were pooled due to the lack of *M. huberi* at GP. The diversity of seed production at the community level was calculated with the Shannon–Weaver diversity index (H') and the Simpson valuation index (1-D; Magurran 2004), only using data on primate-dispersed species, retrieved

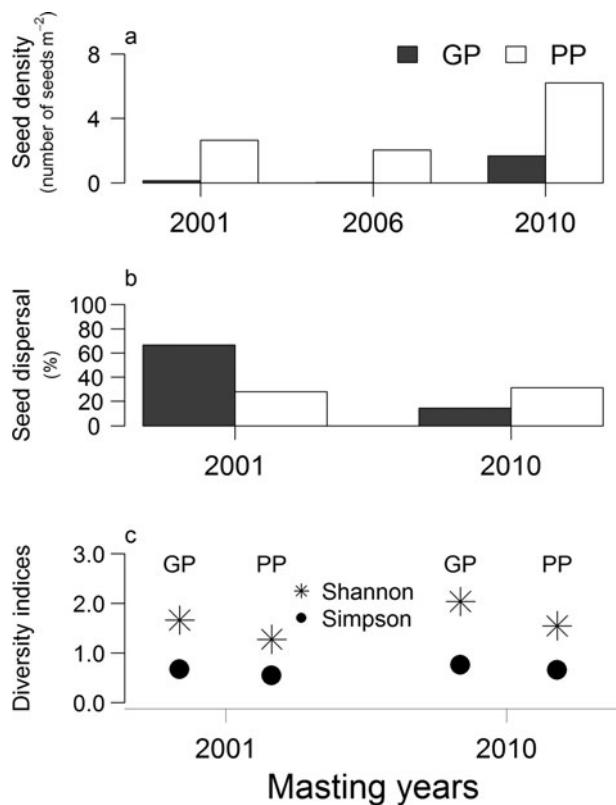


Figure 1. Barplots represent seed density (number of seeds m⁻²) of *Manilkara* estimated from seeds, fruits and remains retrieved in seed traps (a) and the proportion of seeds dispersed (*Ds*) per masting year and habitat studied (GP = Grand Plateau, dark bars; PP = Petit Plateau, light bars). Diversity indices (* = Shannon–Weaver index; • = Simpson valuation index) calculated per habitat and study year using values of fruit production found in seed traps. We only included primate-consumed species (c).

from seed traps. All statistical analyses and graphs were performed with the software R, version 3.1.2.

The 58 traps sampled a total of 237 entire seeds, 210 free pedicels, 64 entire fruits, and 700 g of dry mass of remains, the equivalent of 152 consumed fruits, during the 10-y monitoring. Although immature or aborted fruits were present during all study years, viable fruits and seeds only appeared during three years (2001, 2006 and 2010), therefore considered the three masting events of the species. Immature fruits were easily distinguishable from mature ones given their smaller size, attached pedicel, and poor development of the mesocarp.

There was a significant variability of seed production among masting events; the estimated number of *Manilkara* seeds was greater in 2010 (3.37 seeds m⁻²) than in 2001 (1.06 seeds m⁻²) and 2006 (0.78 seeds m⁻²; $\chi^2 = 187$, df = 2, P < 0.001; Figure 1). During the three masting events, seed production was overwhelmingly larger at PP than at GP (Figure 1), presumably a direct

Table 1. Minimum adequate model for explaining the proportion of seeds dispersed (*Ds*) in relation to habitat and year. We fitted a Generalized Linear Model with a binomial distribution and a logit link. Model was estimated using a restricted maximum likelihood (REML). AIC = 190.17; Total df = 41; Residual deviance = 153.9 on 38 df. Total number of estimated seeds were included as weights in the model.

	Estimate	Standard error	Z	P
Intercept	-0.69	0.86	-0.8	0.42
Habitat	-0.26	0.90	-0.29	0.78
Year	-3.72	1.33	-2.81	0.005
Habitat × Year	3.74	1.36	2.74	0.006

consequence of contrasting *Manilkara* adult density on the plateaux.

Due to low sampling of *Manilkara* seeds in 2006 (only 1 seed at GP), we removed this year for consequent analyses. In 2001, dispersal proportion of *Manilkara* seeds (*Ds*) was higher at GP (66.7%) than at PP (27.8%; Figure 1), whereas the pattern was the opposite in 2010, when *Ds* was significantly greater at PP (35.9%) than at GP (14.3%). The minimum adequate model for *Ds* retained three parameters: habitat, year and the interaction between habitat and year (Table 1). According to our two diversity indices, GP showed the highest values of diversity for primate-preferred species compared with PP in both years (Figure 1): 2001 (H' = 1.66; 1-D = 0.67 for GP vs. H' = 1.28, 1-D = 0.55 for PP) and 2010 (H' = 2.04; 1-D = 0.76 for GP vs. H' = 1.55, 1-D = 0.66 for PP).

Our results showed that seed dispersal proportion was greater in 2001 compared with 2010, the year of higher seed production, which is consistent with our initial hypothesis of frugivore satiation. However, there was a spatio-temporal effect in the pattern of satiation that relates to the community context. First, the two study areas differed in *Manilkara* tree density, lower at GP than at PP for both species. Second, the composition of primate-dispersed seed rain was more diverse at GP than at PP during both years (see Ratinarison & Forget 2011 for similar results), possibly a result of overall contrasting tree composition and drainage between plateaux (Poncy *et al.* 2001), and differences in foraging of primates across the landscapes (Simmen & Sabatier 1996).

Manilkara tree species had a major contribution in the community fruit production during each mast seeding event (16% in 2001 and 39% in 2010 of the total number of seeds retrieved in traps each year; Mendoza *et al.* unpubl. data). This might explain that, despite relatively low density of adult trees, massive crops of *Manilkara* seem to be able to affect predators and dispersers. At GP, in a relatively poor year in terms of fruit production (2001), the proportion of *Manilkara* seeds dispersed was greater than in a year with an overall context of higher diversity of

primate-dispersed fruit production (2010). Seed dispersal proportions were similar at PP between both years.

Massive fruit production of *Manilkara* therefore resulted in seed waste (*sensu* Howe 1980) during the year with the largest crop (2010). However, seed dispersal is a multi-stage process (Schupp *et al.* 2010) and satiation of frugivores might not necessarily lead to final reduced establishment (Herrera *et al.* 1998). Seed predation by rodents ranged 36–68% in *M. huberi* in 2001 (Chauvet *et al.* 2004), but predation proportion could be lower when the availability of undispersed seeds is higher (e.g. 2010), as observed by Nyiramana *et al.* (2011).

In conclusion, our initial hypothesis that seed masting would satiate frugivores was not generally supported, but rather depended on spatio-temporal variability of fruit production at the community level. Factors such as the composition of the frugivore guild, the community diversity of seed production and tree densities seem to affect the satiation phenomenon. Recommended future directions should include further experiments on the effect of climate variability on fruit availability and frugivore satiation, seed establishment and the recruitment of plants in the longer term.

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