

Fruit availability drives dietary, activity and ranging patterns of
invasive *Macaca fascicularis* in Mauritius: implications for
conservation of *Pteropus niger* and native forests

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Introduction

Macaca spp. are omnivorous primates with a wide geographical distribution and are native to South, East and Central Asia, North Africa and Southern Europe (Richard et al. 1989). Even though *Macaca* spp. are highly opportunistic and can adapt their diet depending on habitat (Tang et al., 2016), seasonality (Hanya, 2004; Ruslin et al., 2019) and anthropogenic disturbances (Riley, 2007; Sha and Hanya, 2013), a large number of *Macaca* spp. mostly consume ripe fruit (Yeager, 1996; O'Brien and Kinnaird, 1997; Krishnadas et al. 2011; Albert et al. 2013a) and/or typically prefer fruits over other foods (Hanya, 2004; Huang et al., 2015; Sengupta and Radhakrishna 2016; Ruslin et al., 2019). Just like other frugivorous primates (Terborgh 1983; Wallace 2005), food items such as mature leaves, flowers, immature fruits, and seeds are often increasingly consumed as fruits become more scarce (Lucas and Corlett, 1991; Sengupta and Radhakrishna, 2016; Tang et al., 2016; Gazagne et al. 2018). Therefore, these food items are typically referred to as 'fallback foods' (Marshall et al., 2009). This highly adaptable and frugivorous nature is well illustrated by *Macaca mullata* and *M. assamensis*, which mostly consume leaves in limestone forests, but shift to a more frugivorous diet when scarce fruits become available (Huang et al., 2015; Tang et al., 2016).

Furthermore, in disturbed habitat where forest fruits are usually scarce, various *Macaca* spp. are known to rely on anthropogenic foods (Angetsuma, 2007; Riley et al. 2013; Sha and Hanya, 2013). Even though some *Macaca* spp. are considered 'weed' species (e.g., *M. mullata*) that intentionally occupy habitat disturbed by humans to consume anthropogenic foods (Richard et al. 1989), consumption of anthropogenic foods is also often promoted by low availability of forest fruits (Sha and Hanya, 2013; Gazagne et al. 2020a) or partly related to the more stable availability of cultivated vs. forest fruits (Riley et al. 2013). Even in undisturbed habitat seasonal scarcity of forest fruits can promote consumption of anthropogenic foods (Albert et al. 2013b). Consequently, availability of forest fruits is an important driver of dietary patterns in macaques.

Movement and ranging patterns of many *Macaca* spp. are also commonly driven by forest fruit availability (Albert et al., 2013b; Sengupta and Radhakrishna, 2016; Gazagne et al., 2018). *Macaca* spp. commonly adopt both energy maximizing and minimizing strategies in periods of fruit scarcity (Agetsuma and Noma, 1995; Albert et al., 2013b). Energy-maximizing strategies involve increasing ranging distance during periods of fruit scarcity to meet dietary needs and obtain high-quality or preferred food items (Hall, 1962). On the other hand, energy-minimizing strategies involve decreasing daily travel distances and increasingly foraging on 'fallback foods' (Wrangham, 1977). Moreover, ranging patterns can also be affected by habitat disturbance and human influence, as home range can be small in provisioned macaques when they have access to a reliable year-round anthropogenic food source (Ruppert et al., 2018), unlike unprovisioned macaques (Caledecott et al. 1996; Kogenezawa and Imaki, 1999). On the other hand, when human food sources are less reliable or patchily distributed, provisioned macaques can also have larger home ranges than their unprovisioned counterparts in order to access spatially and temporally unpredictable food sources (Sha and Hanya, 2013) or various remote food sources (Riley, 2008).

This behavioural flexibility combined with their dietary plasticity make macaques incredibly resilient frugivores that can cope relatively well with habitat degradation and human disturbances (Albert et al., 2013c). As a result, they can become important seed-dispersers in areas where other large seed-dispersers have disappeared (Lucas and Corlett, 1998; Albert et al., 2013c; Sengupta et al., 2014; Gazagne et al., 2020b). *Macaca* spp. may be especially

reliable seed dispersers for 82 species in three plant genera and are potentially reliable dispersers for a total of 11 plant families throughout their native range (Sengupta et al. 2020).

However, the resilience and adaptability of *Macaca* spp. can also cause various problems in some cases. The long-tailed macaque, *Macaca fascicularis*, is a macaque species native to most of Southeast Asia and occurs in a broad variety of habitats (Aldrich-Blake, 1980; Gumert et al., 2011). Like other macaques, this species is a highly opportunistic omnivore (Gumert et al., 2011), prefers feeding on fleshy fruits (Lucas and Corlett, 1991; Ruslin et al., 2019), mostly eats ripe fruits (Ungar, 1995; Ruslin et al. 2019) and can be an effective seed disperser (Lucas and Corlett, 1998). However, *M. fascicularis* has been both deliberately and accidentally introduced to oceanic islands across the globe (GISD, 2019). *Macaca fascicularis* adapts remarkably well to habitat disturbed by humans (Medway, 1970; Van Schaik et al., 1996; Sussman et al., 2011; Mohammad and Wong, 2019), which is typically present on islands. Consequently, they have a number of economic and ecological impacts on islands, including crop raiding, predation of eggs and chicks of native birds, destroying native fruits and seeds and changing the composition of the vegetation (Carter and Bright, 2002; Kemp and Burnett 2003; Sussman et al. 2011). As a result, *M. fascicularis* is included in the IUCN invasive species specialist group's list for the 100 most invasive species worldwide (GISD, 2019). Introduced non-hominid primates worldwide, including *M. fascicularis*, are either partly or completely accountable for at least 69 island extinctions and extirpations (Jones et al., 2018).

Mauritius is a perfect example of an oceanic island where early introduction of *M. fascicularis* (Sussman and Tattersall, 1986) may have greatly contributed and is still contributing to the ongoing degradation of the fragile ecosystem. The island was once almost completely covered by forests (Cheke, 1987), but now the majority of land cover is made up of urban areas and agricultural land. At present, forests cover about 25% of Mauritius (MAIFS, 2015), but only a small portion (1%) is good quality native vegetation that is not dominated by alien invasive plants (forests with >50% native plant cover; MAIFS, 2015). Of the remaining highly endemic flora (Baider et al. 2010) about 80% is threatened (Strahm, 1993), and most of the remaining endemic vertebrates are threatened too (Jones, 2008). *Macaca fascicularis* is likely to play a role in the ongoing degradation of the ecosystem by preying on eggs and chicks of endemic birds (Jones et al., 1992; Safford, 1994), destroying flowers and young shoots of endemic plants (Baider and Florens, 2006), and mostly consuming unripe fruit of native plants (Baider and Florens, 2006; Krivek, 2017; Reinegger et al., 2021a).

The native fruits that remain in what is left of Mauritius' native forests are mostly shared between *M. fascicularis*, other invasive animals (e.g., *Rattus rattus* and *Psittacula krameri*) and the endemic flying fox *Pteropus niger*. The flying foxes are persecuted by the government because they feed on commercially valuable orchard crops in plantations and private backyards (Vincenot et al. 2017; Oleksy et al. 2018; Tollington et al. 2019). Meanwhile, the macaque population is likely to have grown in size in the last 20 years (Bertram, 1994). Even though the current size of the macaque population is unknown, and the export of wild monkeys has limited population growth to some degree (Sussman et al. 2011), reports of macaques moving into urban areas and harassing residents have become common (L'Express, 2015; L'Express, 2017; L'Express, 2020a; L'Express, 2020b). This suggests that insufficient suitable forest habitat and resources are available. Furthermore, a recent study by Reinegger et al. (2021a) suggests that *M. fascicularis* may reduce the availability of native fruits to *P. niger*, potentially forcing *P. niger* to become more dependent on commercial fruits. Unlike *M. fascicularis*, *P. niger* mostly eats

native fruit when ripe (Krivek et al., 2020; Reinegger et al., 2021). Therefore, effective seed dispersal of native plants is also potentially disrupted by *M. fascicularis*.

In summary, it is likely that *M. fascicularis* has come to rely largely on 'fallback foods and anthropogenic food sources in Mauritius because of the potentially low fruit availability in the fragmented and disturbed forest habitat. Previous studies on *M. fascicularis* in Mauritius found that *M. fascicularis* spends a larger proportion of their feeding time consuming leaves, flowers, grass and sugarcane (42%) than fruits (38%) (Sussman et al., 2011). However, during this study food availability was only measured for seven months, making it difficult to make inferences about food preference or seasonal fruit scarcity (Sussman et al. 2011). Furthermore, earlier studies never focused on the consumption of native fruits, because they were mostly carried out in Mon Vallon in the Southwest of the island. This area consists of degraded open shrublands and savannah, which does not contain substantial patches of native vegetation (Sussman et al. 2011). Therefore, there is no robust evidence for seasonal fruit scarcity or that consumption of unripe native fruit by *M. fascicularis* is a result of scarcity.

Therefore, we aimed to study the relationship between seasonal fruit availability, ranging patterns and diet composition of *M. fascicularis* in a degraded native forest remnant to determine *M. fascicularis'* food and fruit preferences in Mauritius. Furthermore, we aimed to quantify the consumption and drop of both exotic and native fruits by *M. fascicularis* and the yield of forest trees within their home range to provide insights into the intensity of fruit scarcity and food competition with *P. niger*. Consequently, we hypothesized that *M. fascicularis* spends a larger proportion of feeding time consuming fruits during periods of high fruit availability than in periods of low fruit availability. We also tested the hypothesis that *M. fascicularis* feeds on more ripe fruits when fruits are more abundant. Furthermore, because the distribution of forest resources is likely to be patchy, we hypothesized that *M. fascicularis* uses energy-maximizing strategies to acquire preferred food sources during periods of low fruit availability. Additionally, we tested the hypothesis that *M. fascicularis* limits availability of scarce native fruits to *P. niger* by exploiting unripe fruits. We then discuss the implications of our findings for the conservation of *P. niger* and native forests. Based on our findings and earlier work on *M. fascicularis* in Mauritius, we also give recommendations for appropriate methods for estimating the current population size of *M. fascicularis*.

Methods

Study site

This study was carried out in a forest remnant in the North of Mauritius (Fig. 1), which was selected because of the relatively rich native plant community (Reinegger et al. 2021b) and the presence of various *M. fascicularis* troops. The site is located in the Calebasses Mountain Range, which consists of two mountains: Calebasses Mountain range and Mariannes (lat: -20.181203°, long: 57.584498°). This area is between 420 and 580 m asl and receives 1,800 – 2,200 mm of rainfall per year (Willaime, 1984). The forest was made up of semi-dry vegetation at lower elevations and sub-humid vegetation at higher elevations. However, the forest was extremely degraded at lower elevations and mostly consists of a remnant pine plantation (*Pinus nigra*) and dense thickets that were made up of invasive *Flacourtia indica*, *Hiptage benghalensis*, *Ligustrum robustum*, *Litsea* spp., *Psidium cattleianum*, *Rhamnus nepalensis* and *Syzygium jambos*.

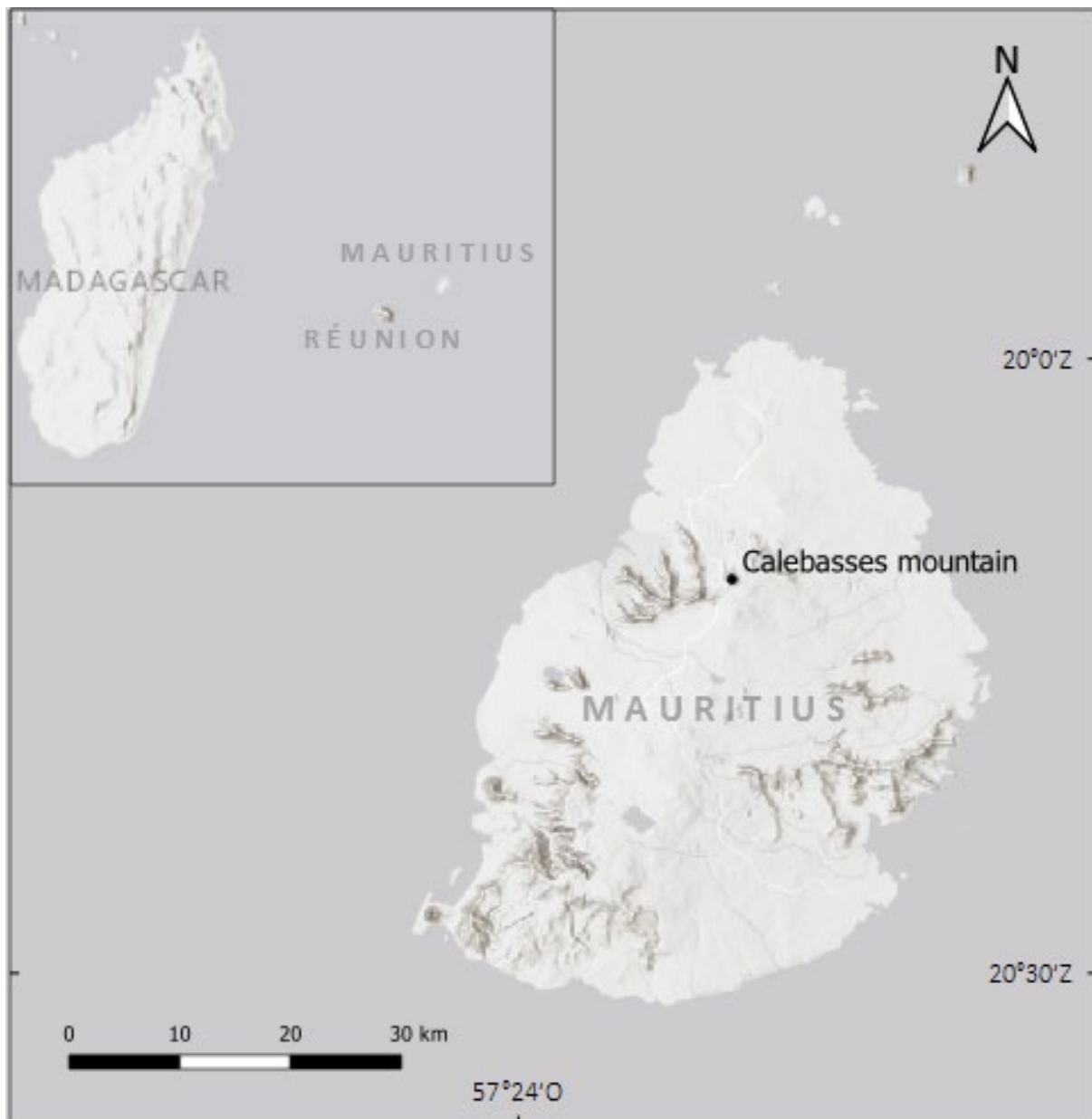


Figure 1: Location of the study site

Dietary and behavioural data collection

A troop of macaques occupying a steep, densely vegetated, northwest facing slope on Calebasses Mountain were partially habituated during October – November 2019 (Fig. 2). Chasing animals was avoided as much as possible by memorizing areas they frequently visited during the day, so that the animals could run into the researcher instead of vice versa. The troop consisted of 19 – 23 individuals and was followed three to four times a week from December 2019 until December 2020. The troop was followed from the moment the macaques left their sleeping site (05:30 – 6:00) until 13:30 or from 11:00 until the macaques returned to their sleeping site (18:00 – 18:30) or until the troop was lost by the researcher for longer than 1.5 hours. These day intervals were chosen over full days (05:30 – 18:30) because the high topographical relief in the area combined with steep slopes made following the group very physically straining. Furthermore, Sussman et al., (2011) found that activity patterns of Mauritian *M. fascicularis* were very consistent throughout the day, suggesting that our chosen day interval can be representative for the whole day. Dietary and behavioural data was

collected by scan sampling the troop at 5-min intervals (Altmann, 1974), typically within five to 20 m distance from the troop. During scans, each visible troop member was observed for 15 - 20 seconds to record its behaviour. Behavioural activities were divided into seven categories: resting, moving, feeding, grooming, playing, mating and fighting. Feeding was defined as the manual handling of food items and then putting them into the mouth or oral handling of food items when they were directly taken by the mouth. When an individual was feeding, the first item that was consumed was recorded: pinecone, insect, fruit, leaf, bark, flower, egg, seed, grass or crop. When a plant food was consumed, the name of the plant species was also recorded. Whenever food items or a plant species could not be clearly identified, because of poor visibility, they were recorded as unknown. For each activity, we also recorded whether it occurred in the canopy or on the ground. Activity patterns were analysed in R (R Core Team, 2020) by calculating the relative proportion of scans that macaques were engaged in each activity every month. Additionally, diet composition and relative use of plant species were analysed by calculating the relative proportion of time the macaques spent feeding on every food item and plant species. Unfortunately, we had to omit January 2020 from our dataset, because frequent cyclones and torrential storms made data collection nearly impossible during this month.



Figure 2: Members from our study troop resting near their sleep site on the north-west facing slope of Calebasses Mountain.

Food availability and fruit yield

To assess fruit availability within the home range of our study group we first estimated tree density by marking all stems with diameter at breast height (DBH) ≥ 5 cm along four vegetation transects. Two were oriented in the North–South direction and two were oriented East–West. Each transect was 2 m wide and 200 m to 400 m in length, covering a total area of 0.24 ha. Because *M. fascicularis* is considered an opportunistic feeder in its native range (Gumert, 2011) as well as in Mauritius (Sussman et al., 2011), all tree and liana species present in the vegetation transects were included. Every month, the phenological state of all stems was recorded along three transects (presence/absence of flowers and ripe and unripe fruit). Based on the percentage of crown area covered by fruit (visual estimation), trees were ranked on a 5-point scale where a score of 0 implied no fruit and 1, 2, 3, and 4 implied 1–25 %, 26–50 %, 51–75 %, and ≥ 76 % of the crown area covered by fruit respectively (Albert et al., 2013b; Sengupta and Radhakrishna, 2016). Flower cover was also recorded using the same 5-point scale. The total Fruit Availability Index (FAI) was then calculated for each month:

$$FAI = \sum_{i=1}^n D_i B_i P_{im}$$

Here, D_i is the mean density of species i in the home range, B_i is the mean basal area of trees of species i (cm^2) and P_{im} is the mean score of fruit cover in species i in month m . This is then totalled for all species (n) in the phenology transects. The same method was used to calculate an availability index for flowers (FAI), where P_{im} was replaced with the mean score of flower cover in species i in month m . Furthermore, we also calculated a pinecone availability index (PcAI). Because pine trees (*Pinus nigra*) were only present in the valley between Calebasses Mountains and Mariannes, we established an additional vegetation transect (2 m by 300 m). Pinecone cover on trees was recorded every month using the same 5-point scale as for the FAI and FAI. The PcAI was then calculated by multiplying B_{pine} by P_{pine} for every month. Pinecone availability could only be recorded from March 2020 until December 2020.

Lastly, we also measured fruit yield for every tree and liana species by counting fruits on all stems marked along three vegetation transects monthly. For trees > 4 m tall, yield was estimated by counting the number of fruits using binoculars along three large branches on a tree that were selected on an *ad libitum* basis. The mean number of fruits per branch was calculated and then multiplied by the number of major branches on the tree. For small trees (≤ 4 m tall) all the fruits were counted. Similar methodologies have been used for estimating fruit abundance of tropical trees in other studies (Dinerstein, 1986; Chapman et al., 1992). An important limitation of this method is that fruits that drop from the tree (either naturally or removed by an animal) in between measurements cannot be accounted for. This is mostly a problem for species that drop large quantities of small fruits, such as *Ficus reflexa*, *F. rubra* and *Litsea* spp.

Home range and daily path length

The location of the study troop was manually recorded with a handheld GPS (Garmin eTrex 30x) every 30 min while following the troop. Because we could not collect an equal number of GPS points every month, we randomly selected 40 GPS points per month (equal to the least number of points collected in a month). QGIS and R were then used to map the monthly and total home range and calculate the length of daily paths. Estimates of limits and surfaces of the day range were derived by using the least square cross-validated fixed kernel density estimation (LSCV KDE) in R (script can be found in Appendix 1). This method is widely used and is an accurate

method for home range size estimation (Seaman and Powell 1996; Albert et al., 2013b). The 95% confidence region of the kernel density estimation (95% KDE) was used to represent the full home range and reflects the area associated with a 95% probability of finding the animal. The 50% confidence region (50% KDE) was also calculated, reflecting the core area that is disproportionately more used by the animals than other areas of the home range (Rühmann et al., 2019). The monthly and total 95% and 50% KDE's created in R were exported as shapefiles and mapped in QGIS. We could not calculate total daily path lengths because of an unequal number of daily GPS points. Additionally, sometimes we would lose the troop for more than an hour. Therefore, we first calculated distances between all of the consecutively recorded GPS points (30 minutes apart). For every day, we then randomly selected four of these 30-minute distances (total of two hours) and used them as substitute for daily path length. Days during which we could not record five GPS points consecutively were omitted.

Quantification of ripe vs. unripe fruit consumption and drop

The consumption and drop of ripe vs. unripe fruit by *M. fascicularis* were assessed by opportunistically quantifying fruit drop during feeding observations by using focal sampling. Both the exact time that a macaque or a group of macaques started feeding and the number of feeding individuals were recorded. We then randomly selected one feeding individual and observed it for as long as the feeding event lasted to determine the fruit parts it was consuming (whole fruit, pericarp, seed). The state of ripeness of fruits was also determined (ripe/unripe) and the type of fruit consumption was recorded: swallowed (when the entire fruit was ingested), spat out (when the fruit was taken into the mouth, mostly stored in cheek pouches, cleaned of the pulp and the seeds spat out), partly eaten (when portions of fruits, e.g., epicarp, were fed upon and then discarded), destroyed (when seeds were crunched by macaques) and dropped (when fruits were picked and discarded without being fed upon or accidentally dropped).

After the macaques finished feeding, we counted the discarded partly eaten pericarp of ripe and unripe fruits beneath the feeding tree to determine the number of consumed fruits (fruit consumption). For plant species with small fruit that only contained a single seed, we counted spat out or discarded seeds instead of discarded pericarp (e. g. *Litsea* spp.). We also determined the total number of fruits dropped by *M. fascicularis* by counting fruits that were dropped intact (either picked and discarded or accidentally dropped) and adding them to the number of consumed fruits. Fruit were either counted for 2 – 3 minutes or collected and stored in zip-lock bags so that they could be counted after field activities on the same day. The total number of consumed and dropped fruits were then divided by the total number of macaques on the tree to estimate consumption and drop by a single macaque, as distinguishing fruits handled by different individuals on the same tree in dense vegetation was often not possible. This method was suitable for most canopy species with medium to large-seeded fruits. However, very small, seeded fruits, such as *Ficus reflexa* and *F. rubra*, sometimes got swallowed whole, so quantification was limited for these species. Furthermore, seeds of *Litsea* spp. were too big to be swallowed, but the small fruits were often stored in *M. fascicularis*' cheekpouches (Fig. 3). Therefore, some fruits of this species were likely missed.



Figure 3: A macaque feeding on pinecone of *Pinus nigra* (left), a macaque eating fruits of *Psidium cattleianum* (middle) and a macaque chewing on fruits of *Litsea* spp. and *Flacourtia indica* stored in its cheekpouches (right).

Furthermore, the fruit consumption by *M. fascicularis* recorded during our feeding observations was compared to the fruit drop measured under native canopy trees in our study site. Fruit drop was measured for a total of three to four canopy tree replicates in a total of 15 randomly allocated plots (10 m by 10 m). Canopy species that were sufficiently abundant to be replicable were selected: *Aphloia theiformis*, *Calophyllum tacamahaca*, *Eugenia pyxidata*, *Labourdonnasia calophylloides*, *Mimusops maxima*, *Psiloxylon mauritianum*, *Syzygium glomeratum* and *Syzygium duponti*. The three to four replicates in every plot were a random subset of these species. Fruit drop was measured with seed traps, constructed of polyester fabric loosely stretched along a square pvc frame (1 m by 1 m). Two frames were placed under the canopy of every replicate and tied at least 0.5 m above the ground at all edges with plastic string to minimize fruit and seed removal by rats (Fig. 4). The seed traps were checked on a weekly basis from the start of the flowering until the end of the fruiting period for each tree. All fruits (intact and eaten) and seeds (intact and eaten) were recorded. Fruits eaten by *M. fascicularis* were characterized by large round canine and/or incisor marks (Krivek, 2017; Reinegger et al., 2021a). The teeth marks could be easily distinguished from marks left by other common large canopy feeders: *P. niger* leaves a typical triangular-shaped canine imprint (Banack 1998; McConkey and Drake 2015; Reinegger et al. 2021a), invasive rats (*Rattus rattus*) leave gnawing marks with their two upper and lower incisors and ringneck parakeets (*Psittacula krameri*) create V-shaped marks with their under and upper mandibles (VSG, 2018). Additionally, a single camera trap was placed on the trunk of one fruiting tree replicate per species and aimed at the canopy. A 10 second video was recorded when motion is detected, and the camera trap was left for two weeks.



Figure 4: Seed traps placed under the canopy of native trees in the study site.

Statistical analyses

Dietary, behavioural and ranging patterns

To determine food preference of *M. fascicularis*, we calculated Spearman's correlation coefficients between the different food availability indices (FAI, FIAI and PcaI) and the proportion of time *M. fascicularis* spent feeding on various food items every month. Furthermore, we calculated Spearman's correlation coefficients between exotic and native fruit availability and the proportion of time *M. fascicularis* spent feeding on native and exotic fruit every month. To determine whether fruit availability also influenced activity budgets, we calculated Spearman's correlation coefficients between FAI and the percentage of time *M. fascicularis* spent doing various activities, such as moving, feeding and resting. Moreover, the relationship between home range size, daily travel distance and food availability was assessed by calculating Spearman's correlation coefficients between monthly home range, mean daily path length (expressed as mean 2 hourly path length) and the different food availability indices.

We also calculated preference indices (S_i) for every plant species that *M. fascicularis* consumed fruits of to investigate fruit species preference using the formula from Sengupta et al. (2016):

$$S_i = \frac{f_i}{a_i}$$

Here, f_i is the percentage of total fruit feeding time *M. fascicularis* spent feeding on the fruits of species i of total fruit feeding time in the period that species i was available and a_i the percentage of total fruiting trees that species i constituted in the period it was available. A preference index of > 1 indicated that the species was preferred.

Ripe vs. unripe fruit preference

To determine whether macaque preferred ripe vs. unripe fruit and whether macaque ate and dropped riper vs. unripe fruit of native compared to exotic plant species, we first standardized the number of ripe vs. unripe fruits consumed and dropped by macaques. They were expressed as the proportion of ripe vs. unripe fruit consumed and dropped per macaque per minute. We then used generalized linear models (GLM's) to test the effects of Species (native/exotic) and monthly FAI on the proportion of ripe vs. unripe fruits consumed per macaque per minute and on the proportion of ripe vs. unripe fruits dropped per macaque per minute. Because our response variables are count-based proportions, we fitted the GLM's with binomial distribution.

We kept the models simple because we had an unequal number of samples in different months and during some months *M. fascicularis* did not feed on native fruits at all. Therefore, we only included Species (native/exotic) and monthly FAI as predictors in both models. A backwards model selection procedure based on the second order Akaike Information Criterion (AICc) was used to find the most parsimonious models among a set of models containing all possible variable combinations (Table 1). Models were then validated with residual diagnostic plots from package DHARMA (Hartig 2020).

Table 1: AICc table of a priori models explaining effects of monthly FAI and Species (native/exotic) on the proportion of ripe vs. unripe fruits consumed per macaque per minute and on the proportion of ripe vs. unripe fruits dropped per macaque per minute. Models are ranked in ascending order of AICc. The difference between model AICc and lowest AICc in the model set (Δ AICc) and AIC weight (ω) are also provided for every model.

Effects of FAI and Species on prop. ripe vs. unripe consumed	k	AICc	Δ AICc	ω
Prop. ripe vs. unripe ~ FAI + Species	3	94.4	0.0	0.58
Prop. ripe vs. unripe ~ FAI	2	95.0	0.7	0.42
Prop. ripe vs. unripe ~ 1	1	132.4	38.1	<0.001
Effects of FAI and Species on prop. ripe vs. unripe dropped				
Prop. ripe vs. unripe ~ FAI + Species	3	92.6	0.0	0.87
Prop. ripe vs. unripe ~ FAI	2	96.3	3.7	0.13
Prop. ripe vs. unripe ~ 1	1	127.2	34.6	<0.001

Fruit yield vs. fruit drop by M. fascicularis

To determine whether *M. fascicularis* made fruits of various tree species unavailable to *P. niger*, we estimated the percentage of yearly fruit yield per tree species within the macaque's home range that was dropped by the whole troop. Even though *M. fascicularis* also dropped intact fruits that can still be consumed by other animals, Old world Pteropodids such as *P. niger* are primarily canopy feeders (Fleming et al. 1987) and are thus unlikely to forage on the ground. Therefore, dropped intact fruits are likely to become unavailable to *P. niger*. We first estimated total yearly fruit yield per tree or liana species by averaging the maximum fruit yield recorded across individuals along our vegetation transects and then multiplying it by the average density of the species across our vegetation transects and the total home range. Total yearly fruit drop by *M. fascicularis* was then estimated for every tree or liana species that *M. fascicularis* used during our study period. Subsequently, we estimated yearly fruit drop per macaque for every tree species by calculating mean number of fruits dropped per macaque per minute, based on the feeding events for which we recorded fruit drop. Afterwards, we extrapolated fruit drop per macaque to a full year by multiplying it by the proportion of time that *M. fascicularis* spent feeding on the fruits of a particular species during our study period (based on the scan samples). Finally, it was multiplied by the total number of troop members (based on the minimum number of members counted: 19) so we could calculate the percentage of yield dropped by the troop.

Moreover, we compared the percentage of yield dropped by *M. fascicularis* per native plant species in the study site with the percentage of fruits eaten by *M. fascicularis* as measured with our seed traps.

Results

Fruit availability

We recorded 1288 trees belonging to 39 species along our phenology transects (Appendix 2). The majority of stems along transects was exotic (86%; Appendix 2). The FAI ranged from 21645 in March to 1739 in November (mean \pm *SD* = 11483 \pm 7310 per month). The fruit abundance period was defined as February - June 2020, when monthly FAI scores exceeded 15000 (Fig. 5). Exotic species accounted for the majority of the total FAI (70%) and also constituted the largest proportion of FAI during the fruit abundance period (72%). Only three exotic species accounted for the bulk of total FAI (63% by *F. indica*, *Litsea* spp., and *P. cattleyanum*; Appendix 2). The non-exotic portion of total FAI was mostly made up of three native species (24% by *Canarium paniculatum*, *P. mauritianum* and *S. glomeratum*; Appendix 2). Native species produced little fruit compared to exotics: only 15 out of 29 native species produced fruits, whereas 8 out of 10 exotic species produced fruit (Appendix 2). Additionally, only 45% of native stems produced fruit, whereas 73% of exotic stems produced fruit (Appendix 2). Overall, FAI showed a clear peak and trough. This was caused by the almost simultaneous fruiting peaks (February – March 2020) of *F. indica*, *P. cattleyanum* and *P. mauritianum* (33%, 15% and 16% of total FAI respectively; Appendix 2). Native FAI was more stable than exotic FAI, showing a less clear peak than exotic FAI and a slower decline in August (Fig. 5). Unlike native FAI, exotic FAI plummeted to zero (Fig. 5).

Activity budget and dietary patterns

We collected a total of 2764 scans (mean \pm *SD* = 2 \pm 1 individuals per scan; range = 1 – 9 individuals) over 75 days (3.1 \pm 1.8 hours per day) from December 2019 until December 2020 (19.2 \pm 7.3 hours per month). Our study troop was highly arboreal, spending 79% of their time in trees. Troop members mostly travelled on the ground when climbing slopes or when foraging on cliffs, in low canopy vegetation or near the forest edge. The macaques also crossed fields to access orchards and isolated patches of invasive pioneer vegetation. The macaques spent largest proportion of the time feeding (37%), followed by moving (33%), resting (16%) and grooming (7%). The monthly percentage of time that *M. fascicularis* spent feeding was positively correlated with FAI ($|r|$ = 0.59, P < 0.05) and the monthly percentage of time that *M. fascicularis* spent moving was negatively correlated with FAI ($|r|$ = -0.71, P < 0.05). This indicates that *M. fascicularis* spent significantly less time feeding and more time moving as FAI decreased.

Furthermore, the majority of *M. fascicularis* diet was made up of fruit (40.4%), followed by pinecone (26.3%), leaves (15.5%), invertebrates (6.0%), flowers (4.0%) and crops (2.7%; Fig. 5). Other food sources included tree bark (0.5%), grasses (0.3%) and eggs (0.2%). A small proportion of the diet could not be identified due to poor visibility (3.9%). The proportion of time *M. fascicularis* spent feeding on fruit was positively correlated with FAI ($|r|$ = 0.85, P < 0.001; Fig. 5). No significant correlations were found between the proportion of *M. fascicularis* spent feeding on flowers and FAI ($|r|$ = 0.29, P > 0.05) and the proportion of time *M. fascicularis* spent feeding on pinecone and FAI ($|r|$ = 0.35, P > 0.05). Furthermore, we found negative correlations between FAI and the proportion of time *M. fascicularis* spent feeding on leaves ($|r|$ = -0.59, P < 0.05), invertebrates ($|r|$ = -0.84, P < 0.01), flowers ($|r|$ = -0.73, P < 0.01) and crops ($|r|$ = -0.66, P < 0.05), suggesting that fruits are a preferred food source and that *M. fascicularis* increasingly feeds on leaves, flowers, invertebrates and crops as forest fruits become scarcer.

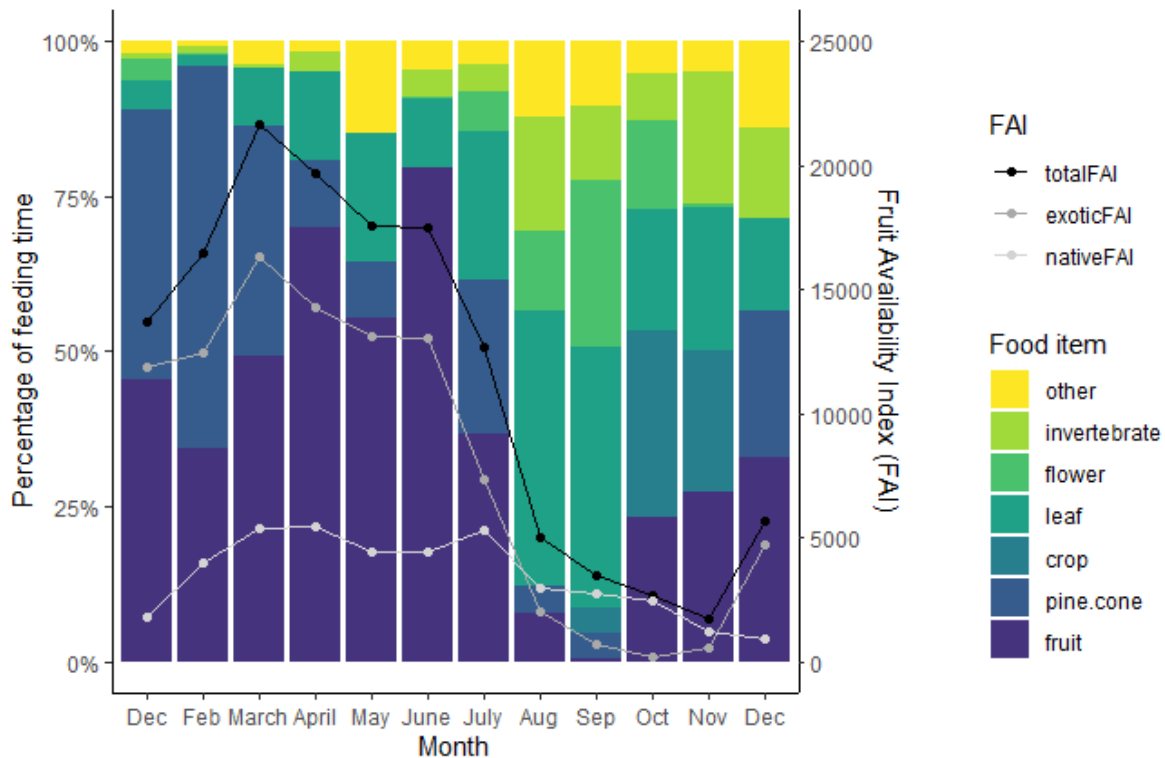


Figure 5: Percentage of time *M. fascicularis* spent feeding on various food items every month (left y-axis) and the monthly Fruit Availability Index (FAI) scores for all plant species (totalFAI), exotic plant species (exoticFAI) and native plant species (nativeFAI) (right axis).

Furthermore, *M. fascicularis* consumed plant parts of 36 plant species and the fruits of 17 plant species (Appendix 3). Exotic species made up the majority of the time *M. fascicularis* spent feeding on total plant foods (98%) and fruits (97%; Appendix 3). Of the time *M. fascicularis* spent feeding on fruits, invasive *Litsea* spp. and *P. cattleyanum* constituted the majority (40.2% and 39.3% respectively, Appendix 3), followed by invasive *F. indica* (9.5%) and exotic *Mangifera indica* (4.9%). Of the little time *M. fascicularis* spent feeding on native fruits, *E. pyxidata* made up the majority (24.1%), followed by *F. rubra* (20.7%) and *F. mauritiana* (13.8%). The proportion of exotic fruits in *M. fascicularis*' diet was positively correlated with exotic FAI ($|r| = 0.86$, $P < 0.001$). No significant correlation was found between the proportion of native fruits in *M. fascicularis*' diet and native FAI ($|r| = 0.17$, $P > 0.05$), indicating that exotic fruits are preferred over native fruits. The most preferred fruiting species based on preference index were *Litsea* spp., *S. jambos*, *S. dupontii* and *P. cattleyanum* (Appendix 3).

Moreover, of the invertebrates *M. fascicularis* ate, only the native cicada *Abricta brunnea* could be identified, which constituted 2.7% of *M. fascicularis* invertebrate diet. We could not determine to what species the gecko eggs *M. fascicularis* consumed belonged to.

Home range, daily path length and fruit availability

Our study troop had a total home range of 35.7 ha and a mean monthly home range of 13.1 ha with an *SD* of 6.7 ha (range = 3.2 – 28.4ha; Fig. 6). Daily path lengths (two hourly path lengths) could be calculated for a total of 51 days (mean \pm *SD* = 4 ± 2 days per month). Mean daily path lengths were slightly lower inside the fruit abundance period (241.2 ± 132.4 m) than outside of it (257.3 ± 152.6 m), but this difference was not significant. Both home range and mean daily path length were negatively associated with FAI ($|r| = -0.29$ and $|r| = -0.27$ respectively), but these correlations were not significant. The weak correlation between home

range and FAI was largely influenced by a home range outlier in November (Fig. 5). Mean monthly home range outside of the fruit abundance period (December 2019 and July – December 2020) was 15.4 ha ($SD = 7.8$) and November was the only month under 10 ha (3.2 ha). Removal of November resulted in a significant correlation between home range and FAI ($|r| = -0.66$, $P < 0.05$). In October 2020, when FAI was almost at its lowest, the troop started descending down the northern slope of Calebasses Mountain and moved towards the north-western forest edge next to the orchards and agricultural fields in Vallée du Paradis (Fig. 6). The troop remained here until the end of our study period.

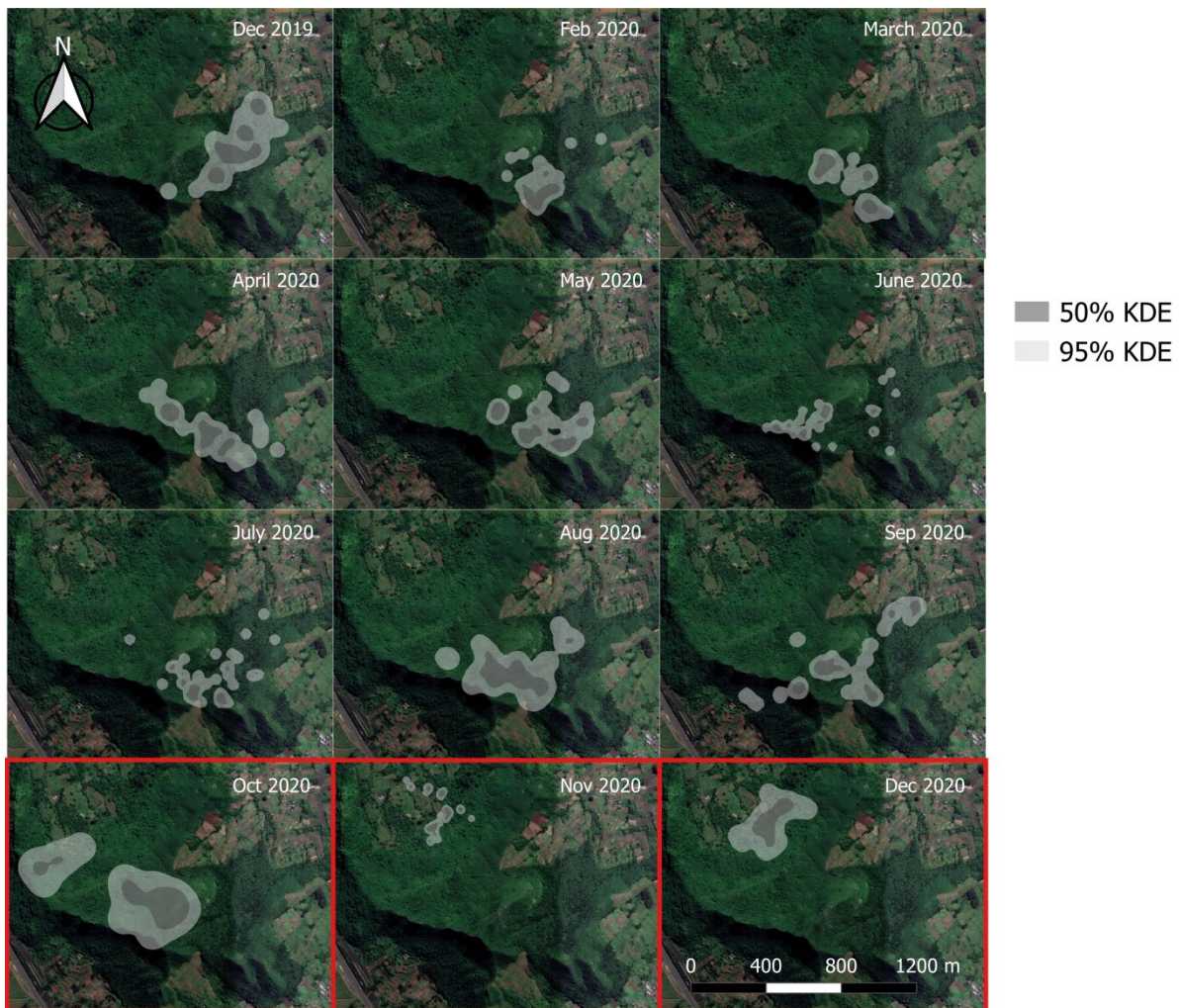


Figure 6: Monthly home ranges of the study troop from December 2019 until December 2020, represented by the 95% KDE. Core areas are represented by the 50% KDE. The period October – December 2020 has been highlighted in red, because the troop moved into a new area that it had not used in the months prior to October.

Ripe vs. unripe fruit

Fruit consumption and drop was quantified for a total of 114 feeding events (total feeding time = 14 hours) spread across 39 days from December 2019 until December 2020 (mean $\pm SD = 11 \pm 9$ events per month). The majority of fruit consumed and dropped by *M. fascicularis* was exotic (105 out of 114 total feeding events) and consumption and drop of native fruits was mostly recorded outside of the fruit abundance period (7 out of 9 native fruit feeding events). Overall, *M. fascicularis* consumed more ripe than unripe fruit (61% ripe, Table 3), but dropped less ripe than unripe fruit (35% ripe, Table 3). Most of the ripe fruits were consumed and dropped by *M. fascicularis* during the fruit abundance period (94% and 76% respectively;

February – June). The percentages of ripe vs. unripe fruits consumed and dropped by *M. fascicularis* were much smaller for native species (2% and 8% respectively) than for exotic species (72% and 38% respectively, Table 3). *Macaca fascicularis* consumed ripe fruits of only one native species (Table 3). The plant species with the largest percentages of ripe vs. unripe fruit consumed and dropped by *M. fascicularis* were *F. indica* (95% and 52% respectively) and *P. cattleyanum* (84% and 80% respectively). Moreover, the most common fruit treatments by *M. fascicularis* recorded during the feeding events were partly eating the fruit pulp and discarding the rest, plucking and dropping intact fruits and seed crunching (Table 3). Seed spitting was only recorded for invasive *Litsea* spp. (Table 3). The average percentage of dropped vs. consumed fruit per plant species was high (mean \pm SD: 50 \pm 31%) but varied greatly between species (range = 0 - 100%; Table 3). This indicates that overall *M. fascicularis* was a wasteful fruit consumer, especially for *Citrus* sp., *F. reflexa*, *F. rubra*, *F. indica*, and *Litsea* spp. (Fig. 7).

Table 3: Total, median and *IQR* for number of ripe and unripe fruits consumed and dropped by a single macaque for the following plant species: *Citrus* sp., *Eugenia pyxidata* (Eug pyx), *Ficus mauritiana* (Fic mau), *Ficus reflexa* (Fic ref), *Ficus rubra* (Fic rub), *Flacourtia indica* (Fla ind), *Litsea* spp., *Mangifera indica* (Man ind), *Noronhia broomeana* (Nor bro), *Psidium cattleyanum* (Psi cat), *Syzygium dupontii* (Syz dup) and *Syzygium jambos* (Syz jam). The status (St: native = Na or exotic = Ex), size of the seed (S: s = diameter < 1 cm, m = diameter \geq 1 cm but \leq 3 cm, l = diameter > 3 cm), treatment of the fruit (De = seeds crunched and destroyed, Di = fruit partly eaten and discarded, Dr = fruit dropped intact, Sp = seed cleaned of pulp and then spat out, Sw = fruit swallowed whole), total number of sampled feeding events (n) and total feeding time in minutes (t) are also given for every species. At the bottom of the table the total across all plant species is provided.

Species	St	S	Treatment	n	t	Consumed/ macaque: sum (median [<i>IQR</i>])		Dropped/ macaque: sum (median [<i>IQR</i>])	
						Ripe	Unripe	Ripe	Unripe
Citrus sp.	Ex	m	Di/Dr	1	16	-	2	-	11
Eug pyx	Na	m	De/Di/Dr	2	21	-	62 (31 [16 - 46])	-	96 (35 [18 - 52])
Fic mau	Na	s	Di	2	13	-	19 (10 [7 - 12])	-	19 (10 [7 - 12])
Fic ref	Na	s	Di/Dr/Sw	2	13	-	-	11 (6 [3 - 8])	21 (11 [6 - 15])
Fic rub	Na	s	Di//Dr/Sw	1	18	2	1	3	11
Fla ind	Ex	s	Di/Dr	10	79	53 (3 [1 - 9])	3 (0 [0 - 0])	79 (6 [1 - 13])	72 (5 [1 - 9])
Litsea spp.	Ex	m	Dr/Sp	33	272	142 (0 [0 - 10])	50 (0 [0 - 1])	364 (7 [1 - 16])	818 (14 [5 - 40])
Man ind	Ex	l	De/Di/Dr	19	170	2 (0 [0 - 0])	48 (2 [1 - 3])	2 (0 [0 - 0])	82 (3 [2 - 5])
Nor bro	Na	m	De/Di/Dr	1	3	-	4	-	5
Psi cat	Ex	s	Di/Dr	40	218	168 (3 [1 - 6])	33 (0 [0 - 1])	203 (4 [1 - 7])	53 (0 [0 - 2])
Syz dup	Na	m	De/Di/Dr	1	8	-	5	-	9
Syz jam	Na	m	De/Di/Dr	2	11	-	9 (5 [2 - 7])	-	13 (7 [3 - 10])
			Total:	114	842	367	236	662	1210



Figure 7: Intact and partly eaten fruits dropped by *Macaca fascicularis* during feeding observations: A) unripe partly eaten fruits of *Ficus mauritiana*, B) intact and partly eaten ripe and unripe fruits of *Flacourtia indica*, C) partly eaten ripe and unripe fruits of *Psidium cattleianum* and D) intact and partly eaten fruits of *Eugenia pyxidata*. The fruits in picture A were dropped by a single individual in one minute, fruits in pictures B dropped by two individuals in 10 minutes, fruits in picture C by two individuals in 22 minutes and the fruits in picture D were dropped by two individuals in 16 minutes.

Our GLM's showed that there was a weak significant difference in the proportions of ripe vs. unripe fruit consumed and dropped per macaque per minute between native and exotic species (Fig. 8; Appendix 4). Furthermore, we found highly significant effects of FAI on both the proportions of ripe vs. unripe fruit consumed and dropped per macaque per minute (Fig. 8; Appendix 4). This indicates that a larger proportion of native fruit is consumed and dropped unripe compared to exotic fruit and that ripe fruit is preferred over unripe fruit.

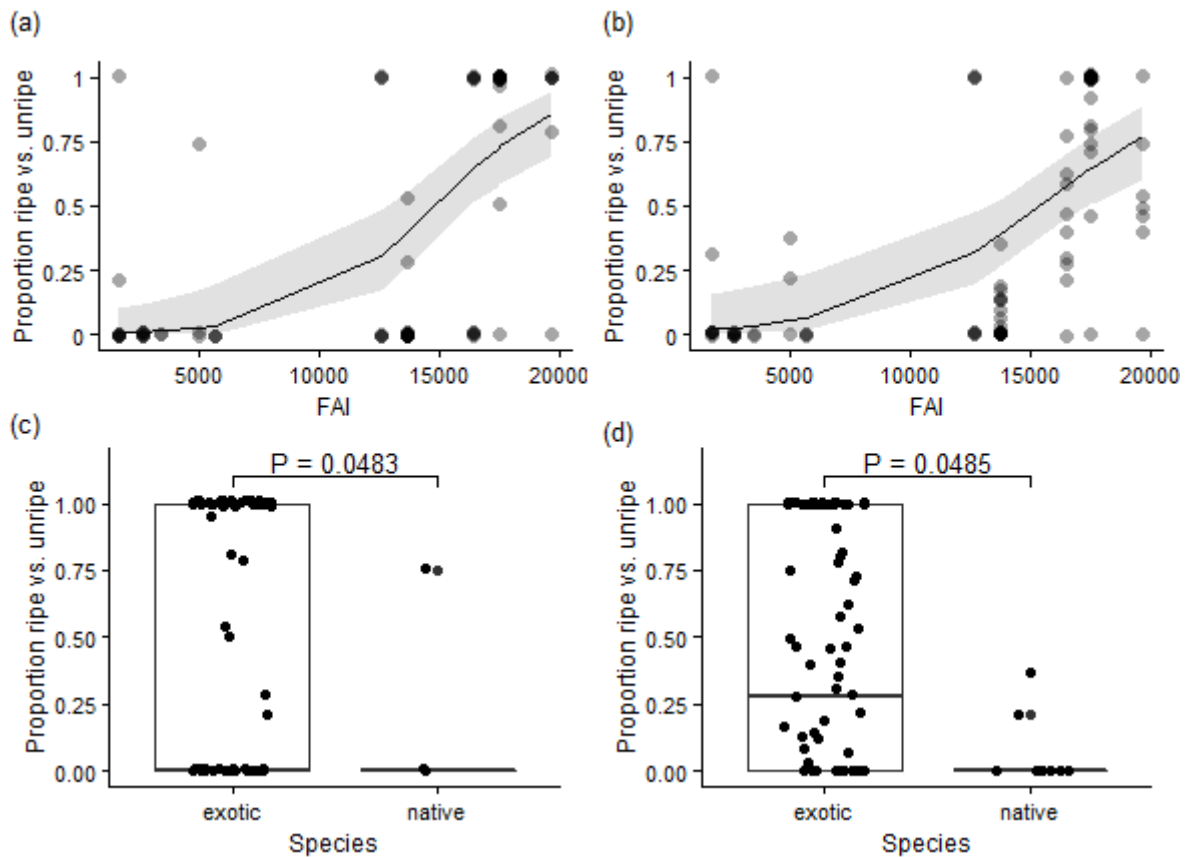


Figure 8: Line of best fit with confidence intervals estimated by the most parsimonious binomial GLM's expressing a) the relationship between FAI and the proportion of ripe vs. unripe fruit consumed per macaque per minute and b) the relationship between FAI and the proportion of ripe vs. unripe fruit dropped per macaque per minute. The bottom figures contain boxplots for c) the proportion of ripe vs. unripe fruits consumed per macaque per minute for native and exotic plant species and d) the proportion of ripe vs. unripe fruits dropped per macaque per minute for native and exotic plant species. The P -values for the difference in group means as predicted by the most parsimonious binomial GLM's are also provided. The full description of these models can be found in Table 1.

Fruit yield vs. drop by *M. fascicularis*

Macaca fascicularis did not feed on all plant species that were marked along our transects. Furthermore, some of the species included in *M. fascicularis* fruit diet were not present along the transects, because they were restricted to forest edges (e.g., *M. indica*) or very rare (e.g., *Noronhia broomeana*). Therefore, estimation of the percentage of total fruit yield in the home range that was dropped by *M. fascicularis* was limited to seven plant species (Table 4). The estimates indicated that *M. fascicularis* dropped all fruits of two native plant species (*E. pyxidata* and *F. mauritiana*) and the majority of another native species (*S. dupontii*) within their home range (Table 4), which accounted for ~6% of native FAI and ~2% of total FAI (Appendix 2). Additionally, they dropped all fruit of three exotic plant species (*Litsea* spp., *P. cattleyanum* and *S. jambos*) and the majority of exotic *F. indica* fruits (Table 4). Combined these species accounted for 66% of total FAI and ~91% of time *M. fascicularis* spent feeding on fruits (Appendix 3), suggesting that *M. fascicularis* plucked and dropped the majority of fruit available in their home range.

Table 4: Median and interquartile range (*IQR*) for fruits dropped per macaque per minute (Fruit macaque/minute) for various plant species (Eug pyx = *Eugenia pyxidata*, Fic mau = *Ficus mauritiana*, Fla ind = *Flacourtia indica*, Litsea spp. = *Litsea glutinosa* and *monopetala*, Psi cat = *Psidium cattleianum*, Syz dup = *Syzygium dupontii* and Syz jam = *Syzygium jambos*), status of the plant species (St: Na = native, Ex = exotic), the percentage of total observation time *M. fascicularis* spent feeding on fruits of a particular species (% of total time), median and *IQR* for estimated number of fruits dropped by our study troop/year based on minimum number of troop members and % of total time (fruit/year/troop), median and *IQR* for estimated yearly fruit yield of every plant species inside our study troop's home range (Fruit yield in home range) and the percentage of this yield that *M. fascicularis* dropped based on median fruit drop/year/troop (% of yield dropped).

Species	St.	Fruit macaque/minute (median [<i>IQR</i>])	% of total time	Total fruit/year/troop (median [<i>IQR</i>])	Fruit yield in home range (median [<i>IQR</i>])	% of yield dropped
Eug pyx	Na	2.2 [1.6 – 2.8]	0.1046	22,981 [16,713 – 29,248]	2,502 [0 – 21,270]	100
Fic mau	Na	3.08 [2.12 – 4.04]	0.0598	18,393 [12,660 – 24,126]	3,640 [0 – 8,770]	100
Fla ind	Ex	1.96 [1.17 – 2.26]	1.42	277,941 [165,914 – 320,484]	287,254 [0 – 3,858,344]	97
Litsea spp.	Ex	4.06 [2.5 – 8]	6.0	2,432,687 [1,497,960 – 4,793,472]	229,949 [0 – 344,924]	100
Psi cat	Ex	0.88 [0.73 – 1.67]	5.875	516,296 [428,291 – 979,791]	88,686 [0 – 532,117]	100
Syz dup	Na	1.12	0.0448	5,011	6,222 [3,111 – 9,333]	81
Syz jam	Ex	1.08 [0.54 – 1.62]	0.1495	16,124 [8,062 – 24,186]	0 [0 – 12,719]	100

The percentages of fruits eaten by *M. fascicularis* measured with the seed traps were largely consistent with the estimated percentages in table 4 and the dietary patterns we observed during our study period. About 91% of the *E. pyxidata* fruits and 100% of *S. dupontii* fruits recorded in the seed traps were eaten by *M. fascicularis* (Fig. 9), reflected by our estimates in table 4 and the extremely small proportion of FAI these species accounted for (Appendix 2). Furthermore, *M. fascicularis* consumed < 0.5% of *S. glomeratum* fruits and no fruits of *P. mauritianum* (Fig. 9). This is reflected by the extremely small percentage of time that *M. fascicularis* spent feeding on fruits of *P. mauritianum* and the absence of *S. glomeratum* in *M. fascicularis*' fruit diet (Appendix 3), even though they accounted for 16 times the FAI percentages of *E. pyxidata* and *S. dupontii* combined (Appendix 2). Moreover, the fruits of *A. theiformis* and *S. mauritianum* recorded in the seed traps were not eaten by *M. fascicularis*, reflected by the absence of feeding records for these species in our observational data (Appendix 3). The other 3 native species that we monitored with seed traps did not produce fruits (*C. tacamahaca*, *L. calophylloides* and *M. maxima*).

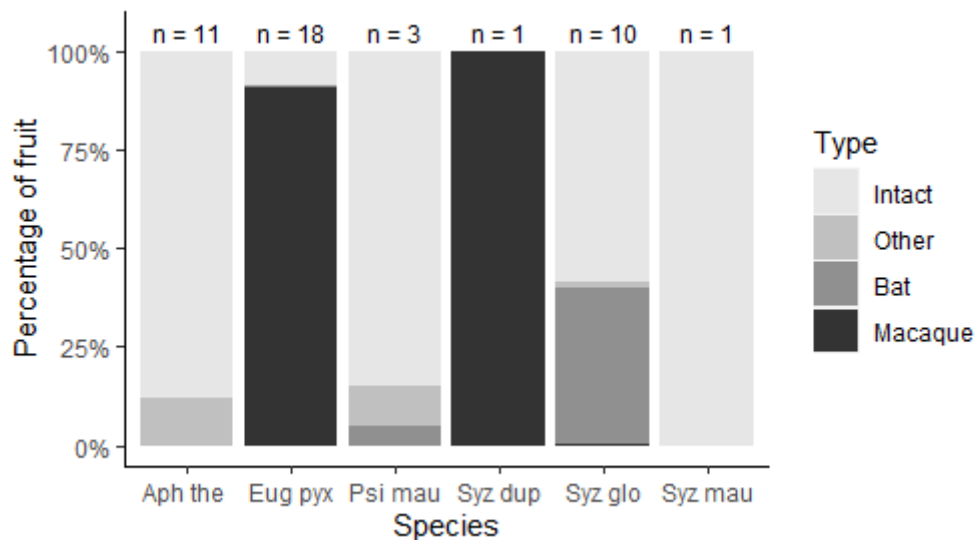


Figure 9: Percentage of fruits sampled with seed traps that remained intact or were eaten by either *Macaca fascicularis* (macaque), *Pteropus niger* (bat) or other animals (other) for *Aphloia theiformis* (Aph the), *Eugenia pyxidata* (Eug pyx), *Psiloxylon mauritianum* (Psi mau), *Syzygium dupontii* (Syz dup), *Syzygium glomeratum* (Syz glo) and *Syzygium mauritianum* (Syz mau). The number of tree replicates per species has been provided at the top of each bar (n). Species for which no fruits were recorded have been omitted.

Anecdotal observations

Seed dispersal

Even though we did not quantify seed dispersal, we frequently recorded what seeds were present in faeces of *M. fascicularis* while doing behavioural observations during the fruit abundance period (February – June 2020). Faeces typically contained fully developed seeds of invasive *F. indica* and *P. catteyanum*.

Neighbouring troops

We could identify three neighbouring troops during our study period (Fig. 10). The first neighbouring troop was identified early during our study, because it shared some our troop's home range in December 2019. It was similar in size to our study troop (~20 individuals) and during December 2019 – February 2020 the group sometimes crossed paths with our study troop in the late morning, which resulted in fighting. When fights broke out, we could not distinguish between troops, but one group would always leave the Calebasses Mountain Range in the late afternoon through a forest corridor in the East (Fig. 10), indicating they used a different sleeping site from our study troop. On confusing days like these, we always made sure to revisit our study troop's sleeping site in the early evening to confirm their return. The second neighbouring troop was identified a bit later in March, because their sleeping site was located on Les Mariannes, a mountain opposite of Calebasses Mountain. We visited the troop three days in a row. The troop was small (~7 individuals) and appeared to mostly occupy the eastern edges of the forest to avoid running into our study troop. A fight between this troop and our study troop was observed once. The third neighbouring troop was identified in October when our troop moved towards the north-western forest edge to feed on orchard trees. This troop occupied the eastern forest 'arm' of the Calebasses mountain range and was about twice the size of our study troop (~40 individuals). This troop appeared to raid farmlands daily but was never observed crossing paths with our study troop.

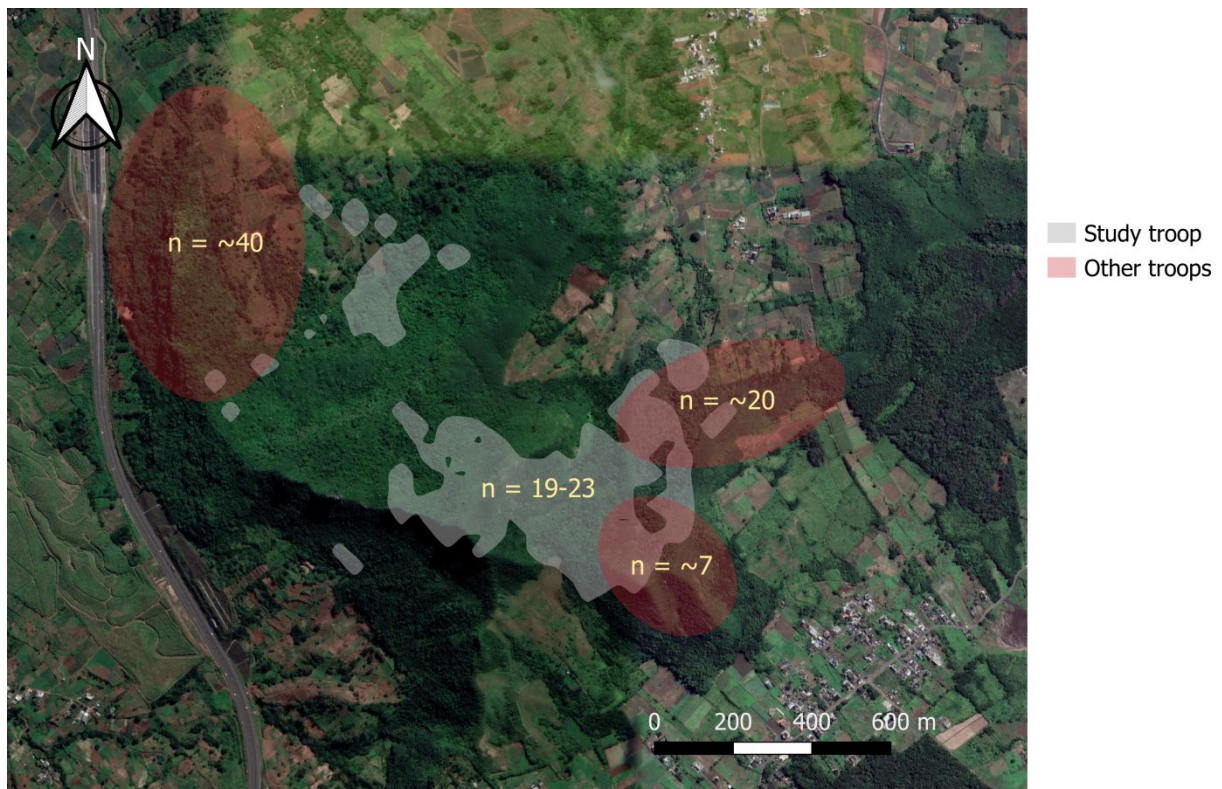


Figure 10: Map of the Calebasses Mountain Range with the total home range of our study troop in grey (based on the 95% KDE) and the approximate locations of the neighbouring troops in red. Estimated number of individuals is also provided for every troop (n).

Raiding of farmlands/orchards and monkey trapping

Because our troop moved towards a new area in October 2020 to feed in orchards for the first time, we visited three fruit farmers in Vallée du Paradis to ask about the macaques. We asked how often *M. fascicularis* visited their fields, how many troops visited the farmlands, from what direction the troops entered the farmlands and whether they had noticed a difference in macaque raiding frequency between the Mauritian winter (high fruit abundance in the study site) and summer (fruit scarcity in study site and commercial fruit season). The farmers all confirmed the macaques visited their farm fields all year round, but that the raiding frequency increased end of winter/ early summer. They all said they commonly saw a large group of about 50 individuals coming from the eastern forest ‘arm’, confirming the presence of the third neighbouring troop. One farmer said he frequently saw one group coming from the direction of our study troop, but he could not confirm whether he had only witnessed this in summer. Moreover, they all said there was one additional troop which did not come from the Calebasses Mountain Range, but from a strip of pioneer vegetation to the North that was surrounded by farmlands. We did not have time to confirm the presence of this troop. Furthermore, the farmers mentioned that macaques were frequently captured year-round near the north-western edge. We could confirm this because we found several cage traps with minor rust stains in this area. As far as we are aware, no capture/trapping activities were carried out when our troop moved into this area.

Discussion

Refuging behaviour and troop size

Macaca fascicularis is considered a ‘refuging species throughout its range, returning to a central sleeping site every night (Van Schaik et al., 1996; Sussman et al., 2011). Our study troop also

showed typical 'refuging' behaviour and their sleeping site was located on a steep, densely vegetated, north-west facing slope on Calebasses Mountain. Even though our troop sometimes used the forest on the south-eastern slope of Calebasses Mountain as sleeping site, our findings largely align with the findings of Sussman and Tattersall (1981) and Sussman et al. (2011). Their research also shows that *M. fascicularis* uses hillslopes and cliffs with dense thickets of vines as sleeping site in Mauritius. This contrasts with undisturbed habitat in *M. fascicularis*' native range, where sleeping sites are usually located around rivers (Wheatley, 1980; Van Schaik, 1996).

However, our study troop was much smaller than the troops studied by Sussman et al. (2011) and our macaques spent most of their time in trees (79%) instead of on the ground. This mostly arboreal nature is shared with *M. fascicularis* populations in most of Southeast Asia, especially in places where they are sympatric with terrestrial *M. nemestrina* (71% and 97% of time spent in trees) (Crocket and Wilson, 1980; Wheatley, 1980). The availability of contiguous vegetation in our study site may have allowed the macaques to stay in trees, contrary to study sites of Sussman et al. (2011), which consisted mostly of shrubland and savannah. Furthermore, the small troop size could be explained by the abundance of dense vegetation, leaving the troop less exposed to predators (stray dogs) and thus being part of a large group was not as important as in open shrubland. However, we also confirmed recent macaque capture activities near the north-western forest edge, which could also be an important factor contributing to small group sizes (Sussman et al. 2011). Depending on the frequency of trapping efforts in recent years, the troops in Calebasses Mountain Range may have been reduced in size. Nevertheless, these findings highlight spatial variation in behaviour and ecology of introduced *M. fascicularis* and the ability of *M. fascicularis* to adapt to a wide variety of habitats.

Fruit availability driving patterns in activity budget, diet and home range

Our study troop spent the majority of its time feeding (37%) and moving (33%). This activity pattern is similar to what Sussman et al. (2011) found in Mon vallon (32% feeding and foraging, 25% moving and travelling), most likely because most forest habitat is highly disturbed/degraded, resulting in patchy distribution of food sources. As a result, *M. fascicularis* has to spend more time travelling and foraging when it has no access to clumped resources that are available year-round, such as food provisioned by humans on a daily basis (Son, 2004). Similar patterns were also recorded in disturbed forest on the Malay Peninsula (MacKinnon and MacKinnon, 1980) and Borneo (Mohammad and Wong, 2019), where resources were patchily distributed. Furthermore, our findings indicate *M. fascicularis* spends more time moving and less time feeding as fruits become scarcer. This was to be expected as lower fruit availability would require more travelling to find high-quality food and obtain sufficient nutrients. These variations in activity budget driven by fruit availability have also been recorded for other *Macaca* spp., such as *M. maura* that spends more time feeding when in fruit rich habitat compared to fruit poor habitat (Albani et al. 2020) and *M. silenus* that spends more time moving around trees in search of food when fruits are scarce (Menon and Poirier, 1996).

The proportion of fruits in the diet of *M. fascicularis* (40%) was very similar to a previous study on *M. fascicularis* in the Southwest of Mauritius (38%, Sussman et al., 2011), indicating that the degree of frugivory is similar across the island but smaller than in unprovisioned *M. fascicularis* in its native range (64% - 67%) (Ungar, 1995; Yeager, 1996). Furthermore, fruits are increasingly consumed as fruits become more abundant, contrary to leaves, flowers, invertebrates and crops, indicating that fruit is a preferred food source. These findings show *M. fascicularis* has a similar response to fruit availability in Mauritius as in its native range (Lucas

and Corlett, 1991; Yeager et al. 1996; Ruslin et al., 2019). Sussman et al. (2011) were not able to properly assess food preference, but the percentages of leaves (22%), flowers (9%) and crops (6%) in their troop's diet were also quite similar to what we found (15.5%, 4.0% and 2.7% respectively). Therefore, the troop studied by Sussman et al. (2011) may have responded similarly to fruit availability as our troop.

Furthermore, *M. fascicularis* barely fed on native species and the majority of *M. fascicularis* plant and fruit diet is made up of exotic plant species. Our findings show that this is a result of *M. fascicularis* preference for exotic over native fruits and the much higher exotic vs. native stem density and fruit availability (70% of available fruit in home range is exotic). Especially *Litsea* spp., *S. jambos* and *P. cattleyanum* were highly preferred exotic species. Their preference for *P. cattleyanum* may be caused by the sweet, slightly acidic and juicy pulp of its fruits, which made up 39% of time *M. fascicularis* spent feeding on fruit. *Macaca fascicularis* is known to prefer ripe and succulent fruits that are often sweet and acidic (Ungar, 1995). *Psidium cattleyanum* fruited simultaneously with native *P. mauritianum* and *S. glomeratum*, which produce small fleshy drupes with little pulp that are less sweet and acidic than *P. cattleyanum*. These native species provided the majority of native fruit (62%) but were almost completely ignored by *M. fascicularis* (0.1% of time spent feeding on fruits).

Furthermore, ripe *P. cattleyanum* fruits are bright red/yellow, whereas ripe *P. mauritianum* fruits are pale yellow/green and *S. glomeratum* fruits dark purple/red. Primates are known to select bright yellow or orange fleshy fruit (Gautier-Hion et al., 1985; McConkey et al. 2002) and in some instances also bright red (Terborgh, 1983; Gautier-Hion et al., 1985; Julliot, 1996; Skalníková et al. 2020). This is attributed to their trichromatic vision, which allows them to distinguish yellow, orange and red from green (Mollon, 1991) and potentially gives them an advantage in detecting brightly coloured ripe fruits (Onstein et al. 2020; Skalníková et al. 2020). Aslan and Rejmánek (2012) proposed that fruit traits of native plants can dictate how well an exotic plant competes for native seed-dispersers. Based on our findings, we argue that this theory probably also works in the other direction: that fruit traits of exotic plants can dictate how well a native plant competes for exotic seed-dispersers.

However, other factors are likely to influence fruit choice too, since *Litsea* spp. was a highly preferred species, even though the ripe fruits are small dark drupes with little fruit pulp (similar to *S. glomeratum*). Both *Litsea* and *Syzygium* were found to be key genera in the diet of *Macaca* spp. (present in diet of >50% of *Macaca* spp. and eaten in >50% of habitats where *Macaca* spp. are present) and were also considered preferred plant genera and yearly staple foods for *Macaca* spp. (Sengupta et al. 2020). The reason *S. glomeratum* fruits were ignored and *Litsea* fruits were not may be that *Litsea* was mostly available when *P. cattleyanum* was not. Therefore, relative fruit abundance may also explain preference by *M. fascicularis*, as both *Litsea* spp. and *P. cattleyanum* were highly abundant. Fruit abundance is known to be an important cue for frugivorous birds to select fruits (Sallabanks, 1993). However, *M. fascicularis* also showed preference for other *Syzygium* spp. (*S. dupontii* and *S. jambos*, Appendix 3), which were not very abundant. Nutrient and energy content analysis of these fruits may reveal why *M. fascicularis* prefers these fruits. For example, energy content partly explains preference for invasive over native fruits by frugivores in California (Vilá and D'Antonio, 1988) and why *M. tonkeana* is so attracted to cultivated cacao (Riley et al. 2013).

Moreover, another important food source was pinecone. We did not find a significant correlation between the percentage of time *M. fascicularis* spent feeding on pinecone, pinecone availability and fruit availability. Nevertheless, the woody pinecone is high in cellulose and should be more

difficult to digest and thus less nutritious than fleshy fruits for hindgut-fermenting macaques (Chivers, 1994). Therefore, pinecone was probably not a preferred food source and more likely to be a 'fallback' food. The use of pinecone as 'fallback' food has also been observed in howler monkeys in Argentina (*Alouatta* spp.), which are known to exploit pinecone during periods of fruit scarcity (Agostini et al., 2010). *Alouatta* spp. and *M. fascicularis* are both hindgut-fermenters, persist in highly disturbed forests (Crocket, 1998) and have some of the highest seasonal dietary variability among primates (Chapman and Chapman, 1990), emphasizing their opportunistic and adaptive abilities. However, this is the first time that *M. fascicularis* has been reported to spend a relatively large proportion of time feeding on pinecone.

Ranging patterns also appeared to be related to fruit availability. Even though the negative correlation between monthly home range and FAI was very weak, removal of November 2020 resulted in a significant negative correlation. Monthly home range in November was much smaller than in the other months outside of the fruit abundance period and may be explained by the fact the troop moved towards the orchards in October 2020. In November 2020 our study troop had settled near the orchards and was mostly feeding on mango trees on farmlands and on the forest edges. The temporary abundance of food probably made travel redundant. In the following month home range increased again, possibly because the troop had depleted local fruit sources and had to range further again in order to find sufficient food. Remarkably, our study troop did not go near these orchards during October – November 2019, while we were still in the process of habituating the troop. This may be explained by the ongoing capture of *M. fascicularis* near the forest edges, resulting in size reduction of other local troops that may have occupied these areas in 2019. In October 2020 our study troop may then have grabbed the opportunity to move close to the orchards in search for food, because fruits were scarce. Therefore, our findings indicate *M. fascicularis* probably used energy maximizing- strategies as forest fruits became scarce.

Because ranging patterns and dietary patterns are often on an annual cycle for *Macaca* spp. (O'Brien and Kinnaird, 1997; Hanya et al. 2003) and macaque females are usually philopatric (Noordwijk and Van Schaik, 1999; Xia et al. 2019), we assume that we observed a troop migration in October 2020. Migration by single individuals is common, as males typically split from their natal troop and join adjacent troops (Noordwijk and Van Schaik, 1985; Kuester and Paul, 1999). However, migration or 'expeditions' by an entire troop or large groups are not common because in undisturbed habitat other areas are likely to be inhabited by other troops (Noordwijk and Van Schaik, 1985). Scarce resources and lack of adjacent troops may facilitate ranging outside of their original home range (Sugiyama and Ohsawa, 1982; Hanya et al. 2002). For example, there are various cases of *M. fuscata* troops either splitting into separate troops (Sugiyama and Ohsawa, 1982) or migrating completely (Hill and Angetsuma, 1995; Hanya et al. 2002). Similar to our troop, these troops occupied a habitat heavily modified by humans, consisting of a mosaic of forest, farmlands and human settlements (Sugiyama and Ohsawa, 1982; Hill and Angetsuma, 1995; Hanya et al. 2002), or experienced capture by humans (Sugiyama and Ohsawa, 1982). Expeditionary ranging by our study troop was probably also driven by food scarcity and facilitated by macaque capture. This also emphasizes the resilience of *M. fascicularis* and their ability to quickly react to changes in their environment.

Fruiting patterns driving consumption of unripe fruit

Macaca fascicularis preferred ripe fruit and increasingly consumed unripe fruits as fruits became scarcer. The vast majority of native fruit consumed by *M. fascicularis* was unripe, aligning with the findings of Florens and Baidar (2006), Krivek (2017) and Reinegger et al. (2021a).

However, the majority of exotic fruit consumed by *M. fascicularis* was ripe, meaning that overall *M. fascicularis* does consume more ripe than unripe fruit in Mauritius, because the majority of fruits consumed by *M. fascicularis* were exotic. The reason that *M. fascicularis* consumed a significantly larger proportion of native than exotic unripe fruits was probably due to the fact that *M. fascicularis* generally preferred exotic over native fruits and mostly consumed native fruits outside of the fruit abundance period. Additionally, the vast majority of ripe fruits were consumed during the fruit abundance period (94%; February – June). Therefore, our findings suggest that *M. fascicularis* can only rely on ripe fruits for a few months in the disturbed forest habitat in Calebasses Mountain while for the rest of the year it mostly feeds on unripe fruits.

This was likely a result of the extreme peak and trough in fruit availability, caused by the simultaneous fruiting of two exotic and one native species that combined made up 64% of total fruit availability. Furthermore, the poor fruiting success of native compared to exotic species also contributed to this fruiting pattern, as native FAI showed a less extreme peak and trough than exotic FAI. There were nearly twice as many native as exotic species along our transects, but the majority of fruit was produced by exotic species. Furthermore, only three highly invasive species (*F. indica*, *Litsea* spp. and *P. cattleyanum*) accounted for the bulk (90%) of exotic fruit. This imbalance in fruit production is a common phenomenon in Mauritius, because invasive species are gradually replacing the native vegetation (Strahm, 1993; Baider and Florens, 2011; Florens et al. 2017) and also reduce flower (Monty et al. 2013) and fruit production of native trees (Monty et al. 2013; Krivek et al. 2020). Therefore, it is likely that *M. fascicularis* has similar dietary patterns elsewhere in Mauritius, because *F. indica*, *Litsea* spp. and *P. cattleyanum* dominate various sub-humid and wet forests across the island. However, the composition of the native fruit diet is likely to vary, because native species dominance and frequency often vary greatly between forest patches (Reinegger et al. 2021b).

Nevertheless, the majority of fruit dropped by *M. fascicularis* (including 'wasted' intact fruit) was unripe and for many plant species large percentages of fruit dropped by *M. fascicularis* were intact. As a result, large quantities of fruit were wasted. The only plant species likely to be effectively dispersed by *M. fascicularis* were invasive *F. indica*, *P. cattleyanum* and *Litsea* spp. For example, seed spitting, which is considered an effective seed dispersal mechanism (Gross-Camp and Kaplin, 2011), was only observed for invasive *Litsea* spp. Furthermore, the majority of *F. indica* and *P. cattleyanum* fruits were consumed and handled when ripe and mature seeds of invasive *F. indica* and *P. cattleyanum* were often found in the faeces of *M. fascicularis*. These three species also made up the majority of time *M. fascicularis* spent feeding on fruits. Consequently, the chance of successful seed dispersal by *M. fascicularis* was generally low but highest for invasive *F. indica*, *P. cattleyanum* and *Litsea* spp.

Additionally, according to our estimates *M. fascicularis* dropped the majority of available fruit within its home range, suggesting that less than 34% of available fruit remains for canopy feeding frugivores, such as *P. niger*. Furthermore, our findings also indicate *M. fascicularis* consumed and dropped the vast majority of fruits of at least three native species (*F. mauritiana*, *E. pyxidata* and *S. dupontii*) at an unripe stage, which was largely reflected by our seed trap measurements. Additionally, even though we did not measure fruit availability for *N. broomeana*, the fruits were likely also depleted at an unripe stage by *M. fascicularis*, because the plant is very rare in the study site. The not preferred fruits of native *C. paniculatum*, *P. mauritianum* and *S. glomeratum* (24% of available fruit), were probably the most considerable fruit resources still available to *P. niger* within our study troop's home range.

In summary, these dietary patterns indicate that *M. fascicularis* is likely an important disperser of invasive *F. indica*, *Litsea* spp. and *P. cattleyanum* in Mauritius. However, *M. fascicularis*' seed dispersal effectiveness for native species in Mauritius is probably limited because the majority of fruit handled by *M. fascicularis* is plucked at an unripe stage. Even though in some cases fruit does not have to be ripe in order for seeds to germinate (Cruz-Tejada et al. 2018), generally ripeness of a fruit is an indicator for seed germination success (Sumner and Mollon, 2000). Therefore, *M. fascicularis* likely halts the regeneration of at least four native species, by exploiting unripe fruits and preventing seed-dispersal by *P. niger*. Consequently, *M. fascicularis* likely plays an important role in the ongoing degradation of Mauritius' native remnant forests. There are other examples of invasive animals promoting forest degradation by facilitating plant invasion. Invasive black rats (*R. rattus*) in Hawaii may promote plant invasion by predated more native than invasive species (Shiels and Drake, 2011) and invasive silver pheasants (*Lophura nycthemera*) in Argentina disperse more exotic than native seeds (Martin-Albarracin et al. 2018). However, the role of an invasive animal in forest degradation will always be context dependent, as invasive birds in Hawaii probably have a positive effect on forest regeneration by being important dispersers of native plants (Foster and Robinson, 2007).

Nevertheless, there are not many cases of *Macaca* spp. primarily consuming unripe fruits because of fruit scarcity. For example, exploitation of unripe fruit has been reported for *M. mulatta* in limestone forest habitat (Tang et al., 2016). Due to limited fruit availability *M. mulatta* is predominantly folivorous throughout the year. However, when fruits become available, they are mostly consumed unripe (Tang et al., 2016). Shifts from a diet of mostly ripe fruits to a diet of mostly unripe fruits when fruits become scarcer have also been recorded for birds (Foster, 1977). However, there are no examples of fruit availability patterns as a result of human disturbance promoting this particular feeding strategy in macaques.

Our example in Mauritius is probably unique, as various factors likely contribute to this particular feeding strategy in *M. fascicularis*. For example, many native plants show adaptations to bat dispersal, as the ripe fruits of large-seeded native plants predominantly have inconspicuous colours (green/ brown) and strong odours (Nyhagen, 2004). Therefore, *M. fascicularis* may have difficulty selecting ripe native fruit, because unlike flying foxes, they do not have an acute sense of smell. Instead, they are more likely to depend on their trichromatic vision to detect and select ripe fruit (Onstein et al. 2020; Skalníková et al. 2020), which is not useful if the fruit does not turn yellow, orange or red when ripe. Additionally, *M. fascicularis* was introduced only 400 years ago, possibly not long enough to develop the ability to efficiently detect ripe native fruits that are green or brown in colour. The combination of these factors, *M. fascicularis*' fruit preference and the imbalance in fruit availability as a result of forest degradation largely explain why *M. fascicularis* predominantly consumes unripe native fruits in Mauritius.

Nevertheless, tropical forests degraded by human activities are rapidly expanding (Wright, 2005; Chazdon, 2008). Additionally, human disturbance already has a number of effects on feeding strategies of macaques. For example, human provisioning can decrease the amount of time macaques spend foraging and/or moving (Alami et al. 2012; Dhawale et al. 2020) and reduce fruit consumption and seed dispersal (Sengupta et al. 2015). In our example we have studied a tropical *Macaca* spp. outside of its native range, but we argue that the ongoing habitat degradation caused by human disturbance may force tropical macaques to adopt similar feeding strategies in their native range as *M. fascicularis* in Mauritius depending on fruit preference, the relative abundance of exotic vs. native fruit and fruit traits of exotic species.

Other ecosystem impacts

Macaca fascicularis had a number of other impacts on the native biota, both flora and fauna. Consumption of young shoots of *E. pyxidata*, *F. reflexa*, *F. mauritiana*, *Mimusops maxima* and *Sideroxylon puberulum* was sometimes observed. However, the low frequency at which this occurred and the limited number of shoots that were consumed during a feeding event suggest that this may not have a great impact on plant growth. Nevertheless, *F. reflexa*, *F. mauritiana* and *M. maxima* are scarce in the study site and even infrequent feeding on shoots may have a considerable impact on the few individuals that are present. Mauritian native trees have evolved in the absence of mammalian herbivores and the only endemic herbivores on the island were not able to reach the arboreal foliage (Cheke and Hume, 2008). Therefore, it is likely that native trees lack herbivore defences such as enhanced recovery after foliage damage. This is illustrated by the overall slow growth of the Mauritian native flora (Virah-Sawmy et al., 2009).

Furthermore, *M. fascicularis* fed on *Abricta brunnea* (Orian, 1954), a native cicada in our study site that seemed abundant during some of the summer months (December 2019 – February 2020). The macaques were very skilled at chasing and catching these cicadas. The conservation status of this species is unknown, but *M. fascicularis* may limit local population size to some extent. Additionally, when fruits were scarce, *M. fascicularis* spent a large proportion of time feeding on invertebrates. Invertebrates were often removed from behind bark, which was either peeled off with their hands or broken off with their teeth. Sometimes dead branches were broken apart with their teeth to get access to wood-boring grubs. These invertebrates could not be identified to genus or species level but judging by the large amount of time *M. fascicularis* spent feeding on invertebrates, it is likely *M. fascicularis* eats other native insects besides *A. brunnea*.

Moreover, when *M. fascicularis* moved to the orchards in October 2020, the troop discovered another food source: gecko eggs. The eggs may have belonged to native *Phelsuma ornata*, as we frequently spotted it in our study site and *P. ornata* is known to use invasive traveller's palm (*Ravenala madagascariensis*) as refuge site and for egg laying (Harmon et al. 2007). These palms were largely absent in our study troop's home range during December 2019 – September 2020, but abundant near the north-western forest edge. On some days during October – December 2020 our troop would spend the whole morning travelling from traveller's palm to traveller's palm to forage on gecko eggs in between the leaves. Adult males usually started foraging in between the palm leaves and once they finished younger, probably lower ranking individuals would search the palm again and look for leftovers. *Phelsuma ornata* is not threatened, but it is considered a keystone pollinator for various threatened endemic plants (Nyhagen et al. 2001; Hansen et al. 2006). Therefore, depending on how common this feeding strategy is among Mauritian long-tailed macaques, gecko egg predation by *M. fascicularis* may have consequences for both *P. ornata* and endemic plant populations. However, we could not confirm whether the eggs belonged to *P. ornata*.

Recommendations for estimating population size

The last estimate of the *M. fascicularis* population size in Mauritius was provided by Bertram (1994). The biggest limitation of the methods used by Bertram (1994) and earlier studies (Sussman and Tattersall, 1986) is that they relied on extrapolation of macaque densities based on the combined annual home range of only two adjacent troops. These troops were located in Mon Vallon in the Southwest of the island. However, because of differences in vegetation composition, habitat types and the mosaic nature of landscapes, densities are likely to vary greatly across the island (Sussman and Tattersall, 1986). Nevertheless, Bertram (1994) argued

that suitable habitat within 1 km of farmlands could probably support densities as high as what was reported by Sussman and Tattersall (1986) (1.3 macaques/ha) and that habitat > 1 km away from farmlands could only support half of that (0.65 macaques/ha).

Therefore, we argue that the method from Bertram (1994) should not be used for a new population estimate, as the macaque density estimate is derived from a single area and does not account for overlap with all adjacent troops. In the Calebasses Mountain Range, multiple troops seem to have considerable home range overlap. Furthermore, because of macaque capture, the annual home range of troops may be variable from year to year. The annual home range of our troop would have been significantly smaller without the expeditionary ranging in October 2020, which was probably facilitated by capture of *M. fascicularis* near the north-western forest edges. This makes estimating macaque densities considerably more difficult. Furthermore, habitat that is suitable for *M. fascicularis* should be redefined. Bertram (1994) does not include some forest areas in the North of the island (e.g., Daruty Forest, known to be inhabited by *M. fascicularis*) or any shrublands similar to the areas that were extensively used by a macaque troops close to our study site (Vallée du Paradis). Moreover, based on the information provided by farmers, *M. fascicularis* may not necessarily require large forest areas, as one troop was said to permanently occupy a relatively small patch of pioneer vegetation surrounded by farmlands. Therefore, new methods are needed obtain a reasonable estimate of the *M. fascicularis* population.

Moreover, regardless of the precise size of the population, we argue that the population may already be at carrying capacity. Guidi and Sussman (2009) argued that the population size may have been as low as 8000 individuals in 2009 due to macaque capture. However, the population dynamics model from Bertram (1994) indicate that the population is able to double in 6 years if it is below carrying capacity and completely recover to its original size (40,000 individuals) in 11 years if it was reduced to only 10,000 individuals. Our findings suggest our troop's expedition was most likely driven by scarcity of forest resources and may have been facilitated by removal of other troops. If the macaques near the north-western forest edge were captured early 2020, it means they were replaced within a relatively short time period (8 – 10 months) by our study troop. This could mean that troops inhabiting forest habitat frequently look for opportunities to access food-rich areas outside of their home range because they struggle to find food at the end of the dry winter. This suggests current macaque densities may be too high to be supported by only forest habitat. Frequent crop raiding by *M. fascicularis* across Mauritius and the common *M. fascicularis* related incidents in some urban regions also suggest forest resources may not be sufficient and that the population has exceeded the carrying capacity of forested areas.

We highly recommend exploring the possibilities of applying drones in population census of *M. fascicularis*. In recent years, thermal infrared imaging with drones has become an extremely promising method for carrying out primate surveys with great accuracy (Spaan et al. 2019; Zhang et al. 2020). Thermal infrared imaging relies on the detection of animal heat signatures with an infrared thermal sensor mounted to a drone and comparing these with the specific body temperature ranges of the study animal (Zhang et al. 2020). Depending on how high the drone flies, distinguishing between animals of similar shape and size is possible (Spaan et al. 2019). As *M. fascicularis* and *P. niger* are the largest animals that inhabit Mauritian forests, we suggest using this method to obtain a reasonable estimate of the *M. fascicularis* population.

Conclusion

Availability of forest fruit was a strong driver of dietary patterns, activity budget and probably ranging patterns of *M. fascicularis* during our study. *Macaca fascicularis* preferred fruits and increasingly fed on flowers, leaves, invertebrates and crops as fruits become scarcer.

Furthermore, *M. fascicularis* spent more time moving and less time feeding as fruits became scarce. Additionally, our findings indicate that *M. fascicularis* probably used energy maximizing strategies when fruits became scarce, resulting in a troop migration that may have been facilitated by capture of macaques near the forest edges.

Moreover, *M. fascicularis* preferred ripe fruit, and increasingly consumed unripe fruit when fruits became scarcer. *Macaca fascicularis* prefers exotic over native fruits and mostly consumed native fruit when unripe, unlike exotic fruit. Overall, *M. fascicularis* was not a very effective seed disperser because for many plant species *M. fascicularis* wasted a large percentage of fruit. Nevertheless, our findings indicate that *M. fascicularis* may be an important seed disperser for invasive *F. indica*, *Litsea* sp., and *P. cattleyanum*, because these species made up the majority of time *M. fascicularis* spent feeding on fruits and for *F. indica* and *P. cattleyanum* the majority of fruits were consumed when ripe. Additionally, *Litsea* sp. was the only species for which seed-spitting was observed. Contrarily, *M. fascicularis* is probably a poor seed disperser for native species as the majority of native fruit is consumed when unripe.

Our findings indicate that the consumption of unripe native fruit by *M. fascicularis* is largely driven by *M. fascicularis*' fruit preferences and the imbalance in fruit production between native and exotic species. Only three invasive species accounted for the majority of all available forest fruit and about half of the native species in our study site did not fruit. Moreover, we argue that fruit traits, higher fruit availability of exotic vs. native species and *M. fascicularis*' potential lack of ability to detect ripe native fruits that are green/brown in colour all likely contribute to fruit selection by *M. fascicularis* in Mauritius.

Furthermore, our findings indicate that *M. fascicularis* likely dropped the majority of available fruit from trees within their home range and depleted nearly all fruits of at least four native species at an unripe stage. Consequently, the most considerable fruit resource that probably remained available to *P. niger* within our study site were native *C. paniculatum*, *P. mauritianum* and *S. glomeratum*, accounting for 24% of available forest fruit. Even though native forest composition can largely vary across the island, invasive *F. indica*, *Litsea* spp. and *P. cattleyanum* have invaded most forested areas. Therefore, a similar imbalance in fruit availability between native and invasive species and similar dietary patterns of *M. fascicularis* are expected to be observed elsewhere on the island. Consequently, availability of forest fruits to *P. niger* is potentially limited by *M. fascicularis*.

In summary, we report the first case of how fruit preference and the imbalance in fruit production between native vs. exotic species in a fragmented forest habitat can promote consumption of unripe native fruits and dispersal of invasive plant species by an invasive frugivore, potentially restricting the diet of a native, key-stone seed disperser.

Additional note: macaque tracking vs. habituation

Initially, we started this study by capturing and radio-collaring (MI-2, Holohill, USA; 110 g in weight) four adult macaques (three females and one male) with assistance from the local macaque breeding company Noveprim Ltd. Red hair dye was applied to both flanks so that tagged individuals could be visually identified from a distance. These macaques were part of a larger group, which stuck around while the macaques were equipped with collars. The macaques were then radio-tracked from the ground with a three-element Yagi antenna and

receiver (Sika Biotrack, US). However, both trapping and collaring procedures resulted in a great setback, since the collared macaques became terrified of people. The location of their sleeping site was discovered through radio-tracking, but contact could barely be established in the dense vegetation. The collared macaques also appeared to have split off from the larger group, as radio-collared individuals were mostly encountered together in groups not bigger than three individuals. However, most of the time they would run off when hearing the sounds of the approaching researcher, often before the researcher could see the macaques. We then focused on habituating the larger group, which was encountered coincidentally while trying to find the collared macaques. The radio signals indicated that the collared individuals were never anywhere near the large group. We were able to come within 20 m to 40 m of the large group after just a few days. These macaques were then selected as study troop and their sleeping site was located by successfully following them for an entire day. Remarkably, the sleeping site of the four collared individuals was located in a slightly different area than the sleeping site of the study troop. There was probably still interaction between the groups as camera trap footage indicated (Fig. 11) that they still utilized the same areas. Furthermore, the signals were checked at least once a month while following our study troop, showing that the collared individuals remained an independent group. This indicates possible negative consequences of radio-collaring primates for behavioural studies.



Figure 11: Radio-collared female caught on camera trap in *Eugenia pyxidata* in November.

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Appendices

Appendix 1: R-script for least-squared cross validation kernel density estimation (LSCV KDE) for estimating monthly home ranges.

```
#####  
## clear workspace and set working directory #####  
#####  
# Clear plots  
if(!is.null(dev.list())) dev.off()  
# Clear console  
cat("\014")  
# Clean workspace  
rm(list=ls())  
# Set working directory  
setwd("C:/insert working directory")  
  
## attach data  
mydata<-read.table("insert coordinate file name.txt",header=T,sep="\t")  
  
attach(mydata) # attach the data into R  
  
##install packages  
#install.packages("adehabitatHR")  
#install.packages("rgdal")  
#install.packages("rgeos")  
#install.packages("smoothr")  
library(adehabitatHR)  
library(rgdal)  
library(rgeos)  
library(smoothr)  
library(dplyr)  
library(tidyr)  
  
#group and then randomly select 40 coordinates per months  
randomsample <- newdata %>% group_by(Month)  
set.seed(1234)  
randomsample <- sample_n(randomsample, 40)  
attach(randomsample)  
  
#####  
### Estimate monthly home ranges (95% KDE and 50% KDE) ###  
#####  
#only include three columns (Month, x, and y coordinates) for estimating monthly home ranges  
HomeCalc <- randomsample[, c("Month", "xcoord", "ycoord")]  
#set coordinates to right CRS  
coordinates(HomeCalc) <- c("xcoord", "ycoord")  
proj4string(HomeCalc) <- CRS("+init=epsg:3857" )  
  
#calculate kernel density with least squares cross validation as smoothing parameter  
#keep grid at 100 or even bigger, otherwise function 'getverticeshr' runs into errors later
```



```

kernel.lscv <- kernelUD(HomeCalc, h = "LSCV", grid = 100) # Least square cross validation

#get area for 95% kernels
homecalc.kernel.poly <- getverticeshr(kernel.lscv, percent = 95)
print(homecalc.kernel.poly) # returns the area of each polygon

#####
##### create and export shapefiles #####
#####
#we can now export the 95% and 50% as shapefiles
#make polygons for 95%
KDE95 <- getverticeshr(kernel.lscv, percent = 95)
#Now 50%
KDE50 <- getverticeshr(kernel.lscv, percent = 50)
# smooth with kernel smoothing for better end result
KDE95 <- smooth(KDE95, method = "ksmooth")
KDE50 <- smooth(KDE50, method = "ksmooth")

#Write your 95% and 50% MCP into a shapefile that can be loaded into Q-GIS
writeOGR(KDE95, dsn = ".", layer = "KDE95", driver="ESRI Shapefile")
#A dsn value of "." will output the file in your working directory folder,
#layer is the file name, driver is the type of file that is being made.
#Repeat for the 50% MCP
writeOGR(KDE50, dsn = ".", layer = "KDE50", driver="ESRI Shapefile")

```

Appendix 2: Plant species recorded along our phenology transects. Status (native or exotic), total number of recorded stems (DBH \geq 5 cm) across all four transects (N), percentage of stems that successfully fruited (% fr. success) and percentage of total Fruit Availability Index (% FAI) are also provided for every species. A hyphen indicates that the species produced no fruits during our study period at all.

Family	Species	Status	N	% fr. success	% FAI
Achariaceae	<i>Erythrospermum monticolum</i>	Native	28	35	2.43
Aphloiaceae	<i>Aphloia theiformis</i>	Native	12	22	0.12
Apocynaceae	<i>Tabernaemontana persicariifolia</i>	Native	9	-	-
Burseraceae	<i>Canarium paniculatum</i>	Native	2	100	5.44
Calophyllaceae	<i>Calophyllum tacamahaca</i>	Native	8	-	-
Ebenaceae	<i>Diospyros boutoniana*</i>	Native	1	100	0.06
	<i>Diospyros neraudii</i>	Native	1	-	-
Euphorbiaceae	<i>Claoxylon sp.</i>	Native	2	-	-
	<i>Securinega durissima</i>	Native	23	-	-
Lamiaceae	<i>Premna serratifolia</i>	Native	1	50	0.02
	<i>Rothea serrata</i>	Exotic	3	100	0.07
Lauraceae	<i>Cinnamomum camphora</i>	Exotic	1	-	-
	<i>Litsea sp.</i>	Exotic	143	46	14.73
Loganiaceae	<i>Geniostoma borbonicum</i>	Native	6	17	0.28
Malpighiaceae	<i>Hiptage benghalensis</i>	Exotic	19	100	0.79
Melastomataceae	<i>Memecylon cordatum</i>	Native	1	100	0.01
Moraceae	<i>Ficus mauritiana</i>	Native	4	50	0.46
Myrtaceae	<i>Eugenia elliptica</i>	Native	3	-	-
	<i>Eugenia pyxidata</i>	Native	26	58	0.88
	<i>Psidium cattleianum</i>	Exotic	534	48	15.28

	<i>Syzygium commersonii</i>	Native	3	50	0.08
	<i>Syzygium dupontii</i>	Native	3	50	0.31
	<i>Syzygium glomeratum</i>	Native	18	36	2.72
	<i>Syzygium jambos</i>	Exotic	112	14	0.55
	<i>Syzygium mauritianum</i>	Native	4	75	0.14
Oleaceae	<i>Ligustrum robustum</i>	Exotic	76	58	4.81
Phyllanthaceae	<i>Margaritaria anomala</i>	Native	1	100	1.04
	<i>Phyllanthus sp.</i>	Native	1	-	-
Pittosporaceae	<i>Pittosporum senacia</i>	Native	5	33	0.06
Primulaceae	<i>Ardisia elliptica</i>	Exotic	8	100	1.33
Psiloxylaceae	<i>Psiloxylon maritimum</i>	Native	7	80	15.82
Salicaceae	<i>Casearia coriacea</i>	Native	2	-	-
	<i>Flacourtia sp.</i>	Exotic	180	59	32.59
Sapindaceae	<i>Molinaea alternifolia</i>	Native	1	-	-
Sapotaceae	<i>Labourdonnaisia glauca</i>	Native	1	-	-
	<i>Mimusops maxima</i>	Native	4	-	-
	<i>Sideroxylon puberulum</i>	Native	3	-	-
Stilbaceae	<i>Nuxia verticillata</i>	Native	2	-	-
Rhamnaceae	<i>Rhamnus nepalensis</i>	Exotic	14	-	-

Appendix 3: Family and species name of every exotic and native plant species in *M. fascicularis* diet and the percentage of total plant feeding time *M. fascicularis* fed on any of their plant parts (% plant diet) and percentage of total fruit feeding time that *M. fascicularis* fed on their fruits (% fruit diet). A hyphen indicates that no fruits of this plant species were eaten by *M. fascicularis*. The plant parts *M. fascicularis* consumed are also provided for every species: ripe (r) and unripe (u) fruit (Fr), seed (Se), flower (Fl), leaf (L), stem (St), bark (B) and male and female pinecone (Pc). Finally, the fruit preference index is provided for every species (S_i). For some species in *M. fascicularis'* fruit diet, fruit availability could not be measured because the species was either extremely rare in the study site or restricted to one particular forest area (*Olea lancea* and *Mangifera indica*).

Family	Species	Status	Parts consumed	% plant diet	% fruit diet	S_i
Acanthaceae	<i>Justicia gendarussa</i>	Exotic	L	4.4×10^{-2}	-	-
Anacardiaceae	<i>Mangifera indica</i>	Exotic	Fr (r/u), Se	2.2	4.9	-
Arecaceae	<i>Livistona chinensis</i>	Exotic	Fl, L, S	0.8	-	-
Bignoniaceae	<i>Tabebuia pallida</i>	Exotic	L	0.2	-	-
Caprifoliaceae	<i>Lonicera sp.</i>	Exotic	L	4.4×10^{-2}	-	-
Fabaceae	<i>Fabaceae sp.</i>	Exotic	L	0.3	-	-
Lauraceae	<i>Litsea sp.</i>	Exotic	Fr (r/u), L, Fl, St	25.0	40.2	4.1
Malpighiaceae	<i>Hiptage benghalensis</i>	Exotic	Fr (r/u), Se, L, Fl	6.4	0.7	0.6
Malvaceae	<i>Ruizia blackburniana</i>	Native	L	4.4×10^{-2}	-	-
Melastomataceae	<i>Clidemia hirta</i>	Exotic	S	4.4×10^{-2}	-	-
	<i>Ossaea marginata</i>	Exotic	L	8.7×10^{-2}	-	-
Moraceae	<i>Ficus mauritiana</i>	Native	Fr (u), L	0.3	0.4	0.7
	<i>Ficus reflexa</i>	Native	Fr (r/u), L	0.4	0.3	-
	<i>Ficus rubra</i>	Native	Fr (r/u)	0.3	0.6	-
Myrtaceae	<i>Eugenia pyxidata</i>	Native	Fr (u), Se, L	0.4	0.7	0.4
	<i>Psidium cattleianum</i>	Exotic	Fr (r/u), L, B	17.6	39.3	1.1
	<i>Syzygium dupontii</i>	Native	Fr (u), Se	0.1	0.3	1.2
	<i>Syzygium glomeratum</i>	Native	L	0.2	-	-
	<i>Syzygium jambos</i>	Exotic	Fr (u), Se, L, Fl	1.2	1.0	2.3
Oleaceae	<i>Ligustrum robustum</i>	Exotic	Fr (r/u), Se, L, Fl	3.7	0.7	0.1

	<i>Noronhia broomeana</i>	Native	Fr (u), Se	4.4*10 ⁻²	0.1	-
	<i>Olea lancea</i>	Native	Fr (u), Se, L	8.7*10 ⁻²	0.1	-
Phyllanthaceae	<i>Securinega durissima</i>	Native	L	0.1	-	-
Pinaceae	<i>Pinus sp.</i>	Exotic	Pc, B, St	28.8	-	-
Piperaceae	<i>Piper borbonense</i>	Native	L	4.4*10 ⁻²	-	-
Pittosporaceae	<i>Pittosporum senacia</i>	Native	Fr (u), L	0.2	0.3	0.5
Poaceae	<i>Bambusoideae sp.</i>	Exotic	L	0.1	-	-
	<i>Poaceae sp.</i>	Unknown	L	0.3	-	-
Primulaceae	<i>Ardisia elliptica</i>	Exotic	L	4.4*10 ⁻²	-	-
Psiloxylaceae	<i>Psiloxylon mauritianum</i>	Native	Fr (r)	8.7*10 ⁻²	0.1	0.1
Rutaceae	<i>Citrus sp.</i>	Exotic	Fr (r/u)	0.4	0.8	-
Salicaceae	<i>Flacourtia sp.</i>	Native	Fr (r/u), L	5.6	9.5	0.5
Sapotaceae	<i>Mimusops maxima</i>	Native	L	8.7*10 ⁻²	-	-
	<i>Sideroxylon puberulum</i>	Native	L	0.1	-	-
Verbenaceae	<i>Stachytarpheta jamaicensis</i>	Exotic	L	8.7*10 ⁻²	-	-
Unknown	Unknown	Unknown	L	4.5	-	-

Appendix 4: Regression coefficients, standard errors (SE) and P – values (*P < 0.05, ***P < 0.001) for all predictors included in our top-ranked GLMM's explaining the effects of FAI and Species (native/exotic) on the proportion of ripe vs. unripe fruits dropped per macaque per minute (for both partly eaten and partly eaten and intact fruits combined).

Model and predictors	Estimate	SE	P-value
Prop. ripe vs. unripe (partly eaten)			
FAI	3.67*10 ⁻⁴	9.37*10 ⁻⁵	***
Species: Exotic - native	2.31	1.37	*
Prop. ripe vs. unripe (partly eaten and intact)			
FAI	2.8*10 ⁻⁴	7.69*10 ⁻⁵	***
Species : Exotic - native	2.32	1.46	*

The effects of invasive plant removal on forest regeneration and the availability of native fruits
to *Pteropus niger*

Rufford report 2020 - 2021
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Methods

Study site

This study was carried out in a forest remnant in the North of Mauritius (Fig. 1), selected for its native plant richness, high degree of forest degradation (Reinegger et al. 2021b), and the presence of *M. fascicularis* and *P. niger*. The forest covered two mountains: Calebasses mountain range and Mariannes (lat: -20.181203°, long: 57.584498°). This area was between 420 and 580 m asl and rainfall is 1,800 – 2,200 mm/year. The forest was made up of semi-dry vegetation at lower elevations and sub-humid vegetation at higher elevations. Furthermore, the forest was extremely degraded at lower elevations and mostly consists of a remnant pine plantation (*Pinus nigra*) and dense thickets that were made up of invasive *Hiptage benghalensis*, *Ligustrum robustum*, *Litsea* spp., *Psidium cattleianum* and *Syzygium jambos*.

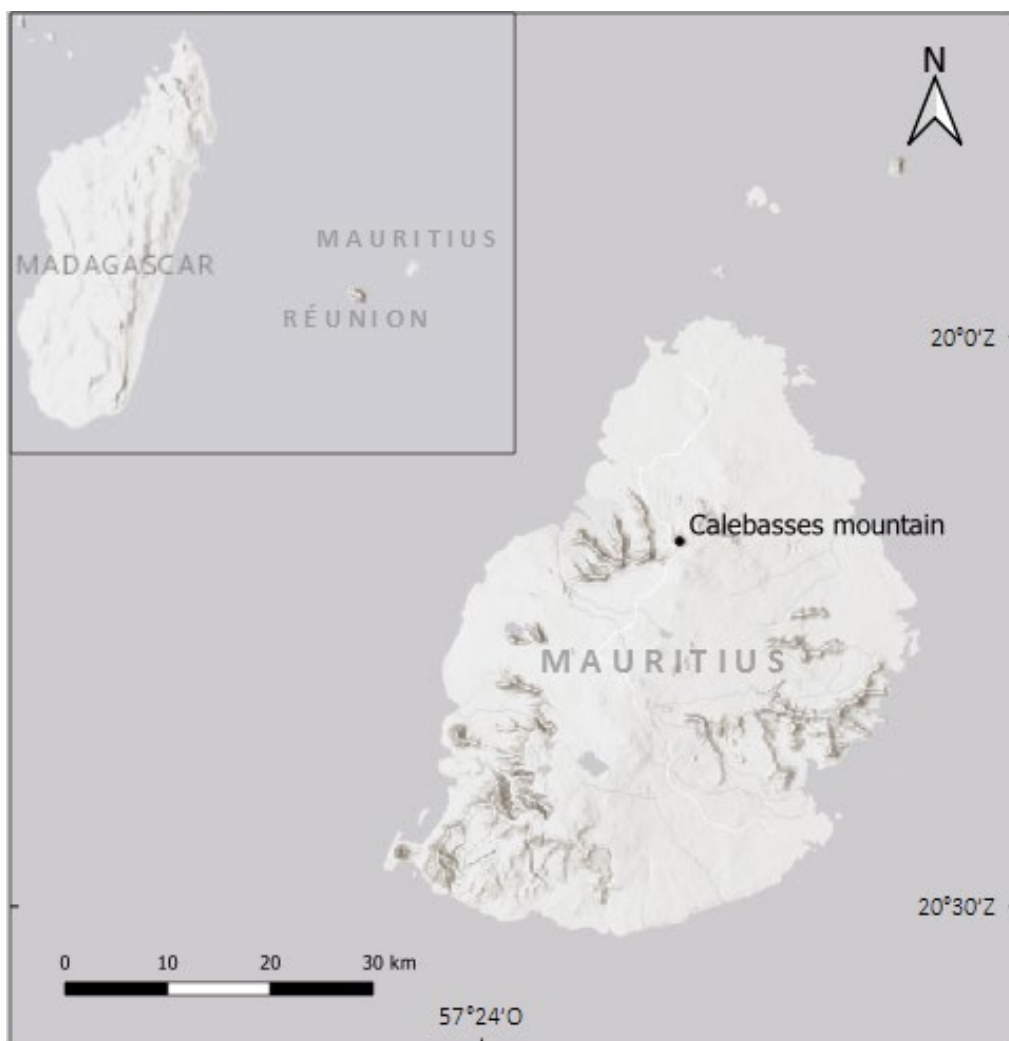


Figure 1: Location of the study site

Invasive plant impact on native fruit production

To assess the impact of invasive plants on fruit production of native plants, fruit and flower drop by canopy species that are primarily dispersed by *P. niger* were measured in pre-weeded and post-weeded conditions. Fruit drop of a total of three to four canopy tree replicates was measured in a total of 15 plots (10 m by 10 m). The plots were placed at > 10 m distance away from each other and divided into three treatments with five plots each: a control, a clear-cutting treatment (treatment 1) and a drilling treatment (treatment 2). In treatment 1 all invasive and exotic plants < 10 cm diameter at breast height (DBH) were cut down as close to the base of the trunk as possible and treated with herbicide (Roundup Energy, Bayer-Monsanto, Leverkusen). All invasive and exotic trees > 10 cm DBH were ring-barked and also treated with herbicide. In the treatment 2, only the invasive and exotic understory (< 3 cm DBH) was removed. In all invasive and exotic trees > 3 cm DBH we drilled three holes that reached the centre of the trunk and injected a total of 2 - 3 ml of herbicide with plastic slip-tip syringes.

We then selected native canopy species that were sufficiently abundant to be replicable in the study site: *Aphloia theiformis*, *Calophyllum tacamahaca*, *Eugenia pyxidata*, *Labourdonnasia calophylloides*, *Psiloxylon mauritianum*, *Sideroxylon puberulum*, *Syzygium glomeratum* and *Syzygium duponti*. The three to four replicates in every plot were a random subset of these species. The replicates were selected three to five meters away from the edge of the plots, to minimize edge-effects after weeding. Fruit drop was measured with seed traps, constructed of polyester fabric loosely stretched along a square pvc frame (1 m by 1 m). Two frames were placed under the canopy of every replicate and tied at least 0.5 m above the ground at all edges with plastic string to minimize fruit and seed removal by rats (Fig. 2). Fruit production was monitored in the pre-weeded stage in every plot from October 2019 until July 2020. The seed traps were checked on a weekly basis from the start of the flowering until the end of the fruiting period for each tree. All fruits (intact and eaten), seeds (intact and eaten) and bat ejecta pellets (compressed fibrous material that remains after *P. niger* squeezes the juice from the flesh) were recorded. Fruits eaten by *P. niger* were identified by their typical triangular-shaped canine imprint (Banack 1998; McConkey and Drake 2015; Reinegger et al. 2021a). The teeth marks could be easily distinguished from marks left by other common large canopy feeders: the invasive long-tailed macaque (*Macaca fascicularis*) leaves large round canine marks (Krivek, 2017; Reinegger et al., 2021a), invasive rats (*Rattus rattus*) leave gnawing marks with their two upper and lower incisors and ringneck parakeets (*Psittacula krameri*) create V-shaped marks with their under and upper mandibles (VSG, 2018). Additionally, a single camera trap was placed on the trunk of one fruiting tree replicate per species and aimed at the canopy. A 10 second video was recorded when motion is detected, and the camera trap was left for two weeks. This was repeated for every selected canopy species so that the identity of animals feeding on the species could be confirmed.



Figure 2: Seed traps placed under the canopy of native trees in the study site.

In July – August 2020, all plots except the control plots were weeded (Fig. 3 and 4). Some of the the most common invasive woody plants in our study area that we removed were: *Ardisia crenata*, *Ardisia elliptica*, *Flacourtia indica*, *Justicia gendarussa*, *Clidemia hirta*, *Ligustrum robustum*, *Litsea glutinosa*, *Litsea monopetala*, *Ossaea marginata* and *Psidium cattleianum*. Fruit production is currently still being measured and will continue to be measured until July – August 2021.



Figure 3: Plot with treatment 1 (clear-cutting) before (left) and after weeding (right).



Figure 4: Plot with treatment 2 (drilling) before (left) and after weeding (right).

Herbaceous layer plots

To assess the impact of invasive plants on regeneration of the native vegetation, we established two random 2 m by 2 m plots within every 10 m by 10 m plot. In these plots, we measured all plants in the herbaceous layer (< 1 m in height) and recorded species abundance, frequency and percent cover. Percent cover was estimated by overlaying the 2 m by 2 m plots with a rectangular 1 m by 1 m ground quadrat in every corner, which was divided into a grid of 10 cm by 10 cm units. We also tagged all plants > 1 m in height and < 1 cm DBH and recorded height and DBH in order to measure plant growth. Measurements were taken straight after weed removal (August 2020) and six months after weed removal (February 2021).

Measurements will be taken again 12 months after weed removal (August 2021). Saplings in the herbaceous layer that had grown > 1 m were then also tagged. Changes in native plant cover and density in the herbaceous layer and sapling growth and establishment in higher vegetation strata (> 1 m in height) were then compared between the control plots and the two treatments.

Data analysis

The only species that produced fruits in post-weeded conditions so far was *A. theiformis*. Therefore, we limited analysis of flower and fruit production to *A. theiformis*. All data analyses were carried out in R (R Core Team, 2020). We used Generalized Linear Models (GLM's) with negative binomial distribution to test the effects of treatment and year on fruit drop and flower drop of *A. theiformis*. We included a two-way interaction between date and treatment as predictor in both models. Furthermore, we used Generalized Linear Mixed Models (GLMM's) with beta distribution to test the effect of treatment on native plant cover in the herbaceous layer. To account for the nested structure of the herbaceous layer plots, we included herbaceous layer plot ID nested within large plot ID as random effect. We then used a backwards model selection procedure based on the second order Akaike Information Criterion (AICc) to find the most parsimonious models among a set of models containing all possible variable combinations (Table 1). Models were then validated with residual diagnostic plots from package DHARMA (Hartig 2020).

Table 1: AICc table of a priori GLM's explaining effects of the two-way interaction between treatment and date fruit and flower drop and GLMM's explaining the effect of the two-way interaction between treatment and date on native plant cover in the herbaceous layer. Models are ranked in ascending order of AICc. The number of parameters (K), the difference between

model AICc and lowest AICc in the model set ($\Delta AICc$) and AIC weight (ω) are provided for every model.

Effects of treatment and date on fruit drop (<i>A. theiformis</i>)	K	$\Delta AICc$	ω
Fruit drop ~ 1	2	0.0	0.74
Fruit drop ~ Year	3	2.5	0.21
Fruit drop ~ Treatment + Date	5	5.6	0.04
Fruit drop ~ Treatment*Date	7	11.5	0.0024
Effects of treatment and date on flower drop (<i>A. theiformis</i>)			
Flower drop ~ Year	3	0.0	0.66
Flower drop ~ 1	2	1.3	0.34
Flower drop ~ Treatment*Date	7	1446.7	<0.001
Flower drop ~ Treatment + Date	5	1519.8	<0.001
Effects of treatment and date on native plant cover			
Native plant cover ~ Date	5	0.0	0.394
Native plant cover ~ 1	6	0.1	0.371
Native plant cover ~ Treatment + Date	8	1.2	0.212
Native plant cover ~ Treatment*Date	10	5.6	0.024

Preliminary results and discussion

We are currently measuring fruit drop in the post-weeded stage (since August 2020) and some species have not yet started producing fruits (*E. pyxidata*, *P. mauritianum*, *S. glomeratum*). Furthermore, *E. pyxidata* produced large quantities of fruits in October 2019 (pre-weeded stage) but did not produce any fruits in October 2020 (post-weeded stage). Recently, *E. pyxidata* started producing large quantities of flowers again (February 2020) suggesting that it does not fruit every year. Furthermore, *M. maxima* did also not produce any flowers or fruits in 2020, but produced flowers in February 2021, indicating that *M. maxima* may also have interannual variation in flower production. Therefore, we are not able to make meaningful comparisons between the pre-weeded and post-weeded stages for most species yet. Nevertheless, we could compare flower and fruit drop of *A. theiformis* between years. Our GLM explaining variation in flower drop of *A. theiformis* indicated that flower drop was higher in the pre-weeded than in the post-weeded stage across all treatments ($P < 0.05$; Fig. 5). Furthermore, the increase in flower drop was not significantly different between treatments, as the most parsimonious GLM only included date as predictor. These findings show that the increase in flower drop was most likely due to annual variation. Furthermore, there was no significant increase in fruit drop, as our GLM explaining variation in fruit drop was not significantly different from a null model. Nevertheless, it is too early to draw conclusions about treatment effectiveness, because most species still have not finished flowering or produced fruits in the post-weeded stage. Additionally, the effects of weeding are more likely to become clearer after multiple years.

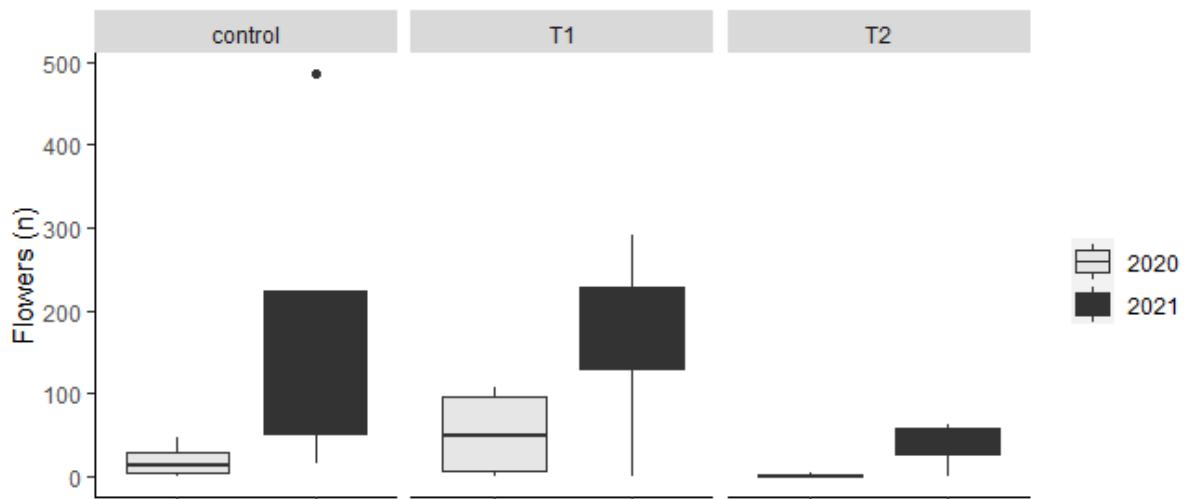


Figure 5: Number of flowers sampled under *Aphloia theiformis* trees in the control plots, treatment 1 plots (T1) and treatment 2 plots (T2) both in the pre-weeded (2020) and post-weeded stage (2021).

For *E. pyxidata*, almost all fruits recorded in our seed traps were eaten at an immature stage by *M. fascicularis* (Fig. 6). Footage from camera traps (23-10-2019 until 2-11-2019) indicates that *M. fascicularis* most frequently fed on *E. pyxidata* fruits and also dropped fruit intact (Fig. 6). The macaques mainly consumed the fleshy portion that is closest to the pedicel and drop the part closest to the pistil and petal remains (Fig. 6, right). Consumption of *E. pyxidata* fruit by *P. niger* was only recorded once, at the end of *E. pyxidata*'s fruiting period. The fruit consumed by *P. niger* was ripe. We were not able to compare feeding intensity by *P. niger* and *M. fascicularis* on *E. pyxidata* between the pre-weeded and post-weeded stage yet, because *E. pyxidata* did not fruit in 2020.



Figure 6: *Macaca fascicularis* feeding on immature fruits of *Eugenia pyxidata* (left and middle). Intact immature *E. pyxidata* fruits and immature *E. pyxidata* fruits eaten by *M. fascicularis* (right).

Nevertheless, we recorded an increase in consumption of *L. calophylloides* flowers by *P. niger*. *Pteropus niger* consumed flowers of this species in both the pre-weeded and post-weeded

stage and we recorded an increase in both flower drop (from 351 to 1467) and flower ejecta (from 2 to 48) between the two stages. However, only one out of two *L. calophylloides* replicates was visited by *P. niger* in both the pre-weeded and post-weeded stages, even though both replicates were located in plots with treatment 1 or 2. Therefore, at this stage it is not possible to determine whether increased foraging on the flowers of this species is a result of interannual variation in flower production or weed removal. It is essential that flower and fruit drop of this species is measured for another year in order to determine whether weed removal results in increased foraging by *P. niger*.

The most parsimonious beta GLMM explaining the variation in plant cover only included date, indicating that overall native plant cover in the post-weeded stage was lower than in the pre-weeded stage ($P > 0.05$; Fig. 7) and that there was no difference between treatments. Therefore, it is likely that this variation in native plant cover is seasonal, because most newly germinated seedlings that occur in clumped groups are expected to die. Nevertheless, it will be essential to measure plant cover again at the 12-month point (August 2021) in order to detect potential differences in native plant cover between treatments, because these changes are expected to be very slow.

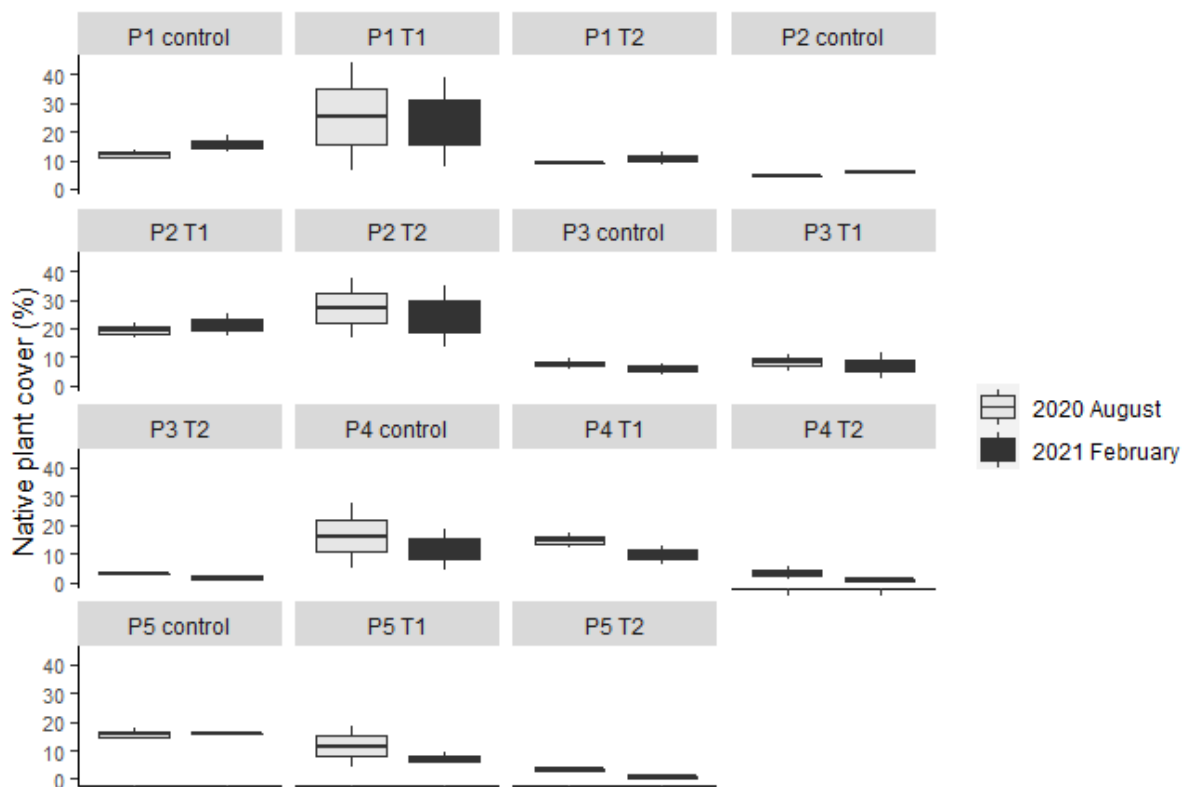


Figure 7: Native plant cover measured at the pre-weeded stage (2020 August) and post-weeded stage (2021 February) in all 15 plots. T1 and T2 refer to treatment 1 and treatment 2 respectively.

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