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The influence of invasive alien plant control on the foraging habitat quality of the Mauritian flying fox (*Pteropus niger*)

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Gabriella Krivek

ABSTRACT

The last surviving Mauritian fruit bat species, *Pteropus niger*, although endangered, provides essential seed dispersal and pollination services for the threatened native flora. However, their foraging habitats in native forest remnants are dominated by alien invasive plants and are inhabited by invasive alien animals like long-tailed macaques. Competition for food resources and a decrease of native fruiting trees appear to force fruit bats to top up their diet with cultivated fruits. Consequently, a rapidly escalating conflict with local farmers resulted in a mass cull initiated by the Mauritian government that decimated around 50% of the fruit bat population. Here, I investigate the impact of invasive alien plant control on the foraging habitat quality of fruit bats, by quantifying fruit production and fruit bat foraging intensity in weeded and non-weeded forest areas using ground quadrats. Moreover, I examine how native tree traits and fruit characteristics affect tree and fruit selection of flying foxes and long-tailed macaques. Weeding significantly increased both native fruit production and fruit bat foraging intensity. Fruit bats preferred to forage in weeded areas on tall trees with a large crown. In addition, fruit bats preferred large and ripe fruits, while long-tailed macaques more often used small unripe fruits. Peak of native fruit use by macaques coincided with lower use by fruit bats, suggesting resource competition. The results suggest that weeded forests provide a better foraging habitat for *P. niger* than non-weeded areas, and emphasize the importance of weeding for the recovery of native plant communities and their associated biodiversity. I conclude that weeding and controlling of the introduced long-tailed macaque population may be solutions to mitigate the current human-wildlife conflict. In the long term, failure to improve native foraging habitats of fruit bats is likely to increase their extinction risk on Mauritius.

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1. INTRODUCTION

Tropical rainforest biodiversity is particularly threatened due to over-exploitation by rapidly growing and developing human populations and increased land degradation (Butchart et al. 2010). Continued destruction of these productive and complex ecosystems may lead to mass extinctions and to massive loss of important ecosystem services provided by these species (Ceballos et al. 2015; Morris 2010). Globalization also presents new challenges, among which invasive alien species are one of the major causes of environmental degradation (Reaser et al. 2007) and extinctions of threatened native species (Pyšek et al. 2017). The growing global transport and travel network provide plenty of opportunities for invasive species to overcome natural dispersal barriers and colonize new locations – even isolated islands (Walsh et al. 2016). Isolated tropical islands with unique biodiversity are particularly susceptible to the negative effects of alien species and habitat loss (Caujapé-Castells et al. 2010). Most of the recent native and endemic species extinctions on islands are due to invasions (Blackburn et al. 2004; Clavero & Garcia-Berthou 2005). Restoration is a key component of conservation (Aronson & Alexander 2013) as removal of alien species may reverse degradation of ecosystem functions and prevent further extinctions (Kaiser-Bunbury et al. 2017; McCann 2007). Although the cost of restoration imposes pressure on other development and conservation goals (Walsh et al. 2016), restoration projects are often profitable and high-yielding investments (Groot et al. 2013). The management of invasive alien species is essential to conserve the biodiversity of many islands (Glen et al. 2013), which may also serve as important models to assess the impact of invasive species on the native biota of other tropical areas (Baider & Florens 2011; Florens 2013).

The volcanic island of Mauritius – part of the Western Indian Ocean Islands biodiversity hotspot – has a unique biota with a proportionally high concentration of endemic species (Myers et al. 2000). However, its biota encompasses some of the most threatened biodiversity in the world (Florens 2013). Since its human colonization, the native forest cover has been reduced to 5% of the island's area (Florens & Baider 2013). The extinction rate of native species is high and currently amounts to 11% of the endemic angiosperms, 63.2% of the endemic land birds and 31.3% of the endemic reptiles (Florens 2013). Today, alien plant invasions further threaten the remaining wildlife that is strongly associated with native vegetation (Florens et al. 2010). The most problematic invasive woody plants on Mauritius are strawberry guava (*Psidium* *cattleianum*), privet (*Ligustrum robustum*), rose apple *(Syzygium jambos*) and cinnamon (*Cinnamomum verum*; Florens & Baider 2013). Invasive alien vertebrates may further accelerate the dispersal of invasive alien plants (Lorence & Sussman 1986) and damage native vegetation directly through browsing, trampling and seed predation (Strahm 1999). Mammals were introduced intentionally to the island, like the Javan deer (*Rusa timorensis*), the wild pig (*Sus scrofa*) and the long-tailed macaque (*Macaca fascicularis*). Accidentally introduced rats (*Rattus rattus* and *R. norvegicus*) contributed to the extinction of several endemic birds and reptiles (Cheke & Hume 2008). Species introduced to eradicate other alien species are also posing a threat on their own, like the feral cat (*Felis catus*) and mongoose (*Herpestes javanicus*), which were introduced to Mauritius to control rats (Roy et al. 2002). The common mynah (*Acridotheres tristis*) and the red-whiskered bulbul (*Pycnonotus jocosus*) are among the most common introduced birds that compete with native species (Nichols et al. 2004). The only native mammals of Mauritius are bats, including two insectivorous microbats, *Taphozous mauritianus* and *Mormopterus acetabulosus* (Goodman et al. 2008) and *Pteropus niger* (Pteropodidae: Chiroptera), the last surviving of three fruit bat species of Mauritius (Florens 2016; Figure 1).

Figure 1. Mauritian flying fox (*Pteropus niger*) in captivity on Ile aux Aigrettes, southeast Mauritius.

Fruit bats (*Pteropus* spp.) play a vital role in the regeneration of native forests by providing essential ecosystem services, such as seed dispersal and pollination (Fujita & Tuttle 1991; Kunz et al. 2011; Vincenot et al. 2017), especially in oceanic-island ecosystems due to the lack of alternate species to fill these roles (McConkey & Drake 2015). Because of the recent human-induced extinctions of all the other large potential seed dispersers, *P. niger* is the only native species left on Mauritius able to disseminate the seeds of most native canopy trees (Vincenot et al. 2017). Canopy trees play a key structural role in forests, regulate hydrological cycles, provide carbon stocks and essential conditions for forest-dependent species (Florens et al. in review; Nyhagen et al. 2005). However, it is known that before *Pteropus* becomes rare, its function as an effective seed disperser decreases or disappears due to changes in its social interactions and foraging behaviour (McConkey & Drake 2006). Therefore, a decline of Pteropoidae fruit bats may cause a cascade of linked native plant and animal population declines or extinctions (Vincenot et al. 2017). The loss of regenerating native canopy species could lead to the functional collapse of native ecosystems (D'Antonio & Dudley 1995; O'Dowd et al. 2003).

Foraging habitat is one of the most important limiting resources for fruit bats (Mickleburgh et al. 1992). This is particularly the case for *P. niger*, which has suffered from massive habitat loss and the quality of remaining forests is on the decrease due to alien plant invasions. The diet of *P. niger* is mainly composed of fruits, occasionally supplemented with flowers, nectar and leaves (Nyhagen 2004). This species generally prefers native forest resources, but around 35% of the species included in its diet comprise plants of introduced to the island (Florens et al. in review). This suggests that high density of invasive plants, together with the rarity of some native plant species and their decreased fitness, strongly influences the fruit bat's foraging behaviour and diet selection. Almost 10% of the native food plants of *P. niger* are threatened and their availability continue to decrease due to land-use changes and habitat degradation by invasive alien plants (Florens et al. 2017; Vincenot et al. 2017).

Fruit bats also top up their diet with cultivated fruits (Oleksy 2015), probably due to the lack of native fruit resources or due to the easier access and high abundance of fruits in plantations and backyards. This habit makes commercial fruit growers and orchard owners across the island to see fruit bats as pests (Nelson et al. 2000). Although the species was classified as Vulnerable (IUCN 2013), the Mauritian government has implemented two large-scale culls of fruit bats since 2015 due to the increasing conflict with fruit growers, which abruptly reduced their population by more than 50% (Vincenot et al. 2017). After this rapid population reduction of *P. niger*, which has a generation time of 7-8 years, the population is likely to recover very slowly (Vincenot et al. 2017). Moreover, the death toll exceeds the number of officially culled bats, due to illegally killed, wounded and orphaned bats, and electrocution (MWF 2015). In addition, fruit bats are highly vulnerable to stochastic events such as cyclones, resulting in high levels of mortality, starvation and loss of roost trees (Cheke & Hume 2008). Cyclones are predicted to become more frequent and intense on Mauritius due to ongoing climate change (Vincenot et al. 2017). All these factors together therefore increase the extinction risk of the species in the near future (Florens 2015).

The few remnants of native Mauritian forests are highly invaded (Florens et al. 2016) and the progressing invasion poses a threat to native plant communities and also to their associated biodiversity (Florens et al. 2017; Florens et al. 2010). Invasive alien species on Mauritius also cause high mortality among canopy trees used by bats (Baider & Florens 2006), but removal of invasive species reverses this trend (Baider & Florens 2011; Vleut et al. 2013). Weeding out invasive plants improves the fitness of individual trees and of native plant communities by increasing density and species richness of seedlings, individual growth and survival rates, and flower and fruit production of native canopy and understory species (Baider & Florens 2006; Baider & Florens 2011; Florens 2008; Monty et al. 2013). Increased flower and fruit availability, accessibility and variety of native food plants are positively correlated with fruit bat abundance (Vleut et al. 2013). Restoration of native habitats on Mauritius could therefore improve their quality and attractiveness to fruit bats (Amavassee 2015). Restored areas would in turn sustain larger bat populations and could result in reduced bat visits to orchards.

Although there is a good understanding of the effects of alien plant weeding on native plant communities, little is known about how the recovery of native vegetation affects the associated biodiversity, particularly the last surviving fruit bat species of Mauritius. There is also a lack of data on food resource competition between invasive alien animals and fruit bats. The aim of this study was to investigate the impact of invasive alien plant control on the foraging habitat selection of the Mauritian flying fox and its adequacy as a restoration and conservation measure. More specifically, I attempt to answer the following questions: 1) What are the effects of invasive alien plants on the foraging habitat selection of *P. niger*? 2) Is there a relationship between native tree traits and their importance as food resources for *P. niger*? 3) Is there resource competition between *P. niger* and *M. fascicularis* that could exacerbate or create potential food shortages for fruit bats in native forests? This study will contribute to the understanding of how native habitat restoration is beneficial to both native flora and fauna of Mauritius.

2. MATERIALS AND METHODS

2.1 Study area

The study was carried out at Mt. Camizard, located in the southeast of Mauritius (Figure 2A) near Anse Jonchée village (3 km to the southeast) and sugar cane fields (Figure 2B). The sampled forest (Figure 3A) is situated on the windward slope of the Bamboo Mountains (20° 19' 51" to 20° 20' 10" S, 57° 42' 52" to 57° 43" 02" E). The forest occurs at an elevation between 250 to 320 meters above sea level on ferralitic soil, derived from 7.5 to 5.2 million years old basaltic lava flows (Montaggioni et al. 1988). The area is characterized by a super humid, mesothermal climate with 2,000–3,000 mm rainfall per year (Halais & Davy 1969). The forest is divided into four blocks, each enclosed at least partially by a fence. *Pteropus niger* is known to actively forage and roost at the site (Robin 2007; Sookhareea 2011). From the 45 native woody plant species known to occur in high relative frequency at Mt. Camizard, 17 (38%) provide important food resources for fruit bats (Florens et al. 2012).

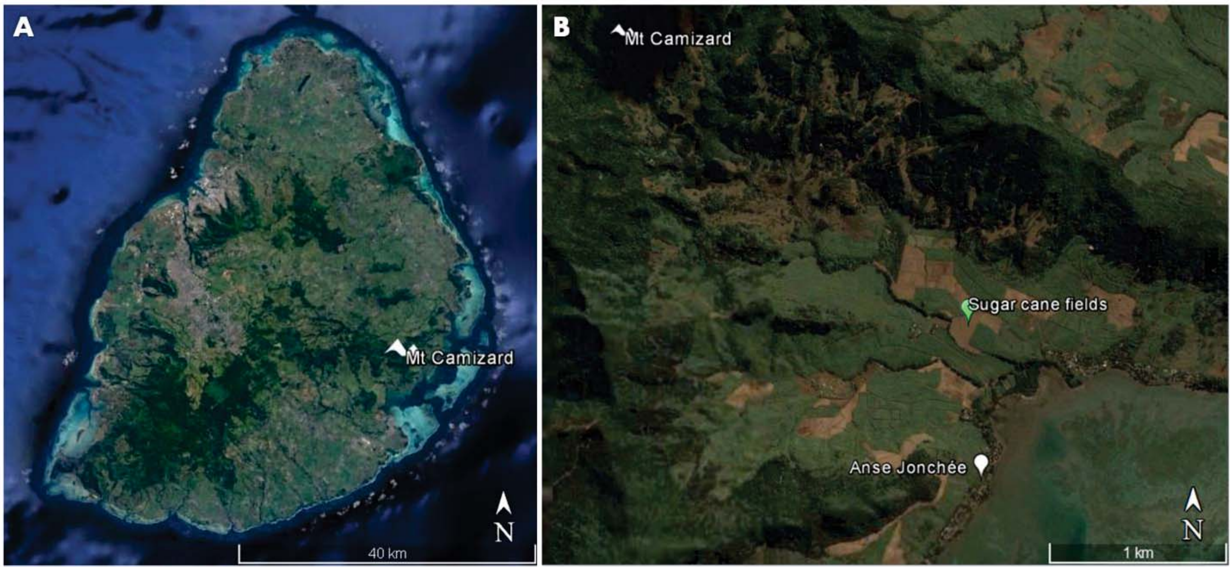

Figure 2. The study area of Mt. Camizard, (A) located in the southeast of Mauritius, (B) near Anse Jonchée village and sugar cane fields.

The area is considered protected as it is designated as a mountain reserve, and it is among the most preserved and least disturbed native wet forests on Mauritius (Florens et al. 2012). The forest canopy is dominated by native species, although exotic species dominate the forest in terms of stem density (Florens & Baider 2013; Florens et al. 2016). The forest consists of a mosaic of well-preserved, moderately and highly invaded areas (Florens et al. 2012), along with patches that have been cleared of invasive alien plants since 2005 (Florens & Baider 2013). Weeded and non-weeded areas (Figure 3B, C) are located close to each other within the same forest (Figure 4), resulting in two similar study sites apart from the removal of invasive alien plants. This provides an experimental design that allows investigating the influence of weeding on the foraging habitat quality of fruit bats within the same type of native vegetation growing in similar abiotic conditions.

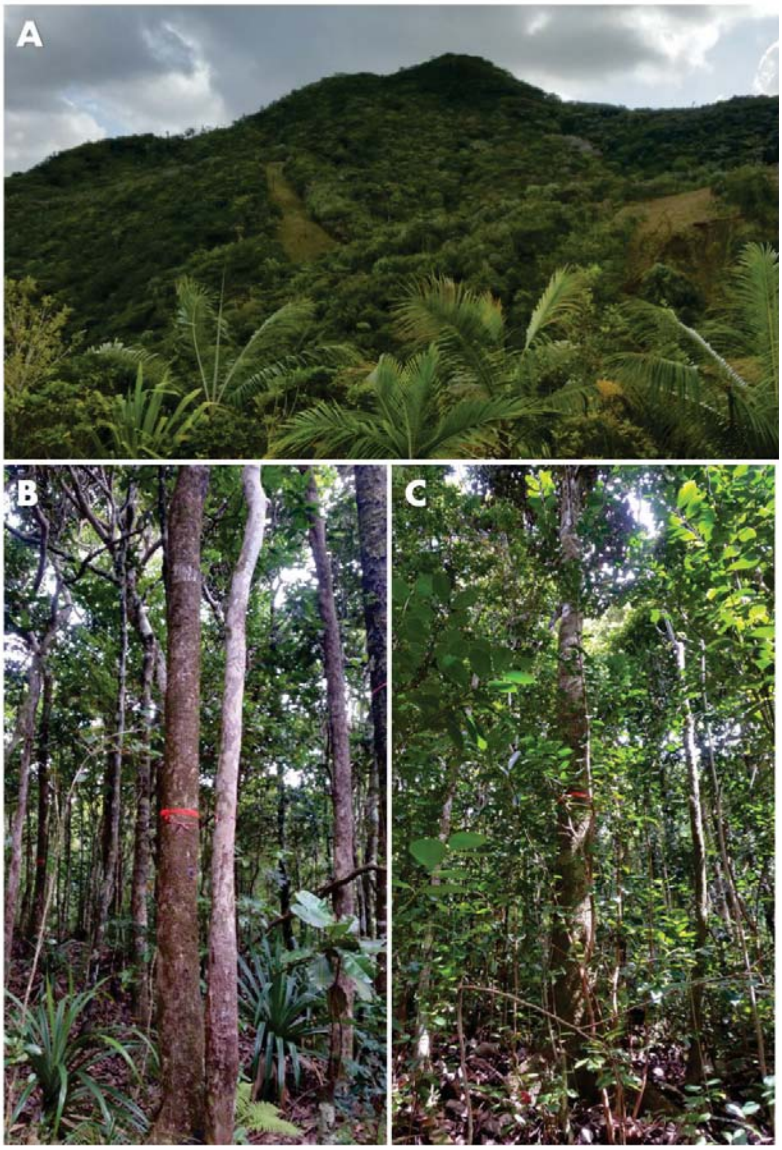

Figure 3. (A) The sampled forest at Mt. Camizard and the two study sites: (B) the weeded and (C) the non-weeded forest, showing a denser understorey comprising of a majority of invasive alien plants.

2.2 Study design

To compare the resource utilization of fruit bats in weeded and non-weeded areas, focal native tree species were selected based on the following criteria:

a) they are present in a sufficiently large number at Mt. Camizard to allow for adequate replication both in weeded and non-weeded areas;
a) their fruits are known to be consumed by *P. niger* (based on direct observations of fruit bat foraging behaviour, indirect observations by ejecta found under the trees, along with previous data gathered on resource use from literature review, respectively);
b) they are known to fruit during the sampling period - between July and November - based on field observations, literature and vouchers from The Mauritius Herbarium.

Two endemic primary forest canopy species, belonging to the family Sapotaceae, met the requirements and were selected as focal species: *Labourdonnaisia glauca* Bojer and *Mimusops maxima* (Poir.) R. E. Vaughan - nomenclature following Friedmann (1981). Focal trees were tagged with coloured tapes, marked with specific species codes (LAGL, MIMA) and numbers (herein tree ID). Their spatial coordinates were recorded using a handheld GPS (Garmin 62s) device. The surveyed area (Figure 4) was 80 m × 120 m, however, in the non-weeded forest an additional forest block was surveyed to reach sufficient number of focal individuals. Including trees near clearings along the edge of each block may introduce a bias to the data due to increased visibility, accessibility and fitness due to greater resource availability. Therefore, individuals falling within 10 m of the edge of the forest blocks were discarded to avoid atypical conditions due to edge effects.

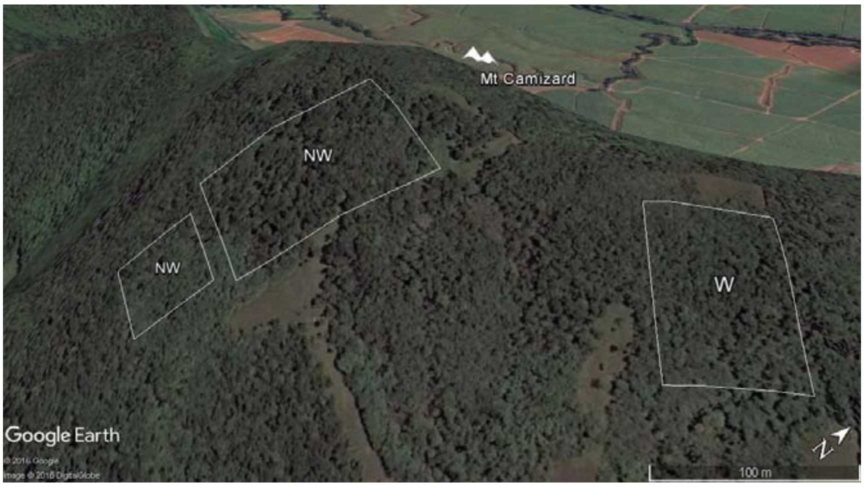

Figure 4. The sampled weeded (W) and the non-weeded (NW) forest areas at Mt. Camizard.

The diameter at breast height (dbh) of each focal tree was measured with a dbh tape, using a 1.3 m long wooden stick placed on the east side of the stem, to standardize the height of the measurement. The dbh of the smallest fruiting individual was used as threshold value to determine adult trees for each species. Trees below the threshold were excluded from the study as they were considered non-reproductive and, therefore, do not provide fruits for fruit bats. The minimum and maximum values represent the smallest and largest tree (based on dbh) that were fruiting during the survey period. The dbh range of reproductive trees were divided into three categories for *L. glauca* (small: 10.0 - 15.0, intermediate: 15.1 – 20.0 and large: 20.1 – 43.5), and two for *M. maxima* (small: 0.3 – 5.0, large: 5.1 – 17.5). This was done to standardize data collection, so that an equal number of individuals were randomly selected from every dbh category (20 individuals of *L. glauca* and, due to lower density, 6 individuals of *M. maxima*). In total, 60 individuals of *L. glauca* and 12 individuals of *M. maxima* were randomly selected for monitoring both in the weeded and non-weeded area.

The crown size of each tree individual was estimated by measuring the distance of the crown edge from the tree trunk in the four cardinal directions. The height of the focal individuals was estimated visually with the aid of a 1 m long stick placed along the stem against the east side of the plant as a reference. The distances from the forest edges in the four cardinal directions from each focal tree were measured using spatial data obtained with the GPS. This data was imported into Google Earth and an "effective distance" was calculated by counting the harmonic mean of distances to the different edges, thus incorporating an eventual effect of multiple edges.

2.3 Data collection

Fruit bat ejecta pellets are created from indigestible fibrous fruit pulp, when the bats squeeze out juices by compressing chewed fruits between their tongue and palate. Ejecta are abundant underneath fruiting trees used by bats and can be easily collected without need to capture and handle bats. By collecting ejecta, it is possible to avoid potential temporal and spatial bias of tree species close to the net and food plants recently consumed by netted animals (Banack 1998). As the number of ejecta beneath fruiting trees positively correlates with fruit abundance (Banack 1998), ejecta were used to provide a quantitative estimate of resource use by fruit bats.

Quadrats of 1 m^2 cleared of leaf litter were set in the four cardinal directions of each focal tree, on the midpoint between the tree trunk and the crown edge. The four corners of each quadrat were marked with orange (N-S) or pink (E-W) colour-taped wooden sticks. Ejecta pellets, ripe and unripe intact fruits, ripe and unripe fruits chewed by bats or macaques were collected underneath focal trees once per week (preferably on the same day) during 4 months (from the end of July to the end of November 2016). Ejecta and fruits found inside the quadrats were removed each week to avoid double counting. This method was chosen as it provided an area based approach to quantify resource use of fruit bats in weeded and non-weeded forest. Ground quadrats are also cheaper and less labour intensive than other methods, such as fruit traps, which are probably also more prone to losing ejecta during strong winds or be raided by long-tail macaques or rats.

Fruits of *L. glauca* were collected and placed in zip-lock bags labelled with the tree ID. Fruit and seed size were measured using a 0.01 mm precision calliper (Figure 5A). Fruit size was expressed as fruit dimension, determined by multiplying fruit length and fruit width. Fruits above the average fruit dimension (500 mm^2) were categorized as “large”, while fruits below this value were considered “small”. Fruit bat attacks were identified by their typical triangular-shaped tooth imprint (Figure 5C; Banack 1998), contrary to the rounded teeth marks of macaques (Figure 5D). To characterize ejecta from *L. glauca* and *M. maxima*, the dimension of 30 randomly collected ejecta were measured with a calliper and their morphology was described based on colour and texture (Figure 5B).

Figure 5. Measuring the dimension of *Labourdannaisia glauca* (A) fruit and (B) ejecta. The teeth-marks of (C) *Pteropus niger* and (D) *Macaca fascicularis* on a fruit of *Mimusops maxima*.

Using ground quadrats, there was a risk that fallen ejecta and fruits could be removed by other frugivores or that ejecta were destroyed by invertebrates or rainfall. Camera traps were set to check if other animals (e.g. rats, macaques, deer, pigs) would remove a significant amount of ejecta or fruits from underneath fruiting trees. An experimental quadrat of 1 m^2 with 10 fresh fruits and 20 ejecta was set up to determine the percentage of disappearance, which was monitored during 3 months. The experimental quadrat was placed on the ground between two fruiting focal trees outside of their crown cover, to avoid confounding factors such as arrival of new ejecta and fruits from above. The fruits and ejecta were replaced with fresh ones each week, handling them with gloves to avoid human smell or contact with mosquito repellent. As ejecta removal by snails has previously been observed (Banack 1998), trials were also conducted to determine if the invasive alien Giant African land snail (*Lissachatina fulica*) would remove ejecta at the study site. Fresh ejecta were placed in front of the snails on a leaf (without touching the ejecta directly), and their behaviour was observed for 5-10 minutes. No ejecta or fruit disappearance was recorded during the monitoring of experimental quadrats and the 10 replicated trials with *L. fulica*. Data collected from ground quadrats were thus used without data correction.

In addition, six ejecta were placed in a cleared area on the ground in the weeded forest to determine how long they stay recognizable. Ejecta on the ground stayed recognizable even after one month and did not disintegrate (Figure 6). However, during this time the colour changed to dark brown and the ejecta shrunk in size. This made them harder to observe on the ground, particularly in the dense non-weeded forest, suggesting that weekly collection of bat ejecta was optimal.

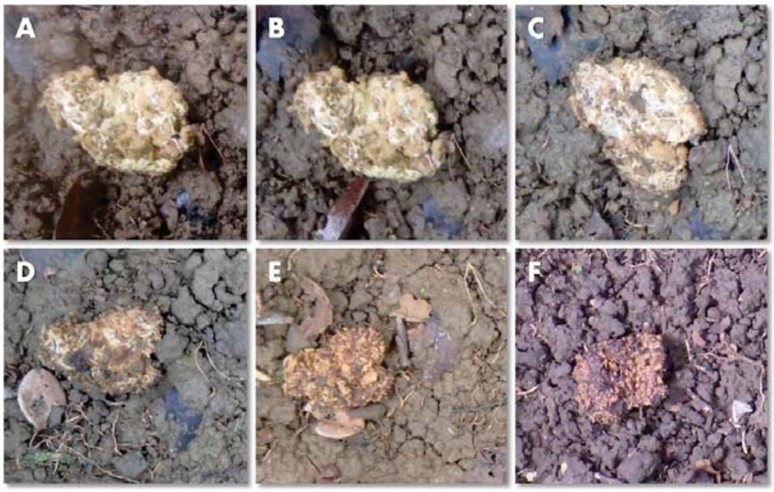

Figure 6. Ejecta placed on the ground on the first day (A), after 1 week (B), 2 weeks (C), 3 weeks (D), 4 weeks (E) and 5 weeks (F).

2.4 Data analysis

Statistical analyses were performed with R version 3.3.1. Generalized linear mixed-effects models (GLMMs) were used to test whether weeded forest is selected over non-weeded as a foraging habitat by fruit bats, to identify important characteristics of bat-used trees and the effect of weeding on fruit production. These analyses were performed in the ‘lme4’ package (Bates et al. 2014). The response variables were count data with negative binomial distribution. The full model contained tree crown size, tree height, tree dbh, harmonic mean of distances from the forest edges, treatment (weeded and non-weeded), tree species and their interaction as explanatory variables, and tree ID as a random effect.

Fruit availability and consumption over time were analyzed using generalized linear models (GLMs). Weekly total ejecta counts were the response variables (count data with negative binomial distribution), while explanatory variables were the number of macaque-attacked fruits and the overall number of fruits found in the quadrats per week. Fruit type preference was analyzed by a GLM model in which the number of fruits was the response variable, while ripeness (ripe, unripe) and attack type (macaque, bat) was the explanatory variable. The GLM model analyzing fruit size preference contained fruit dimension as a binomial response variable (small, large), while explanatory variables were ripeness (ripe, unripe) and fruit type (macaque-attacked, bat-attacked, intact). Unripe and intact fruits were used as reference level in the model.

After describing the full models, automatic model selection was performed using the dredge function in the ‘MuMIn’ package (Barton 2013) to find the best fitting models. Models with Delta < 2 were considered to have substantial support therefore model averaging was performed using these models. The best fitting models were determined to analyze habitat selection (based on the number of ejecta and bat-attacked fruits) and fruit production (Table S1), fruit availability and consumption over time (Table S2), fruit type and size preference (Table S3).

3. RESULTS

3.1 Fruits and ejecta abundance and morphometrics

Labourdannaisia glauca ejecta (Figure 7A) were characterized by pale yellow-green colour and sticky texture, with an average length of 31.01 ± 0.90 (mean ± SE), width of 24.62 ± 0.32 and height of 7.68 ± 0.17 (N=30). *Mimusops maxima* ejecta (Figure 7B) had a reddish green colour, was non-sticky with a fibrous texture, and had an average length of 21.99 ± 0.37 (mean ± SE), width of 19.79 ± 0.55 and height of 7.29 ± 0.15 (N=30).

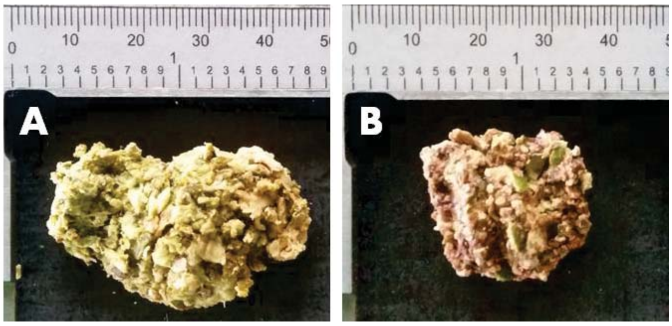

Figure 7. Ejecta of (A) *Labourdonnaisia glauca* and (B) *Mimusops maxima*.

A total of 10,900 (mean 129.8 ± 20.1 SE) and 2,469 (33.4 ± 7.1) ejecta, 217 (2.6 ± 1.6) and 40 (0.5 ± 0.2) macaque-attacked fruits, 151 (1.8 ± 0.5) and 28 (0.4 ± 0.1) bat-attacked fruits, 360 (4.3 ± 0.9) and 131 (1.8 ± 0.4) intact fruits were found in the quadrats of weeded and non-weeded forest, respectively (Table 1). Out of 690 *L. glauca* fruits, 15.94% were attacked by fruit bats, 14.06% were attacked by macaques and the rest were intact fruits. Out of 237 *M. maxima* fruits, 67.51% were attacked by macaques, 29.11% by bats and only 8 intact fruits were found.

Table 1. Number of ejecta, intact and attacked fruits by macaques and bats, including mean ± SE (in brackets) of two endemic plant species in weeded and non-weeded forest at Mt. Camizard.

Species	Sample	Weeded	Non-weeded
Labourdannaisia glauca	Ejecta	9849 (136.8 ± 21.3)	2450 (39.5 ± 7.6)
	Attacked fruit (macaque)	58 (0.8 ± 0.2)	39 (0.6 ± 0.2)
	Attacked fruit (bat)	84 (1.2 ± 0.2)	26 (0.4 ± 0.1)
	Intact fruit	352 (4.9 ± 0.9)	131 (2.1 ± 0.4)
Mimusops maxima	Ejecta	1051 (87.6 ± 9.7)	19 (1.6 ± 0.3)
	Attacked fruit (macaque)	159 (13.3 ± 4.0)	1 (0.08 ± 0.03)
	Attacked fruit (bat)	67 (5.6 ± 1.1)	2 (0.2 ± 0.07)
	Intact fruit	8 (0.7 ± 0.2)	0

3.2 Fruit production and foraging habitat selection

Both tree species were fruiting at the time of the study, but the GLMM model showed that the total number of fruits found in the quadrats was significantly higher in weeded than non-weeded forest (Figure 8A, Table 2). The interaction term showed that *L. glauca* had a trend of lower fruit abundance in the non-weeded area, while *M. maxima* fruit abundance was significantly lower in the non-weeded compared to the weeded forest (Figure 8B, Table 2). The total number of *M. maxima* fruits was significantly lower than *L. glauca* fruits (Table 2). Trees with bigger crown size produced significantly more fruits than trees with smaller crown, but tree height had no significant effect on fruit production (Table 2).

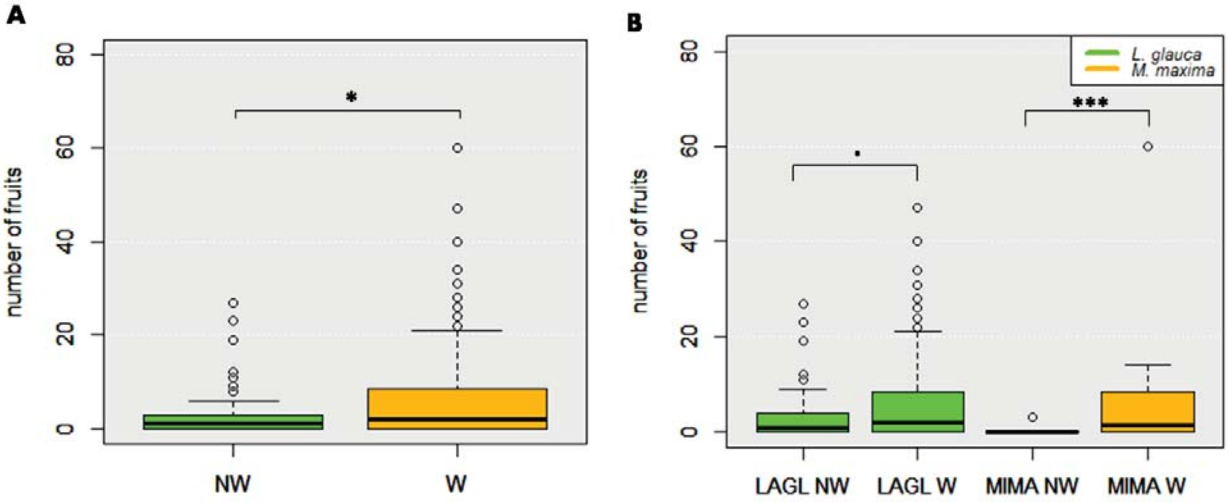

Figure 8. (A) Total number of fruits in the weeded and non-weeded forest at Mt. Camizard. (B) Number of *Labourdonnaisia glauca* and *Mimusops maxima* fruits in weeded and non-weeded forest at Mt. Camizard. The trend was indicated by • p ≈ 0.05, while the level of statistical significance by * p<0.05 and *** p<0.001.

Table 2. GLMM model best explaining fruit production and analysis of the significant interaction term for *Mimusops maxima* (MIMA) and *Labourdonnaisia glauca* (LAGL) in the weeded (W) and non-weeded (NW) forest at Mt. Camizard.

	Estimate	Std. Error	z value	p value	Significance
(Intercept)	-0.99466	0.47458	2.080	0.03749	*
Crown	0.05851	0.01362	4.261	<0.001	***
SpeciesMIMA	-1.88813	0.92542	2.024	0.04298	*
TreatmentW	0.66922	0.32475	2.044	0.040940	*
SpeciesMIMA:TreatmentW	3.35711	1.02543	3.247	0.001160	**
Height	0.01411	0.05039	0.278	0.780900	

Species = LAGL

Contrast	Estimate	SE	z.ratio	p value
NW - W	-0.63613	0.32995	-1.928	0.0539

Species = MIMA

Contrast	Estimate	SE	z.ratio	p value
NW - W	-4.00309	0.97818	-4.092	< 0.001

Bat foraging intensity, reflected by the number of ejecta, was significantly higher in weeded than in non-weeded areas (Figure 9A, Table 3). The number of ejecta of both *L. glauca* and *M. maxima* were significantly lower in the non-weeded forest (Figure 10B, Table 3). The overall number of ejecta for *M. maxima* was significantly lower than for *L. glauca* (Table 3). Of the measured tree characteristics, crown size and tree height had a significant positive effect on the number of ejecta, while tree diameter at breast height and the harmonic mean of distances from the forest edges had no significant effect (Table 3).

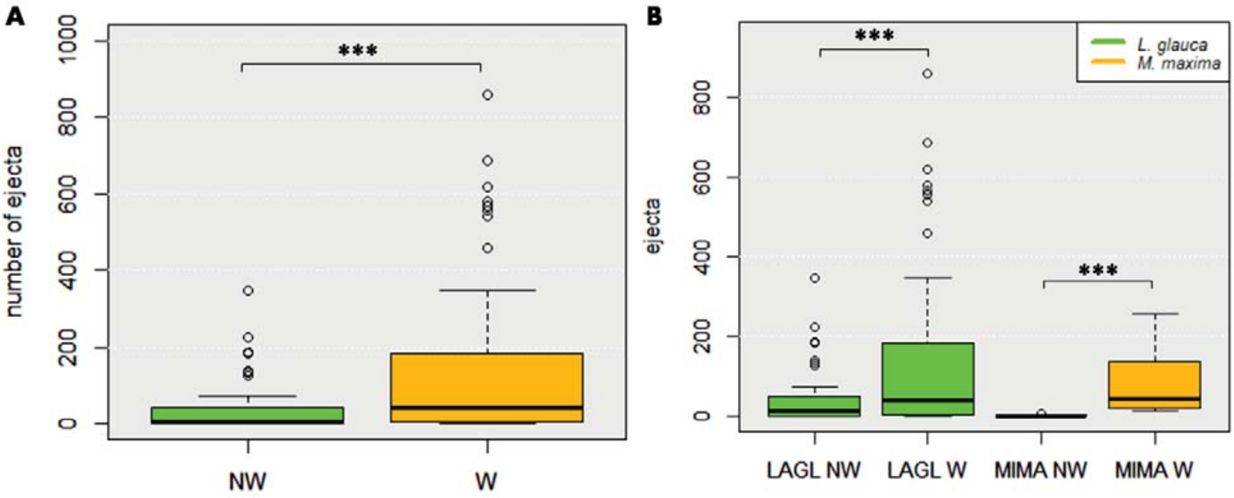

Figure 9. (A) Number of ejecta found in the weeded and non-weeded forest at Mt. Camizard. (B) Number of *Labourdonnaisia glauca* and *Mimusops maxima* ejecta in weeded and non-weeded forest at Mt. Camizard. The level of statistical significance is indicated by *** p<0.001.

Table 3. GLMM model best explaining foraging habitat selection based on the number of ejecta and analysis of the significant interaction term for *Mimusops maxima* (MIMA) and *Labourdonnaisia glauca* (LAGL) in the weeded (W) and non-weeded (NW) forest at Mt. Camizard.

	Estimate	Std. Error	z value	p value	Significance
(Intercept)	2.88989	0.81743	3.510	<0.001	***
Crown	0.09647	0.01889	5.068	<0.001	***
Height	0.26023	0.10664	2.425	0.0153	*
SpeciesMIMA	-1.94946	0.62581	3.091	0.0020	**
TreatmentW	1.50243	0.44020	3.386	<0.001	***
SpeciesMIMA:TreatmentW	3.66592	0.61738	5.891	<0.001	***
DBH	-0.01967	0.02954	0.663	0.5071	
Distance	-0.00267	0.00786	0.337	0.7362	

Species = LAGL

Contrast	Estimate	SE	z.ratio	p value
NW - W	-1.5432	0.45228	-3.412	< 0.001

Species = MIMA

Contrast	Estimate	SE	z.ratio	p value
NW - W	-5.1261	0.45077	-11.372	< 0.001

Similarly, when considering bat attacked fruits only, these were significantly more abundant in weeded than in non-weeded areas (Figure 10A, Table 4). The analysis of the interaction indicated that the number of bat-attacked fruits of both *L. glauca* and *M. maxima* were significantly less abundant in the non-weeded compared to the weeded forest (Figure 10B, Table 4). Although not significant, data indicates that trees with bigger crown had more bat-attacked fruits beneath them. Tree species and tree height had no significant effect on the number of bat-attacked fruits (Table 4).

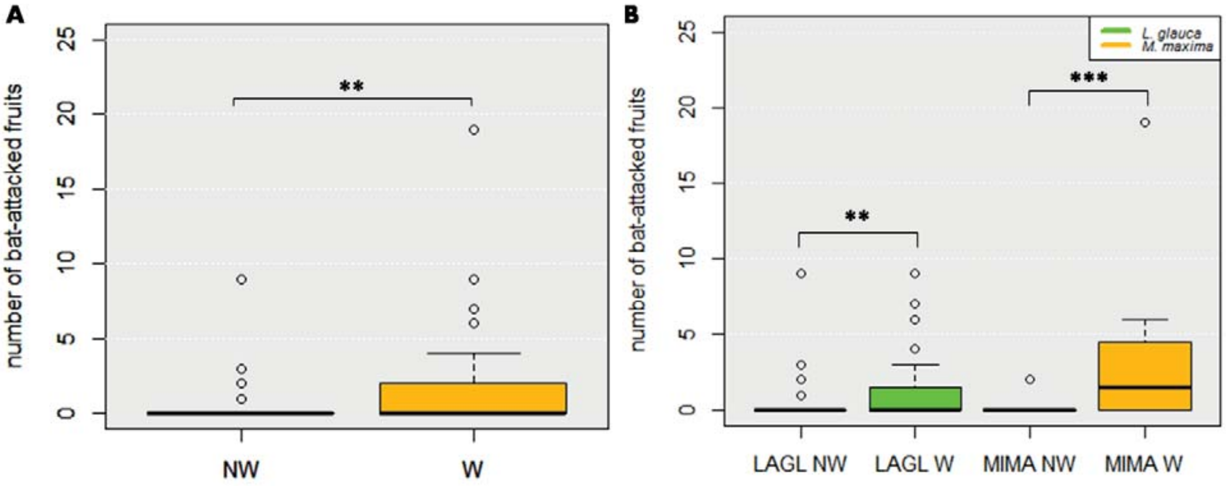

Figure 10. (A) Total number of bat-attacked fruits in the weeded and non-weeded forest at Mt. Camizard. (B) Total number of bat-attacked fruits of *Labourdonnaisia glauca* and *Mimusops maxima* in the weeded and non-weeded forest at Mt. Camizard. The level of statistical significance is indicated by ** p<0.01 and *** p<0.001.

Table 4. GLMM model best explaining foraging habitat selection based on the number of bat-attacked fruits and analysis of the significant interaction term for *Mimusops maxima* (MIMA) and *Labourdonnaisia glauca* (LAGL) in the weeded (W) and non-weeded (NW) forest at Mt. Camizard.

	Estimate	Std. Error	z value	p value	Significance
(Intercept)	-3.17123	0.79082	3.982	<0.001	***
Crown	0.03286	0.01841	1.771	0.07660	.
SpeciesMIMA	-0.25148	1.09991	0.227	0.82057	
TreatmentW	1.20217	0.46104	2.587	0.00968	**
SpeciesMIMA:TreatmentW	2.77249	1.20209	2.288	0.02214	*
Height	0.11628	0.10729	1.076	0.28173	

Species = LAGL

Contrast	Estimate	SE	z.ratio	p value
NW - W	-1.20200	0.46193	-2.602	0.0093

Species = MIMA

Contrast	Estimate	SE	z.ratio	p value
NW - W	-3.90893	1.12848	-3.464	< 0.001

3.3 Fruit bat and macaque fruit selection

Bat foraging intensity on *L. glauca* significantly increased with increased fruit availability (Table 5), and peaked in August and September, when the overall number of fruits was highest (Figure 11A). When macaque attacks on *L. glauca* were more frequent, the number of ejecta significantly decreased (Table 5). Similarly, in the non-weeded forest, bat foraging intensity on *L. glauca* also significantly increased (Table 5) with the number of fruits (Figure 11B). The number of ejecta decreased when macaque attacks were more frequent, but this was not statistically significant (Table 5).

Table 5. GLM models explaining *Labourdonnaisia glauca* (LAGL) fruit consumption by bats in comparison with macaques in the weeded (W) and non-weeded (NW) forest at Mt. Camizard.

	Estimate	Std. Error	z value	p value	Significance
(Intercept)	5.27274	0.17545	30.052	<0.001	***
LAGL macaque W	-0.35762	0.08502	-4.206	<0.001	***
LAGL all fruits W	0.06544	0.01179	5.550	<0.001	***
	Estimate	**Std. Error**	**z value**	**p value**	**Significance**
(Intercept)	3.19723	0.38822	8.236	<0.001	***
LAGL macaque NW	-0.10388	0.07943	-1.308	0.191	
LAGL all fruits NW	0.12207	0.02355	5.183	<0.001	***

In the weeded forest, bat foraging intensity on *M. maxima* significantly increased when there were more fruits (Table 6), with a peak in August and another in September (Figure 12A). As for *L. glauca*, the number of ejecta significantly decreased when macaque attacks on *M. maxima* were more frequent (Table 6). It was not possible to test relations for *M. maxima* in the non-weeded forest, because few ejecta and fruits were found (Figure 12B).

Table 6. GLM model explaining *Mimusops maxima* (MIMA) fruit consumption by bats in the weeded (W) forest at Mt. Camizard.

	Estimate	Std. Error	z value	p value	Significance
(Intercept)	16.190	16.158	1.002	0.3334	
MIMA macaque W	-9.492	1.961	-4.841	<0.001	***
MIMA all fruits	9.765	1.851	5.275	<0.001	***

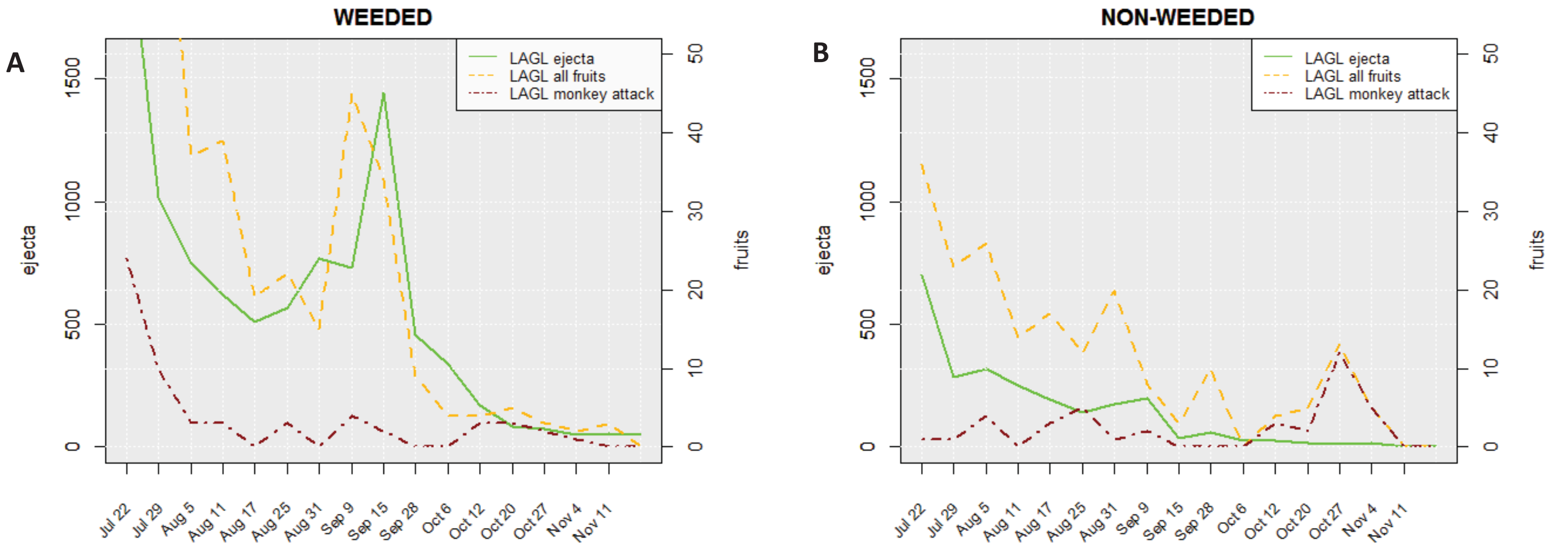

Figure 11. Total weekly ejecta, fruits and macaque-attacked fruits of *Labourdonnaisia glauca* in (A) weeded and (B) non-weeded forest over time at Mt. Camizard.

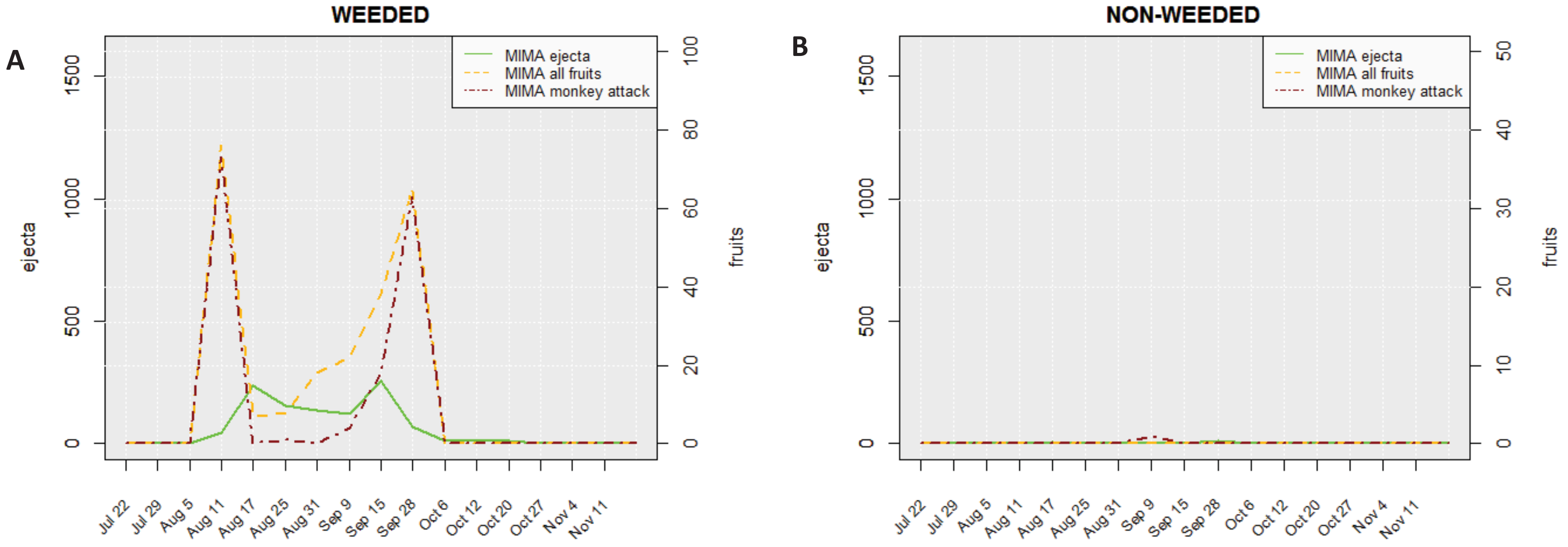

Figure 12. Total weekly ejecta, fruits and macaque-attacked fruits of *Mimusops maxima* in (A) weeded and (B) non-weeded forest over time at Mt. Camizard.

Pteropus niger attacked significantly more ripe fruits of *L. glauca*, while *M. fascicularis* attacked significantly more unripe fruits (Table 7, Figure 13A). The same pattern was also observed for *M. maxima* (Table 8, Figure 13B). Of the macaque-attacked *L. glauca* fruits, 54.64% were unripe, while 60.91% of the bat-attacked fruits were ripe. In the case of *M. maxima*, 72.5% of the macaque-attacked fruits were unripe and 89.86% of the bat-attacked fruits were ripe.

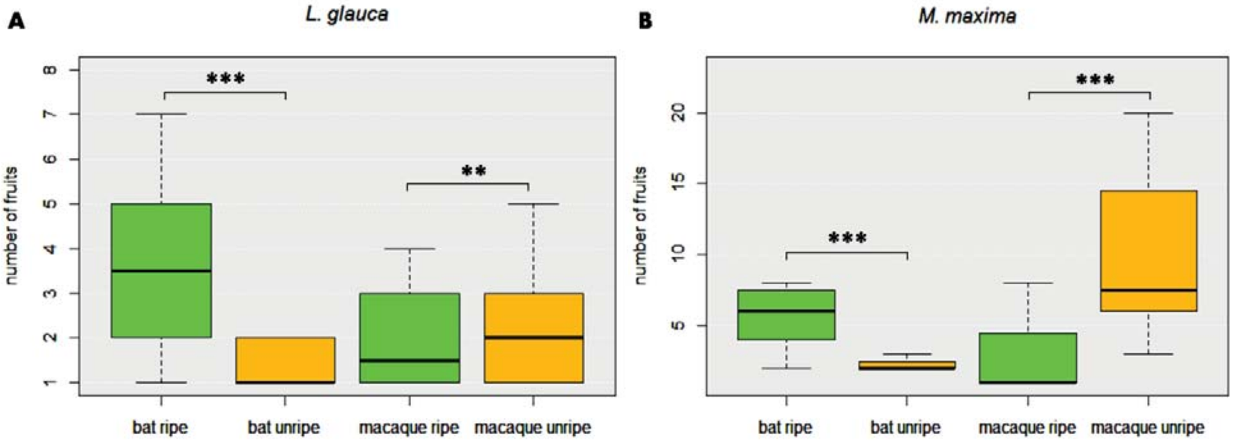

Figure 13. Number of ripe and unripe fruits of (A) *Labourdonnaisia glauca* and (B) *Mimusops maxima* attacked by *Pteropus niger* or *Macaca fascicularis* at Mt. Camizard. The level of statistical significance is indicated by ** p<0.01 and *** p<0.001.

Table 7. Pair-wise comparison of the least-squares means of ripe and unripe *Labourdonnaisia glauca* fruits attacked by *Pteropus niger* and *Macaca fascicularis* at Mt. Camizard.

Species = bat					Species = macaque				
Contrast	Estimate	SE	z.ratio	p value	Contrast	Estimate	SE	z.ratio	p value
ripe - unripe	2.3784	0.1507	15.782	< 0.001	unripe - ripe	0.4861	0.1525	3.187	0.0041

Table 8. Pair-wise comparison of the least-squares means of ripe and unripe *Mimusops maxima* fruits attacked by *Pteropus niger* and *Macaca fascicularis* at Mt. Camizard.

Species = bat					Species = macaque				
Contrast	Estimate	SE	z.ratio	p value	Contrast	Estimate	SE	z.ratio	p value
ripe - unripe	3.303	1.7291	1.91	< 0.001	unripe - ripe	6.9792	1.0138	6.884	< 0.001

Ripe *L. glauca* fruits were significantly larger than unripe fruits (Figure 14A, Table 9). Both bat- and macaque-attacked *L. glauca* fruits were significantly larger compared to intact fruits of *L. glauca* found on the ground (Figure 14B, Table 10). However, bat-attacked *L. glauca* fruits were significantly larger than macaque-attacked fruits (Figure 14B, Table 10).

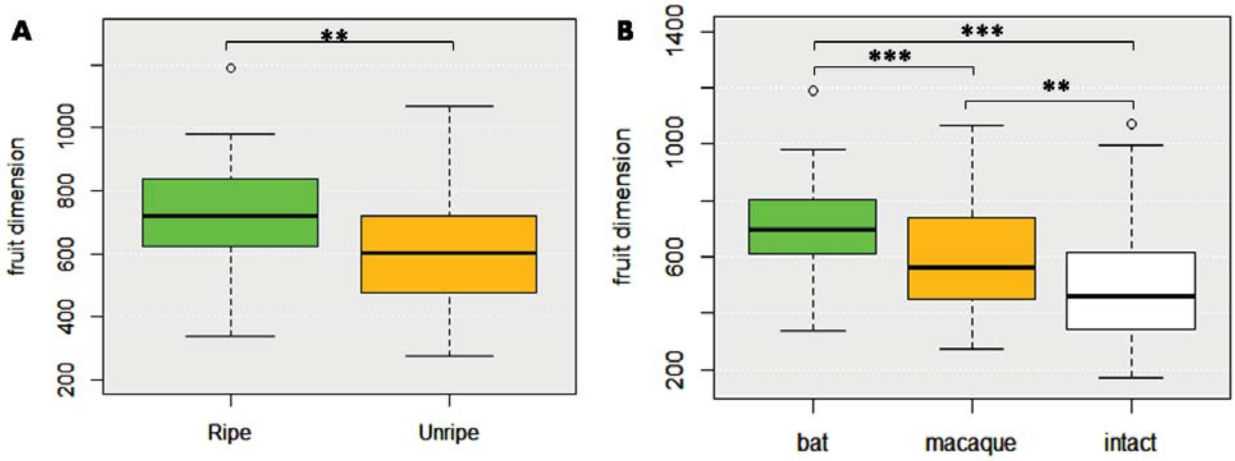

Figure 14. Fruit dimension of (A) ripe and unripe, (B) bat-attacked, macaque-attacked and intact *Labourdonnaisia glauca* fruits found at Mt. Camizard. The level of statistical significance is indicated by ** p<0.01 and *** p<0.001.

Table 9. GLM model explaining *Labourdonnaisia glauca* fruit size preference of *Pteropus niger* and *Macaca fascicularis* at Mt Camizard.

	Estimate	Std. Error	z value	p value	Significance
(Intercept)	-0.6519	0.1488	-4.381	<0.001	***
Ripe	0.5844	0.2179	2.682	0.0073	**
Attack bat	2.8439	0.4120	6.903	<0.001	***
Attack macaque	0.9363	0.2846	3.290	0.0010	**

Table 10. Pair-wise comparison of the size of intact, bat-attacked and macaque-attacked *Labourdonnaisia glauca* fruits found at Mt. Camizard.

Contrast	Estimate	SE	z.ratio	p value	Significance
intact - bat	-2.84389	0.41197	-6.903	<0.001	***
intact - macaque	-0.93631	0.28460	-3.290	0.0029	**
bat- macaque	1.90758	0.47703	3.999	<0.001	***

4. DISCUSSION

4.1 Fruit production and foraging habitat selection

In this study, the total number of *L. glauca* and *M. maxima* fruits was significantly higher in weeded compared to non-weeded areas. Since the studied forests are similar in all aspects except for the management of invasive alien plants, the recorded increased fruit yield of native species is likely because of enhanced plant fitness after weed removal. Indeed, invasive alien plants are known to have a negative impact on the resource acquisition capacity of native trees, ultimately reducing their flower and fruit production (Baider & Florens 2006; Baider & Florens 2011; Monty et al. 2013). As fruit abundance is likely to determine *P. niger* foraging habitat selection, weeded areas provide a better foraging habitat for fruit bats due to increased native fruit production.

Indeed, I collected significantly more ejecta and bat-attacked fruits in the weeded area compared to the adjacent non-weeded area, which strongly suggests that fruit bats prefer to feed in weeded habitats where fruit abundance is higher. These findings agree with a preliminary study that also showed that weeding had a positive effect on fruit bat habitat selection (Amavassee 2015). However, the differences between restored and non-managed areas elsewhere on Mauritius are likely to be even more pronounced than results shown here, because the studied forest sites at Mt. Camizard tend to have a lower alien stem density compared to other well preserved forest remnants elsewhere on the island (Florens et al. 2016). This further highlights the importance of invasive alien plant removal as a biodiversity conservation action. Indeed, secondary forest management in Mexico also increased fruit availability and had a positive effect on fruit bat abundance, suggesting that restored forests are important for frugivorous bats across different continents.

Tree characteristics can also affect the reproductive output of native trees, thereby influencing the resource availability to fruit bats. As expected, I found that native trees with a larger crown produced more fruits than trees with smaller ones. This may be due to their increased capacity to support fruits as they are less affected by competition with surrounding trees or because large trees that reached their maximum vegetative growth can allocate more resources to reproduction (Muller-Landau et al. 2006). Tree height had no effect on fruit production of native trees. However, I found that *P. niger* preferred to forage on tall trees with a large crown. Previous studies also found that tree height and crown size have a positive impact on fruit bat foraging intensity (Nowak 1994; Oleksy 2015; Utzurrum 1995; Vleut et al. 2013). Besides providing more fruits, bats may prefer large trees as they are more easily located and accessed. Although large native trees are less prone to the negative effects of invasive alien plants compared to smaller ones, they have an increased mortality rate in highly invaded areas due to competition (Baider & Florens 2006; Florens 2008). Thus, a lack of invasive alien plant control will with time cause a loss of larger native trees that provide important food resources for fruit bats (Florens et al. 2017), which would further limit native fruit availability.

Although fruit bats prefer to fly above the forest canopy, they were also observed foraging on trees with height below 2 meters in weeded areas (Figure 15). In addition, there are historical records of Mascarenes fruit bats foraging on the ground (Cheke & Hume 2008). These observations suggest that fruit bats are able to use resources of the forest understory in weeded areas. However, the higher density of invasive stems in the understory of the non-weeded forest could prevent fruit-bats from utilizing understorey resources in these forests due to their large wingspan (Norberg 1994). Similarly, birds (Namah 2010) and butterflies (Florens et al. 2010) tend to fly and use less frequently the non-weeded forests of Mauritius. However, weeding not only allows understorey plants to produce more fruits, but it likely makes these resources more accessible to bats due to increased flight efficiency in the lower vegetation density.

Figure 15. ***Pteropus niger*** **feeding on a 2-meter high** ***Mimusops maxima*** **tree in the weeded forest at Mt. Camizard (camera trap photo).**

4.2 Fruit selection by flying foxes

Fruit bats clearly consumed more *L. glauca* than *M. maxima* fruits. Yet, the fruits of both tree species are important food resources for these bats and show typical characteristics of bat-fruits, including dull-green coloration, sweet flavour, easily accessible position and large size (Nyhagen 2004). Therefore, *P. niger* fruit selection could have been driven by fruit availability rather than fruit characteristics, as *L. glauca* trees were more common in the landscape and were fruiting more and longer than *M. maxima*. The shortage of *M. maxima* fruits suggests that *L. glauca* fruits are more reliable food sources. However, other fruit traits may influence the preference of bats, such as nutrient content of fruits, but we lack information for these species.

Apart from the two focal species, the Mauritius black ebony (*Diospyros tessellaria*) also produces typical bat-fruits and this species has high relative density at Mt. Camizard (Florens et al. 2012). A recent study found that the mortality rate of *L. glauca* and *M. maxima* is at least three times higher compared to *D. tessellaria* in the non-weeded areas (Babajee 2017), suggesting that invasive alien plants are changing the forest community composition. The shift in abundance of these species would result in a more homogenous forest composition with a lower diversity of native fruits. As *D. tessellaria* is dioecious, only female individuals produce fruits. However, no fruits were found in 2016 suggesting that this species has an irregular fruiting cycle. Having common species with dioecy and an irregular fruiting cycle may further worsen the level of the native fruit shortage for flying foxes in gap years. However, during the study, ejecta consisting of male *D. tessellaria* flowers were found in October. This shows that fruit bats also use other food resources, which could help them to overcome periods of fruit scarcity.

Bat foraging intensity on *L. glauca* and *M. maxima* increased with the number of available fruits and peaked in August and September, when the fruit availability was highest. Although flying foxes tend to be specialists when a preferred fruit is abundant, they also show generalist behaviour when resources drop below a certain level (Banack 1998; Nakamoto et al. 2015). In other words, *Pteropus* species can show dietary plasticity to survive periods of food shortage (Nakamoto et al. 2015; Picot et al. 2007), and become more generalistic under unpredictable food conditions (Fleming 1986). In such situations, they require large areas of native forest that can provide sufficient, complementary types of native fruits (Nelson et al. 2000).

Fruit bats are usually attracted to conspicuous, spatially and temporally abundant food patches that are easily harvested (Fleming 1986; Marshall 1983; Marshall 1985). Apart from the spatio-temporal availability of resources, visual and olfactory cues are used in fruit selection to evaluate fruit size, ripeness and nutritional content (Sánchez 2006). I found that bat-attacked fruits of *L. glauca* and *M. maxima* were mostly ripe and large. These results agree with other studies showing that fruit bat fruit selection depends on the size (Utzurrum 1995) and that they prefer odorous and juicy ripe fruits (Banack 1998; Bollen & Elsacker 2002). Although unripe fruits may provide comparable levels of nutrients with ripe fruits of the same species, ripe fruits are more palatable with softer pulp and pericarp, and contain higher concentration of sugars and lower levels of secondary metabolites (Nyhagen et al. 2005). Their preference for ripe fruits is also explained by their foraging behaviour – they feed on juice squeezed from fruits and discard the fibrous fruit pulp. The selection of large fruits may be because they provide more energy, therefore, selecting a few large fruits over more, but small fruits would decrease the commuting and approach flight for a similar nutritional reward (Kalko et al. 1996).

However, as I did not perform focal observations of fruit choice in the field, the results should be interpreted with some caution. The attacked ripe fruits found in the ground quadrats could in fact have been discarded by the bats. Indeed, flying foxes are known to be extremely selective in choosing fruit within a tree, probably due to subtle changes in food quality (Banack 1998). They often smell and bite fruits before they actually choose one (Banack 1998), which may account for part of the ripe bat-attacked fruits found in the quadrats. Nevertheless, their known preference for ripe fruit suggests that the bat-attacked ripe fruits on the ground are more likely a result of quarrels or neighbouring bats moving on the trees. When many bats are feeding on the same tree, they may steal fruits from one another and while moving from branch to branch they may knock each other over and cause partially eaten fruits to fall.

Despite their preference for large ripe fruits, it has been observed that fruit bats may increase their consumption of smaller, unripe fruits during the tropical dry season or following cyclones, when fruit availability is low and there is a scarcity of ripe fruits (Grant et al. 1997; McConkey et al. 2004). However, fruit bats mainly feed on ripe fruits, therefore they are likely to disseminate seeds from fruits that they feed on through their feces and ejecta (Bollen & Elsacker, 2002; Corlett, 1998; Nyhagen et al., 2005), or by carrying the fruits to other trees to eat them away from other bats (McConkey & Drake 2006). Dispersal of seeds away from parent trees may reduce predation rate and increase seedling establishment (Connell 1971; Janzen 1970; McConkey & Drake 2006). In addition to providing mobility for seeds, fruit bats affect the density and dispersion patterns of their food species (Fleming & Heithaus 1981). Ingestion of small seeds may also enhance germination success by breaking seed coat layers or increasing its permeability to water and gases (Oleksy 2014; Traveset et al. 2008). Although fruit bats ingest few seeds of species they consume, they remove fruit pulp from larger seeds, which can be a potential source of infection by pathogens (Oleksy 2014). Therefore, apart from dispersal, fruit bats may increase seed survival and germination success by reducing microbial attack on seeds (Nyhagen et al. 2005; Oleksy 2014). Although the seeds of *L. glauca* are removed from the pulp, they often stay attached to the ejecta due to the high latex concentration in the fruit pulp (Figure 16A). However, ejecta are much drier than the fleshy fruit pulp, thus they are less suitable for microbial growth. Moreover, germinating *L. glauca* seeds attached to ejecta were found during the study and in other sites (Figure 16B; Babajee 2017), suggesting that being attached to the ejecta has no inhibitory effect on seed germination.

Figure 16. (A) Intact seed of *Labourdonnaisia glauca* attached to the sticky bat ejecta at Mt. Camizard. (B) A germinated seed of *Labourdonnaisia glauca* attached to dry ejecta at Brise Fer.

4.3 Competition between fruit bats and long-tailed macaques

Human-caused extinctions of large frugivorous vertebrates on Mauritius (e.g. other *Pteropus* species, giant tortoises and the dodo) have increased the relative importance of *P. niger* for seed dispersal on the island (Florens et al. in review). As *P. niger* is the only native vertebrate known to feed on *L. glauca*, their seed dispersal is today possibly dependent on fruit bats (Oleksy

2015). The majority of seeds dispersed by fruit bats are mature and undamaged (Figure 17A; Nyhagen et al. 2005). Beside *P. niger*, the introduced *M. fascicularis* is the only other vertebrate foraging on *L. glauca* fruits (Nyhagen 2004). However, contrary to fruit bats, I found that long-tailed macaques preferentially attack smaller unripe fruits of *L. glauca* and destroy most of the seeds in the fruits that they consume (Figure 17B). Macaques are therefore unlikely to provide important dispersal service for this tree species. On the contrary, macaques are likely to reduce the regeneration of *L. glauca.* Considering that macaques have been on the island for more than four centuries, it is plausible that such seed predation has also been causing a long-term shift towards lower densities of this important native canopy species and reducing foraging habitat quality of fruit bats through a different mechanism as shown by my results.

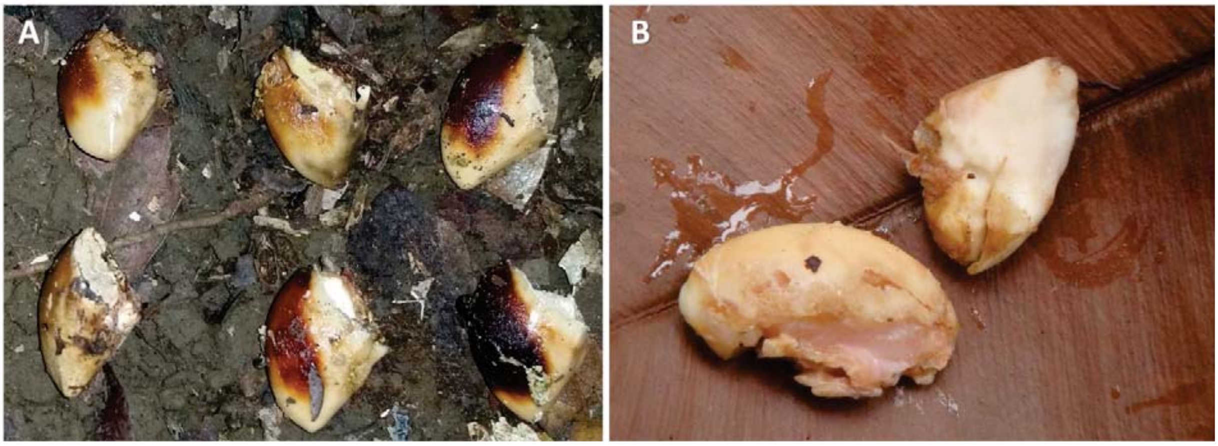

Figure 17. (A) Intact ripe seeds of *Labourdonnaisia glauca* dispersed by *Pteropus niger*.
(B) Unripe *Labourdonnaisia glauca* seeds destroyed by *Macaca fascicularis.*

As the number of fruits attacked by macaques increased, the number of ejecta and bat-attacked fruits of the same species decreased. As macaques depleted fruits before ripening, fruit bats consequently have a lower number of preferred ripe native fruits to feed on. This indicates a possible exploitative competition between flying foxes and long-tailed macaques for native food resources. As native fruit production is already limited by invasive alien plant species, the competition with macaques may force fruit bats to accept alternative resources to native fruits and search for food in orchards and plantations. An increased consumption of commercial fruits by bats could worsen the fruit growers' negative perception of fruit bats and result in illegal hunting.

Macaques consumed a similar amount of *L. glauca* fruits as fruit bats, but attacked twice as many *M. maxima* fruits than bats. These fruits were mainly unripe (Figure 18A, B), which has a negative impact on the reproductive success of the tree. This may further limit native tree dispersal, density and fruit availability to fruit bats and other endemic species, particularly during periods of food shortage (Nyhagen 2004). In fact, the extent of native fruit resource depletion is high as macaques may destroy nearly all the fruits on a given tree, before their seeds have become mature (Baider & Florens 2006). By destroying immature seeds, macaques might impede the fruit bats' ecological role as seed dispersers. Although macaques are able to disperse large mature seeds, a high proportion of seeds are spat out under parent trees, thereby decreasing potential seedling survival (Corlett & Lucas 1990).

Figure 18. (A) The introduced *Macaca fascicularis* feeding on *Mimusops maxima* fruits. (B) Unripe *Mimusops maxima* fruits attacked by *Macaca fascicularis*.

Strawberry guava (*P. cattleianum*) is one of the worst invasive alien plant species in Mauritius and usually reaches 2-8 metres in height. Fruit bats were only occasionally observed to feed on guava fruits on trees that were emergent and not surrounded by dense vegetation. Contrary to bats, macaques have a preference to forage on low trees that are easily accessible, therefore they are expected to consume much higher amount of guava fruits (Sussman & Tattersall 1986). Although macaques may be less efficient seed dispersers of large seeds than fruit bats, the small seeds of guava can be swallowed and therefore dispersed through feces. The seed dispersal of *P. cattleianum* and other invasive alien plants by macaques may thus also contribute to the further degradation of the remaining native forests.

5. CONCLUSION

Although the importance of invasive alien plant control has been recognised on Mauritius, weeded forests cover only 1% of the remaining native vegetation (Monty et al. 2013). Weeding clearly increases native fruit abundance and creates a better foraging habitat for the Mauritian fruit bat. Previously, high costs were considered the biggest obstacle to weed invaded forests, but newer methods provide a ten-fold cost reduction (Florens & Baider 2013). Therefore, weeding could now be extended to incorporate larger areas of the remaining forest. Nevertheless, when funds are limited, targeted weeding around tall native trees with large crown should be given priority. Selective weeding around large native trees in highly invaded areas may lead to a significant improvement in fruit production and could be of higher importance for restoration in more degraded patches since fruit bats favour such trees. Another necessary conservation measure appears to be effective population control of *M. fascicularis,* given their resource competition with fruit bats and negative impact on the native flora and fauna.

Previous studies have shown that *Pteropus* species consumed commercial fruits only during shortages of preferred native fruits or when native fruit crops failed (Nelson et al. 2000; Parry-Jones & Augee 1991). The cultivated fruit availability on Mauritius is seasonal and short (usually from November to February). In these periods, fruit bats are attracted to plantations as they provide easier and more reliable food sources than their highly invaded and degraded native habitats (Florens et al. 2016). Due to the high level and speed of degradation of the native forests, natural recovery may not be fast enough to solve the immediate human-wildlife conflict on Mauritius. However, increasing native fruit abundance by weeding out invasive alien plants is likely to limit the fruit bat damage caused to commercially important fruits in the long-term. Weeding would therefore present a potential way to mitigate the conflict between local fruit growers and bats that currently puts the fruit bats' existence on Mauritius at risk.

The conservation of fruit bats on Mauritius should be considered as an essential element of sustainable development by both protecting biodiversity and maintaining ecosystem functions on the island. Weeding would carry co-benefits for both native flora and fauna, suggesting that the implementation of an ecosystem approach, instead of a species-centred approach, in the conservation and management of native biota is preferable. Restoration of the remaining forest fragments on the island would lead to a conservation success at ecosystem level by preserving the endangered fruit bats and many other threatened native species dependent on native forests.

Since weeding of native habitats is a long-term process, additional methods such as exclusion nets, pruning, dwarf varieties, deterrents and decoy crops, could be implemented simultaneously to further minimize fruit orchard use by bats. Environmental education campaigns are also important to counter the misconceptions regarding bats at all levels of the society and to raise awareness about the ecological and economic importance of flying foxes. Education material that incorporate local knowledge and values with tangible examples, instead of generalized concepts, may be more effective in changing negative attitudes towards bats (Scanlon et al. 2014). The increasing conflict between people and fruit bats on Mauritius could be reduced by providing the general public, media and decision makers with correct and scientifically supported information about flying foxes. The failure to launch these constructive initiatives and changes may result in the extinction of the last remaining fruit bat species of Mauritius and lead to an accelerated degradation of the unique biodiversity on the island.

6. SUPPLEMENTARY MATERIAL

Table S1. GLMM models, included in the average best-model, explaining the habitat selection of *Pteropus niger* and fruit production at Mt. Camizard.

Test	Response variable	Fixed explanatory variables	Random effect	df	AICc	Delta	Weight
1.1. Habitat selection, ejecta	Ejecta ~	Treatment * Species + Crown + Height	(1|treeID)	8	1565.03	0	0.38
1.2. Habitat selection, ejecta	Ejecta ~	Treatment * Species + Crown + DBH + Height	(1|treeID)	9	1565.4	0.37	0.32
1.3. Habitat selection, ejecta	Ejecta ~	Treatment * Species + Crown + Harmonic + Height	(1|treeID)	9	1566.88	1.85	0.15
1.4. Habitat selection, ejecta	Ejecta ~	Treatment * Species + Crown + DBH + Harmonic + Height	(1|treeID)	10	1566.97	1.94	0.15
2.1. Habitat selection, bat-attacked fruits	Batattack ~	Treatment * Species + Crown	(1|treeID)	7	386.92	0	0.52
2.2. Habitat selection, bat-attacked fruits	Batattack ~	Treatment * Species + Height	(1|treeID)	7	388.26	1.34	0.27
2.3. Habitat selection, bat-attacked fruits	Batattack ~	Treatment * Species + Height + Crown	(1|treeID)	8	388.74	1.82	0.21
3.1. Fruit production	Allfruit ~	Treatment * Species + Crown	(1|treeID)	7	752.19	0	0.72
3.2. Fruit production	Allfruit ~	Treatment * Species + Height + Crown	(1|treeID)	8	754.07	1.87	0.28

Table S2. Best fitting GLM models explaining *Labourdonnaisia glauca* (LAGL) and *Mimusops maxima* (MIMA) fruit availability and consumption by *Pteropus niger* and *Macaca fascicularis* in the weeded (W) and non-weeded (NW) forest.

Test	Response variable	Fixed explanatory variables	df	AIC	Delta	Weight
1.1. Fruit availability and consumption, LAGL	EjectaW ~	MonkeyW + AllfruitW	4	239.2	0	0.987
1.2. Fruit availability and consumption, LAGL	EjectaNW~	MonkeyNW + AllfruitNW	4	73.4	0	0.407
1.3. Fruit availability and consumption, MIMA	EjectaW ~	MonkeyW + AllfruitW	4	191.4	0	0.996

Table S3. Best fitting GLM models explaining fruit type and size preference of *Pteropus niger* and *Macaca fascicularis* at Mt. Camizard.

Test	Response variable	Fixed explanatory variables	df	AIC	Delta	Weight
2.1.1. Fruit type preference, LAGL	Number of fruits ~	Attack : Ripeness	4	289	0	1
2.1.2. Fruit type preference, MIMA	Number of fruits ~	Attack : Ripeness	4	232.6	0	1
2.2. Fruit size preference	Fruit dimension ~	Attack + Ripeness	4	556	0	0.931

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