# The role of frugivores in determining Seed removal and dispersal in the Neotropical nutmeg

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**Research Article**

# The role of frugivores in determining seed removal and dispersal in the Neotropical nutmeg

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Abstract
At the Nouragues field station (French Guiana), we studied the seed dispersal system of two sympatric tropical tree species that differ in seed size, *Virola kwatae* and *V. michelii* (Myristicaceae), to evaluate the degree of interaction between *Virola* species and their dispersers, and consistency in the fruit traits affecting seed removal rate. Only the spider monkey (*Ateles paniscus*) and three species of ramphastid toucan dispersed the large (4.8g) *V. kwatae* seeds. These four animal species, as well as three smaller-bodied bird species, also dispersed the small *V. michelii* seeds (2.1g). Annual fecundity of both *Virola* species did not affect seed removal rate. However, variation in *V. kwatae* seed size within tree populations, and increased seed removal rate due to fruit selection on seed size, suggest a potential for an evolutionary response of seed size to selection by large-bodied frugivores in this species. In contrast, seed size did not affect *V. michelii* seed removal rate, and the interactions between *V. michelii* and its dispersers are interpreted to be too diffuse to result in strong selection on plant traits affecting seed removal rate. Because hunting pressure is greater on larger than on smaller frugivores, extinction of *A. paniscus* (the main large-bodied seed disperser of the study *Virola*) is likely to affect the long tail of dispersal kernel, thus decreasing recruitment away from fruiting adult trees.

**Keywords:** coevolution, frugivores, Myristicaceae, Neotropics, seed dispersal, seed size, *Virola* spp.

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## Introduction

In tropical forests, fruit-frugivore interactions are thought to result mostly from diffuse coevolution [1] between groups of plant and animal species exerting selective pressures on each other [2-6]. It has also been suggested that seed dispersal may be an important selective force determining evolutionary changes in these animal-plant interactions, due to effects of the interaction on the fitness of both parties: the fruit choices of frugivores could cause natural selection on some fruit and seed traits [7-11]. The evolution of fruiting traits in response to fruit selection by dispersers requires: 1) variations in these traits within the plant population; 2) non-random fruit choice by frugivores based on these traits; 3) increased plant recruitment due to disperser preferences; and 4) variations in traits at least partly heritable [12]. Here, we investigate the extent to which the first two criteria are met in a well-studied seed dispersal model system, the Neotropical tree genus *Virola* (Myristicaceae) and a variety of frugivores.

Fruit syndromes provide evidence that fruit and seed attributes may have evolved in relation to such selective pressures by different sets of consumers rather than from specific pairwise interactions [6, 8, 13-15]. For instance, the bat-dispersal fruit syndrome is a green, yellow or white berry exposed away from foliage, enclosing small to large seeds embedded in pulp that are swallowed and dispersed after gut transit [14, 16]. The plant family Myristicaceae (nutmegs) illustrates another syndrome, with fruits that are dehiscent at maturity and expose a brightly-coloured aril surrounding large seeds that are dispersed by birds and primates, with intact seeds being either regurgitated or dropped in faeces [6, 13, 17]. Fruit selection by frugivores can be viewed as a cost-benefit balance involving the feeding abilities of frugivores (cost), on one hand, and the available fruit reward (benefit), on the other hand [18, 19]. Many factors may therefore influence fruit selection and seed dispersal, including fruit and seed size [13, 20, 21], pulp to seed ratio [10, 20], nutrient content and secondary compounds [22-24], crop size [25-27], phenology [28, 29], distance to nearest neighbours [30], and plant community structure and diversity [5, 31]. According to their sensory, physiological, morphological and behavioral features, seed disperser species differently integrate these factors when choosing fruits, [18, 32, 33]. Moreover, temporal and spatial variation in fruit selection may occur [3, 34]. Cumulatively, these effects could lead to variability in fruit choice among frugivore species, affecting fitness through inconsistent natural selective pressures on reproductive traits related to seed dispersal.

In this study, we investigated the consistency in the factors of fruit selection affecting seed removal rate by examining interspecific variations in feeding assemblages and fruit selection. Specifically, we quantified the dependence of visitation and seed dispersal by flying and arboreal frugivores on the fruiting and seed traits of two sympatric and congeneric tree species (*Virola kwatae* and *V. michelii*). We hypothesized that the smaller seeded *V. michelii* tree would be visited by a greater number of smaller bodied frugivores species than the large seeded *V. kwatae* tree species, whose fruits are almost exclusively removed by large toucans and one primate species [35, 36]. Frugivores are beneficial to *Virola* tree recruitment simply by removing aril from seeds and facilitating germination [20]. In addition, seed removal by frugivores may allow seeds to escape from predation beneath parent trees, especially by terrestrial vertebrates that often forage in high-density patches of seeds (peccaries [37, 38], S. Ratiarison, pers. obs.). The genus *Virola* represents a model seed dispersal system, its numerous species displaying fruits with similar fruit morphology and a large range of size of the dispersal unit (i.e. arillate seed). Thus, a comparative approach can be used to gain insight into the underlying evolutionary factors involved in plant/disperser interactions.

## Methods

### *Study site and species*

The study was carried out from November 2000 to March 2001 in a pristine continuous lowland high rainforest [39] in the forest surrounding the inselberg in the Nouragues Biological Station (4°05’N, 52°40’W), French Guiana [40] (Fig. 1). Nouragues is free from anthropogenic pressures, thus the natural coterie of frugivores is present. Mean annual rainfall is 2,990 mm, with most rainfall between November and July. Vegetation is characteristic of tall mature lowland rainforest, Lecythidaceae, Sapotaceae and Burseraceae being among the most common tree families [39]. The community level fruiting peak occurs in February-May during the long rainy season in French Guiana [41-43].

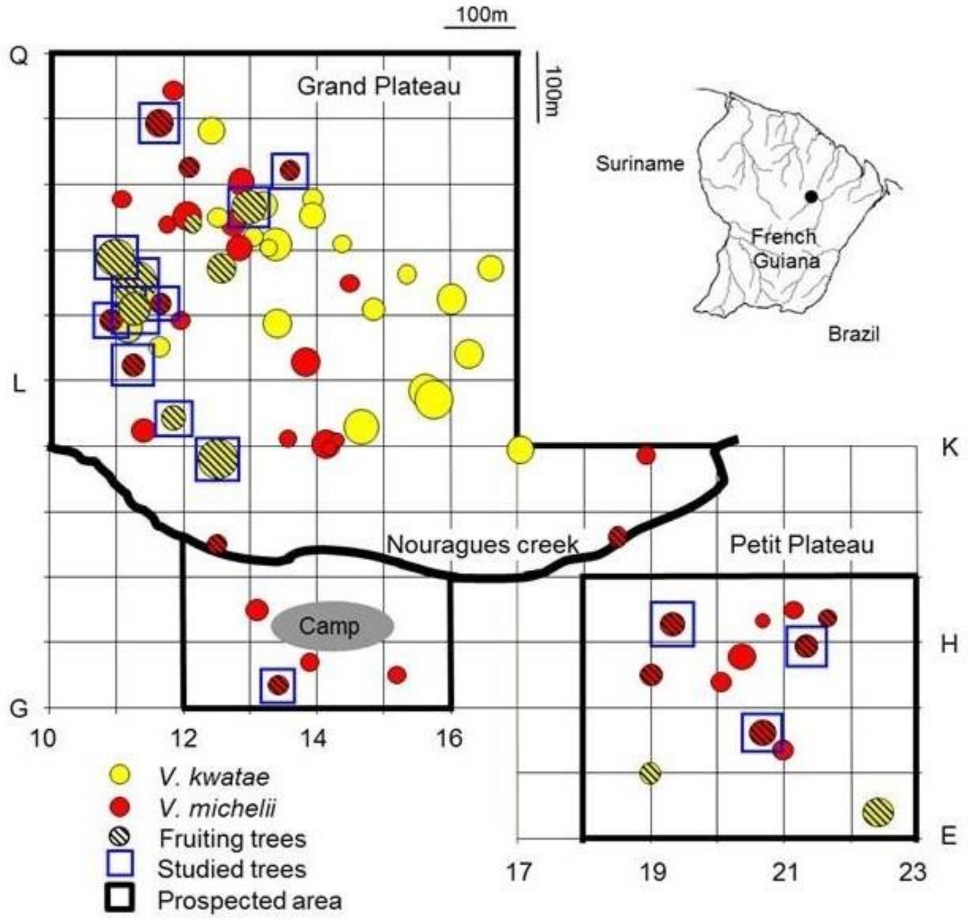

**Fig. 1: Location of *Virola kwatae* (Yellow circles) and *V. michelii* (red circles) adult trees at Nouragues. The 100 × 100 grid indicates trails 100-m apart from each other, numbered by numbers (10 to 23) and letters (G to Q). Circle size is proportional to trunk diameter at breast height (dbh). Trees having fruited in the prospected areas (thick frames) between October 2000 and March 2001 are hatched and focal trees are framed in blue (see symbol legend inset). Inset: French Guiana with location (black dot) of the Nouragues research field station.**

Five *Virola* species have been inventoried at Nouragues [44]. Here we focus on the two species (*Virola kwatae* Sabatier [36] and *V. michelii* Heckel [45]) which both grow at low density and account for most of the *Virola* tree species with diameter at breast height (dbh) > 25 cm recorded at study plots [46] (Fig. 1 and Appendix 1). *Virola* are dioceous trees (Fig. 2a,b) that fruit yearly between September-March, and produce bivalved dehiscent fruits which open to expose one seed surrounded by a lipid-rich aril [47] (Appendix 1). Fruiting periods of *V. kwatae* and *V. michelii* partly overlap and occur during the low fruiting season, with peaks following each other at the onset of the high fruiting season [35, 48]. The two focal study species differ in tree size, fruit colour and size, and seed size (Fig. 2c), but show similar aril to seed ratio (i.e. aril fresh mass/seed fresh mass – Appendix 1).

The avian community includes 157 frugivorous or granivorous species. Large canopy frugivorous birds (e.g. toucans, guans) are common. There are 45 species of arboreal and flying frugivorous mammals [49]. Red howler monkeys (*Alouatta seniculus*), capuchins (*Cebus olivaceus* and *C. apella*) and black spider monkeys (*Ateles paniscus*) dominate in terms of primate biomass.

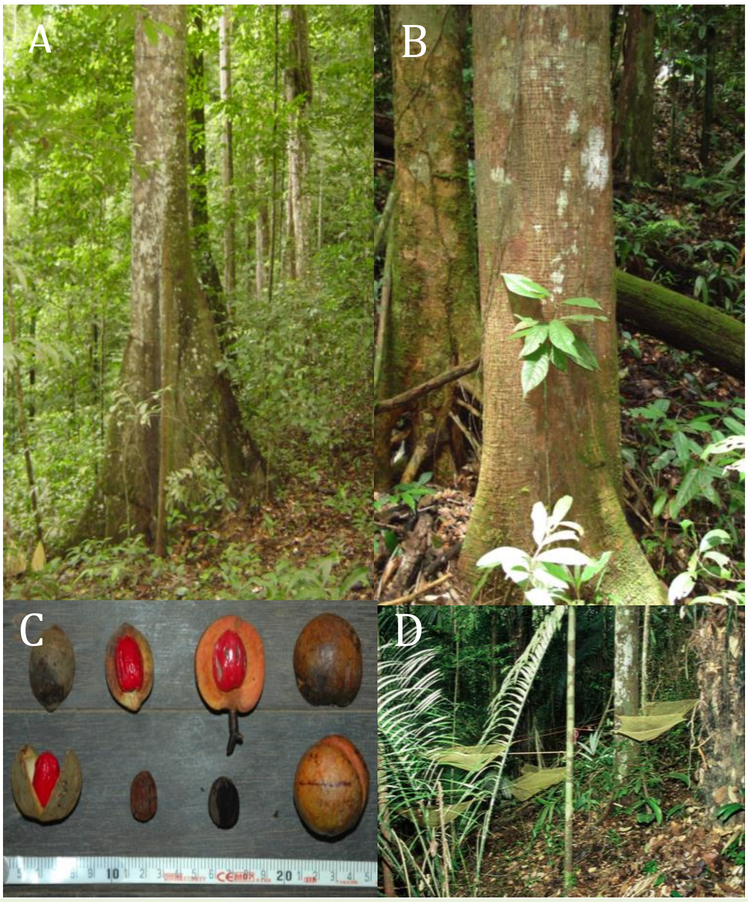

**Fig. 2: *Virola* trees (A : *V. kwatae* ; B: *V. michelii*) fruits and seeds (C : *V. michelii*, left; *V. kwatae*, right) and litter traps (D) underneath a *V. michelii* tree crown in Guianan rainforests (all © Pierre-Michel Forget).**

### *Data collection*

The entire populations of mapped *V. kwatae* and *V. michelii* trees were surveyed for fruit production within an 88-ha area between October 2000 and March 2001 (Fig. 1) [48]. All observed fruiting *V. kwatae* (N = 6) and *V. michelii* (N = 9) trees were equipped with 1-m² litter traps, and their dbh measured. Traps were randomly located within the horizontal projected crown area of focal trees and hung at 1.5 m above ground (Fig. 2d) [20, 35, 50]. Trap design and setting precluded seed loss due to bounce back and predation. Sampling effort was 4-8% and 7-16% of tree projected crown area at individuals of *V. kwatae* and *V. michelii*, respectively. Traps collected single intact valves and pieces of valves chewed by animals, especially primates and rodents. Following Howe and Kerckhove [20], we estimated seed crop size and fate (i.e. proportions of seeds removed, regurgitated/defecated, preyed on prior to dispersal) at both study species.

For all traps under a focal tree, we estimated the total number of fruit valves by dividing the total biomass of chewed valves by the mean mass of an intact valve, plus all intact valves (including those from entire fruits). The total number of fruits (A) corresponding to these valves was then estimated by dividing the total number of valves by two. Collected seeds were classified as: (1) arillate seeds alone or in entire fruits (2) aril-free seeds regurgitated or defecated by consumers, and (3) seeds showing traces of vertebrate predation, especially rodent tooth marks. At each focal tree, the original seed crop size (B) was calculated as B = A / proportion of the crown area sampled. The number of seeds carried away from each focal tree (4) was assessed by subtracting the number of seeds collected (1+2+3) from B. Seed fall from category 1 resulted from wind or frugivore handlings and movements in tree crowns, whereas categories 2, 3 and 4 resulted from fruit consumption by animals. Three seed fate categories were then defined: 1) seeds removed from the parent (seeds unaccounted for), 2) seeds regurgitated or defecated (seeds processed by a frugivore, but not removed from the projected crown area of the parent), and (3) seeds with evidence of pre-dispersal predation. The estimate for each category was expressed as the percentage of the total seed crop. We collected the following fruit and seed trait data, measured on fresh mature fruits collected at each focal tree (N = 5-10 fruits per tree): seed and aril fresh mass, seed length and width (measured both on aril-free dispersed seeds and on non-dispersed seeds cleared from arils), and aril to seed fresh mass ratio.

Censuses of diurnal consumers were conducted at each focal tree species between 30 October and 12 December 2000, and from 3-17 February 2001, i.e., during the *Virola* peak and late fruiting periods. During the entire study period (N = 60 days), three census sets (7:00-9:00, 11:30-13:30 and 16:00-18:00) were performed daily at all focal trees producing mature fruits, in all weather conditions but rain (N = 6 days). Ordering trees randomly within each census set, each focal tree crown was scanned from the ground using binoculars (7x40) for 10 minutes, once per set. All sightings of animals eating arils and/or seeds were recorded. A total of 246 ten-minute censuses were conducted at each tree species. Though some marsupials (Didelphidae) [51] and the kinkajou (*Potos flavus*) [52] are known to consume *Virola* fruits at night, no observation was conducted after dark since *Virola* species contribute little to the diet of these frugivores and nocturnal visitation appears generally infrequent [20, 35, 37].

### *Data analysis*

The goals were to identify between-species differences in fruiting and seed traits (seed fresh mass, length and width, aril fresh mass, and aril to seed ratio) and quantify the effect of variation in these traits on 1) fruit choice by frugivores and 2) seed fate (the categories defined above). Nested analyses of variance (ANOVAs) were used to compare seed traits between and within tree species to identify potential discriminating traits that could affect fruit selection by frugivores. Student's t-tests were used to compare seed traits among random samples of aril-free dispersed seeds and non-dispersed seeds (cleared from arils) within each tree species. Correlations of seed fate categories with fruiting and seed traits were tested using Pearson's correlation tests. One-way analysis of covariance (ANCOVA) with diameter at breast height (dbh) as a covariate was used to compare fruit production between species. Since seed fate categories (removed/ regurgitated/defecated/predated) are dependent variables, one-way multivariate analysis of variance (MANOVA) was used to compare seed fate between species. Arcsine square root transformed values for seed fate percentages and square root transformed values for fruit production were used. Analyses were performed with the software SPSS [53]. When response variable data violated the assumptions of normality and/or homoscedasticity, either transformations or non-parametric alternatives (Kolmogorov-Smirnoff Z-test, Wilcoxon signed-rank test, Spearman's rank correlation) were used.

## Results

*Virola kwatae* and *V. michelii* trees differed significantly in all seed and aril traits except aril to seed ratio (Table 1 and Appendix 1). Seeds of *V. kwatae* were significantly heavier, longer and wider than *V. michelii* ones. There were also significant differences in all of these traits among trees within species, but between-species variations explained most variation in all seed traits. Aril fresh mass also significantly differed among species and trees within species. Within-tree variation was especially high in *V. kwatae*, explaining 76% of aril mass variation at this species vs. 19% in *V. michelii*. Finally, aril to seed ratio did not differ significantly between species, nor among trees. For both tree species, seed fresh mass was positively correlated to seed length (Pearson correlation test, $r = 0.848$; $p < 0.001$ and $r = 0.745$; $p < 0.001$ for *V. kwatae* and *V. michelii*, respectively), width ($r = 0.564$; $p < 0.001$ and $r = 0.688$; $p< 0.001$, respectively), and to pulp fresh mass ($r = 0.512$; $p < 0.001$ and $r = 0.719$; $p < 0.001$). *Virola kwatae* non-dispersed seeds were significantly wider (Appendix 1) than dispersed seeds (Student t-tests, $t = 2.94$; $p = 0.004$), but neither heavier, nor longer ($t < 1.57$; $p > 0.12$). In contrast, there were no significant differences between *V. michelii* non-dispersed and dispersed seeds in fresh mass, length and width ($t < 0.72$; $p > 0.48$).

Table 1. Comparison of *Virola kwatae* (N = 6 trees) and *V. michelii* (N = 9 trees) fruit traits (N = 5-10 fruits per tree). Results of unbalanced nested ANOVAs and percentages of the total variance explained by the different levels are presented.

| | **Between species** | | **Within species** | | **Within trees** | **R²** |
|---|---|---|---|---|---|---|
| | **$F_{1,108}$** | **%** | **$F_{13,108}$** | **%** | **%** | |
| Seed fresh mass | 49.0** | 80.7 | 12.5** | 11.4 | 7.9 | 0.91 |
| Seed length | 12.0** | 56.2 | 43.8** | 37.0 | 6.8 | 0.93 |
| Seed width | 36.7** | 63.1 | 3.8** | 9.6 | 27.4 | 0.71 |
| Aril fresh mass | 8.1* | 35.8 | 4.0** | 20.9 | 43.3 | 0.66 |
| Aril to seed ratio | $0.1^{ns}$ | — | $1.4^{ns}$ | — | — | — |

$^{ns}$: not significant; *: significant at $p \leq 0.05$; **: significant at $p \leq 0.01$

Despite difference in tree diameter between species, average fruit production was comparable ranging between 440-9,200 (2,700 ± SE 1,350) fruits for *V. kwatae* trees and 70-5,430 (2,200 ± SE 580) fruits for *V. michelii* trees (Fig. 2). There was a significant interaction ($F_{1,11} = 6.02$, $p = 0.011$) between trunk diameter and crop size, the nine smaller *V. michelii* trees producing a greater number of fruit (19,655) than the six larger *V. kwatae* trees (16,307) in 2000-2001. No fruit or seed traits were significantly correlated with seed crop size ($p > 0.05$ for *V. kwatae* and *V. michelii*, respectively, for all traits).

During censuses, a total of six and eight frugivore species, accounting for 51 and 110 sightings, consumed *V. kwatae* and *V. michelii* fruits, respectively (Appendix 2). Four species (*Ramphastos tucanus*, *R. vitellinus*, *Selinedera culik* and *Ateles paniscus*) fed on both fruit species. Toucans and toucanets (Ramphastidae) were the most frequently observed consumers in *V. michelii* (censuses: 61%; watches: 38%) and V. *kwatae*, (censuses: 52%; watches: 51%), the smallest species (*S. culik* and *R. vitellinus*) accounting for a larger percentage of sightings at the smaller seeded *V. michelii*, and *vice versa* for the largest *R. tucanus* more frequently visiting the large seeded *V. kwatae* (Appendix 2). Spider monkeys (*A. paniscus*) accounted for 31% and 33% of sightings at *V. kwatae* and *V. michelii*, visiting trees mostly singly or in small groups (usually familial units with one adult female, one young and one juvenile). Feeding only on mature fruits, spider monkeys acted as seed dispersers by swallowing the seeds in 85 ± 5% and 83 ± 3% of the fruits they handled per visit at *V. kwatae* and *V. michelii*, respectively. When leaving feeding trees after a long visit (average visit duration: 37 ± 8 min per visit, N = 25 visits, pooling both tree species), all members of a group tended to defecate one after the other in the vicinity of the crown edge. These defecations contained 1–8 different seed species (N = 6 faeces, 4 ± 1 seed species) scattered over several-m² areas. Only one contained *Virola* seeds (7 seeds of V. *michelii* dropped close to a conspecific tree). Squirrels (Sciuridae) were the only seed predators observed in *Virola* tree crown, though infrequently.

A total of 73% *V. kwatae* and 67% *V. michelii* of seeds produced were removed from focal trees (Table 2). When not removed, seeds were dropped beneath trees either by regurgitation or defecation (15% *V. kwatae* and 21% *V. michelii*) or fell undispersed (12% and 12%) as unopened immature fruits. Pre-dispersal seed predation by insects and/or rodents was very low for both tree species (0.3% and 0.5%). There was no significant difference between *Virola* species in seed fate (MANOVA with arsine-square-root transformed data, $F_{3,11} = 1.483$; Lambda = 0.273; p = 0.712). Seed fate was not correlated with seed crop size (*V. kwatae*: p> 0.40; *V. michelii*: p > 0.10, for all percentages). However, the relationships between seed fate and fruit and seed traits did differ significantly between species: in *V. michelii*, seed fate was not correlated with seed traits (p > 0.15), pulp fresh mass (p > 0.14) or aril to seed ratio (*p* > 0.17). In contrast, in *V. kwatae,* seed removal significantly decreased with seed width, suggesting that narrower seeds were dispersed more frequently ($F_{1,5}$ = 15.1; p= 0.018; $R^2$ = 0.74), while seedfall significantly increased with seed width, suggesting that wider seeds were less likely to be removed ($F_{1,5}$ = 24.4; p= 0.008; $R^2$ = 0.82) away from *Virola* trees that were primarily visited by toucans and toucanets, and secondarily by spider monkeys.

Table 2. Seed fate (removed, regurgitated or defecated, predated) at *Virola kwa*tae and *V. michelii* tree crowns at Nouragues. Data are individual mean proportions ± SE. Univariate analyses associated with the MANOVA testing for species effect on variables of seed fate are presented.

| | ***V. kwatae*** | ***V. michelii*** | $F_{1,13}$ |
|---|---|---|---|
| Removal | 72.3 ± 6.7 | 67.3 ± 3.4 | $0.74^{ns}$ |
| Regurgitation/Defecation | 15.1 ± 3.5 | 20.5 ± 2.5 | $1.95^{ns}$ |
| Predation | 0.3 ± 0.2 | 0.5 ± 0.2 | $1.02^{ns}$ |

## Discussion

### *Effect of forest type and fruit availability*

Overall, there was little difference in the interactions between the two *Virola* species and their seed-dispersing frugivores. Over the entire *Virola* fruiting season, no significant relationship was found between annual fruit production and seed removal rates for both species. The weak influence of individual tree fecundity on the high proportions of seed removal at both tree species, despite their successive timing of fruiting peaks, suggested that all *Virola* fruits were preferred food resources from November to March at Nouragues. This is consistent with previous observations that *V. kwatae and V. michelii* rank first in the diet of *Ateles paniscus* in Guianan and Amazonian forests (for instance [5, 48, 54]), and that *Virola* fruits are regular food sources for ramphastids in other Amazonian forests [10, 50].

Our results contrast with those of Daniel Sabatier [35, 36] on *V. kwatae* at the ‘Saut Pararé’ site, along the Arataye river eight km from our study site. At ‘Saut Pararé’, the forest hosts a different floristic composition, the Myristicacae species with a dbh greater than 10 cm ranking among the most abundant family, with *Virola kwatae* and *V. michelii* as leading species [39]. Sabatier [35] indeed observed that *V. kwatae* removal rate (67 %) was mostly due to visits by *A. paniscus* (50%) at Saut Pararé forest. Thus, the frequency of visits by frugivores at specific fruiting trees may be influenced by forest type and fruit productivity, which are both known to affect the local density of frugivores [55]. However, as emphasized by Peres [55], there is greater tree density (3.4 trees/ha) at Saut Pararé [36] than at Nouragues Inselberg (0.30 trees/ha, this study), thus fruit productivity and an expected greater *A. paniscus* density at the former site may explain Sabatier's results. Crop size also appeared to be three times greater in 1980-1981 (7,300 fruits per tree in average, range 2,400-16,400, N = 6 trees) in Sabatier's study than in the present one (see Results). Further, much may have changed in these forests in the 20 years between the studies.

We suggest that *A. paniscus* were less attracted to sparse fruiting *V. kwatae* trees with smaller crops, allowing more Rhamphastidae to visit trees at Nouragues Inselberg site during this study year. The lower percentage of non-dispersed (dropped) seeds at Nouragues Inselberg (12%) compared to the Saut Pararé forest site (25%) is therefore consistent with the greater frequency of toucans visiting the tree crown compared to spider monkeys at the former site.

### *Effect of fruit and seed size on frugivores visits*

Our study demonstrated that contrasting seed size between the two sympatric and congeneric tree species likely influenced the probability of disperser visitation by different guilds of highly frugivorous animal species. Seed width appeared as the main plant attribute relevant to *V. kwatae* seed removal rate. Toucans acted as seed dispersers at both tree species, usually regurgitating seeds at perching trees located more than 20 m away from parent trees. In contrast, toucanets were not efficient seed dispersers, often regurgitating seeds beneath parent trees at *V. kwatae* and *V. michelii*. Similarly, the smallest recorded bird species (*Trogon melanurus*, Trogonidae) also regurgitated all the seeds below *V. michelii* tree crowns. Except guans (*Penelope marail*, Cracidae), which removed *V. michelii* seeds, other recorded bird species (Icteridae, Momotidae) dropped seeds beneath both *Virola* tree species.

Although smaller seeds showed lower fruit reward (i.e. food supply vs. seed ballast), fruit selection based on seed width occurred at *V. kwatae*, implying the preferential removal of the narrowest seeds and greater chance of a seed being dropped beneath parent trees displaying the widest seeds. We could not determine which disperser species exerted such selection, but it is likely that, for such large-seeded fruits, both birds and monkeys selected for smaller seeds [20]. In contrast, at *V. michelii*, no significant relationships were detected between seed traits and seed removal rate despite smaller-bodied bird species feeding on this fruit species. This suggested that the maximum size of *V. michelii* seeds was below the discriminating threshold size of seeds for being swallowed by its main disperser species: whatever the factors of fruit selection by smaller-bodied bird species, the impact of such fruit selection on seed removal rate was probably low and counterbalanced by greater fruit use by large frugivorous species independently of seed size.

Several researchers [8, 12] have reported the potential response of fruit size to natural selection by dispersers, especially gape-limited birds that swallow fruits whole. In dehiscent fruits such as nutmegs, only the arillate seeds will be swallowed, so that seed width could experience selection pressure [56] that normally applies to fruit diameter or width. At *V. kwatae*, variation in seed size between and within trees, non-random fruit selection based on seed size, and increased seed removal rate due to fruit selection on seed size, all suggest the potential for an evolutionary response of seed size to selection by dispersers [12]. In contrast, at *V. michelii*, plant-disperser interactions were probably too diffuse to result in strong selection on plant traits affecting seed removal. However, the heritability of seed size and effective increase of plant recruitment following seed removal have still to be demonstrated. Moreover, conflicting selective forces might also operate on seed size, such as requirements for germination and establishment that may vary according to environmental conditions [57-60].

Comparisons of *Virola* seed dispersal systems both at a local and a larger spatial scale may show strong mutual dependency between *Virola* and a few disperser species, especially highly frugivorous ones, and spatial consistency in the functional relationship between seed size and seed removal rate. Similar disperser assemblages among *Virola* species might result from phylogenetic relatedness, the functional relationship between seed size and seed removal rate within genus *Virola* simply reflecting that a common ancestor passed on this relationship [10, 61]. To determine the origin of such similar disperser assemblage within genus *Virola* and to evaluate if this disperser assemblage exerted directional selection on fruit and seed traits affecting seed removal rate, phylogenetic information is needed, as well as evidence of genetic basis of traits, and evaluation of increased plant fitness resulting from fruit selection by dispersers.

## Implications for Conservation

Because hunting pressure is greater on larger than on smaller frugivores [62-65], defaunation would impact dispersal and recruitment of larger-seeded frugivore-dispersed tree species more than smaller-seeded species in Neotropical rainforests [66]. The largest primate spider monkey *A. paniscus* and the largest toucan *R. tucanus* were the main consumers and dispersers of *V. kwatae* seeds observed at Nouragues. The population densities of spider monkeys and toucans might also be affected by forest type and *V. kwatae* tree density. In contrast, smaller frugivores were more often observed in the small-seeded *V. michelii* tree crowns. Because the diet of spider monkeys is dependent on forest richness and the abundance of fruit throughout the year, especially the occurrence of *V. kwatae* fruit species during the lean season, a reinforced level of protection is needed in all rainforests where *Virola* or other large-seeded nutmeg tree species occur, in order to conserve this key seed disperser [5, 67]. One may expect that if large frugivores, especially *A. paniscus,* experience greater population declines due to hunting [50, 54, 68], then the seed shadow, especially the long tail of the dispersal kernel, of large seeded *Virola* species will be altered, with potentially adverse effects on seedling establishment and recruitment away from parent trees. Conversely, because hunting pressure only marginally affects large toucans as observed in Ecuador [50] or French Guiana (Boissier et al., unpubl. data), large toucans such as *R. tucanus* and other smaller-bodied frugivores that are able to ingest and disperse *Virola* seeds will likely continue to ensure seed removal and dispersal, though at shorter distances from parents [69, 70] (dispersal distances being overall shorter among toucans [50, 71] than among primates [54, 72] with seedling aggregation around parent trees [37, 38]). Indeed, as observed for *V. michelli* in a Guianan forest lacking *A. paniscus* [38], *Virola* seedling recruitment in the near proximity of parents is still possible, allowing for some resilience in continuous ecosystems where larger frugivores have been extirpated. Nonetheless, if the forest is additionally fragmented, it is possible that dispersal effectiveness of *Virola* species will likely be adversely affected in the long-term [68].

### *Conclusion*

The seed dispersal ecology of two *Virola* species with contrasting seed size is very comparable after analysing the frequency of visits by two guilds of frugivores (birds and primates) and the percentage of seed removal in tree crown. However, each guild may differ in their frequency in Neotropical forests as a result of the interaction between the floristic composition and animal density, and the effect of anthropogenic pressures threatening wildlife habitats [55]. Though the primate *A. paniscus* was equally observed in both *Virola* species, the diversity of avian frugivore species differed among trees at Nouragues. The large toucan *R. tucanus* was more frequently observed in the large seeded species *V. kwatae*, and conversely for the smaller ramphastids and the smaller seeded *V. michelii*. Since large-bodied frugivores more often suffer from hunting, *Virola* species with small seed size might be less affected in human-modified landscapes and should show a greater resilience to disturbances. Still, without the larger seed dispersers, either primates and/or large toucans, seed removal of both species is likely to be dramatically affected, with altered dispersal kernels having the long tail reduced to shorter distances around the parent trees.

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Appendix 1. Tree density and tree and fruit traits of Virola kwatae and V. michelii at Nouragues. Tree, fruit and seed (only mature fruits and arillate seeds extracted from fruits) data (mean ± SE) are based on focal trees.

| | ***V. kwatae*** | ***V. michelii*** |
|---|---|---|
| **Adult tree density** | dbh ≥ 35 cm[1] | dbh ≥ 25 cm[1] |
| | GP: 24 for 68ha | GP: 27 for 68ha |
| | PP: 2 for 20ha | PP: 9 for 20ha |
| **Trees** | n = 6 | n = 9 |
| Trunk dbh (cm) | 115 ± 15 | 50 ± 3 |
| Mean crown radius (m) | 8.9 ± 0.8 | 5.4 ± 0.3 |
| **Fruit valves** | n = 100 | n = 103 |
| Fresh mass (g) | 17.54 ± 0.62 | 5.11 ± 0.19 |
| Colour at maturity (outside / inside) | Yellow / orange | Light brown, tomentuous / light green |
| **Seeds** | n = 50 | n = 73 |
| Fresh mass (g) | 4.77 ± 0.14 | 2.09 ± 0.05 |
| Length (cm) | 2.83 ± 0.06 | 2.05 ± 0.03 |
| Width (cm) | 1.82 ± 0.03 | 1.42 ± 0.02 |
| **Aril** | n = 50 | n = 73 |
| Fresh mass (g) | 1.78 ± 0.10 | 0.82 ± 0.05 |
| Aril:seed ratio | 0.37 ± 0.02 | 0.39 ± 0.02 |
| Nutrient content (% dry mass)[2] | | |
| Protides | ≥ 3.7 | ≥ 5.2 |
| Lipides | ≥ 11.7 | 49.0 |
| Soluble sugars | --- | 14.6 |

[1] Minimal trunk diameter at breast height (dbh) of all fruiting trees recorded in the study area (GP: Grand Plateau; PP: Petit Plateau); [2] Data from [47]

Appendix 2. Flying and arboreal diurnal consumers of Virola fruits at Nouragues. For each consumer species, the related proportions of sightings during censuses (C) and watches (W), pooled over the two observation periods and over all focal trees are presented. Values in bold are the sum for all birds and all mammals. Body mass (g), range of group size (n ind) and visit duration (min) of consumer species are indicated. Nomenclature follows [73] for birds, for primates [74] and [75] for other mammals.

| | | | ***V. kwatae*** | | | | ***V. michelii*** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Family** | **Species** | **Body mass** | **C** | **W** | **Group size** | **Visit duration** | **C** | **W** | **Group size** | **Visit duration** |
| **All birds** | | | **64.7** | **62.6** | | | **66.4** | **58.2** | | |
| Cracidae | *Penelope marail* | 1024-2048[1] | | | | | 3.6 | | 2 | — |
| Icteridae | *Psarocoluis viridis* | 256-512[1] | 3.9 | 25.0 | 1-4 | 17 | | | | |
| Momotidae | *Momotus momota* | 128-256[1] | | | | | 0.9 | | 1 | — |
| Ramphastidae | *Ramphastos tucanus* | 512-1024[1] | 39.2 | 12.5 | 1-4 | 2-20 | 5.5 | 4.5 | 1-2 | 5-6 |
| | *Ramphastos vitellinus* | 256-512[1] | 9.8 | 6.3 | 1-2 | 5-6 | 17.3 | 14.9 | 1-3 | 2-25 |
| | *Pteroglossus aracari* | 128-256[1] | | 12.5 | 2 | 35 | | | | |
| | *Selenidera culik* | 128-256[1] | 11.8 | 6.3 | 1-2 | 9-16 | 29.1 | 31.3 | 1-3 | 3-82 |
| Trogonidae | *Trogon melanurus* | 64-128[1] | | | | | 10.0 | 7.5 | 1-2 | 5-45 |
| **All mammals** | | | **35.3** | **37.4** | | | **33.6** | **41.8** | | |
| Atelidae | *Ateles paniscus* | 13500[2] | 31.4 | 37.4 | 1-9 | 3-133 | 32.7 | 37.3 | 1-3 | 8-150 |
| Cebidae | *Cebus apella* | 3000[2] | | | | | | 4.5 | 3 | 7 |
| Sciuridae | *Sciurus aestuans* | < 500[2] | 3.9 | | 1 | — | | | | |
| | *Sciurillus pusillus* | < 300[2] | | | | | 0.9 | | 1 | — |

[1] Mean body mass categories from [76]; [2] [77]