

The feeding competition between the invasive crab-eating macaque *Macaca fascicularis* and the Mauritian flying fox *Pteropus niger*

Mr Raphael Reinegger (University of Bristol, UK)

1. Introduction

Mauritius has a long history of direct and indirect defaunation, either through the active hunting and harvesting of native animals, or the introduction of invasive species and logging of native forests (Cheke and Hume, 2008). Mauritius has lost over 98% of its endemic and native forests and 81.7% of the remaining indigenous plant species are threatened according to the IUCN Red List criteria (Baider et al., 2010). The forests have become largely devoid of large native seed dispersers and only three large potential seed dispersers remain: the Mauritian flying fox *Pteropus niger*, the echo parakeet *Psittacula eques* and the pink pigeon *Nesoenas mayeri* (Cheke and Hume, 2008). Of these three frugivorous species the Mauritian flying fox *P. niger* is the biggest and also the last endemic large frugivore that exists in high numbers (Cheke and Dahl, 1981; Cheke and Hume, 2008). Large-seeded endemic plants are likely to be dependent on the flying fox for their dispersal and survival (Cheke and Hume, 2008; Hansen and Galetti, 2009) and many of the remaining endemic and native plants show signs of adaptation to dispersal by *P. niger*. The Mauritian flying fox is known to disperse the fruits of a wide variety of native and endemic species (Nyhagen et al., 2005; Florens et al., 2017), some of which provide important services and resources to other plants and animals (Motala et al., 2007). The Mauritian flying fox is capable of long distance flight and seed dispersal, which can reduce distance- or density-dependent mortality of seeds and seedlings (Howe and Smallwood, 1982; Hardesty et al., 2006). Furthermore, there are indicators that fruit treatment by *P. niger* can promote seed germination (Oleksy 2016 unpublished; Krivek, 2017). Therefore, *P. niger* plays an important role in forest ecosystems (Nyhagen, 2004; Nyhagen et al., 2005; Florens et al., 2017; Vincenot et al., 2017).

However, Mauritius has lost its entire primary forest cover and with the little of the forests left, *P. niger* still face many threats and conservation challenge. The Mauritian flying fox is widely regarded as a pest, and claimed to do considerable damage to commercial fruit crops, particularly litchi and mango (Oleksy, 2015). This has fuelled a conflict between Mauritian fruit growers and *P. niger*, which has supplied the Mauritian government with an incentive to weaken biodiversity protection laws and legalize mass-culling campaigns of *P. niger* (Florens, 2016). The extinction or ecological extinction of large vertebrate dispersers will affect the populations of plant species and can even lead to the extinction of plant species (Redford, 1992). A forest in which the majority of animal species are ecologically extinct will not be able to last and is often referred to as an 'empty forest' (Redford, 1992). Flying foxes can become ecologically extinct long before becoming rare (McConkey and Drake, 2006), meaning that future mass-culling could have large consequences for native forest.

Furthermore, invasive mammals pose a serious threat to Mauritian forest (Florens, 2015) and may negate the flying fox's positive effects on forest regeneration to a certain extent. The invasive crab-eating macaque (*Macaca fascicularis*) was introduced in Mauritius about 400 years ago (Cheke and Hume, 2008) and is likely to have greatly altered the forest ecosystems. The macaques were shown to destroy unripe fruits (Florens, 2015; Krivek, 2017), and are capable of almost completely depleting the fruits on a tree, before the seeds have become mature (Baider and Florens, 2006). Therefore, the macaque's feeding behaviour could have a significant negative impact on the regeneration of Mauritian forest. Furthermore, the macaque compete for the remaining forest food resources with the flying fox, limiting the native food availability to the flying foxes even more (Sussman et al., 2011; Florens, 2015) thus preventing the flying foxes from effective seed dispersal. This competition may force bats to feed in commercial plantations, causing human-bat conflict (Oleksy, 2015; Vincenot et al., 2017).

Additionally, wild boar (*Sus scrofa*) and deer (*Rusa timorensis*) were introduced around the same time as the *M. fascicularis* and are likely to have affected the survival and establishments of the native

plants. The wild boar *S. scrofa* are known to have a negative impact on seedling recruitment throughout their introduced range (Ickes, 2001; Barrios-Garcia and Ballari, 2012; Florens, 2015). They damage seed bank and decrease seedling survival either by rooting (Ickes, 2001; Mitchell et al., 2007) or direct consumption of seeds (Ickes et al., 2001; Barrios-Garcia and Ballari, 2012). In Montserrat wild boar reduce abundance of native plant species and enhance establishment conditions for the invasive java plum (*Syzygium cumini*) and guava (*Psidium guajava*) (Peh et al., 2015).

Finally, introduced exotic plant species pose another threat to the survival of native plants, because they outcompete the native plant species, invade the forest and reduce or inhibit the growth of native tree species (Lorence and Sussman, 1986; Virah-Sawmy et al., 2009). Species like *Psidium cattleianum*, *Litsea monopetala*, *Ligustrum robustum*, *Ardisia crenata*, *Clidemia hirta* and *Schinus terebinthifolius* can outcompete native plant species for light, space and nutrients, suffocating and outgrowing the native flora (Cheke et al. 1984; Virah-Sawmy et al., 2009; Baider and Florens, 2011). Research by Lorence and Sussman (1986) indicated a big difference in regeneration rates between exotic and native species in some areas in Mauritius, which was leading to a destabilization of forest composition. This destabilization is illustrated in a paper by Virah-Sawmy et al. (2009), showing a dramatic increase in the abundance of exotic plants and decrease of native plant species over the course of 60 years in Mauritius. Many native species have difficulty regenerating in the degraded forest, contrary to invasive species that tend to thrive (Lorence and Sussman, 1986; Virah-Sawmy et al., 2009). Research from the last decade in Mauritius suggests that invasive plant species may be driving the ongoing decline of native plant species (Baider and Florens, 2011; Monty et al., 2013), supported by the fact that removal of invasive plants can result in dramatic recovery of native plants (Baider and Florens, 2011). Additionally, invasive mammals, such as the invasive macaque and wild boar, may promote the exotic invasion in Mauritian forest by dispersing the seeds of invasive plants (Lorence and Tattersall, 1986).

1.2 Aims

Firstly, this study aims to assess the competition for forest resources between the invasive crab-eating Macaque *M. fascicularis* and the Mauritian flying fox *P. niger*. Native forest resources are already scarce in Mauritius and further resource depletion by macaques may force flying foxes to forage on commercial fruits and prevent them from effective performance of their ecological role in the forest. Secondly, the study aims to provide insights into the impact of *M. fascicularis*, *S. scrofa* and *R. timorensis* on the regeneration of the native plant species and the contribution to forest degradation. Thirdly, the project aims to assess the woody plant diversity, quality and the level of degradation of various forest remnants. Many of these remnants have remained largely unassessed and they might hold great conservation potential. These sites could provide quality habitat for bats and function as buffer zones and biological corridors to enhance landscape connectivity (Chazdon, 2008).

Hypothesis	Data collection methods	Type of collected data
The crab eating macaques (<i>M. fascicularis</i>) reduces the fruit availability to bats	Seed traps placed at equal distances in four cardinal direction from the fruiting tree	The percentage of fruits eaten by macaques and fruit bats
Macaques (<i>M. fascicularis</i>) damage the seeds of the trees they feed on.	Seed trapping	Quantitative data about number of destroyed and intact seeds, damaged and intact ripe or unripe fruit, faeces, bat ejecta and seeds.
Deer <i>R. timorensis</i> and boar <i>S. scrofa</i> reduce seedlings recruitment in forests.	Plot exclusion experiment	The proportion of seedlings established in the exclusion plots and in the control plots

<p>Predation by Macaque <i>M. fascicularis</i> decreases the reproductive success of targeted species and the number of seedlings in close proximity to the parental tree.</p>	<p>Line transects in four cardinal directions from the fruiting tree.</p>	<p>Frequency and number of seedlings of targeted native plant species in understory in close proximity to the parental trees.</p>
--	---	---

2. Description of study areas

Lower Gorges

The site is located in the area around 'Pilgrim trail' in the Black River Gorges National Park (Fig. 1; lat: -20.388660°, long: 57.432560°). It has an altitude between 150 and 300 masl and receives less than 1500 mm of rainfall/year. It classifies as a dry to semi-dry forest (Sevathian and Atkinson, 2007) and the forest is mostly composed of exotic species (Page and d'Argent, 1997). However, many native species are still present, such as *Cassine orientalis*, *Cossinia pinnata*, *Diospyros melanida*, *Diospyros tessellaria*, *Eugenia tiniflora*, *Foetidia mauritiana*, *Margaritaria anomala*, *Ochna mauritiana* and *Stadmania oppositifolia*. This area is frequently raided by macaques (*M. fascicularis*), and frequently visited by boar (*S. scrofa*) and deer (*R. timorensis*). It also borders one of the largest Mauritian flying fox (*P. niger*) roosts in the Lower Gorges.

Chassée Senneville

Chassée Senneville is a private estate bordering the Black River Gorges National Park (Fig. 1; lat: -20.383055°, long: 57.415780°). The site is located at an altitude between 150 and 300 masl. Just like in the Lower Gorges in the National Park the vegetation type here ranges from dry forest to semi-dry forest (Sevathian and Atkinson, 2007) with less than 1500 mm/year of rainfall. The forest seems to be better preserved than in other parts of the Lower Gorges and contains a large number of native species, such as *C. orientalis*, *C. pinnata*, *E. tiniflora*, *D. melanida*, *F. Mauritiana*, *M. anomala* and *Stilingea lineata*. Both *S. scrofa* and *R. timorensis* are known to frequently visit the area.

Brise Fer CMA

The study area is located in the closed management area (CMA) in Brise Fer in the Black River Gorges National Park (Fig. 1; lat: -20.395461°, long: 57.436237°). It is a patch of well preserved forest located at an altitude of 600 masl. The rainfall is up to 4500 mm/year and the forest is classified as an upland wet forest (Sevathian and Atkinson, 2007). In this area invasive species were successfully removed and exotic plants are frequently weeded to prevent them from dominating the understory. The majority of forest canopy is formed of native and endemic species, such as *Canarium paniculatum*, *D. tessellaria*, *Mimusops maxima*, *Labourdonnaisia callophyloides*, *Labourdoinnaisia glauca*, *Protium obtusifolium*, *Securinega durissima* and *Sideroxylon cinereum*. The area has been initially well fenced, however due to the fence corrosion *M. fascicularis*, *S. scrofa* and *R. timorensis* access this forest patch frequently.

Brise Fer semi-weeded

This area is located next to the Mare Longue CMA not far from the Brise Fer CMA (Fig. 1; lat: -20.394667°, long: 57.437469°). The forest here is less intact than in the Brise Fer CMA, because weed removal here started many years after the weeding in the CMA. The canopy is not as dense as in the CMA, but the native species composition appears to be similar to the CMA.

Bon Amour

Bon Amour is a small mountain bordering Long Mountain in the North of the island (Fig. 1; lat: -20.144482°, long: 57.582571°), and is covered by a degrading forest that is still relatively rich in native species. It is located at an altitude between 180 and 240 masl and the rainfall is less than 1500 mm/year, classifying it as dry to semi-dry forest just like the Lower Gorges. The native species occurring in this area are typical of Mauritian dry forest and include: *C. pinnata*, *D. melanida*, *E. lucida*, *E. tiniflora*, *F. Mauritiana*, *M. maxima* and *S. oppositifolia*. The slopes are gentle and the area is easy to access.

Mariannes

Mariannes is a mountain opposite of Mont Deux Mamelles and Pieter Both in the North of the Island (Fig. 1; lat: -20.181203°, long: 57.584498°). The site on Mariannes is located in a patch of degraded forest at an altitude between 500 and 600 masl. The rainfall in this area is between 2500 and 4500 mm/year and the forest classifies as sub-humid to upland wet forest, which is similar to Brise Fer. The forest is highly degraded by Chinese guava (*Psidium cattleianum*), Madagascar plum (*Flacourtia indica*) and privet (*Ligustrum robustum*), but contains a large number of native species typical of a Mauritian wet forest, including *L. revoluta*, *S. puberulum*, *S. glomeratum* and at least one species of *Tambourissa*. The area can be accessed via a path that starts on the gentle slope starting at Nouvelle Découverte village.

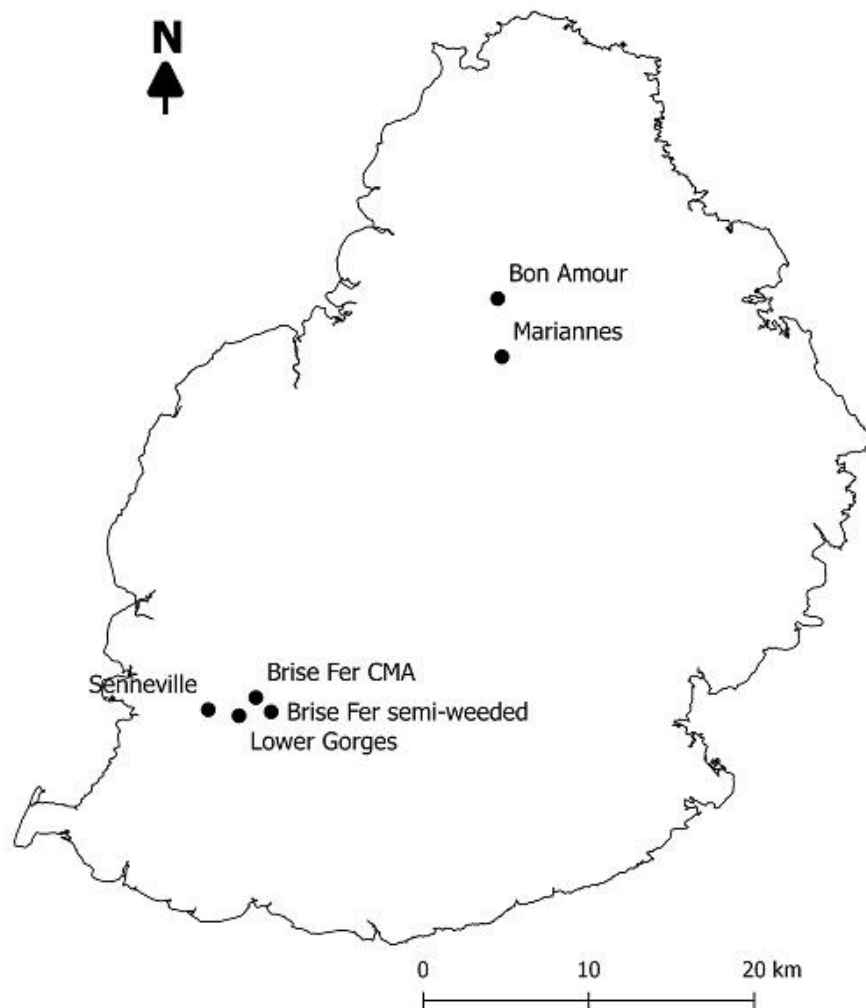


Figure 1: Study site locations across Mauritius

3. Methods and Analysis

3.1 Macaque impact on food availability and regeneration

To assess the impact of macaque on food availability to flying fox and regeneration of the native species, 19 canopy species primarily dispersed by the flying fox are studied (Tab. 1).

Table 1: Tree species in each site and number of replicates used.

Site	Tree species	Replicates	Seed traps placed	Start of flowering
Bon Amour				
	<i>Cassine orientalis</i>	3	yes	July
	<i>Cossinia pinnata</i>	3	yes	February
	<i>Diospyros leucomelas</i>	3	yes	February
	<i>Diospyros tessellaria</i>	6	yes	September
	<i>Eugenia sp. 3</i>	3	No	-
	<i>Eugenia tiniflora</i>	3	no	-
	<i>Foetidia mauritiana</i>	3	yes	March
	<i>Mimusops petiolaris</i>	4	yes	February
	<i>Protium obtusifolium</i>	3	yes	March
	<i>Stadmania oppositifolia</i>	3	yes	April
	<i>Terminalia bentzoë</i>	3	yes	February
Brise Fer semi-weeded				
	<i>Diospyros tessellaria</i>	6	yes	September
	<i>Labourdonnasia glauca</i>	3	yes	June
	<i>Labourdonnasia revoluta</i>	4	yes	April
	<i>Sideroxylon cinereum</i>	3	no	-
	<i>Syzygium glomeratum</i>	4	yes	April
Brise Fer CMA				
	<i>Canarium paniculatum</i>	5	no	-
	<i>Cassine orientalis</i>	5	yes	July
	<i>Diospyros tessellaria</i>	6	yes	September
	<i>Labourdonnasia glauca</i>	5	yes	June
	<i>Mimusops maxima</i>	5	yes	July
	<i>Protium obtusifolium</i>	5	no	-
	<i>Sideroxylon grandiflorum</i>	5	yes	-
	<i>Syzygium glomeratum</i>	5	yes	June
Lower Gorges				
	<i>Cassine orientalis</i>	3	yes	June
	<i>Cossinia pinnata</i>	3	yes	February
	<i>Diospyros leucomelas</i>	3	yes	February
	<i>Diospyros tessellaria</i>	6	no	-
	<i>Eugenia sp. 1</i>	3	no	-
	<i>Eugenia tiniflora</i>	3	no	-
	<i>Foetidia mauritiana</i>	3	yes	March
	<i>Mimusops petiolaris</i>	3	no	-
	<i>Protium obtusifolium</i>	3	yes	June
	<i>Stadmania oppositifolia</i>	3	yes	April
Mariannes				
	<i>Eugenia sp. 4</i>	3	No	-
	<i>Labourdonnasia revoluta</i>	3	Yes	April
	<i>Sideroxylon cinereum</i>	3	No	-
	<i>Syzygium glomeratum</i>	3	Yes	June
	<i>Syzygium duponti</i>	3	yes	August

The seed traps used for sampling fallen fruits and flowers were constructed by stapling water-permeable mesh onto wooden frames, which were raised 30cm above the ground to minimize seed removal by animals. Seed traps were placed under three to six individuals of the 19 focal species in each study site as described in Table 1. The traps were checked on a weekly basis from the start of the flowering until the end of the fruiting period of each tree. All fruits and flowers (intact and eaten),

seeds (intact and eaten), bat ejecta pellets (compressed fibrous material that remains after the flying fox squeezes the juice from the flesh Fig. 2 and 3) and faeces of various animals were recorded. Fruits eaten by *P. niger* were identified by their typical triangular-shaped canine imprint (Banack, 1998), contrary to the larger rounded canine imprints and large incisor marks of *M. fascicularis* (Fig. 2; Krivek, 2017).

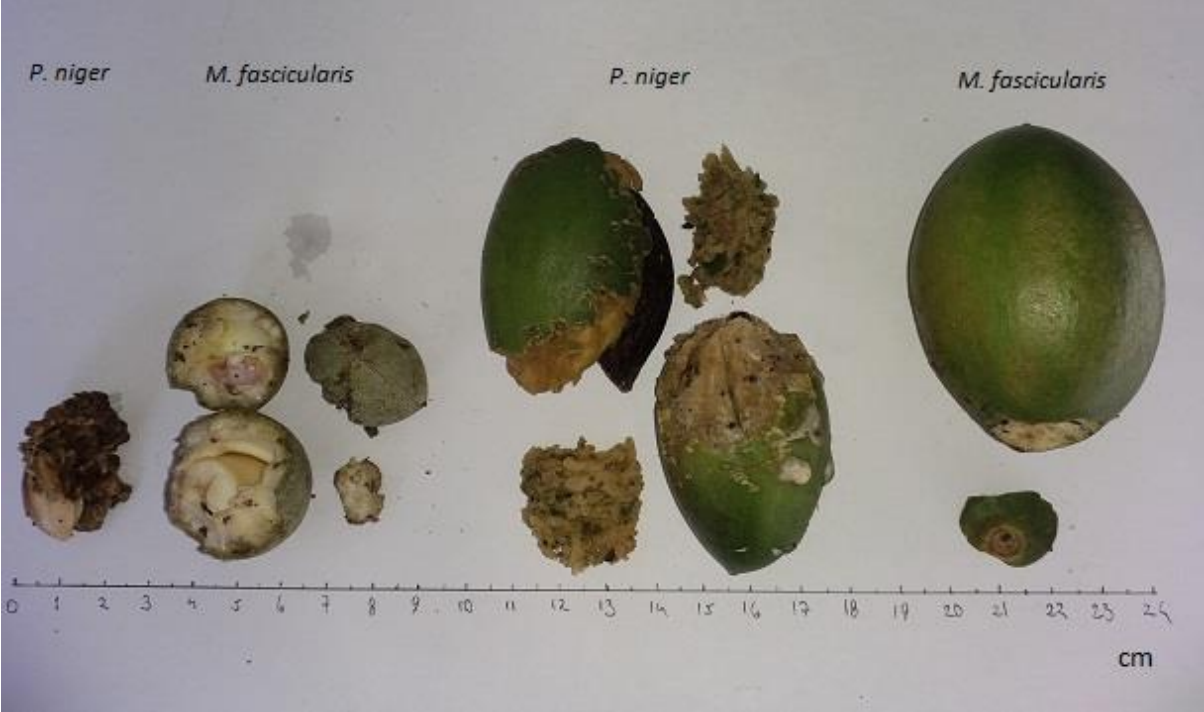


Figure 2: Fruits of *Labourdonnaisia glauca* (left) and *Mimusops maxima* (right) eaten by *P. niger* (with ejecta pellet) and *M. fascicularis*.

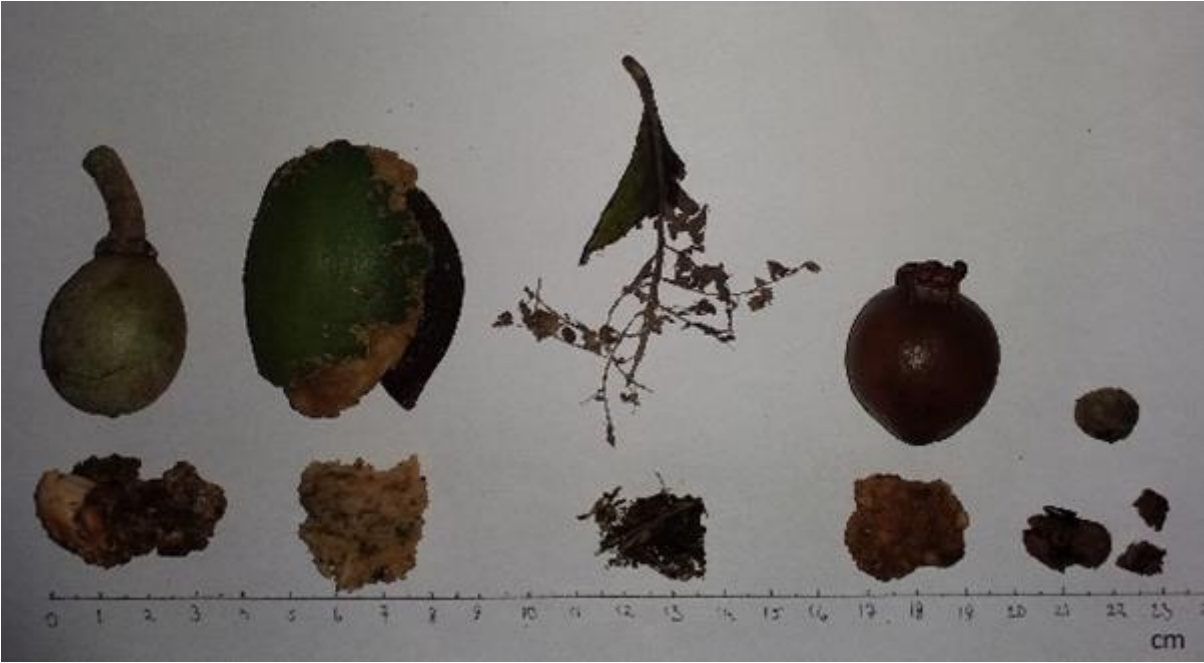




Figure 3: Intact fruits and leaves (top) and ejecta pellets of the same fruits and leaves left by *P. niger* after consumption (bottom). From left to right: *Labourdonnaisia glauca* fruit, *Mimusops maxima* fruit, *Hugonia serrata* leaf, *Psidium cattleianum* fruit and *Syzygium glomeratum* fruit. The flying fox usually consumes the entire fruit of *L. glauca* and *Psidium cattleianum*, leaving behind only an ejecta pellet that contains the seeds.

Each fruit sampled in the seed traps was examined for seed maturity by opening the fruit and extracting the seed (mature seeds were hard and looked fully developed while immature seeds were soft and empty inside). Ripe fruits were characterized by soft flesh and sweet smell, while unripe or premature fruits were typically tough and had soft seeds that could easily be squished between thumb and index finger. To confirm the identity of the animals which were visiting the studied trees, camera traps were attached to the trunk of the trees and aimed at the canopy or feeding branches. Each camera was left on the tree for one month and checked on a weekly basis. Finally, seedlings recruitment of each of the studied trees was assessed within 2m x 15m transect starting from the trunk of the parental tree in each of the four cardinal directions. This part of the study is carried out in all study sites. Either a multi-factor ANOVA or a non-parametric equivalent will be used to test for differences in numbers and ripeness of fruits between macaque eaten fruits and flying fox eaten fruits across species and sites, depending on the distribution. The effects of consumption type (flying fox vs. macaque) and ripeness of consumed fruits (ripe vs. unripe) will be tested on number of consumed fruits and number of seedlings.

3.2 Diet of *P. niger* and *M. fascicularis*.

To indicate other feeding sources for *P. niger* and *M. fascicularis*, a 500m transect was established in every site (Fig. 4). Because most of the study areas are located on steep slopes, the transects followed the paths that were previously established with GPS and were known to be safe. The following parameters were recorded: food plant species, type of plant part that was consumed (leaves, flowers, unripe and ripe fruit), type of animal that had consumed the plant part (flying fox, macaque, rat or bird) and the number of consumed plant parts. Consumption of fruits by rats (*R. rattus*) could be recognized by the scrape marks left behind on the fruit by the two upper and two lower rat incisors. Fruits eaten by parrots (either *Psittacula eques* or *Psittacula krameri*) could be distinguished from fruits eaten by other animals by the rounded beak marks on two sides of the fruit, similar to the round incisor mark left by macaques but much smaller. This provides an indication of plant species that were fed on

by flying foxes, macaques or other animals in a particular month. A similar methodology has been used to create a better understanding of the feeding ecology of the Seychelles black parrot *Coracopsis barklyi* (Reulleaux et al., 2014).

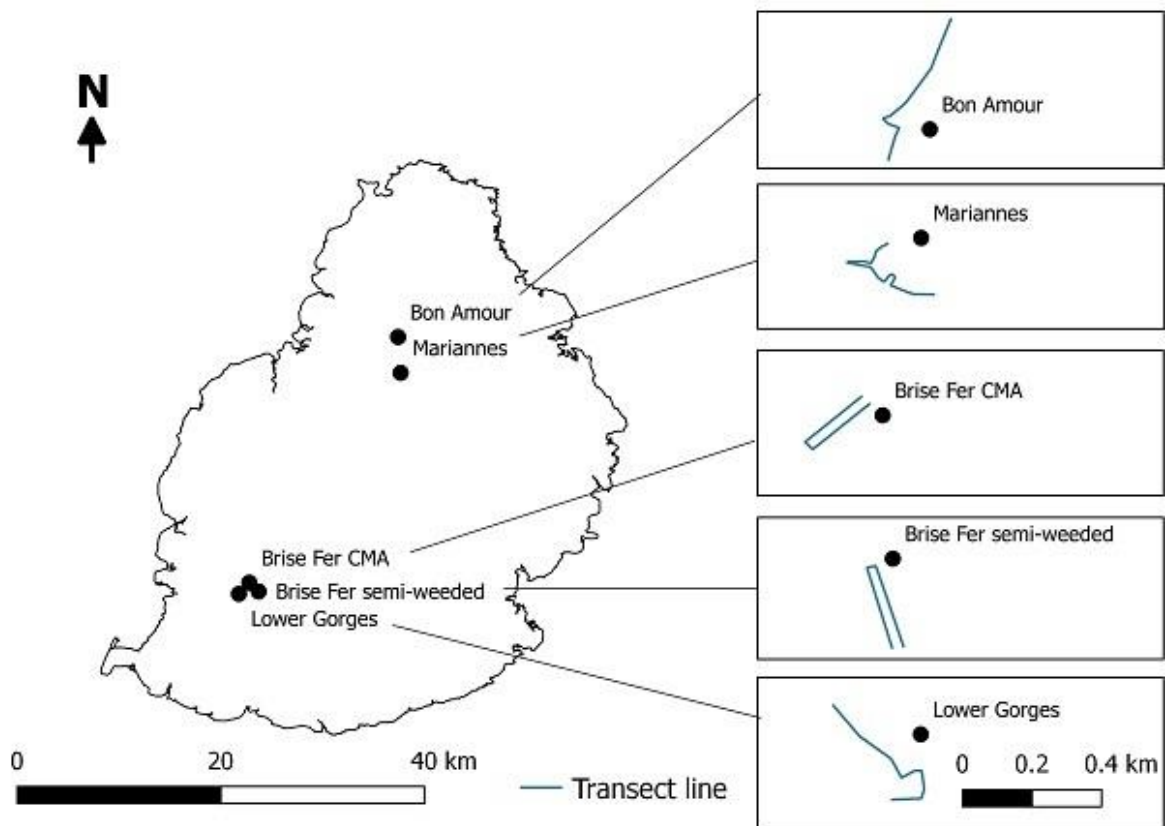


Figure 4: The 500m - transects established in the five study sites. The blue line indicates the path of the transect that was walked monthly.

3.3 Seed germination experiment

To provide insights into the seed dispersal by *M. fascicularis*, faeces from *M. fascicularis* were collected monthly from March until December in three sites: Lower Gorges, Bon Amour and Brise Fer. An equal amount of faecal samples ($n = 20$) was collected in every site and the faeces were potted in plastic soil trays that were made up of 4cm by 4cm cells containing a soil medium consisting of 75% top soil and 25% coconut peat. All the tray cells were watered daily and the trays were kept in semi-shaded conditions to prevent overheating and evaporation. The trays were monitored throughout the year to see what seeds germinated from the faeces. Dispersal of exotic species by *M. fascicularis* was assessed by comparing the number of exotic species that germinate from faeces in each of the studied site. Furthermore, all seeds of exotic *Psidium cattleianum* and *Schinus terebinthifolius* found in the faecal samples were counted. Germination success for these plant species was assessed by comparing the number of germinating seeds and the total number of seeds found in faecal samples in every site. This will serve as an indication for dispersal ability of exotic plant species by *M. fascicularis*.

3.4 Boar and deer impact assessment

To assess the impact of boar and deer on native seedling establishment and survival, exclusion plots were used. Exclusion plots are often used to study effects of browsers on the understory (Young et al., 1997; Ickes et al., 2001). A total of three randomly allocated 3m by 3m areas were fenced off with galvanised 15cm by 15cm mesh with a diameter of 3.8mm and fence height of 2m in each site. One 3m by 3m unfenced control plot was placed next to each fenced plot by placing four poles in the ground to indicate each corner of the plot and marking them with coloured tape. All seedlings up to 30cm were recorded in each plot after allocation. Subsequently, every plot was assessed every three months to compare establishment success and survival of seedlings between fenced plots and control plots. This element of the study is limited to Brise Fer CMA, Brise Fer semi-weeded, Chassée Senneville and

the Lower Gorges, since these are the only areas where boars and deer are present. The effect of the treatment (control vs. fenced) will be assessed by the mortality of seedlings, recruitment of new seedlings and number of seedlings with an appropriate parametric or non-parametric test depending on the distribution of the data.

3.5 Forest diversity assessment

To assess the woody plant diversity in the study areas, modified Whittaker plots are used (Stohlgren et al., 1995; Campbell et al., 2002). The modified Whittaker plot is a nested-vegetation plot composed of one 1000m² plot containing subplots of 100m², 10m² and 1m². In the 1m² subplots only seedlings, herbaceous plants and all other plants 1<cm stem diameter at breast-height (DBH) are recorded. In the larger subplots of 10m² and 100m², the DBH of trees is measured and only trees with a DBH of > 1cm and >5cm are recorded respectively. In the 1000m² plot area trees with DBH > 10cm are recorded and the DBH is measured. The 1m² subplots provide a measure of seedling richness and abundance and will be extrapolated to the 1000m² plot. This is helpful in determining how well native species regenerate in various sites and how species present in the overstory are represented in the understory. Voucher specimen of plants that cannot be identified in the field are collected, pressed and subsequently identified at the national herbarium of Mauritius. The number of modified Whittaker plots employed in each site is determined by looking at the pairwise Jaccard's Coefficients between the single modified Whittaker plots in a site (Stohlgren et al., 1997). The within-site diversity variation (β - diversity) will be obtained by comparing the various plots in a particular site. The diversity variation between sites (α - diversity) can be obtained by fitting rarefaction and accumulation curves for the total modified Whittaker plots in every site (Stohlgren et al., 1997; Gotelli and Colwell, 2001). Finally, this method will show how the various sites contribute to total landscape plant diversity (γ - diversity). Species-area curves and rarefaction curves are created to compare plant diversity between sites and provide a measure for the total species richness in the study sites.

4. Results

4.1 Macaque competition

Both *P. niger* and *M. fascicularis* fed on most species selected for this study (Fig. 5). Only a few species have remained untouched in some sites since the start of fruiting: *Cossinia pinnata* and *Protium obtusifolium* in both the Lower Gorges and Bon Amour. There were big differences in feeding intensity of both *P. niger* and *M. fascicularis* between species and sites (Fig. 5). Consumption of fruits by macaques was observed for *L. revoluta*, *Mimusops maxima* and *L. glauca* in Brise Fer, *L. revoluta* in Mariannes, *Foetidia mauritiana* and *D. leucomelas* in the Lower Gorges and *F. mauritiana*, *D. leucomelas* and *M. petiolaris* in Bon Amour (Fig. 5). Consumption of fruits by flying foxes was recorded for *F. mauritiana* in the Lower Gorges and Bon Amour, *Stadmania oppositifolia* and *Terminalia bentzoë* in Bon Amour, *M. maxima*, *L. glauca*, *Syzygium glomeratum* in both of the Brise Fer sites, and *S. glomeratum* in Marianne (Fig. 5). The start of fruiting for many species varied between study sites (tab. 2). The ripe fruits of *S. oppositifolia* and *T. bentzoë* were only consumed by *P. niger* during certain months and ignored during others (Fig. 6).

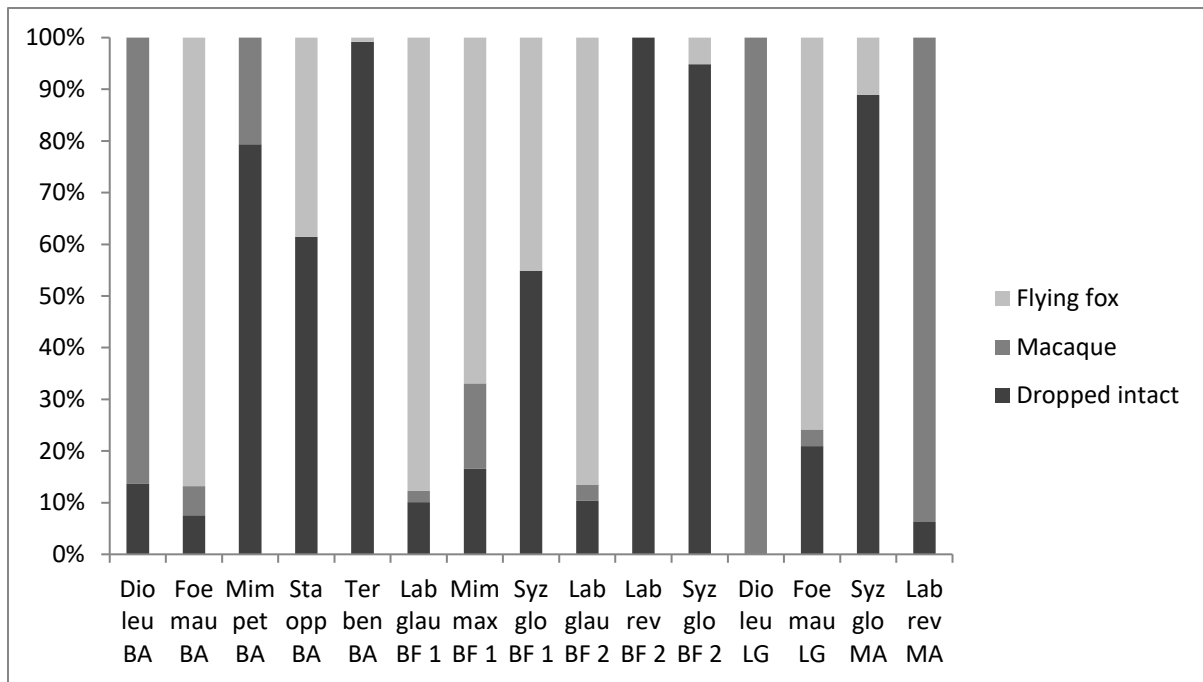


Figure 5: Relative amount of sampled flowers and fruits that remained intact or were eaten by either flying foxes or macaques for *Diospyros leucomelas* (Dio leu), *Foetidia mauritiana* (Foe mau), *Mimusops petiolaris* (Mim pet), *Labourdonnaisia glauca* (Lab glau), *Mimusops maxima* (Mim max), *Labourdonnaisia revoluta* (Lab rev), *Stadmanie oppositifolia* (Sta opp), *Syzygium glomeratum* (Syz glo) and *Terminalia bentzoë* (Ter ben) in Bon Amour (BA), Brise Fer cma (BF1), Brise Fer semi-weeded (BF2) and Marianne (MA).

Table 2: The start of fruiting for all species selected for the competition assessment in the different study sites: Bon Amour (BA), Brise Fer cma (BF 1), Brise Fer semi-weeded (BF 2), Lower Gorges (LG) and Marianne (MA).

Species	BA	BF 1	BF 2	LG	MA
<i>Canarium paniculatum</i>	-	-	-	-	-
<i>Cassine orientalis</i>	Sept.	June	June	June	-
<i>Cossinia pinnata</i>	March	-	-	March	-
<i>Diospyros leucomelas</i>	March	-	-	March	-
<i>Diospyros tessellaria</i>	Sept.	Sept.	Sept.	Oct.	-
<i>Eugenia. sp. 1</i>	-	-	-	Sept.	-
<i>Eugenia. sp. 3</i>	Sept.	-	-	-	-
<i>Eugenia tinifolia</i>	-	-	-	-	-
<i>Foetidia mauritiana</i>	May	-	-	May	-
<i>Labourdonnaisia glauca</i>	-	June	June	-	-
<i>Labourdonnaisia revoluta</i>	-	-	April	-	March
<i>Mimusops maxima</i>	-	July	July	-	-
<i>Mimusops petiolaris</i>	March	-	-	April	-
<i>Protium obtusifolium</i>	March	Sept.	-	Aug.	-
<i>Sideroxylon puberulum</i>	-	Oct.	Oct.	-	Oct.
<i>Sideroxylon grandiflorum</i>	-	-	-	-	Sept.
<i>Stadmanie oppositifolia</i>	May	-	-	April	-
<i>Syzygium glomeratum</i>	-	June	June	-	May
<i>Terminalia bentzoë</i>	Feb.	-	-	-	-

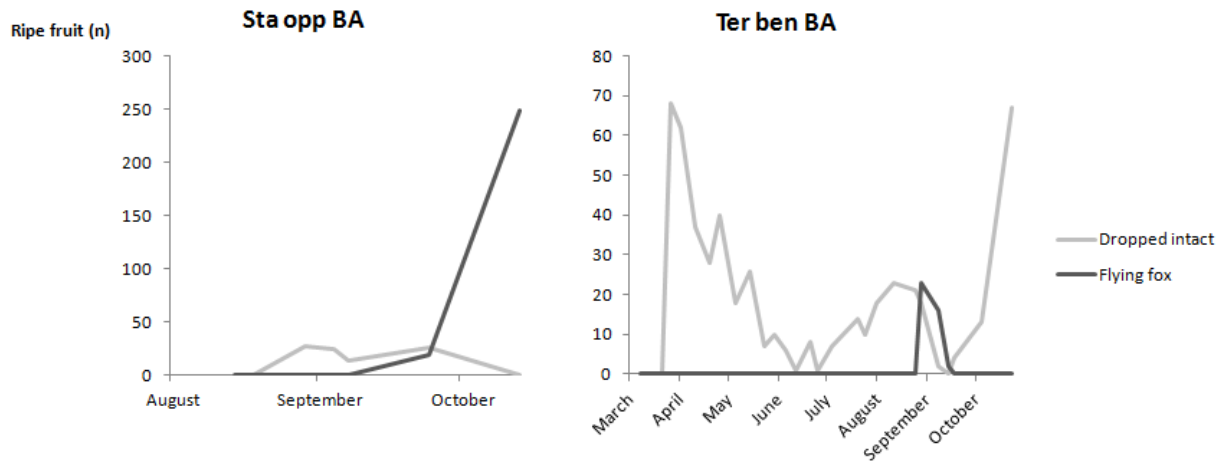


Figure 6: Number of intact ripe fruits that dropped from the trees or were consumed by flying foxes during the fruiting period of *Stadmania oppositifolia* (Sta opp BA) and *Terminalia bentzoë* (Ter ben BA) in Bon Amour.

Additional food species used by *P. niger* and *M. fascicularis* were identified during the monthly transect walks and by collection of faeces of *M. fascicularis* (Appendix 1 and 2). Of the 19 identified food species used by *P. niger*, the flying fox consumed ripe and unripe fruits of 14 species. For 10 out of these 14 species, *P. niger* exclusively consumed ripe fruits (Appendix 1). Furthermore, *P. niger* consumed the leaves of five species (Appendix 1). Lastly, the flying fox only consumed the flowers of one species (Appendix 1). For *M. fascicularis* a total number of 14 food species were identified. Contrary to *P. niger*, the macaque only fed on seeds and ripe or unripe fruits. Furthermore, the macaque only consumed ripe fruits for seven out of 14 species and unripe fruits for nine out of 14 species (Appendix 2). A total number of nine food species were used by both *P. niger* and *M. fascicularis* (Appendix 1 and 2). The only food sources that were exclusively used by *P. niger*, were the leaves of *Dalbergia latifolia*, *Flacourtia indica*, *Hornea mauritiana* and *Hugonia serrata* and the fruits of *Aphloia theiformis*, *Eugenia sp. 1* and *S. glomeratum* (Appendix 1).

Additionally, most of the unripe fruits consumed by *M. fascicularis* were still at a premature or unripe stage, often resulting in damage or consumption of the seeds (Fig. 7). Footage of the camera traps indicated that the macaque tend to only bite the fruit of for example *D. leucomelas*, dropping a big chunk of the fruit with underdeveloped and damaged seeds (Fig. 8). Fruits eaten by *M. fascicularis* of other *Diospyros spp.*, *M. maxima*, *M. petiolaris* and *L. glauca* collected in the seed traps or recorded during transect walks have also been dropped after a single bite, often resulting in damage to the seeds (Fig. 7). The macaque was the only animal that consumed fruits of *D. leucomelas*, *D. boutoniana* and unidentified *Diospyros spp.*, and all the fruits were eaten at a premature stage within one or two month's period (Appendix 2). Some food species, such as *L. revoluta* and *M. petiolaris*, produced fruits over three to four months. However, *P. niger* and *M. fascicularis* exploit these species during different months with no clear overlap. For both *L. revoluta* and *M. petiolaris*, the macaque consumed unripe fruits and seeds before the flying fox started consuming fruits of these species. The flying fox also consumed unripe fruits of *L. revoluta*, but the seeds remained intact. Furthermore, the flying fox exclusively consumed ripe fruits of *M. petiolaris* (Appendix 2).



Figure 7: Macaque damaged premature *Diospyros melanida* fruits with seeds removed (top left and bottom left). Macaque eaten premature *Labourdonnaisia revoluta* fruits (middle top), macaque eaten unripe *Mimusops maxima* fruits (middle bottom), macaque eaten premature *D. boutoniana* (top right) and macaque eaten fresh fruit of *D. boutoniana* with damaged seed (second picture in bottom right corner) and macaque eaten fruit of *D. nodosa*. (first picture in bottom right corner).

Parrots and rats also competed for fruits with *P. niger*, since all the eaten fruits of *Cassine orientalis* that were recorded in the seed traps or during transect walks had been consumed at an unripe stage by either rats or parrots in all the sites where these food species were present (Appendix 2). This did usually not result in damage to the seeds, since unripe fruits of *C. orientalis* already have a tough and hard seed. However, rats did often predate on the seeds of other species, such as *E. monticulum* and *S. oppositifolia* (Appendix 2).



Figure 8: Camera trap footage of Macaque dropping chunks of *Diospyros leucomelas* fruit after taking a bite.

4. 2 Seed germination experiment

The faecal samples of *M. fascicularis* collected in the Lower Gorges contained a large number of *S. terebinthifolius* seeds (Tab. 2). Out of the 259 seeds, 117 germinated (45%).

Table 3: Total number of *Schinus terebinthifolius* seeds found in faecal samples collected in the Lower Gorges and the number of *S. terebinthifolius* that germinated after potting the faecal samples.

Lower Gorges	Total	Germinated
Faecal sample 1	14	5
Faecal sample 2	12	9
Faecal sample 3	42	42
Faecal sample 4	9	9
Faecal sample 5	84	18
Faecal sample 6	24	8
Faecal sample 7	17	11
Faecal sample 8	23	11
Faecal sample 9	21	3
Faecal sample 10	13	1

Other species that were found in the faecal samples collected in the Lower Gorges and in the other study areas were *Flacourtia indica*, *Psidium cattleianum* and *Syzygium cumini*. All of these species are exotic. Of these three species, only *P. cattleianum* and *S. cumini* germinated. Faecal samples only contained very few seeds of these species compared to the high number of *S. terebinthifolius* seeds in the faecal samples collected in the Lower Gorges (tab. 2).

4.3 Exclusion study

The boar and deer exclusion study showed a loss of exotic seedlings in the control plots as compared to no or little loss of exotic seedlings in the fenced plots. In the Lower Gorges the number of exotic *Vitex glabrata* seedlings has decreased in the control plots, whereas the number of exotic *V. glabrata* seedlings has remained unchanged in the fenced plots.



Figure 8: Enclosure inaccessible to boar and deer erected in Brise Fer. Soil dug up by boar can be seen at the bottom of the picture.

4.4 Vegetation assessment

Four Modified Whittaker plots have been completed in Bon Amour, Brise Fer and Marianne and the Lower Gorges. Voucher specimen were collected, pressed and brought to the national herbarium for identification. The species list for Bon Amour and Brise Fer will be completed after all the samples have been retrieved from the national herbarium. For Marianne the majority of collected specimens has already been identified and a species list has been compiled (Appendix 3). However, still 19 samples need identification, so the list is likely to expand.

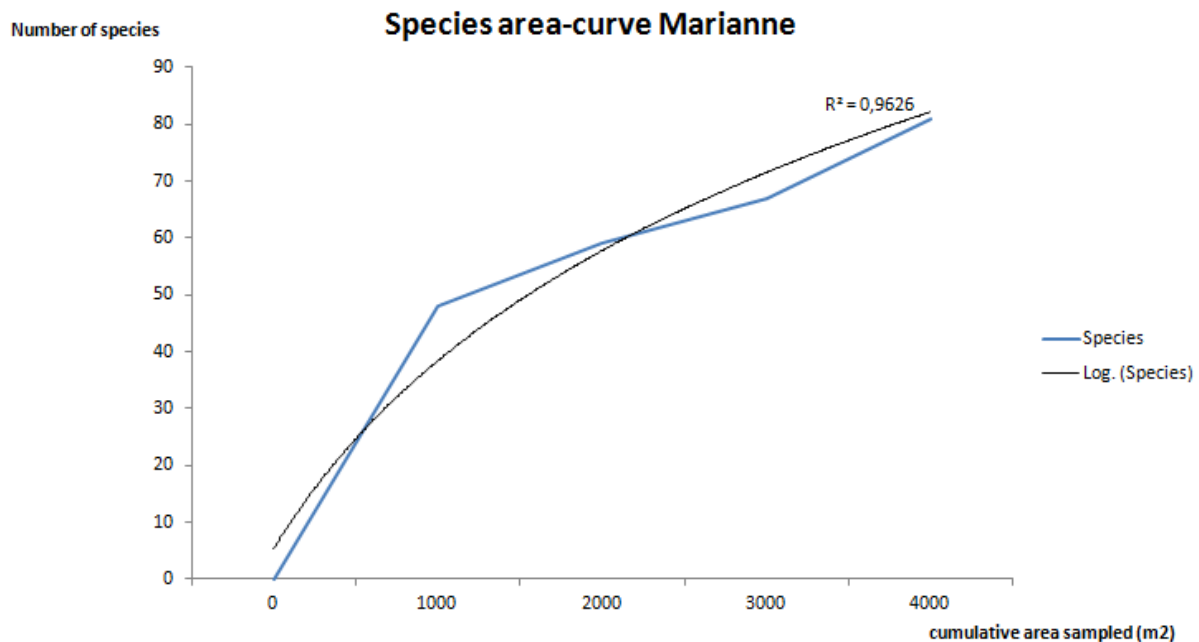


Figure 9: Cumulative species richness sampled over four MWP's in the forest on Marianne with fitted trend line. The blue line indicates the number of additional species sampled with cumulative area.

On Marianne a total number of 61 woody plant species across 52 genera were sampled in a total area of 0.4 hectares. Out of all 61 species, 47 were either endemic or native (Appendix 3). This is 68% of the native richness sampled in an area of 0.9 hectares in the best preserved native forest in Mauritius: Brise Fer. The species-area curve (Fig. 9) shows that the number of woody plant species is likely to increase with additional vegetation plots but will eventually level out and reach an asymptote. Finally, there is a possibility that the *Diospyros sp.* that was sampled in this site (Appendix 3) could be a presumed extinct species: *Diospyros angulata*. The species will be confirmed after the flowers and fruits are analyzed at the national herbarium.

5. Discussion

Many species selected for this study (such as *Foetidia mauritiana*, *Stadmania oppositifolia* or *Syzygium glomeratum*) were ignored by flying foxes until the trees started developing ripe fruits. For *S. oppositifolia*, a dramatic increase in fruit consumption was recorded shortly after the first ripe fruits started to drop into the seed traps. It has been previously shown that flying foxes prefer ripe fruit over unripe fruit (e.g. Krivek, 2017), mainly because they depend on their sense of smell to locate the food source (e.g. Bianconi et al., 2007; McConkey and Drake, 2007; Richter and Cumming, 2008). The same increase in fruits consumption was recorded for *S. glomeratum* in three studied sites after the fruits started ripening. Interestingly, the damage recorded with the seed traps for unripe fruits of *Diospyros leucomelas*, *Labourdonnaisia revoluta* and *Mimusops petiolaris* suggests that *M. fascicularis* can quickly deplete fruits on individual trees before *P. niger* can utilize them. This could have a big impact on native food availability to *P. niger*. Remarkably, the *D. melanida* and *L. revoluta* fruits were depleted by *M. fascicularis* before the seeds inside the fruit had a chance to fully develop. During the transect

walks other *Diospyros* species were encountered that seemed to have been stripped of all the fruits by *M. fascicularis*, based on the large amount of fruits that were predated in similar fashion as *D. leucomelas* around the trees. The fruits that only had shallow canine marks and had remained relatively intact were opened to analyze the development stage of the fruit. The seeds were very soft and could be easily squished between thumb and index finger, suggesting that the feeding behaviour of *M. fascicularis* does not only limit the native food availability to *P. niger* but also has a negative impact on the regeneration of various native plant species. Additionally, not a single seedling of *Diospyros* spp. was found in the area surrounding the trees.

The results indicate that there is an asynchronism of fruiting periods between sites and individual trees, and it has been observed for most of the species that have been sampled so far. In Bon Amour *Protium obtusifolium* started fruiting in March, in the Lower Gorges in July and in Brise Fer in September. *Cassine orientalis* started fruiting in the Lower Gorges and Brise Fer in June, but in Bon Amour the fruits appeared in August. Even within a single site, asynchronous fruiting between individual trees of a single species has been observed. Based on the old mature fruits that were encountered around a *M. petiolaris* tree in the Lower Gorges at the start of March, it seemed that the species had stopped fruiting in this site a while ago. However, premature fruits around a single individual were suddenly encountered at the end of May in the same site, suggesting that this individual had started fruiting a lot later than other replicates. Furthermore, the *Diospyros tessellaria* individuals that were selected in February in the Lower Gorges did not start flowering until October. However, one *D. tessellaria* individual with freshly dropped fruits was encountered in April while sampling other species. These differences could be explained by the fact that there can be variations of fruit production for individual trees from year to year, meaning that the chosen replicates could have fruited at a different time compared to other individuals in the same areas.

Additionally, during the transect walks in Bon Amour other *M. petiolaris* individuals were found to be used by *P. niger* almost two months after the individuals selected for this study had already finished fruiting. Damage by *M. fascicularis* was not observed for these trees, suggesting either the diet of *M. fascicularis* had changed during these two months or that *M. fascicularis* had not started foraging in that area yet. It could also suggest that either *P. niger* did not have the chance to consume any fruits of the early fruiting *M. petiolaris* individuals that were used by *M. fascicularis*, or that *P. niger* was depending on other food sources at the time and started changing its diet during the two months that followed. Nevertheless, the observed asynchronism of the flowering and fruiting periods between sites and individuals of a single species could greatly contribute to meeting the nutritional needs of *P. niger* at a particular time of the year. Asynchronous fruiting of species would mean that the presence of the species in various sites across the island increase food availability for bats. The Mauritian flying fox is able to travel the entire island within a single night, feeding in multiple sites across the island before returning to a roost (Oleksy, 2015). It suggests that forest patches, such as the forests in Bon Amour and Marianne, play an important role in providing food to *P. niger* at certain time of the year that would not be available elsewhere.

Some species that have been monitored for several months now since the start of the fruiting, such as *Cassine orientalis*, *Cossinia pinnata* and *Protium obtusifolium*, have still not been touched by *P. niger*, possibly because the bat are exploiting other food sources or because *P. niger* does not eat them at all. It is possible that they will start depending on these currently ignored species at a later time during the year, since some individuals still have fruits or have yet to start fruiting. During June and July invasive Chinese guava (*Psidium cattleianum*) and Governor's plum (*Flacourtia indica*) seemed to have acted as the major food source for the flying foxes in Bon Amour and the Lower Gorges, since a large amount of spatouts and eaten fruits was recorded during the 500m- transect walks. Macaque also consumed a large amount of these fruits, indicated by the large amount of faeces containing *P. cattleianum* and *F. indica* seeds that were found in the sites. Most of the macaque faeces that was collected in the Lower Gorges during the monthly searches contained a large amount of invasive wild pepper (*Schinus terebinthifolius*) seeds, of which almost half (45%) germinated after potting the faeces.

This suggests that *M. fascicularis* contributes to the dispersal of invasive *S. terebinthifolius*, which could be a driver of the ongoing exotic invasion in Mauritian forests.

Additionally, the macaque greatly limits native food availability of certain tree species to *P. niger*. There is clear dietary overlap between both flying fox and macaque, however macaque exploit and predate on 100% of unripe fruits of *Diospyros* spp. that are extremely scarce in the study sites (such as *D. boutoniana*, *D. leucomelas* and *D. nodosa*). This prevents the few individuals that are present in the study sites from developing ripe fruits which would then be dispersed by bats. Other species within the *Diospyros* genus that are more abundant in certain regions of Mauritius (such as *D. tessellaria*, *D. egrettarum* or *D. melanida*) are known to be dispersed by *P. niger*. The *Diospyros* spp. fruits show bat syndrome traits as they are relatively large, visually inconspicuous (green to brown, and non-contrasting against the background), odorous, and are presented away from the foliage suggesting adaptation to be dispersed by bats. Therefore, it is likely that bats would also feed on the scarce *Diospyros* spp. in the study areas if the fruits get a chance to ripen.

Remarkably, not a single seedling of the scarce *D. boutoniana*, *D. leucomelas* and *D. nodosa* was found around the parental trees. Interestingly, individuals of the more abundant endemic *D. tessellaria* usually reproduce well and develop a seedling bank. Furthermore, individuals of the rare and endangered *D. egrettarum* on the offshore islet Ile aux Aigrettes also commonly develop seedlings banks. Ile aux Aigrettes is inaccessible to *M. fascicularis*, and *P. niger* is known to consume the fruits of the *D. egrettarum* here. This suggests that the exploitation and predation of unripe native fruit by *M. fascicularis* has a negative impact on the reproductive success of the tree species. Furthermore, it is likely that *M. fascicularis* limits reproductive success of some species by discarding unripe or ripe fruit after taking a small bite. Seeds are more susceptible to disease and fungal attack when the flesh around the seed is not removed, decreasing the survival chances of the seeds (Corlett, 1998; Traveset, 1998). The flesh also inhibits germination as often the removal of the pulp breaks the seed dormancy (Traveset, 1998). Contrary to *M. fascicularis*, *P. niger* often removes all the fibrous and fleshy material around the seed before discarding it, thus contributing to seed survival (Corlett, 1998) and ultimately the germination (Traveset, 1998).

The vegetation data from Marianne indicates that the area is very rich in native and endemic species that typically occur in intermediate to wet forests. The site contains nearly 2/3 of woody plant species present in the best preserved forest in Mauritius. This species number is likely to increase based on the species-area curve, since the logarithmic trendline fits very well and indicates that more species can still be recorded with an increasing number of plots. Additionally, the site could possibly contain a presumed extinct *Diospyros* species. Therefore, Marianne holds great conservation potential. However, many invasive plant species, such as *Psidium cattleianum*, *Litsea* spp., *Ossaea marginata* and *Clidemia hirta* seem to suppress the regeneration of native forest. Weeding of invasive species would promote the regeneration of native forest by reducing competition for space, light and nutrients and boosting native fruit production. Various studies showed that weeding of invasive species can increase native regeneration (e.g. Baider and Florens, 2011) and fruit production of native trees (Krivek, 2017). This would increase the native food availability to *P. niger* and promote the seed dispersal and thus passive forest regeneration.

Conclusion

It is clear that the crab-eating macaque *Macaca fascicularis* limits food availability to the Mauritian flying fox *Pteropus niger* by competing for scarce native resources across the island. The predation on immature fruits by macaque leads to unavailability of certain fruits to flying foxes and negatively affects the regeneration of native plants. Rare species seem to be most affected by the macaque's feeding behaviour, since exploitation of immature fruits of the few individuals that are present in certain areas prevents the development of mature seeds. Therefore, reproduction of these plant species is completely halted. Furthermore, fruiting patterns of a single species can differ between sites, resulting in the availability of a certain fruit at different times during the year in different areas

across the island. More research into these fruiting patterns is needed to create insights into food availability throughout the year and food selection by *P. niger*. The asynchronous fruiting patterns also emphasize the need to conserve remnant forests, since they can be very rich in plant species and *P. niger* visits these forest to consume fruits. Remnant forest could provide certain food resources at a specific time of the year when they are not available elsewhere on the island. Weeding these remnant forests will be important to increase the fruit yield of native plants, which will in turn promote dispersal by flying foxes. Ultimately, this will lead to the restoration of native vegetation communities and thus the habitat of the native and endemic animal communities. Additionally, populations of invasive macaque should be controlled in order to successfully restore native vegetation communities and increase food availability to *P. niger*.

Literature

Baider, C., Florens, F. B. V., Baret, S., Beaver, K., Matatiken, D., Strasberg, D. and Kueffer, C. (2010). Status of plant conservation in oceanic islands of the Western Indian Ocean. In: Proceedings of the 4th Global Botanic Gardens Congress. [online] Richmond, Surrey: *Botanic Gardens Conservation International*, pp. 7. Available at: <https://www.bgci.org/files/Dublin2010/papers/Baider-Claudia.pdf> [Accessed 4 June 2017]

Baider, C. and Florens, F. B. V. (2011). Control of invasive alien weeds averts imminent plant extinction. *Biological Invasions*, 13, pp. 2641 – 2646.

Banack, S. A. (1998). Diet selection and resource use by flying foxes (genus *Pteropus*). *Ecology*, 79, pp. 1949 – 1967.

Barrios-Garcia, M. N. and Ballari, S. A. (2012). Impact of wild boar (*Sus scrofa*) in its introduced and native range. *Biological Invasions*, 14, pp. 2283 – 2300.

Bianconi, G.V., Mikich, S.B., Teixeira, S.D. and Maia, B. H. N.S., 2007. Attraction of fruit-eating bats with essential oils of fruits: A Potential Tool for Forest Restoration. *Biotropica*, 39, 136-140

Chazdon, R. L. (2008). Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science*, 320 (5882), pp. 1485 – 1460.

Cheke, A. S. and Dahl, J. F. (1981). The status of bats on western Indian Ocean islands, with special reference to *Pteropus*. *Mammalia*, 45(2), pp. 205 – 238.

Cheke, A. and Hume, J. (2008). Lost land of the Dodo: an ecological history of the Mascarene Islands. London: T and AD Poyser, pp.

Corlett, R. T. (1998). Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews*, 73, pp. 413 – 448.

Florens, F. B. V. (2016). Biodiversity law: Mauritius culls threatened fruit bats. *Nature*, 530, pp. 33.

Florens, F. B. V., Baider, C., Marday, V., Martin, G. M. N., Zmanay, Z., Oleksy, R., Krivek, G., Vincenot, C. E., Strasberg, D. and Kingston, T. (2017). Disproportionally large ecological role of a recently mass-culled flying fox in native forests of an oceanic island. *Journal for Nature Conservation*, 40, pp. 85 – 93.

Gotelli, N. J. and Colwell, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, pp. 379 – 391.

Hansen, D. M., Kaiser, C. N. and Müller, C. B. (2008). Seed dispersal and establishment of endangered plants on oceanic islands: The Janzen-Connell model, and the use of ecological analogues. *PLoS One*, DOI: 10.1371/journal.pone.0002111.

- Hansen, D.M. and Galetti, M. (2009). The forgotten megafauna. *Science*, 324 (5923), pp. 42 – 43.
- Ickes, K., Dewalt, S. J. and Appanah, S. (2001). Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest. *Journal of Tropical Ecology*, 17(2), pp. 191 – 206.
- Krivek, G. (2017). *The influence of invasive plant control on the foraging habitat quality of the Mauritian flying fox Pteropus niger*. MSc. Norges Miljø- og Biovitenskapelige Universitet.
- Lorence, D. H. and Sussman, W. S. (1986). Exotic species invasion into Mauritius wet forest remnants. *Journal of Tropical Ecology*, 2(2), pp. 147 – 162.
- Lorence, D. H. and Tattersall, I. (1986). Distribution, abundance, and putative ecological strategy of *Macaca fascicularis* on the Island of Mauritius, Southwestern Indian Ocean. *Folia Primatologica*, 46, pp. 28 – 43.
- McConkey, K. R. and Drake, D. R. (2006). Flying foxes cease to function as seed dispersers long before they become rare. *Ecology*, 87, pp. 271 – 276.
- McConkey, K. R. and Drake, D. R. (2007). Indirect evidence that flying foxes track food resources among islands in a Pacific archipelago. *Biotropica*, 39, pp. 436-440.
- Mitchell, J., Dorney, W., Mayer, R. and McIlroy, J. (2007) Ecological impacts of feral pig diggings in north Queensland rainforests. *Wildlife Research*, 34, pp. 603 – 608.
- Monty, M. L. B., Florens, F. B. V. and Baider, C. (2013) Invasive alien plants elicit reduced production of flowers and fruits in various native forest species on the tropical island of Mauritius (Mascarenes, Indian Ocean). *Tropical Conservation Science*, 6, pp. 35 – 49.
- Motala, S. M., Krell, F. –T., Mungroo, Y. And Donovan, S. E. (2007). The terrestrial arthropods of Mauritius: a neglected conservation target. *Biodiversity Conservation*, 16, pp. 2867 – 2881.
- Nyhagen, D. F. (2004). A study of the bat-fruit syndrome on Mauritius, Indian Ocean. *Phelsuma*, 12, pp. 118–125.
- Nyhagen, D. F., Turnbull, S. D., Olesen, J. M. and Jones, C. G. (2005). An investigation into the role of the Mauritian flying fox, *Pteropus niger*, in forest regeneration. *Biological Conservation*, 122, pp. 491 – 497.
- Oleksy, R. (2015). The impact of the Mauritius fruit bat (*Pteropus niger*) on commercial fruit farms and possible mitigation measures. Detailed final report to the Rufford Foundation. Available at: <http://www.rufford.org/files/14099-B%20Detailed%20FinalReport.pdf> [Accessed 10 June 2018]
- Page, W. and D'Argent, G. (1997). A vegetation survey of Mauritius to identify priority rain forest areas for conservation management. [online] Port Louis: Mauritian Wildlife Foundation, pp. 13 – 27. Available at: <http://npcs.govmu.org/English/Documents/Chapter%202-4.pdf> [Accessed 5 June 2017].
- Peh, K. S. –H., Balmford, A., Birch, J. C., Brown, C., Butchart, S. H. M., Daley, J., Dawson, J., Gray, G., Hughes, F. M. R., Mendes, S., Millett, J., Stattersfield, A. J., Thomas, D. H. L., Walpole, M. and Bradbury, R. B. (2015). Potential impact of invasive alien species on ecosystem services provided by a tropical forested ecosystem: a case study from Montserrat. *Biological Invasions*, 17, pp. 461 – 475.
- Redford, K. H. (1992). The empty forest. *BioScience*, 42, pp. 412 – 422.

Reuleaux, A., Richards, H., Payet, T., Villard, P., Waltert, M. and Bunbury M. (2014). Insights into the feeding ecology of the Seychelles Black Parrot *Coracopsis barklyi* using two monitoring approaches. *Ostrich*, 85, pp. 245 – 253.

Richter, H.V. and Cumming, G. S. (2008). First application of satellite telemetry to track African straw-coloured fruit bat migration. *Journal of Zoology*, 275, pp. 172-176.

Sussman, R. W. and Tattersall, I. (1986). Distribution, Abundance, and Putative Ecological Strategy of *Macaca fascicularis* on the Island of Mauritius, Southwestern Indian Ocean. *Folia Primatologica*, 46, pp. 28 – 43.

Thomson, B. (2002). Australian handbook for the conservation of bats in mines and artificial cave bat habitats. Kenmore: Australian Centre for Mining Environmental Research, pp. 66.

Traveset, A. (1998). Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics*, 1, pp. 151 – 190.

Vincenot, C., Florens, F. B. V. and Kingston, T. (2017). Can we protect island flying foxes? *Science*, 355(6332), pp. 1368–1370.

Virah-Sawmy, M., Mauremootoo, J., Marie, D., Motala, S. and Sevathian, J. –C. (2009). Rapid degradation of a Mauritian rainforest following 60 years of plant invasion. *Oryx*, 43, pp. 599 – 607.

Appendices

Appendix 1: Species documented to have been eaten by *P. niger* and the consumed plant parts (fruit = Fr, unripe = u, ripe = r, flower = Fl, leaves = Lv and seeds = Se) across the five study sites: Bon Amour (BA), Brise Fer semi-weeded (BFs), Brise Fer cma (BFc), Lower Gorges (LG) and Marianne (MA).

Family	Species	Eaten plant part	Site	Period
Aphloiaceae	<i>Aphloia theiformis</i>	Fr (r)	BFs	June
Ebenaceae	<i>Diospyros tessellaria</i>	Fl	BFc	Sept.
Fabaceae	<i>Dalbergia latifolia</i>	Lv	LG	Aug.
Lamiaceae	<i>Vitex glabrata</i>	Fr (r)	LG	Sept.
Lechythidaceae	<i>Foetidia mauritiana</i>	Fr (r)	BA, LG	May – Sept.
Linaceae	<i>Hugonia serrata</i>	Lv	BFc, BFs	July – Aug.
Myrtaceae	<i>Eugenia sp. 1</i>	Fr (r)	LG	July
	<i>Eugenia sp. 2</i>	Fr (r)	BFc	Sept.
	<i>Psidium cattleianum</i>	Fr (r)	BFc, BFs, LG, MA	June – Aug.
	<i>Syzygium glomeratum</i>	Fr (r)	BFc, BFs, MA	Aug. – Oct.
Rubiaceae	<i>Coffea macrocarpa</i>	Fr (r)	BFs	Sept.
Salicaceae	<i>Flacourtia indica</i>	Fr (r), Lv	BA, LG	June – Sept.
	<i>Ludia mauritiana</i>	Lv	LG	July – Aug.
Sapindaceae	<i>Hornea mauritiana</i>	Lv	LG	July – Aug.
	<i>Stadmania oppositi folia</i>	Fr (r)	BA	Sept.
Sapotaceae	<i>Mimusops maxima</i>	Fr (r, u)	BFc, BFs	July – Oct.
	<i>Mimusops petiolaris</i>	Fr (r, u)	BA, LG	May – July
	<i>Labourdonnaisia glauca</i>	Fr (r, u)	BFc, BFs	June – Sept.
	<i>Labourdonnaisia revoluta</i>	Fr (u)	BFs	Aug.

Appendix 2: Species documented to have been eaten by different animals (Type: *M. fascicularis* = M, *R. rattus* = R, *Psittacula eques* or *Psittacula krameri* = P) and the consumed plant parts (Eaten plant part: fruit = Fr, unripe = u, ripe = r, flower = Fl and leaves = Lv) across the five study sites: Bon Amour (BA), Brise Fer semi-weeded (BFs), Brise Fer cma (BFc), Lower Gorges (LG) and Marianne (MA).

Family	Species	Type	Eaten plant part	Site	Period
Achariaceae	<i>Erythrospermum monticolum</i>	R	Fr (u), Se	MA	July
Anacardiaceae	<i>Schinus terebinthifolius</i>	M	Fr (r)	LG	April – May
Celastraceae	<i>Cassine orientalis</i>	R/P	Fr(u)	BFs	
Ebenaceae	<i>Diospyros boutoniana</i>	M	Fr (u), Se	BFs	June – July
	<i>Diospyros leucomelas</i>	M	Fr (u), Se	BA, LG	
	<i>Diospyros tessellaria</i>	M	Fr (u), Se	BFc	March-April
	<i>Diospyros nodosa</i>	M	Fr (u), Se	BFs	Aug.
Lechthyidaceae	<i>Foetidia mauritiana</i>	M	Fl	LG	March
Myrtaceae	<i>Eugenia sp. 2</i>	M	Fr (r)	BFc	Sept.
	<i>Psidium cattleianum</i>	M	Fr (r)	BFs, LG, MA	June – Aug.
Rubiaceae	<i>Coffea macrocarpa</i>	M	Fr (r)	BFs	Sept.
Salicaceae	<i>Flacourtia indica</i>	M	Fr (r, u)	BA	June – July
Sapindaceae	<i>Stadmania oppositifolia</i>	R	Fr(r, u), Se	BA, LG	July – Oct.
Sapotaceae	<i>Mimusops maxima</i>	M	Fr (r, u)	BFc, BFs	July – Sept.
	<i>Mimusops petiolaris</i>	M	Fr (u)	BA, LG	March – May
	<i>Labourdonnaisia glauca</i>	M	Fr (u), Se	BFc, BFs	July – Sept.
	<i>Labourdonnaisia revoluta</i>	M	Fr (u)	MA	July/ Oct.
	<i>Sideroxylon grandiflorum</i>	M	Fr (u)	BFc	Sept.

Appendix 3: List of all woody plant species recorded on Marianne and their status: native/endemic or exotic. The list is not complete yet and more species will be added after all samples have been identified.

Family	Species	Status
Achariaceae	<i>Erythrospermum monticolum</i>	Native/endemic
Aphloiaceae	<i>Aphloia theiformis</i>	Native/endemic
Apocynaceae	<i>Tabernaemontana persicariifolia</i>	Native/endemic
Asteraceae	<i>Ayapana triplinervis</i>	Exotic
Bignoniaceae	<i>Colea coleii</i>	Native/endemic
Boraginaceae	<i>Trochetia blackburniana</i>	Native/endemic
Clusiaceae	<i>Calophyllum tacamahaca</i>	Native/endemic
Connaraceae	<i>Cnestis glabra</i>	Native/endemic
Ebenaceae	<i>Diospyros sp.</i>	Native/endemic
Euphorbiaceae	<i>Acalypha integrifolia</i>	Native/endemic
	<i>Cordemoya integrifolia</i>	Native/endemic
	<i>Homalanthus populifolius</i>	Exotic
	<i>Orfilea neraudiana</i>	Native/endemic
	<i>Securinega durissima</i>	Native/endemic
Lauraceae	<i>Litsea sp.</i>	Exotic
	<i>Ocotea sp.</i>	Native/endemic

Loganiaceae	<i>Geniostoma borbonicum</i>	Native/endemic
Malpighiaceae	<i>Hiptage benghalensis</i>	Exotic
Melastomataceae	<i>Clidemia hirta</i>	Exotic
	<i>Clidemia marginata</i>	Exotic
Memecylaceae	<i>Memecylon cordatum</i>	Native/endemic
Mettuisaceae	<i>Apodytes dimidiata</i>	Native/endemic
Monimiaceae	<i>Tambourissa ficus</i>	Native/endemic
Moraceae	<i>Ficus reflexa</i>	Native/endemic
Musaceae	<i>Ravenala madagascariensis</i>	Exotic
Myrtaceae	<i>Eugenia kanakana</i>	Native/endemic
	<i>Eugenia sp.</i>	Native/endemic
	<i>Eugenia vaughanii</i>	Exotic
	<i>Psidium cattleianum</i>	Native/endemic
	<i>Syzygium commersonii</i>	Native/endemic
	<i>Syzygium duponti</i>	Native/endemic
	<i>Syzygium glomeratum</i>	Native/endemic
	<i>Syzygium jambos</i>	Native/endemic
	<i>Syzygium mauritianum</i>	Exotic
Myrsinaceae	<i>Ardisia crenata</i>	Native/endemic
	<i>Badula multiflora</i>	Native/endemic
Ochnaceae	<i>Ochna mauritiana</i>	Exotic
Oleaceae	<i>Ligustrum robustum var. Walkeri</i>	Native/endemic
	<i>Olea lancea</i>	Native/endemic
Phyllanthaceae	<i>Antidesma madagascariense</i>	Native/endemic
Pittosporaceae	<i>Pittosporum senacia</i>	Native/endemic
Psiloxylaceae	<i>Psiloxylon maritimum</i>	Exotic
Rosaceae	<i>Rubus alceifolius</i>	Exotic
	<i>Rubus rosifolius</i>	Native/endemic
Rubiaceae	<i>Bremeria landia</i>	Native/endemic
	<i>Coffea macrocarpa</i>	Native/endemic
	<i>Danais fragrans</i>	Native/endemic
	<i>Fernelia decipiens</i>	Native/endemic
	<i>Gaertnera psychotriodes</i>	Native/endemic
	<i>Ixora parviflora</i>	Native/endemic
	<i>Psychotria borbonica</i>	Native/endemic
Salicaceae	<i>Casearia coriacea</i>	Native/endemic
	<i>Flacourtia sp.</i>	Exotic
	<i>Homalium sp.</i>	Native/endemic
	<i>Ludia mauritianum</i>	Native/endemic
Sapindaceae	<i>Molinaea alternifolia</i>	Native/endemic
Sapotaceae	<i>Labourdonnaisia calophylloides</i>	Native/endemic
	<i>Labourdonnaisia glauca</i>	Native/endemic
	<i>Labourdonnaisia revoluta</i>	Native/endemic
	<i>Sideroxylon puberulum</i>	Native/endemic
Thymeliaceae	<i>Wikstroemia indica</i>	Exotic