Roads Disrupt Frugivory and Seed Removal in Tropical Animal-Dispersed Plants in French Guiana

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Ecological interactions are being affected at unprecedented rates by human activities in tropical forests. Yet, the continuity of ecological functions provided by animals, such as seed dispersal, is crucial for forest regeneration and species resilience to anthropogenic pressures. The construction of new roads in tropical forests is one of the main boosters of habitat destruction as it facilitates human access to previously isolated areas and increases defaunation and loss of ecological functions. It, therefore, becomes increasingly urgent to rapidly assess how recently opened roads and associated anthropogenic activities affect ecological processes in natural habitats, so that appropriate management measures to conserve diversity can be taken. In this study, we aimed to evaluate the effects of anthropogenic pressures on the health status of a mature rainforest crossed by a newly opened road in French Guiana. For this, we combined different methods to conduct a rapid assessment of the forest's health status. Firstly, we evaluated the activity of frugivores using camera traps deployed in four forest patches located near (<1 km) ecological corridors preserved as canopy bridges over the road during the fruiting periods of four animal-dispersed tree species. Secondly, we analyzed the fate of seeds enclosed in animal-dispersed tropical fruits by calculating the proportions of fruits consumed and seeds removed (either dispersed or predated) by frugivores. Results show that the proportion of fruits opened and consumed was lower in the forest areas located near the road than in the control forest, and this difference was more significant for plant species strictly dependent on large-bodied primates for seed dispersal than for species relying on both primates and birds. Camera traps showed the presence of small primates and kinkajous feeding on *Virola* fruits in the forest impacted by the road, where large primates were absent. It is thus likely that smaller frugivores exert a compensatory effect that maintains

ecological functions near the road. Despite efforts made to preserve forest continuity through ecological corridors, anthropogenic pressures associated with road proximity are affecting wildlife and disrupting associated ecological functions crucial for plant regeneration, contributing to further forest degradation.

INTRODUCTION

Roads facilitate economic development by increasing exchange and access to agricultural land and resources, but they have detrimental effects on natural ecosystems and human populations, especially indigenous people inhabiting remote forested areas (Campbell et al., 2017; Laurance and Arrea, 2017). As a result, most natural ecosystems and protected areas, located far from densely populated urban areas, are increasingly threatened by the rapid expansion of road networks worldwide, which favor rampant anthropogenic activities such as hunting, logging, mining, agriculture and encroachment of small-scale human activities (Laurance et al., 2012). Modern anthropo-ecosystems are becoming a matrix progressively surrounding fragmented protected areas and indigenous people's land, increasing anthropogenic pressures both outside and inside (Laurance et al., 2001, 2012). For instance, the edges of the 100-km^2 squared forest fragment of the Adolpho Ducke Forest Reserve near the city of Manaus (Brazil) were already visible early in the 1990s on Landsat images (Rodrigues et al., 2003). The dramatic report of collapsing protected areas calls for a new paradigm and strategy for road planning to preserve remaining natural tropical habitats. Such areas host most of the wildlife diversity upon which the recruitment of plants and the resilience of forest cover and carbon stocks depends (Laurance et al., 2014; Alamgir et al., 2017, 2020; Brodie and Fragoso, 2020; O'Bryan et al., 2020).

The effects of roads on forest fragmentation and species loss in natural ecosystems are well documented at different scales, particularly in temperate biomes. The negative impacts of road networks on wildlife communities have been reported, on average, five times as much as positive effects (Forman and Alexander, 1998; Trombulak and Frissell, 2000; Coffin, 2007; Fahrig and Rytwinski, 2009; Laurance et al., 2009). Road expansion increases the mortality rate of animals by introducing vehicles and collisions, reducing connectivity among populations, and allowing hunters and poachers better access to the forest. These road-mediated anthropogenic activities contribute to rapidly increasing defaunation of forest habitats, from hundreds of meters up to several kilometers from roadsides (de Thoisy et al., 2005; Laurance et al., 2009, 2012; Clements et al., 2014; Benítez-López et al., 2019; Gallego-Zamorano et al., 2020). The consequences of roads for ecosystem services also depends on species' characteristics (reproduction rate, home range, migration, behavior), with larger animals overall being more impacted than smaller ones (Trombulak and Frissell, 2000; Peres, 2001; Nuñez-Iturri and Howe, 2007; Laurance et al., 2009; Boissier et al., 2020).

There is now a growing consensus to minimize the number of planned roads (Clements et al., 2018; Vilela et al., 2020) and implement so-called "green" or "ecological" corridors. Examples of these, in tropical habitats, are wildlife overpasses or underpasses and canopy walkways across roads. Corridors support the resilience and movement of animals alongside roads and across fragmented landscapes (Ng et al., 2004; Gregory et al., 2017; Shi et al., 2018), although their efficiency to reduce forest defaunation still needs to be evaluated. To our knowledge, few authors have addressed the consequences of changes in wildlife diversity for the ecology of native plants located in the vicinity of roads (Forman and Alexander, 1998; Wright and Duber, 2001; Coffin, 2007; Laurance et al., 2009).

Located in northern South America, the Guianas ecoregion remains well preserved and non-fragmented in comparison to the rest of the Amazon basin (Huber et al., 2002), with remote and isolated protected areas surrounded by vast tracts of mature forests (>50 km in width, *sensu* Laurance et al., 2012). However, anthropogenic pressures in the Guianas are steadily increasing due to the renewed demand from the economic sectors for more roads and infrastructure that bisect and fragment large patches of mature forest, facilitating the exploitation and exportation of natural resources (Hammond, 2005). To establish efficient conservation programs for the resilience of biodiversity to environmental threats such as roads and the anthropogenic activities they promote, it is thus important to assess the current health status of tree species in forested habitats that are crossed by new roads (Boissier et al., 2020).

As in other ecosystems, many tropical forest trees rely on animals for seed dispersal (Markl et al., 2012; Carreira et al., 2020; Emer et al., 2020). The health of tropical forests, therefore, depends on the resilience of frugivore-plant interaction networks to anthropogenic pressures such as fragmentation, selective logging, and hunting (Kitamura and Poonswad, 2013; Corlett, 2017; Dugger et al., 2019; Naniwadekar et al., 2019). Traits such as animal body mass, gape width, animal behavior, fruit morphology and seed dimensions determine whether seeds are swallowed, spat, dropped or carried, and thus whether they will be dispersed further away from parent plants by frugivores (Forget et al., 2007; Naniwadekar et al., 2019; Sivault et al., 2020). Therefore, for evaluating seed dispersal effectiveness is also necessary to estimate the role of smaller-bodied frugivores that may contribute as efficient alternate seed dispersers once the major larger-bodied frugivores are lacking or extinct (Carreira et al., 2020). In French Guiana, for instance, despite an overall reduction in seed removal rates at the plant community level due to modifications of the frugivore community, defaunation differentially impacted seed removal rates between plant families (Boissier et al., 2020).

Using a rapid assessment method to evaluate seed removal, Boissier et al. (2020) observed that the downsizing effect of hunting was greater for plant species in the primate-dispersed family Sapotaceae than for those in the bird-and-primate-dispersed Burseraceae and Myristicaceae. The compensation of the loss of primates was possibly explained by the resilience of birds, especially Ramphastidae (toucans), to anthropogenic pressures (see Holbrook and Loiselle, 2009 for similar results). Using the same method, Hambuckers et al. (2020) observed that the amount of forest cover in an overall fragmented landscape affected seed removal rates, which also differed between two frugivore-dispersed species. They concluded that the health of the forest fragments was similar to that of a disturbed forest, validating the use of seed removal rate as an indirect indicator of forest health and as a proxy to evaluate the activity of frugivores of all body sizes (Nuñez-Iturri and Howe, 2007; Gutierrez-Granados and Dirzo, 2010; Levi and Peres, 2013).

Our present study aims to monitor and analyze the ecological consequences of road-mediated anthropogenic activities along a recently opened road in French Guiana and the compensatory effect of ecological corridors. More specifically, we aimed to evaluate how "green bridges," connecting the recently bisected forest, can effectively contribute to the resilience of ecological services such as animal-mediated seed dispersal. Firstly, we hypothesized that reproductive trees located closer to the road and urbanized areas will face greater anthropogenic pressures (traffic, hunting) than trees located further away or in intact forests. Secondly, we hypothesized that plants relying on a specialized seed dispersal system with fewer large frugivores will be more greatly impacted by road effects than those with a generalized dispersal system comprising a community of small-to-large frugivores (Howe, 1993). To test these hypotheses, we used rapid assessments (Boissier et al., 2014) for evaluating the levels of fruit consumption and seed removal of four animal-dispersed plants, namely *Virola micheli, V. kwatae* (Myristicaceae) and *Manilkara huberi* and *M. bidentata* (Sapotaceae) at the tree population level. In addition, we placed camera traps on the ground and in the canopy of focal fruiting trees to evaluate the diversity of wildlife in the forest areas surrounding the ecological corridors. Results of the forest impacted by the road are discussed and evaluated in comparison to a protected (Nouragues) and another disturbed forest (Montagne de Kaw), where the same tree species and wildlife co-occur.

MATERIALS AND METHODS

Study Sites

French Guiana is a French overseas department located in South America, bordered by Brazil in the East and by Suriname in the West. The climate is humid equatorial with a long rainy season between November and August, eventually interrupted by a small dry season in February or March, followed by a dry season between September and October. The development of road networks in the 1990s included a project of socio-economic development in Eastern French Guiana to improve the mobility

of goods and people between the department and the border with Brazil, as well as offer better access to timber and agricultural lands (Boudoux d'Hautefeuille, 2010).

The study area is a mature rainforest growing along that road, named "Nationale 2" (hereafter RN2; Bens, 2011; Pérez and Archambeau, 2012; Nicolle and Boudoux d'Hautefeuille, 2014) extending from Cayenne (capital city of the department) on the littoral to Saint-Georges in the interior along the Oyapock river, which marks the border between French Guiana and Brazil (**Figures 1A,B** and **Table 1**). In 2017, a bridge connecting French Guiana to Brazil by land was built (Pérez and Archambeau, 2012) and officially opened to traffic, with likely further social, economic and environmental effects on both the inhabitants of Saint-Georges and the forest located along the road (Grenand, 2011). To limit the fragmentation effects and to maintain forest connectivity above the new section of RN2, a total of 13 ecological corridors were created during the opening of the former continuous forest block with tree cover being preserved near roadsides aiming at connecting the two edges of the bisected canopy cover. However, due to degradation of the vegetation cover at both edges as well as inside the corridors, along with tree falls, natural or man-made (to avoid accidents), connectivity is currently far from being complete.

Observations and fruit surveys were carried out in the forest surrounding seven out of the 13 corridors at various distances along RN2 (**Figure 1C**, **Supplementary Figure 1**, and **Supplementary Table 1**). Study sites were all located on hilltops (where the road opening was created to avoid slopes and flooded terrain), generally providing easy access to the mature forest nearby. Forest patches near corridors were chosen after an intensive search for the fruiting study tree species (**Figure 1**). Four areas were defined referring to forest surrounding corridors 1 (hereafter "A"), 2 ("B"), 3 and 4 ("C") and 5, 6, and 7 ("D") (**Figures 1B,C**, **Supplementary Figure 1**, and **Supplementary Table 1**). Elevation increased along RN2 with distance from Saint-Georges (**Supplementary Figure 1**). Forest patches A and B were located near logged forests, while C and D were part of the Parc Naturel Régional de Guyane, a partially protected area with high forest cover and low deforestation rates (**Figure 1C** and **Supplementary Figure 1**).

The forest at study sites was characterized by hilly topography. Hilltop forests present a species richness and a species composition different from downslope forests, as frequently observed in the Guianas (Guitet et al., 2015). Forest types encountered at the study area are described as a mosaic of ecotone and mixed forest types mainly characterized by the abundance of Fabaceae, Sapotaceae, Chrysobalanaceae, Burseraceae and Lecythidaceae (Forget, *pers. obs.*). Canopy height is between 30 and 40 m, with some emergent trees. The type of geomorphological landscape types is referenced as "High Plateaux or Tableland" and "Mountains" (so-called "Montagne") with a mean altitude between 50 and 200 m (e.g., categories G and H, respectively, in Guitet et al., 2015; Guitet et al., 2018). Despite the increasing impact of hunting and other sources of human disturbance, wildlife encountered along RN2 ten years ago led the forest to be regarded as relatively undisturbed, compared to that of the Nouragues Nature Reserve (hereafter Nouragues,
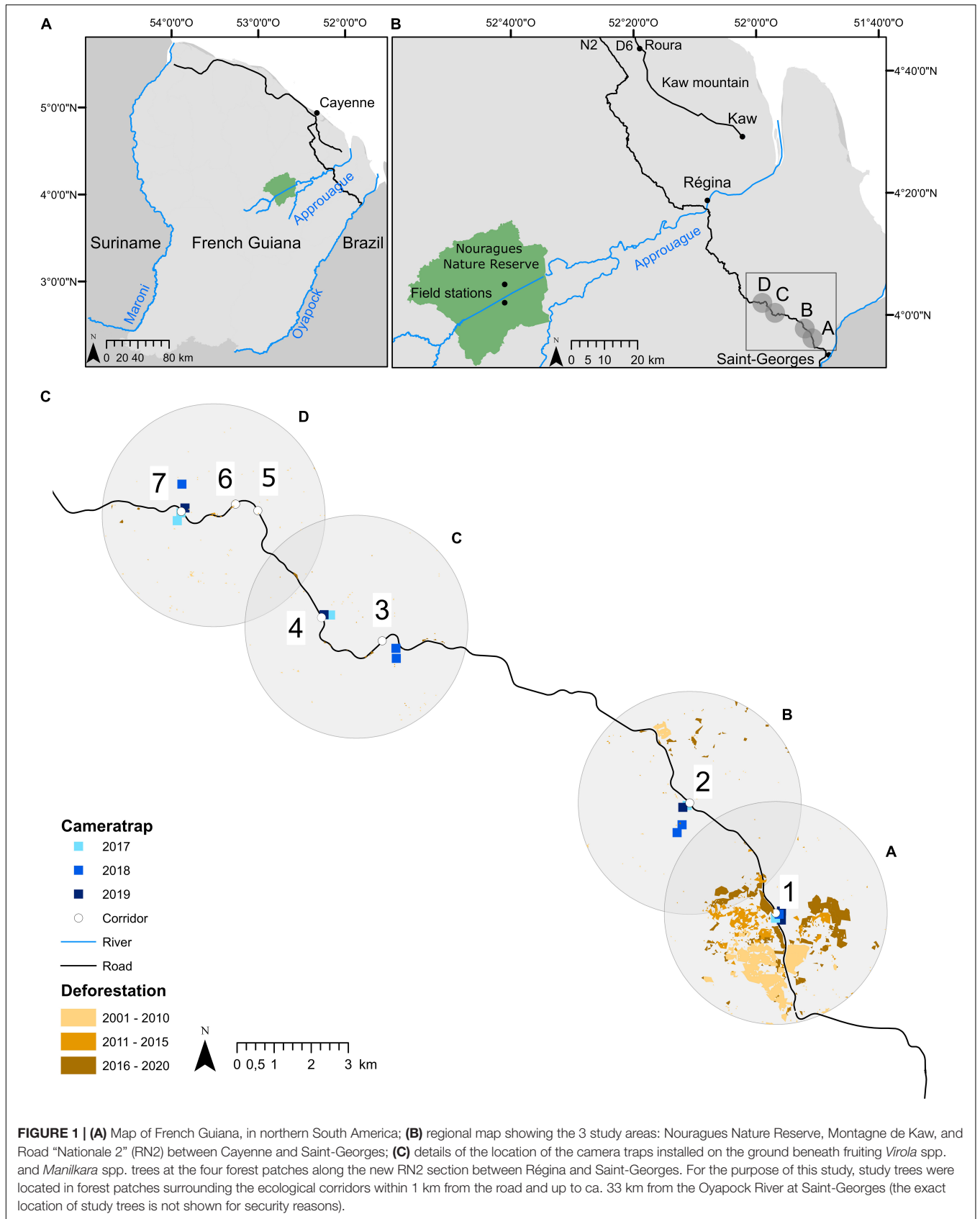
FIGURE 1 | (A) Map of French Guiana, in northern South America; **(B)** regional map showing the 3 study areas: Nouragues Nature Reserve, Montagne de Kaw, and Road "Nationale 2" (RN2) between Cayenne and Saint-Georges; **(C)** details of the location of the camera traps installed on the ground beneath fruiting *Virola* spp. and *Manilkara* spp. trees at the four forest patches along the new RN2 section between Régina and Saint-Georges. For the purpose of this study, study trees were located in forest patches surrounding the ecological corridors within 1 km from the road and up to ca. 33 km from the Oyapock River at Saint-Georges (the exact location of study trees is not shown for security reasons).

TABLE 1 | Study sites in French Guiana, with hypothesized increasing intensities of anthropogenic disturbance (NOURAGUES, Nouragues Field Station; KAW, Montagne de Kaw; RN2, Road "Nationale 2").

Forest	NOURAGUES	KAW	RN2
Coordinates	N4° 02.294′ W52° 40.386′—N4° 05.288′ W52° 40.779′	N4° 36.613′ W52° 16.764′—N4° 29.905′ W52° 03.145′	N3° 55.994′ W51° 50.760′—N4° 02.006′ W51° 59.416′
Forest status	National reserve	National and regional Reserve/State forest	Regional park/State forest
Nearest town	Régina	Roura	Saint-Georges
Accessibility	By river/air	By road (D6)	By road (N2)
Distance to nearest town	>100 km	<30 km	<30 km
Human footprint (2016)[a]	0	4	4–18
Expected Anthropogenic Stressors[b,c]	Nil	Low	Low to High
Main anthropogenic pressures	Scientific research	Vehicle traffic, hunting, logging	Vehicle traffic, hunting, logging
No. of *Virola* trees (years)	44 (2010–2019)[b,c,d]	23 (2009–2011)[c,d]	62 (2013–2015, 2018–2019)[e]
No. of *Manilkara* trees (year)	6 (2010)[c]	6 (2010)[c]	30 (2014)[e]
Wildlife censuses	2010–2011[c]	2010–2011[c]	2017–2019[e]

[a]*de Thoisy et al. (2016).*
[b]*Kocher et al. (2017).*
[c]*Boissier et al. (2020).*
[d]*Boissier et al. (2014).*
[e]*This study.*

Figure 1B; de Thoisy et al., 2010, 2016). However, since the construction of the new section of the RN2 between Régina and Saint-Georges, ca. 20 years ago, the forest became more accessible, and recent studies suggest a recent decrease in species richness and abundance of vertebrate wildlife at a more local scale (Kocher et al., 2017, 2022). This would be comparable to that of Montagne de Kaw (hereafter Kaw, **Figure 1B**) with a impoverished population of large-bodied fruit-eating primates (Boissier et al., 2020; P.-M. Forget, pers. obs. in 2013–2022).

The study area was characterized with a theoretical anthropogenic gradient extending from the Oyapock river and Saint-Georges to the interior (**Figures 1B,C** and **Supplementary Figure 1**), with A and B being the closest (< 20 km) and likely the most disturbed, and C and D the farthest (> 20 km) and least disturbed in accordance with the Human Footprint Index (HFI ranging 4–18; de Thoisy et al., 2010, 2016). Moreover, we also expect an anthropogenic gradient extending from the RN2 to the interior; along this gradient, forest areas located closer to the road should be more disturbed than forest areas located further away from the road. Anthropogenic pressures thus increase with forest accessibility, here defined by two parameters: (1) the distance of trees to the RN2; and (2) the distance of the trees to Saint-Georges (**Supplementary Table 1**).

Data collected at RN2 were analyzed in comparison with other datasets collected in forests at Nouragues (control, HFI = 0) and Kaw (disturbed, HFI = 4) (sites 3 and 4, respectively, in de Thoisy et al., 2016), where the latter comprises the Tresor Regional Nature Reserve (Boissier et al., 2014, 2020; **Table 1**).

Study Trees

We studied two wild nutmeg trees *Virola kwatae* Sabatier, 1997, and *V. michelii* Heckel, 1898 (Myristicaceae), and two canopy bulletwood trees (or balata) *Manilkara bidentata* (A.DC.) A. Chev., 1932 and *Manilkara huberi* (Ducke) A. Chev., 1932

(**Supplementary Figure 2** and **Supplementary Table 2**). *Virola* trees are annual dioecious species that fruit between November and March in French Guiana (Ratiarison and Forget, 2013; Mendoza et al., 2018). *Virola* species produce capsule-like fruit possessing two valves protecting a seed covered by a lipid-rich aril (**Figure 2**). When fruits reach maturity, they naturally dehisce into two valves exposing the red-colored aril. The two valves are firmly attached to each other and do not separate when falling without being handled or processed by a diverse coterie of both arboreal, flying and ground-dwelling vertebrate frugivores (**Supplementary Table 3**). *Virola kwatae* trees grow almost exclusively uphill, on ridges and mountains, and produce larger seeds (seed size average: 2.8 × 1.8 cm) than *V. michelii* (seed size average: 2.0 × 1.4 cm), thus attracting larger frugivores. Due to their large size, *V. kwatae* seeds are mainly dispersed by the black spider monkey (*Ateles paniscus*), kinkajous (*Potos flavus*) and toucans (*Rhamphastos* spp.). *Virola kwatae* was indeed named after the black spider monkey (called "kwata" in the bushi-nenge vernacular name) because it is the main fruit consumer and seed disperser (Forget and Sabatier, 1997; Sabatier, 1997). Other consumers such as red howler monkey (*Alouatta macoonelli*) and green oropendola (*Psarocolius viridis*) only play a minor role in the dispersal of *V. kwatae*'s seeds. The other tree species, *V. michelii*, is also dispersed by spider monkeys, howler monkeys, kinkajous and toucans. In addition, the smaller seed size of *V. michelii* allows dispersion by brown capuchin (*Sapajus apella*) and birds such as marail guan (*Penelope marail*) and the Amazonian motmot (*Momotus momota*). The arboreal mammalian frugivores (e.g., Primates) have prior access to seeds and can consume them before they naturally dehisce. Indeed, these animals can handle and open fruit before dehiscence, reach the arilled seed, swallow it, and drop single-valved fruit to the ground. On the contrary, birds have to wait for fruit dehiscence to reach the edible aril,

FIGURE 2 | Fruits and seeds of **(A)** *Virola kwatae* (left) and *V. michelii (right),* and **(B)** *Manilkara bidentata* (left) and *M. huberi* (right) (all photographs © Pierre-Michel Forget).

and valves remain sealed when dropping after fruit abscission (Boissier et al., 2014).

Manilkara tree species are common trees, 40–50 m tall, with mast fruiting behavior (Norden et al., 2007; Mendoza et al., 2018; **Supplementary Table 2**). Fruits are ripe between March and June, i.e., during the fruit peak at the community level, when ground-dwelling consumers are satiated with fruits and seeds on the ground (Mendoza et al., 2015; **Supplementary Table 3**). Such satiation increases the probability of seed survival (Mendoza et al., 2015), and thus favors seedling recruitment (Chauvet et al., 2004). *Manilkara* fruits are drupes containing one to five medium-sized seeds (seed size average: 2.4 × 1.3 cm) embedded in sugar-rich pulp (**Figure 2**). Fruit and seed traits differ between *M. bidentata* and *M. huberi*, with fruits of the latter being more globose, containing a slightly greater mean number of seeds (1.1 vs. 1.6 on average, respectively) and thus being heavier than the former. During the study, the average weight of fruit and seeds was established to be 14.7 and 9.5 g, respectively, for *M. bidentata*, and 1.7 and 1.2 g, respectively, for *M. huberi* (Ratiarison and Forget, 2011). Fruits of both *Manilkara* are consumed by a diversified community of frugivores and granivores, with the main diurnal arboreal consumers and seed dispersers being primates in the undisturbed forest of the

Nouragues Nature Reserve (Zhang, 1995; Ratiarison and Forget, 2011). Ground-dwelling consumers of *Manilkara* fallen fruits are partially known (Chauvet et al., 2004), and include small spiny rats (*Proechimys cuvieri* and *P. guyannensis*), medium-to-large rodents (*Myoprocta acouchy* and *Dasyprocta leporina*) and peccaries (*Tayassu pecari* and *Pecari tajacu*).

Frugivore Data Collection by Camera Trapping

Camera traps from the brand Reconyx®, model HC600 equipped with a red infrared moving sensor, were placed at *Virola* and *Manilkara* trees in the forest surrounding corridors to characterize the community of frugivores (**Figure 1C** and **Table 2**). Ground cameras were set a few meters away with the lens pointing to the base of fruiting individuals of *Virola* (2017–2019) and *Manilkara* (2017, during a masting event), and attached at nearby tree bases, ca. 50 cm above the ground. For *Virola*, camera traps were installed during 2017, 2018 and 2019 fruiting seasons, after fruit sampling. In 2019, the tree crowns of *Virola* trees were accessed using a single rope climbing method (Picart et al., 2014), and cameras were placed with the lens pointing to large branches possessing fruit at the extremity

TABLE 2 | Camera trap selection for characterizing the ground-dwelling fauna in the entire studied area including forest patches A, B, C and D along the National Road 2 (NR2) between Régina and Saint-Georges, French Guiana.

Year	Recording period	No. days	No. camera traps
2017	21/03/2017–11/06/2017	83	9
2018	07/12/2017–03/02/2018	59	15
2019	03/02/2019–18/03/2019	44	10
Total	21/03/2017–18/03/2019	186	34

First and last events (among all camera traps installed) were set as the first and last days of records for each year.

(Moore et al., 2021). The cameras were then left operational for 6 weeks from early February until mid-March. For *Manilkara*, camera traps were installed in 2017, on trees that were sampled for fruit during the masting event of 2014. Cameras were set up to take five pictures per trigger, with the shortest trigger delay setting and the shortest time setting between successive pictures. The sensor was set at its highest sensitivity. To minimize untimely triggering, which occasionally occurs on the ground and very often in the canopy due to leaf movements, incipient plants, leaves and small branches were cut when they were too close to the camera (around less than 3 m). The shortest distance between two camera traps within forest patches was 225 m. This was in the most disturbed forest where it was difficult to circulate away from the tracks and where study fruiting trees were scarce. The number of cameras installed per fruiting season, the settling and removal days, as well as the length of the recorded periods, are detailed in **Table 2**. **Supplementary Table 3** lists vertebrates known to consume fruits and seeds of the study tree species.

Fruit Consumption and Seed Removal

Trees were searched for at locations where they were most likely to be present, using hunting trails and walking along ridges (**Supplementary Table 4**). Fruit surveys were conducted toward the end of the fruiting season of *Virola* (late January/early February 2009–2019) and during a masting year of *Manilkara* (late May and early June 2014) trees. To count fallen fruits and seeds, 1-m^2 quadrats were randomly placed on the ground 2–3 m from each trunk base (one quadrat per tree from 2010 to 2015 and three per tree from 2017 to 2019, following Hambuckers et al., 2017). This distance avoided sampling areas under branches not bearing fruits, where fruits were less numerous on the ground than expected at random.

Fruits and seeds of *Manilkara* were sampled underneath tree crowns following the method described in Boissier et al. (2020). Within each quadrat, intact fruits were collected and counted. To determine the number of eaten fruits, husk parts were collected, air-dried for 24 h with an indoor electricity-powered fan, then weighed. The weight of the husk parts was divided by the average weight of *Manilkara* fruits (*M. huberi*: 14.73 g; *M. bidentata*: 9.55 g). The number of single, unpredated seeds was also counted. Estimates of the total numbers of seeds were established for *M. bidentata* and *M. huberi* using the average of 1.1 and 1.6 seeds per fruit, respectively (Ratiarison and Forget, 2011). Since seed removal can be affected by the fruit crop, percentages were

determined from the total number of fruits within each quadrat (Boissier et al., 2020).

For both species and within each quadrat, all conspecific fruits and seeds were counted and categorized as (1) intact fruit, (2) eaten fruit, (3) dehisced fruit with both valves still joined together (only for *Virola*), (4) single valve (only for *Virola*) or (5) seed, according to Boissier et al. (2014) and Boissier et al. (2020). Three indices were then calculated from these estimates. (1) The fruit consumption rate (proportion of eaten fruits) in *Manilkara* is calculated as the number of eaten fruits divided by the total number of fruits. (2) The proportion of fruits found as single valves in *Virola* is half the number of single valves (two valves per fruit) divided by the total number of fruits. Both these ratios are proxies to evaluate the activity of arboreal and ground-dwelling consumers and their consumption of fruits. Finally, (3) the seed removal rate is the proportion of seeds that were removed by animals, either dispersed or predated, and are thus missing from the quadrat. It is based on the proportion of remaining seeds, which is calculated as the total number of seeds remaining in the quadrat (either found on the ground or still contained in intact fruits) divided by the total number of seeds expected to be found in the quadrat if none had been taken away by animals (based on the total number of fruits found in the quadrat and the number of seeds per fruit, one for *Virola* and a mean observed number for *Manilkara*). In *Virola*, consumption of entire ligneous fruits is unlikely, only the fleshy aril and seeds are consumed, swallowed or destroyed by consumers. In *Manilkara*, the pericarp is not swallowed in the canopy, then it is dropped beneath the fruiting tree after the pulp surrounding the seeds has been consumed by arboreal frugivores. Uneaten fruits fall entire on the ground where they accumulate when not consumed by ground-dwelling vertebrates. Hence, the seed removal rate is calculated as one minus the proportion of remaining seeds. The quadrat method had proven to be an efficient field "tool" in order to calculate an index of fruit consumption and seed removal below fruiting plants for the two study genera, and more details and formulae can be found in Ratiarison and Forget (2013), Boissier et al. (2014), and Boissier et al. (2020).

Fruit sampling of all species was conducted in 2010, 2011, and 2019 at the two field stations Inselberg and Pararé at Nouragues (**Figure 1B**), and in 2013, 2014, 2015, 2017, and 2018 at RN2. Fruit data from 2010 to 2015 were collected exclusively using one quadrat rather than the three replicates used from 2017 onward. We assessed the effect of the number of quadrats by comparing fruit consumption and seed removal calculated from one quadrat vs. 3 quadrats (for each tree sampled with 3 quadrats) using Student and Mann–Whitney U-tests for paired samples. There was no effect of the number of quadrats (Mann–Whitney U rank test, $U = 341$, $p = 0.28$, $n = 35$; Student test, $t_{(34)} = 0.22$, $p = 0.83$, $n = 35$) on fruit consumption and seed removal.

Data Analyses

The package *camtrapR* was used to organize and extract data from the raw images (Sollmann et al., 2016). *DigiKam* software was chosen to add metadata to the images. Data were extracted into a record table for each year. We took a conservative approach and we considered records as different events when the time

difference between records of the same species at the same station was larger than 60 min.

To characterize the community of frugivores feeding on *Virola* and/or *Manilkara* fruits and/or seeds, we removed all events of species not consuming or predating fruits or seeds, and we compiled all of the events recorded during 2017, 2018, and 2019 (**Table 2**). The package *iNEXT* (Hsieh et al., 2016) was used to compute species accumulation and coverage-based (i.e., sample completeness) sampling curves as well as an estimation of species richness based on the method proposed by Chao et al. (2014).

We used percentages of fruit consumption, fruits found as single valves and seed removal rate as proxies for the activity of both frugivores and seed predators in the canopy and underneath the tree crown. After testing for a species effect on these proxies using Kruskal-Wallis rank-sum tests, proxies were compared between forest patches and between Nouragues, Kaw and RN2 forests with Kruskal-Wallis rank-sum tests and Pairwise-Wilcoxon statistical tests.

Generalized linear mixed models computed with the *lmer* function from the package *lme4* (Bates et al., 2015) were used to test for an effect of the distance to the road and the distance to Saint-Georges on the proportion of fruits found as single valves (for *Virola*), on the fruit consumption rate (for *Manilkara*), and on seed removal rate (for both *genus*). The year of sampling, and the tree species were used as random effects to account for temporal and species-specific variability for *Virola* while species only was used as a random factor for *Manilkara* since the sampling was only conducted in 2014. As the response variable was proportion data, we used a binomial error distribution with a logit link, with the number of fruits implemented as the weight argument. Data analyses were performed with R 3.2.3 (R Core Team, 2021).

RESULTS

Frugivore Community

After *camtrapR* analysis and selection, 770 independent events of frugivore visits were recorded corresponding to 16 species (**Table 3** and **Supplementary Tables 5, 6**). The species accumulation curve of ground and arboreal frugivorous species did not reach a plateau at the end of the survey period (**Figure 3A**). Sampling effort (186 days of records) allowed a sample coverage of 95.2% (**Figure 3B**) and the Chao estimation of species richness was 18.98 ± 4.53 se.

All major known ground-dwelling frugivores of the study species were observed (**Table 3**). Beneath *Virola* spp., we recorded red-rumped agouti (*Dasyprocta leporina*), collared peccari (*Pecari tajacu*) and brocket deer (*Mazama gouazoubira* and *M. americana*), which were grouped in this study because they are almost indistinguishable in photographs (**Figure 4**). At *Manilkara* trees, frequent consumers were the gray-winged trumpeter (*Psophia crepitans*), great tinamou (*Tinamus major*), black curassow (*Crax alector*), red acouchy (*Myoprocta acouchy*), lowland paca (*Cuniculus paca*) and lowland tapir (*Tapirus terrestris*, **Figure 5**). On *Virola* spp. tree crowns,

TABLE 3 | Numbers of detection events of frugivorous species recorded near and in *Virola* and *Manilkara* trees censused with Reconyx® camera traps at the four forest patches along Road "Nationale 2" (RN2), between Régina and Saint-Georges, French Guiana.

| Family	Common name	Species	RN2			
			A	B	C	D
Birds						
Cracidae	Black curassow	*Crax alector*	0	1	6	4
Psophiidae	Gray-winged trumpeter	*Psophia crepitans*	0	3	35	16
Tinamidae	Great tinamou	*Tinamus major*	10	6	14	13
Ground mammals						
Tapiridae	Lowland tapir	*Tapirus terrestris*	0	0	1	0
Cervidae	Red/Gray brocket deer	*Mazama americana* and *M. gouazoubira*	16	4	32	19
Tayassuidae	Collared peccary	*Pecari tajacu*	3	25	38	41
Dasyproctidae	Red-rumped agouti	*Dasyprocta leporina*	14	8	63	69
Dasyproctidae	Red acouchi	*Myoprocta acouchy*	14	6	19	29
Cuniculidae	Lowland paca	*Cuniculus paca*	8	12	16	41
Echimyidae	Spiny rat	*Proechimys* sp.	0	1	10	4
Arboreal mammals						
Atelidae	Guyanan red howler	*Alouatta maconnelli*	0	0	1	0
Cebidae	Tufted capuchin	*Sapajus apella*	0	0	3	0
Callitrichidae	Golden-handed tamarin	*Saguinus midas*	0	0	0	1
Procyonidae	Kinkajou	*Potos flavus*	72	0	50	11
Erethizontidae	Brazilian porcupine	*Coendou prehensilis*	1	0	11	0
Didelphidae	Common opossum	*Didelphis marsupialis*	0	2	6	11

arboreal frugivores such as the kinkajou *(Potos flavus)*, tufted capuchin (*Sapajus apella*), red howler monkey (*Alouatta macconnelli*) and Golden-handed tamarin (*Saguinus midas*) were observed. In addition, two species not known to feed on *Virola* fruits and seeds were recorded: the common opossum (*Didelphis marsupialis)* and the Brazilian porcupine (*Coendou prehensilis*). The arboreal kinkajou was the major visitor of *Virola* and corresponded to 55% of visits in the 2019 survey (**Supplementary Figure 3**).

### Single-Valved Fruits, Fruit Consumption, and Seed Removal

A total of 62 *Virola* and 30 *Manilkara* trees were sampled at RN2 between 2013 and 2019, and in 2014, respectively (**Supplementary Tables 4, 7, 8**).

There was no significant effect between *Virola* species for either percentage of fruits found as single valves (*V. kwatae*: average 42.35%; *V. michelii*: 32.60%) or seed removal (*V. kwatae*: average 76.11%; *V. michelii*: 68.88%) along RN2 ($X^2 = 3.81$,
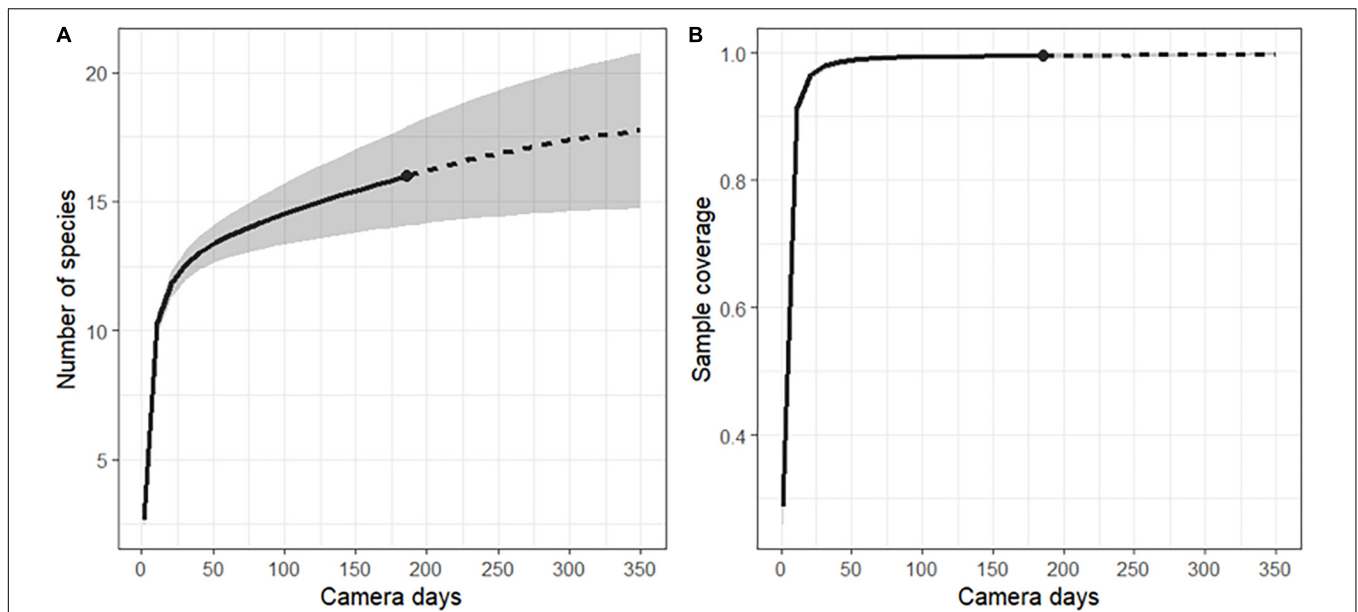
FIGURE 3 | (A) Randomized species accumulation curve and **(B)** coverage-based sampling curve for the ground and arboreal frugivore community of the entire study area (including forest patches A, B, C, and D) recorded in the vicinity of *Manilkara* and *Virola* trees. The shaded area represents the 95% confidence interval. The dot at the limit between the interpolated solid line and the extrapolated dashed line indicates the actual sampling effort of the study (186 days of record).
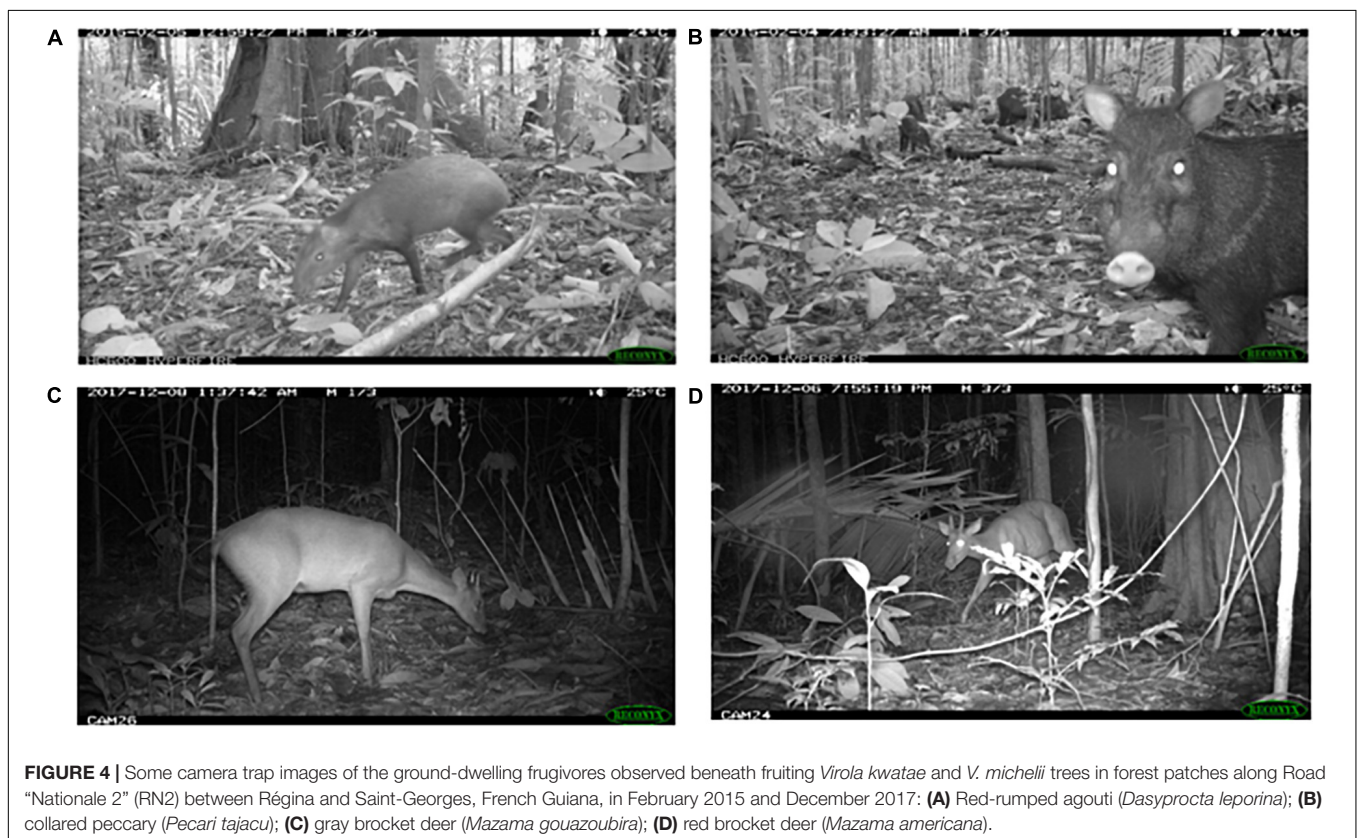
FIGURE 4 | Some camera trap images of the ground-dwelling frugivores observed beneath fruiting *Virola kwatae* and *V. michelii* trees in forest patches along Road "Nationale 2" (RN2) between Régina and Saint-Georges, French Guiana, in February 2015 and December 2017: **(A)** Red-rumped agouti (*Dasyprocta leporina*); **(B)** collared peccary (*Pecari tajacu*); **(C)** gray brocket deer (*Mazama gouazoubira*); **(D)** red brocket deer (*Mazama americana*).

$df = 1$, $P = 0.14$ and $X^2 = 2.15$, $df = 1$, $P > 0.05$, respectively). The proportion of *Virola* fruits found as single valves and seed removal rate did not differ between forest patches ($X^2 = 0.73$, $df = 3$, $P = 0.09$ and $X^2 = 0.65$, $df = 3$, $P = 0.33$, respectively). Overall, the mean proportion of fruits found as single valves at RN2 (37.6%) was similar to Kaw (37.7%) and significantly lower

FIGURE 5 | Some camera trap images of the ground-dwelling frugivores observed beneath fruiting *Manilkara huberi and M. bidentata* trees in forest patches along Road "Nationale 2" (RN2) between Régina and Saint-Georges, French Guiana, in March–May 2017: **(A)** Gray-winged trumpeter (*Psophia crepitans*); **(B)** great tinamou (*Tinamus major*); **(C)** black curassow (*Crax alector*); **(D)** red acouchy (*Myoprocta acouchy*); **(E)** lowland paca (*Cuniculus paca*); **(F)** lowland tapir (*Tapirus terrestris*).

($P < 0.001$) than at Nouragues (66.1%). Similarly, the mean seed removal rate was significantly lower ($P < 0.01$) at RN2 (71.9%) than at Nouragues (83.8%), whilst intermediate at Kaw (81.46%; **Figure 6**).
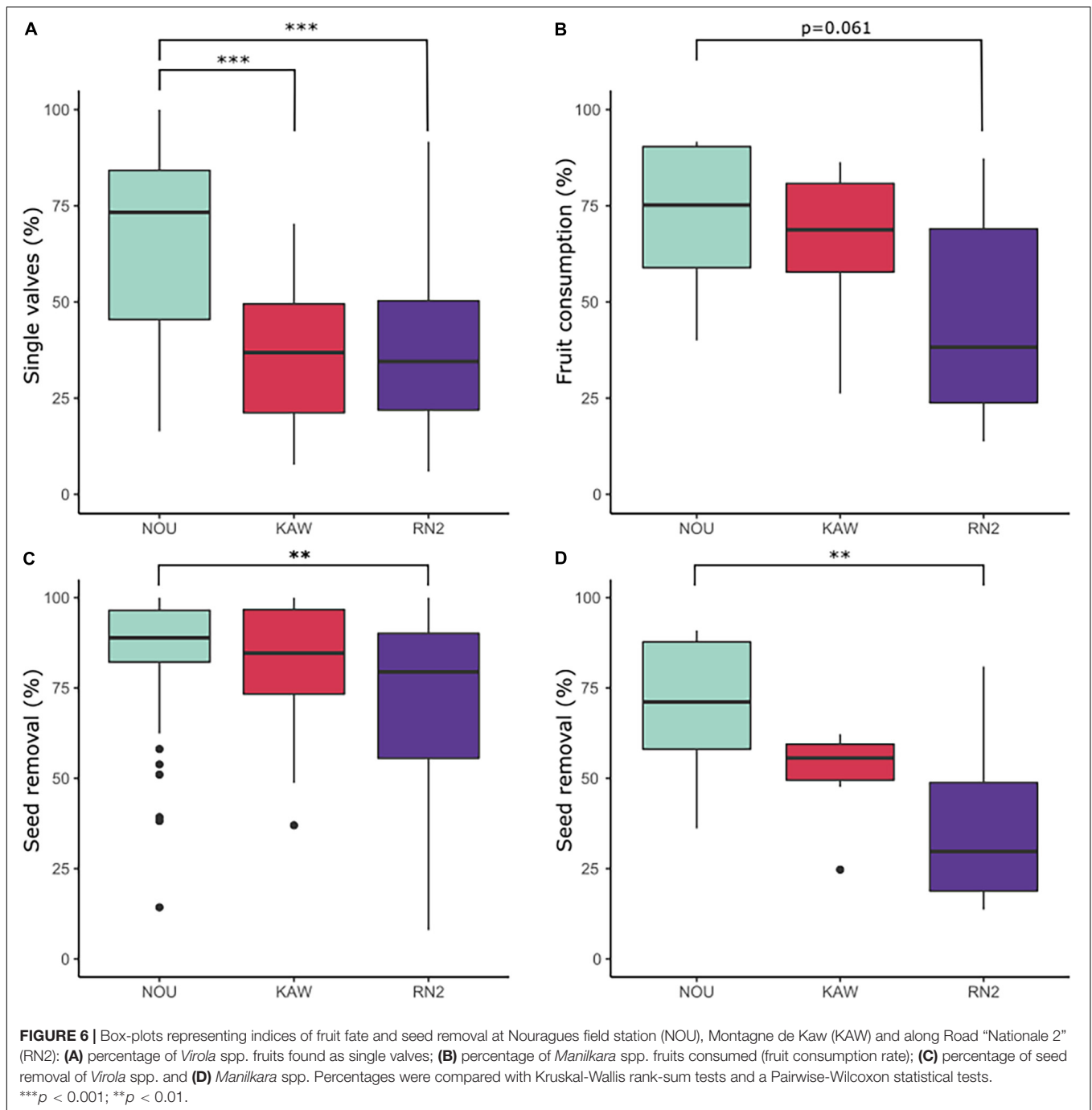
There was no significant effect between *Manilkara* species for either fruit consumption (*M. bidentata*: average 43.8%; *M. huberi*: 46.1%) or seed removal (*M. bidentata*: 30.7%; *M. huberi*: 41.4%) along RN2 ($X^2 = 0.12$, $df = 1$, $P = 0.72$ and $X^2 = 1.30$, $df = 1$, $P = 0.25$, respectively). The proportion of *Manilkara* fruit consumption and seed removal rate did not differ between forest patches ($X^2 = 6.44$, $df = 4$, $P = 0.17$ and $X^2 = 5.75$, $df = 4$, $P = 0.21$, respectively). The mean proportion of *Manilkara* fruit consumed at RN2 (44.9%) was marginally significantly lower ($P = 0.06$) than at both Nouragues (71.8%) and Kaw (64.8%). The mean seed removal rate at RN2 (36.1%) was significantly lower

than at Nouragues (69.4%), with Kaw (51.1%) being intermediate ($P < 0.01$; **Figure 6**).

Effects of Road and Distance to Urbanization

We analyzed the road effect (distance between trees and the road) and the distance to Saint-Georges on the proportion of fruit found as single valves (for *Virola*), on the fruit consumption rate (for *Manilkara*) and on seed removal rates (for both genera).

For *Virola* trees, the mean distance of trees to the road and to Saint-Georges was 403.9 m (range 10.32–894.88) and 25.08 km (range: 7.94–32.45), respectively. There was a significant and positive effect of the distance to the road ($Z = 6.14$, $P < 0.001$, slope $= 1.03 \pm 0.17$; mean $\pm$ se) on the proportion of fruit

FIGURE 6 | Box-plots representing indices of fruit fate and seed removal at Nouragues field station (NOU), Montagne de Kaw (KAW) and along Road "Nationale 2" (RN2): **(A)** percentage of *Virola* spp. fruits found as single valves; **(B)** percentage of *Manilkara* spp. fruits consumed (fruit consumption rate); **(C)** percentage of seed removal of *Virola* spp. and **(D)** *Manilkara* spp. Percentages were compared with Kruskal-Wallis rank-sum tests and a Pairwise-Wilcoxon statistical tests. ***$p < 0.001$; **$p < 0.01$.

found as single valves. We also reported a significant but very weak positive effect of the distance of trees to Saint-Georges ($Z = 5.40$, $P < 0.001$, slope $= 0.04 \pm 0.01$) on the proportion of single valve fruits. The seed removal rate was significantly but weakly affected by the distance to the road ($Z = 4.01$, $P < 0.001$, slope $= 0.67 \pm 0.17$), while no effect of the distance to Saint-Georges was reported.

For *Manilkara* trees, the mean distance of trees to the road and to Saint-Georges was 243.21 m (range 3.31–604.46) and 25.49 km (range: 7.94–32.45), respectively. There was a significant but

weak positive effect of the distance to Saint-Georges ($Z = -2.49$; $P < 0.05$, slope $= 0.02 \pm 0.01$) on the fruit consumption rate while no effect of the distance to road was reported. In addition, there was a significant but weak negative effect of the distance to Saint-Georges ($Z = -2.13$; $P = 0.03$, slope $= -0.02 \pm 0.01$) on seed removal rate, while no effect of the distance to the road was reported.

Overall, there was no significant effect of distance to urban areas for either fruit consumption or removal in all study species.

DISCUSSION

Ecological factors that can act on the visitation of fruiting trees by frugivores are forest type, tree accessibility, fruit occurrences and crop size (e.g., for Primates: Stevenson et al., 2005; Stevenson, 2016). In this study, we compared two seed dispersal systems in four tree species that co-occur in the same forest type (plateau and hilltop). They are all defined as specialized (*sensu* Howe, 1993) and produce large fruit and seeds that are dependent on large frugivores, especially primates and birds, for seedling recruitment away from parents. Abundant literature already demonstrated that the impact of human activities, especially hunting of the main fruit consumers of the study species, could alter their seed dispersal, but no study focused on roads and corridors (Pardo et al., 2019). We investigated here the alteration of these dispersal systems by the construction of a recent road fragmenting and facilitating access to the forest and therefore, promoting road-mediated anthropogenic activities such as hunting, logging and ranching.

A theoretical anthropic gradient was predicted along RN2 with various human activities and pressures across four forest patches, expected to decrease with increasing distance to Saint-Georges. After the bridge opened to traffic across the frontier French Guiana-Brazil in 2017, an increase of anthropogenic pressures along the RN2 was expected, notably with an increase in population and settlements along the road, as well as a development of human activities. We then expected biodiversity and the seed dispersal ecological process to be markedly impacted in the short term (de Thoisy et al., 2010).

Virola Seed Dispersal System

On the one hand, the absence of a significant difference in seed removal rate in *Virola* spp. across forest patches may indicate that seed dispersal is not yet markedly impacted by the predicted anthropic gradient along the RN2. Nevertheless, the lowest rate and the highest variance of seed removal compared to that of the Nouragues demonstrate that seed dispersal and predation occur more heterogeneously along the RN2 than at Nouragues. On the other hand, the high proportion of *Virola* fruits found as single valves at Nouragues, compared to both RN2 and Kaw, suggests that primate density and activity are significantly higher in the control forest, or lower in the environmentally stressed habitats such as a forest close to roads (Boissier et al., 2014, 2020). This higher proportion of *Virola* fruits found as single valves at Nouragues is best explained by the high abundance of black spider monkeys in this nature reserve, which is not a common species in RN2 (observed only once from 2013 to 2019; de Thoisy et al. (2005); P.-M. Forget, *pers. obs.*), and absent at Kaw (Boissier et al., 2020). This primate species is indeed very sensitive to hunting pressure and habitat quality (Nuñez-Iturri and Howe, 2007; Sales et al., 2020) and is one of the first species disappearing with anthropogenic pressures (de Thoisy et al., 2010). The presence of single-valved fruits at the RN2 thus results from the activity of other canopy-foraging animal species that can manipulate fruits to reach the aril, such as the red howler monkey and

brown capuchin, despite them being known to have a minor role in *Virola* spp. seed dispersal at the Nouragues control forest (Ratiarison and Forget, 2013).

In addition, camera traps placed in the canopy revealed that kinkajou is the most frequent visitor of *Virola* trees (**Supplementary Figure 3**). The feeding behavior of this arboreal animal has been argued as comparable to that of primates such as spider monkeys (Kays, 1999). This observation indicates that kinkajou could be ensuring seed dispersal in the canopy along RN2. Kinkajou might therefore contribute to forest resilience, through ecological and functional redundancy (Loiselle et al., 2007), by being an active disperser when other frugivores such as spider monkeys are lacking in the forest (Rother et al., 2016; Moreira et al., 2017). The maintenance of seed dispersal may also be complemented by large toucans, other important dispersers of *Virola* seeds (Howe and Vande Kerckhove, 1980, 1981; Holbrook and Loiselle, 2009; Ratiarison and Forget, 2013). In this study, however, using camera traps in the canopy, we failed to reveal high frequencies of diurnal species and canopy birds including toucans in fruiting *Virola* tree crowns. This may be due to the positions of the cameras in tree crowns as a study showed that wind and sun exposure can severely impact camera triggering, particularly in the canopy where weather conditions are more intense (Gregory et al., 2014). Camera positions were optimized to capture individuals eating fruits but camera exposure to environmental conditions was not considered. Further studies should thus pay more particular attention to camera positioning, and choose the best compromise between exposure and optimal position for observing diurnal animals (Bowler et al., 2017; Moore et al., 2021).

Manilkara Seed Dispersal System

The *Manilkara* 2014 masting event led to the accumulation of entire, uneaten fruit (55%) and non-dispersed seeds (63%) below parent trees standing in the forest along the RN2, with no apparent relation with the distance between trees and road, and a weak effect of the distance to the nearest urban area. Several factors could explain such high level of removal failure also called fruit waste (*sensu* Howe, 1980), including the abundance of fruit resources at the community level, the diversity and density of ground and arboreal consumers, as well as the saturating effect of the masting event among years and sites (Mendoza et al., 2015). However, when comparing fruit and seed fate at three contrasting forest habitats, it is apparent that fruit consumption and seed removal are more affected in the primate-dispersed species (*Manilkara* spp.) than in the more generalist species dispersed by both mammals and birds (*Virola* spp.) at RN2, the most stressed forest. Moreover, our results show that fruit consumption and seed removal rates decrease from the least disturbed (Nouragues) to the most disturbed sites (RN2 and Kaw). The low level of fruit consumption and seed removal at RN2 appeared to be comparable to Kaw. These results illustrate the indirect impacts of the RN2 in the area, which eases accessibility to the forest and promotes human activities such as hunting. The observed fruit waste in *Manilkara* at RN2 compared to Nouragues and Kaw is a common phenomenon within the Sapotaceae family level in stressed environmental

conditions, especially defaunated ones (Gutierrez-Granados and Dirzo, 2010; Anzures-Dadda et al., 2011; Levi and Peres, 2013; Boissier et al., 2020). It suggests a lower population of specialized consumers of *Manilkara* in the canopy, e.g., howler monkeys and brown capuchins (Ratiarison and Forget, 2011), along with the satiation of the overall wildlife cotery on the ground beneath trees where whole fruit and seeds accumulate. Moreover, forest habitats along RN2 have important edge effects and the development of logging and ranching thanks to the construction of the RN2 favored the growth of secondary vegetation with pioneer and successional species bearing small-sized fruit. This concentrates the most favorable ecological conditions suitable for the establishment and persistence of small body-sized primates such as golden-handed tamarins *Saguinus midas* in disrupted forests (Pack et al., 1999), likely responsible for the greater proportion of removal failure. Indeed, because of their small size (Sivault et al., 2020), they can manipulate large fruits but will not ingest them and do not swallow large seeds. They rather spit them out after sucking the pulp, leading to their accumulation on the ground beneath tree crowns, which then attract ground-dwelling granivores such as large rodents and peccaries (Forget et al., 2007).

Frugivore Community

The apparent marginal effect of the National Road on fruit consumption and seed removal, particularly near the closest urban area of Saint-Georges, suggests that the wildlife community was not yet heavily affected by the road and the increased forest accessibility. An alternative hypothesis is that the lack of consumption and removal by the primary consumers and dispersers has been compensated by a greater abundance of secondary frugivores and granivores (Effiom et al., 2013; Moreira et al., 2017; Boissier et al., 2020). Indeed, most of the frugivorous species known to feed on *Manilkara* and *Virola* fruits and/or seeds were recorded in the study area. However, the main consumer of *Virola* fruits, the spider monkey, was never recorded. Frugivores such as large fruit-bats (e.g., *Artibeus* spp. or *Carollia* spp., Phyllostomatidae) known to forage and feed upon *Manilkara* fruit (Lobova et al., 2009) were not recorded either but this is likely due to the method, which was not designed to survey such flying species. Also, the quadrat method cannot evaluate the effect of frugivores that may swallow entire fruit (particularly *Manilkara* fruit), leaving no trace of consumption. However, such a bias is the same for all quadrats and depends on the presence of frugivores (nocturnal and terrestrial). During this study, the use of camera traps allowed enriching the diversity of known consumers by showing that deers and tapir consumed entire *Manilkara* fruits, possibly dispersing their seeds *via* regurgitation or in the feces (Feer et al., 2001), a feeding behavior that was missing in previous literature about their diet in the Guianas (Gayot et al., 2004; Hibert et al., 2011).

Primates are unlikely to forage across a fragmented forest landscape (Ratiarison and Forget, 2005) and the abundance of large terrestrial dispersers may decrease due to hunting (Moreira et al., 2017). Nonetheless, the human population of Saint-Georges remains limited (ca. 4,000 inhabitants), many of them inhabiting along the Oyapock river, where the hunting pressure is concentrated. The study was also carried out at a time when traffic was still relatively sparse since the cross-river international bridge had not yet opened. As a whole, road nuisances may remain relatively limited due to the small size of the human population.

The overall sharp differences in fruit handling, consumption, and seed fate beneath parent trees between Nouragues and RN2 reveal a change in the frugivorous community of the latter. The lower seed dispersal and accumulation of fruits below trees was likely due to the lack of key dispersers in the forest bordering the RN2. Hence, in line with the model of vulnerability, which predicts that population densities generally decline with increasing body mass, (Robinson and Redford, 1986), six species population densities decreased in the hunting area, i.e., three large primate species (spider monkey, howler monkey and capuchin) and the collared peccary (*Tajacu pecari*), black curassow (*Crax alector*) and gray-winged trumpeter (*Psophia crepitans*). Fruiting *Virola* and *Manilkara* trees are mostly visited and their fruits/seeds dispersed by arboreal mammals and birds, and the differences across study sites suggest that the primate community has been more impacted by environmental pressures along the RN2 compared to Nouragues and Kaw.

Limitations

The lack of effect on *Manilkara* fruit consumption between RN2 and Kaw suggests a similar disruption in the wildlife community, along with comparable anthropic pressures at both sites (hunting, logging, and fragmentation). This result is provisional given the small number of trees considered in the comparison (6 at Kaw vs. 30 trees at RN2), and a possible inter-annual effect, with a difference in *Manilkara* fruit production between 2010 and 2014. Still, results for *Manilkara* seed removal at RN2 are consistent with the general finding of low seed removal amongst Sapotaceae species at Kaw (Boissier et al., 2020).

To conduct a more thorough study of the fauna visiting trees, it would be necessary to implement camera traps in canopies at all different forests. The sampling must be improved with more fruiting trees by patch and forest type along the road, and at a greater distance (> 1 km) in the interior (see Miller et al., 2021). Cameras should be set up at different heights to gain greater information about arboreal animals, i.e., small to large, diurnal and nocturnal, visiting the tree crowns or not (Moore et al., 2021; Zhu et al., 2021). We expect that small frugivorous vertebrates are also important, contributing to the resilience of animal-plant interaction networks in stressed and endangered forest habitats (Carreira et al., 2020). Such a study should also be repeated during other years at the forest patches, and across forests, to minimize month effect and year effects that most likely would alter results and comparisons across sites, especially during mast fruiting events of *Manilkara* species (Norden et al., 2007; Mendoza et al., 2015). Furthermore, since the bridge opened to traffic in 2017, it would be interesting to study how resilient the wildlife has been, and to compare how frugivorous species and trees responded to the expected greater road traffic, which has barely been investigated during impact assessments (Vilela et al., 2020).

CONCLUSION

Based on the current data, the study does not indicate a significant effect of distance to the urban area and to the road on frugivorous activity and seed dispersal. This is likely due to a compensatory effect of small mammals replacing large and absent ones in the most impacted forests. However, the comparison across forests revealed significant differences in the type of fruit handling, and the rate of fruit consumption and dispersal rate among tree species, despite only a small number of sampled trees being included for one study tree species (*Manilkara*). Tropical biodiversity conservation research should take into consideration the threats that new bisecting roads (such as RN2 in the last Western forest block) represent for a region that is an excellent natural laboratory to understand the process of human-induced biodiversity degradation and the associated species responses (Kocher et al., 2017, 2022). A decade after the road was asphalted and open to traffic, this study indicates a moderate effect of the road on frugivorous activity and ecological services. This first round of observations would need to be more thorough to explain the origins and causes of the differences observed from an environmental perspective, as well as to evaluate how flora and fauna differ across forest stands within the study sites. Repeated measurements of ecological services throughout time, at 5–10 year intervals, at the same forest patches, and possibly at the same individual trees and species, across forest sites, would allow evaluation of the effects of inter-annual variability and masting years (Norden et al., 2007; Mendoza et al., 2015, 2018) on fruit consumption and seed removal, and the expected greater fruit waste (sensu Howe, 1980) in primate-impoverished animal communities.

The tropical rainforest is a complex ecosystem that relies on plant-animal interactions occurring at each step of the life cycle of a plant (Terborgh et al., 2008). It is therefore vital to urgently evaluate the effects of anthropogenic pressure on animal communities, due to the change of interactions they can induce and to the cascading effects it will have at different scales—local, regional and global. The frugivorous vertebrates, by their role as seed dispersers, are a crucial factor of change and efficiency of seed recruitment, which affect plant diversity in the short term. Indeed, the lower seedling recruitment is below the reproductive tree, the higher species coexistence will be (Terborgh et al., 2008). The impoverishment of the community of large frugivores, because of various anthropogenic pressures (hunting, fragmentation, logging), leads to a downsizing effect at the community level, with an increased population of small-sized frugivores. Within several years or decades, defaunation combined with downsizing effects will have consequences on specialized large-seeded tree species such as *Virola* and *Manilkara* that will fail to recruit (Levi and Peres, 2013), being progressively replaced by generalized small-seeded and small animal-dispersed tree species (Moreira et al., 2017). Conservation programs have to consider interactions between plants and animals to maintain forest diversity despite human pressures. The decrease in hunting pressure on dispersers and increasing connectivity between populations are key points for the conservation of the diversity of plant-animal interactions.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article are available as **Supplementary Tables 5–8**. Pictures from camera traps are included in https://www.agouti.eu and are available upon requests directed to the corresponding author(s).

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because animals were not captured or manipulated.

AUTHOR CONTRIBUTIONS

OC, OB, AB, and P-MF conceived and designed the fruit surveys at all sites. OC, EG, and P-MF conceived the camera trap protocol at RN2. OC, AA-D, OB, CMD, FF, IM, EG, and P-MF performed the fruit and seed surveys. OC, MD, and P-MF performed data analysis and interpretation. OC, MD, OB, IM, and P-MF wrote and edited the manuscript. All authors contributed to the article and approved the submitted version.

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