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Invasive alien plant control improves foraging habitat quality of a threatened island flying fox

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Abstract

Flying foxes play keystone ecological roles in plant reproduction. Yet, they face numerous threats, including persecution for eating commercial fruits. This human-wildlife conflict has recently escalated to culling campaigns of a threatened flying fox on Mauritius. Finding non-lethal solutions to this human-wildlife conflict on the island is therefore extremely important. We hypothesized that invasive alien plants may reduce native fruit availability through competition and that weeding alien plants could improve the native foraging habitat quality of flying foxes – in turn, reducing their consumption of commercially important fruits. We compared native fruit production and foraging intensity of the Mauritian flying fox (*Pteropus niger*) in forests weeded of alien plants a decade previously and adjacent non-weeded forests. Fruits and ejecta were collected weekly during five months under 144 randomly chosen native trees of two canopy species whose fruits are eaten by flying foxes. Intraspecific variations in tree and fruit traits were used to examine flying fox foraging preference. Native fruit production was significantly higher in weeded forests for both tree species, and this was matched by higher flying fox foraging intensity. Flying foxes preferred large trees and fed predominantly on large and ripe fruits. The predominant consumption of ripe fruits emphasizes the importance of flying foxes as seed dispersers. Our results indicate that alien plant invasion substantially reduces native fruit production and that weeded forests provide a much better habitat for flying foxes. Our findings lend support to invasive alien plant control as a management strategy in mitigating such human-wildlife conflicts.

Keywords: Alien plant invasion; fruit bat; frugivory; habitat restoration; intraspecific variation in traits; *Pteropus niger*

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Introduction

Flying foxes of the genus *Pteropus* often play keystone ecological roles through pollination and seed dispersal (Cox, Elmqvist, Pierson, & Rainey, 1992; Nakamoto, Kinjo, & Izawa, 2009), thereby contributing to plant arrival, reproduction and maintenance in the landscape (de la Peña-Domene, Martinez-Garza, Palmas-Perez, Rivas-Alonso, & Howe, 2014; Muscarella & Fleming, 2007; Whittaker & Jones, 1994; Wunderle, 1997). Seeds dispersed by flying foxes are often from canopy trees (Banack, 1998; McConkey & Drake, 2006; Rainey, Pierson, Elmqvist, & Cox, 1995). These trees fulfil structural ecosystem engineer roles in their habitats and enable the development and maintenance of diverse communities within them (Jones, Lawton, & Shachak, 1997). However, flying foxes face numerous threats, such as habitat loss, climate change and invasive alien species (Frick, Kingston, & Flanders, 2019). This may weaken their ecological role even before they become rare (McConkey & Drake, 2006). In addition, flying foxes are often targeted as bush meat (Jenkins & Racey, 2008; Mickleburgh, Waylen, & Racey, 2009; Mildenstein, Tanshi, & Racey, 2016) or persecuted to try to protect domestic fruit crops (Aziz, Olival, Bumrungsri, Richards, & Racey, 2016; Roberts, Catterall, Eby, & Kanowski, 2012).

Persecution of flying foxes, specifically in attempts to protect commercial fruits, is widespread (Frick et al., 2019) and worsening (Epstein et al., 2009; Tait, Perotto-Baldivieso, McKeown, & Westcott, 2014; Vincenot, Florens, & Kingston, 2017). This situation is aided by a general lack of legal protection or adequate law enforcement (Aziz et al., 2016). Although non-lethal strategies like netting of fruit trees exist (Aziz et al., 2016), killing by farmers (e.g. Vincenot et al., 2015) or government-led mass-culling (Florens, 2016) appear to be favoured despite being largely ineffective (Florens & Baider, 2019; Roberts et al., 2012). A poignant example of this is seen in Mauritius, where the country's biodiversity protection law was weakened in 2015 to enable mass-culling of the Mauritian flying fox (*Pteropus niger*) in attempts to protect commercial fruits (Florens, 2012, 2015, 2016). By 2017, two mass-culling events and a surge in poaching (Kingston, Florens, Oleksy, Ruhomaun, & Tatayah, 2018; Vincenot et al., 2017) had halved the population. This situation prompted the International Union for Conservation of Nature (IUCN) to change the species' Red List category from Vulnerable to Endangered (Kingston et al., 2018). Although mass-culling did not improve commercial fruit production, a third mass cull was implemented in 2018 (Florens & Baider, 2019; Florens & Vincenot, 2018) and another in 2019. Given the imminent threat of further culls, it is important and urgent to identify and promote strategies that not only benefit fruit producers, but also avoid unnecessarily elevating the extinction risks of ecological keystone species.

One such strategy could be the control of invasive alien species, particularly those that may reduce natural food resources for flying foxes directly (e.g. long-tailed macaques on Mauritius (Baider & Florens, 2006)) or indirectly (for example through foraging habitat degradation). Invasive alien species are major drivers of habitat degradation, particularly on islands (Caujapé-Castells et al., 2010). For example, prolonged exposure to invasive alien rats may alter the composition of native forests (Harper & Bunbury, 2015). Additionally, invasive alien plants can compete with native plants reducing their fitness (Brown & Mitchell, 2001; McKinney & Goodell, 2010; Stinson et al., 2006; Vilà et al., 2011) and may contribute to a major decrease in large tree density (Florens, Baider, Seegoolam, Zmanay, & Strasberg, 2017). Conversely, habitat restoration by controlling alien plants can increase growth rate, flowering and fruiting of native trees (Baider & Florens, 2006; Monty, Florens, & Baider, 2013), leading to increased native tree regeneration and species richness (Baider & Florens, 2011). Notably, this includes species whose fruits are eaten by *Pteropus* (Florens, Baider, Marday, et al., 2017). Native habitat restoration is thus expected to improve foraging habitat quality for native frugivores, thereby providing easier access to food resources within native habitats. This would in turn reduce

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reliance on commercial fruit trees. However, the effectiveness of native habitat restoration to mitigate such human-wildlife conflicts remains to be tested and quantified.

We investigated the influence of invasive alien plant control on the native foraging habitat quality of *P. niger* by comparing fruit and ejecta density under native canopy trees in areas cleared of alien plants and in adjacent weed-invaded forest controls. More specifically, we aimed to characterise any positive effect that invasive alien plant control may have on native fruit production and the foraging intensity of the Mauritian flying fox to evaluate whether weed removal may improve native foraging habitat quality for flying foxes. In addition, we sought to characterise any influence of tree traits on the foraging site choice of flying foxes to better inform ecological restoration efforts. The potential recovery of native vegetation after weed removal could be further accelerated by the ensuing reinforced seed-dispersal mutualism between flying foxes and native trees. Therefore, we explored whether native fruit traits influence fruit choice of flying foxes to better characterise their role as seed dispersers. We discuss the ecological significance of the results and their application to improve management including for conservation.

Methods

Study area

Mauritius (centred on 20°20' S, 57°34' E; 1,865 km^2; 828 m a.s.l.; 7.8 million years old) is a volcanic island in the Mascarenes, approximately 900 km east of Madagascar (Figure 1). This work was carried out at Mt Camizard (centred on 20°19'54" S, 57°43'14" E; 250-320 m a.s.l.) south-east Mauritius (Figure 1), within a protected forest (Mountain Reserve). The area has ferralitic soil, derived from 7.5-5.2 million years old basaltic lava flows, and has a humid, mesothermal climate (mean annual rainfall and temperature of 2,500 mm and 22°C, respectively). It harbours one of the most well-preserved and least disturbed native wet forests on Mauritius, dominated by native canopy trees and relatively low alien plant invasion compared to most native forest remnants on the island (Florens, Baider, Martin, & Strasberg, 2012). The forest comprises of well-preserved (≥ 70% native cover) and moderately invaded (≥ 50% and <70 % native cover) forest patches (Page and D'Argent 1997). The most invasive plant species are strawberry guava (*Psidium cattleyanum* Sabine), cinnamon (*Cinnamonum verum* J.Presl) and rose apple (*Syzygium jambos* (L.) Alston) (Florens et al., 2016). Although *P. niger* is known to feed on strawberry guava and rose apple (Nyhagen, Turnbull, Olesen, & Jones, 2005), this has been observed very rarely even in highly invaded forests (FBVF & CB, pers. comm.). The branches of strawberry guava are often too short, thin and dense to support foraging *Pteropus.* The rarer rose apple is a relatively shade-loving and slow growing species that provides mostly flowers, as fruit production is known to be low (CABI, 2020).The studied forest contains patches cleared of these invasive alien plants alongside areas that have not been cleared of them (Figure 2), thereby enabling a comparative study between the two habitat types. We sampled non-weeded forests and adjacent forests of the same type and age where the removal of invasive plant species has been implemented since 2006.

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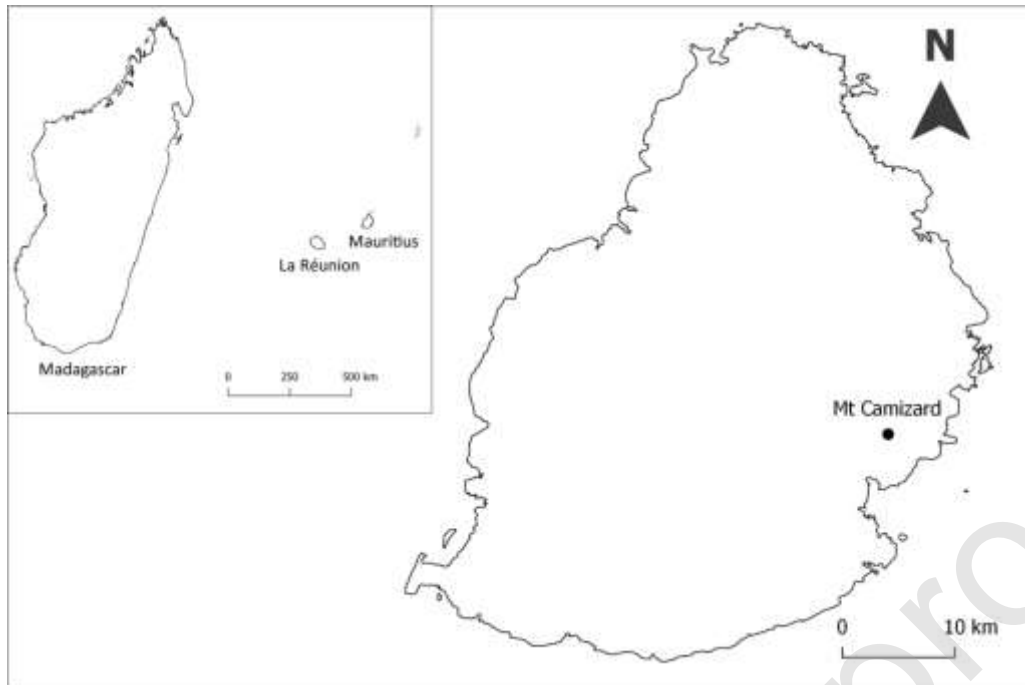

Figure 1. Mauritius, east of Madagascar (insert) and a closer view showing the study site at Mt Camizard in south-east Mauritius.

Figure 2. Ground (top) and aerial view (bottom) of adjacent native forest areas weeded of invasive alien plants (left) and non-weeded (right) on Mauritius.

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Study species

The Mauritian flying fox (*Pteropus niger*) is the last surviving of three original Mascarene-endemic *Pteropus* species on Mauritius (Cheke & Hume, 2008). It feeds on fruits of at least 43 native species, representing approximately 25% of the native woody species and 50% of the tree individuals in any given forest area on the island (Florens, Baider, Marday, et al., 2017). To our knowledge fruit preference between native and alien species has not been studied for *P. niger*. Studies on other Pteropodid bats have pointed out a general tendency to prefer native over alien food resources (Andrianaivoarivelo et al., 2012; Nelson, Miller, Heske, & Fahey, 2000; Parry-Jones & Augee, 1991), although the reverse has been also documented in a setting of farmland versus dry native forest (Luskin, 2010). The replacement of native fruits with farmed ones in the diet of *Pteropus* might have negative nutritional consequences for flying foxes (Nelson et al., 2000) and negative impact on the dispersal of large-seeded native fruits. *Pteropus niger* is the largest remaining native frugivore and seed disperser on Mauritius, following the human-induced extinction of other large fruit-eaters (Cheke & Hume, 2008; Hansen & Galetti, 2009), and may also pollinate several natives species (Nyhagen et al., 2005). It roosts at the study site where it eats fruits of 56% of native tree species, which comprise 78% of the forest trees ≥10 cm diameter at breast height (dbh) (Florens, Baider, Marday, et al., 2017).

Sampling protocol

We sampled (a) fruit and (b) ejecta density on the ground to compare (a) relative native fruit production and (b) foraging intensity of flying foxes respectively, between native forest areas invaded by alien plants and nearby weeded areas. Fruits and ejecta were sampled below two main native forest canopy species (*Labourdonnaisia glauca* Bojer and *Mimusops maxima* (Poir.) R.E. Vaughan - Sapotaceae), whose fruits are eaten by *P. niger*. The ripe fruit season of *L. glauca* typically spans from September to January, and that of *M. maxima* from September to November. Mature trees were randomly sampled in one hectare of weeded forest and one hectare of adjacent non-weeded forest to estimate relative native fruit production and compare ejecta density at their base as a surrogate of flying fox foraging intensity. Trees within 10 m of forest edges were excluded to avoid potential edge effect. An equal number of trees were sampled across the trunk diameter range of reproductive trees for each species, resulting in 60 sampled trees of *L. glauca* and 12 of *M. maxima,* in each of the weeded and non-weeded forest areas. Quadrats of 1 m^2, cleared of leaf litter, were marked on the ground in the four cardinal directions of each sampled tree, centred on the midpoint between the trunk's base and the crown's edge. Fruits and ejecta found in the quadrats (4 m^2 per tree) were collected weekly during five months (July – November 2016) for each of the 144 sampled trees. Fresh seeds were not counted separately because *M. maxima* seeds (one or rarely two per fruit) were always within the fruit pulp and *L. glauca* seeds (one per fruit) were attached to fruit remnants by a sticky latex, thus recognisable as coming from one fruit and counted as such. Intact fruits and fruits remnants bearing *Pteropus* teeth marks were used to estimate relative native fruit production of trees between the weeded and non-weeded areas. We did not attempt to estimate relative fruit production from ejecta counts due to the lack of information about the number of ejecta potentially produced per fruit and because no fruit could be completely eaten by a flying fox, but instead they always discarded the large seeds with at least some pulp attached to it. Ejecta counts were used as proxy for flying fox foraging intensity.

Foraging preferences of flying foxes were examined using intraspecific variation in traits of sampled trees and their fruit characteristics. Tree height was visually estimated using a metre placed along the trunk, a reliable method given the forest's short stature (3-15 m). Crown size was estimated by measuring the distance from the tree trunk's centre to the crown edge in the

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four cardinal directions. Diameter at breast height was measured at 1.3 m along the east side of the trunk. Sampled trees were georeferenced using a handheld GPS (Garmin 62s), for determining the harmonic mean of distances to the forest edges in the four cardinal directions ("effective distance") to incorporate a potential effect of multiple edges. Ripeness of fruits and seeds of *L. glauca* (N=593) and *M. maxima* (N=77) was determined based on the texture of the fruit pulp (softened when ripe) and seed colour (darkened when ripe), and each fruit was classified as either bat-eaten (if they bore typical teeth marks of *Pteropus*) or intact. Length and diameter of *L. glauca* fruits (N=474) were measured using a dial calliper (error: ± 0.01 mm) to obtain a "size index" - the fruit length multiplied by the width in mm. The size of *M. maxima* fruits was not measured, because they were often eaten from their base making accurate measurements impossible due to large missing parts.

Ejecta detectability and secondary removal

A sample of ejecta was visually monitored on the forest floor for five weeks to assess the ease of their detectability through time for informing temporal spacing of sampling effort. Ejecta detectability on the forest floor was reduced after one week due to shrinking and the ejecta turning darker brown. However, ejecta remained easily detectable and had not disintegrated even after five weeks, suggesting that weekly data collection was sufficient for reliable quantification. Although secondary removal of ejecta and fruits has been previously reported by snails and other frugivores (Banack, 1998), no removal was detected during a 3-month camera trapping scheme where 10 fruits and 20 ejecta, that were replaced weekly, were monitored. Additional feeding trials with the invasive alien Giant African land snail (*Lissachatina fulica* (Férussac, 1821) - Achatinidae), common at the study site, confirmed that snails had no significant impact of the number of ejecta (unpublished data). Consequently, ejecta and fruit count data collected from the ground quadrats were used in the analyses without any further data correction for secondary disappearance.

Statistical analyses

Native tree fruit production and flying fox foraging intensity were compared between weeded and non-weeded areas and on native trees with different characteristics by two separate zero-inflated generalised linear mixed-effects models (Table A) using the "glmmTMB" package (Brooks et al., 2017) in R version 3.3.1. (R Core Team, 2016). Pearson correlation coefficients were computed to assess the relationship between tree traits and avoid multicollinearity. Crown size was positively correlated with both trunk diameter at breast height and tree height (Figure A), therefore crown size was used as a general proxy for tree size in the models. GLMMs were fitted with negative binomial distribution to handle over-dispersion and given the nature of the response variables (Lindén & Mäntyniemi, 2011). The interactions between tree species, impact of weeding and other tree traits (crown size and distances from forest edges) were incorporated as fixed effects into the full models while tree identity was included as random effect to account for pseudo-replication. The preferences of flying foxes regarding native fruit size and ripeness were tested by a GLMM (Table A) with fruit condition (intact versus bat-eaten) as a binomial response variable, fruit size (continuous variable) and ripeness (categorical variable) as fixed effects and tree identity as random effect using the *glmer* function of the "lme4" package (Bates, Mächler, Bolker, & Walker, 2015). All model fits were validated using diagnostic plots of the *DHARMa* package (Hartig, 2017). Model selection was performed using the *dredge* function of the "MuMIn" package (Barton, 2016) and the most parsimonious models were identified using the second-order Akaike information criterion (AICc (Burnham & Anderson, 2002), Table A). Subsequently, we conducted post-hoc contrast tests for pairwise comparisons of significant interactions, while correcting for multiple comparisons using the Tukey method with the

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"lsmeans" package (Lenth, 2016). All results are reported as mean ± standard error over the five-month sampling period unless otherwise specified.

Results

Relative native fruit production

Native fruit production, reflected by the number of intact and bat-eaten fruits sampled in the ground quadrats, was on average three times higher in the weeded forest than in the non-weeded forest (8.7 ± 2.11 fruits per tree and 2.7 ± 0.58 fruits per tree, respectively) during the sampling period (July – November). *Labourdonnaisia glauca* fruit production was 6.9 ± 1.23 fruits per tree in the weeded and 3.2 ± 0.68 fruits per tree in the non-weeded forest, and the equivalent figures for *M. maxima* were 19.5 ± 12.84 and 0.3 ± 0.25 in the same areas. Model predictions indicated that weeding significantly increased the fruit production for both species (Figure 3A, Table 1, 2). The best-fitting GLMM exploring the impact of tree characteristics on native fruit yield showed a significantly positive effect of crown size (Table 1).

Table 1. Parameters for significant explanatory variables retained in the best GLMM explaining native fruit production and flying fox foraging intensity on *Labourdonnaisia glauca* (LAGL) and *Mimusops maxima* (MIMA) in weeded (W) and non-weeded (NW) forests at Mt Camizard on Mauritius. Estimates with associated standard error (SE) as well as *Z*-value and adjusted *P*-value are given for each variable.

	Fruit production			*Foraging intensity*		
	Z-value	P-value	Estimate (± SE)	Z-value	P-value	Estimate (± SE)
Species (LAGL vs MIMA)	2.06	*	1.76 (± 0.86)	3.25	**	2.13 (± 0.66)
Habitat type (W vs NW)	2.62	**	0.82 (± 0.31)	4.77	***	1.49 (± 0.31)
Crown size	3.50	***	0.06 (± 0.02)	3.36	***	0.06 (± 0.02)
Species (MIMA) * Habitat type (W)	3.00	**	3.01 (± 1.00)	2.75	**	2.25 (± 0.82)

* p<0.05; ** p<0.01; *** p<0.001

Table 2. Results of the post-hoc contrast tests applied to the most parsimonious GLMM for explaining native fruit production and flying fox foraging intensity, which included interaction between tree species (*Labourdonnaisia glauca* (LAGL) versus *Mimusops maxima* (MIMA)) and weeding (weeded (W) versus non-weeded (NW)). Estimates with associated standard error (SE) as well as *t* ratio and adjusted *P*-value are given for each comparison.

Contrast		*Fruit production*			*Foraging intensity*		
		t ratio	P-value	Estimate (± SE)	t ratio	P-value	Estimate (± SE)
LAGL NW vs	LAGL W	-4.03	***	-3.83 (± 0.95)	-5.07	***	-3.84 (± 0.76)
	MIMA W	-3.08	*	-2.58 (± 0.84)	-5.80	***	-3.80 (± 0.66)
	MIMA NW	2.06	NS	1.76 (± 0.86)	-3.36	**	-2.23 (± 0.67)

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MIMA NW vs	LAGL W	-3.44	**	-2.07 (± 0.60)	-2.76	*	-1.61 (± 0.58)
	MIMA W	-2.62	*	-0.82 (± 0.31)	-4.83	***	-1.57 (± 0.32)
LAGL W vs	MIMA W	2.16	NS	1.25 (± 0.58)	0.08	NS	0.04 (± 0.56)

NS – not significant; * p<0.05; ** p<0.01; *** p<0.001
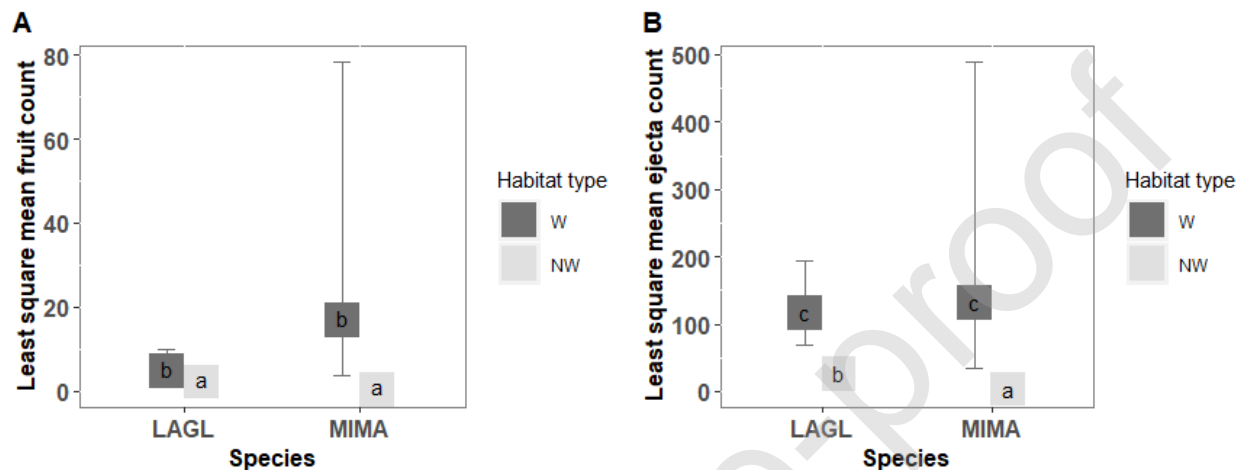
Figure 3. A) Native fruit production and B) flying fox foraging intensity reflected by the number of fruits and bat ejecta collected in the ground quadrats under the sampled *Labourdonnaisia glauca* (LAGL) and *Mimusops maxima* (MIMA) trees in weeded (W) and non-weeded (NW) forests at Mt Camizard on Mauritius. Significant differences (p<0.05) between the predicted means with 95% confidence intervals using the most parsimonious GLMM are marked by letters a, b and c.

Flying fox foraging intensity

Overall, flying fox foraging intensity was much higher in the weeded forest (129.8 ± 20.14 sampled ejecta per tree in the weeded area versus 33.4 ± 7.11 in the non-weeded area), reflected by the number of ejecta collected in ground quadrats during the survey period (July – November). For *L. glauca*, an average of 136.8 ± 23.05 ejecta per tree were sampled in the weeded and 39.5 ± 8.27 in the non-weeded forest, while the corresponding figures for *M. maxima* were 87.6 ± 25.74 and 1.6 ± 0.78 in the same areas, respectively. The post-hoc test showed a significantly positive impact of weed removal on flying fox foraging intensity on both tree species (Figure 3B, Table 1, 2). The best-fitting GLMM exploring the impact of tree characteristics on flying fox foraging intensity showed a positive effect of crown size (Table 1).

Flying fox fruit preference

Fruit size of *L. glauca* ranged from 170 to 1,188 mm^2, with a mean ripe fruit size of 608 ± 9.8 mm^2 and mean unripe fruit size of 483 ± 9.7 mm^2. Of the 110 bat-eaten *L. glauca* fruits sampled, 69.4 % were ripe, whereas 60.5 % of the 483 intact *L. glauca* fruits were unripe. Similarly, of the 68 bat-eaten *M. maxima* fruits sampled, 94.7% were ripe, while only 8 intact *M. maxima* fruits were found, all unripe. The GLMM confirmed that flying foxes feed significantly more on ripe *L.*

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glauca fruits compared to unripe ones and larger *L. glauca* fruits were bearing *Pteropus* teeth-marks significantly more often than smaller fruits of the same species (Table 3, Figure 4). No analysis was performed for *M. maxima* fruits because fruits size could not be measured.

Table 3. Parameters for significant explanatory variables retained in the best GLMM explaining flying fox foraging preference for native fruit size and ripeness on *Labourdonnaisia glauca* at Mt Camizard on Mauritius. Estimates with associated standard error (SE) as well as *Z*-value and adjusted *P*-value are given for each variable.

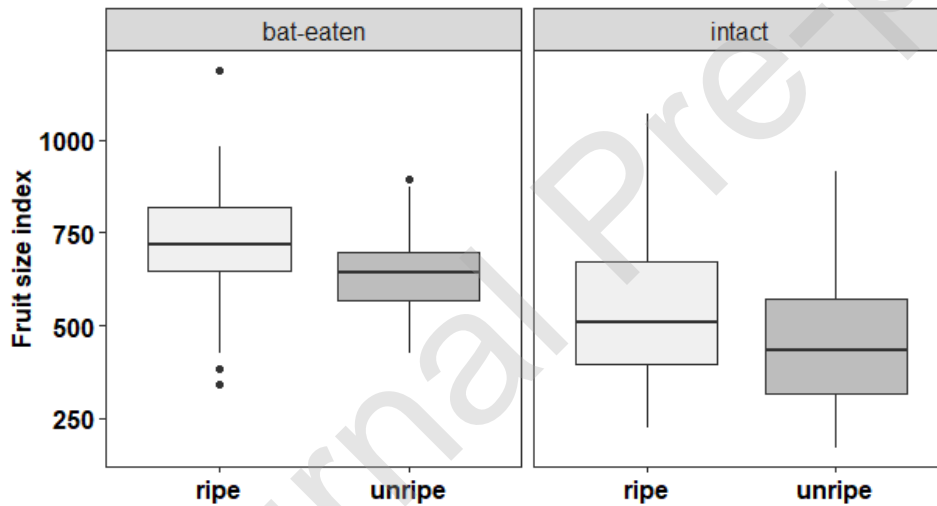|	*Flying fox preference for fruit size and ripeness*		
	Z-value	P-value	Estimate (± SE)
Fruit size index	7.49	*	0.006 (± 0.001)
Ripeness (ripe versus unripe)	2.68	**	0.74 (± 0.28)

* p<0.05; ** p<0.01

Figure 4. Size comparison of ripe and unripe *Labourdonnaisia glauca* fruits that were bearing teeth-marks of *Pteropus niger* (N=110) versus intact (N=483) fruits collected in ground quadrats under sampled *L. glauca* trees in weeded and non-weeded forests at Mt Camizard on Mauritius. Fruit size index was obtained by multiplying fruit length and width in mm.

Discussion

Relative fruit production and foraging intensity

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We found substantially higher fitness of native trees, reflected by the much higher number of fruits sampled per tree where invasive alien plants have been controlled compared to trees growing in the non-weeded forests.The comparison between trees in weeded and non-weeded areas was based on a sample of fruits that were collected in the ground quadrats set up under each sampled tree. We did not set out to estimate total fruit production per tree but we were rather interested in the relative fruit production between trees in weeded versus non-weeded forests. Ejecta counts were not included to estimate relative fruit production because it could not be ascertained how many ejecta could be produced per fruit and seeds were always attached to a remnant of fruit pulp, allowing for including them in fruit counts. Larger trees also produced more fruits than their smaller conspecifics. Increased native fruit production after weed control has been previously noted in several other species bearing fleshy fruits (Auchoybur & Florens, 2005; Baider & Florens, 2006; Monty et al., 2013), suggesting that this trend is general. However, other processes may affect this outcome. For example, despite more abundant flower production after weeding, fewer fruits may be produced because of effects of herbivores and pollinators (Kaiser, Hansen, & Müller, 2008).

The observed increased fruit yield in the weeded forest was accompanied by greater foraging intensity by flying foxes. This shows that ecological restoration of native forest habitats through invasive alien plant control not only improves the quantity of fruits available to flying foxes in terms of per capita fruit production, but that this greater fruit availability is also detectable and exploited by these animals. This is consistent with findings elsewhere (Babajee & Florens, 2017). *Pteropus niger* largely roost in forested areas and must often travel significant distances to reach commercially important fruit trees. Since flying foxes use the increased food resources in native forests after alien plant weeding, this suggests that alien plant control in their native forest habitats would reduce the need for longer distance movements to commercial fruit trees.

Foraging intensity of flying foxes was also much greater in larger trees with wider crown compared to smaller ones of the same species. This result is in line with Old world Pteropodids being primarily canopy feeders (Fleming, Breitwisch, & Whitesides, 1987) and previous findings on Mauritius that larger tree species are more commonly used as fruit sources by *P. niger* than smaller species (Florens, Baider, Marday, et al., 2017). Furthermore, Oleksy et al. (2018) also noted that *P. niger* forages predominantly on larger trees of the commercially grown lychee (*Litchi chinensis* Sonn. - Sapindaceae). Larger trees thus play an important role in providing fruit resources to flying foxes. This may be a consequence of easier detectability and accessibility, as well as these trees carrying more fruits and thus representing more attractive resource patches.

Fruits that *P. niger* feed on are mainly larger and riper compared to fruits that they avoid. This suggests that they are predominantly seed dispersers, although flying foxes may feed on unripe fruits at times of fruit scarcity like after cyclones (Grant, Craig, & Trail, 1997; McConkey, Drake, Franklin, & Tonga, 2004). In this study, fruits were collected from the ground and not directly from trees to avoid changing the foraging behaviour of flying foxes on sampled trees. Intact fruits found on the ground could be a result of natural fall or animal movements while feeding, including flying foxes and monkeys too. Although we recognize that partially-eaten ripe fruits in the ground quadrats could have been also discarded by *P. niger*, flying foxes have the potential to disseminate the seed of the plucked fruit whether it is eaten or not afterwards. Seed dispersal is indeed known to be a major ecological role fulfilled by *Pteropus* species (Cox et al., 1992; Nakamoto et al., 2009). Critically, this ecosystem service tends to collapse with population reductions even before flying foxes become rare (McConkey & Drake, 2006). Flying foxes are also known to increase germination success of seeds that have been ingested (Traveset, Rodríguez-Pérez, & Pías, 2008) and to reduce microbial attacks by separating fruit pulp from larger seeds (Nyhagen et al., 2005; Oleksy, 2012), further enhancing their vital role in maintaining native forest regeneration.

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Conservation implications

The control of invasive alien plants in native forests as a restoration measure (Florens, 2013; Florens & Baider, 2013) improves the availability of fruits which flying foxes are able to locate and feed on. Our results likely reflect a conservative estimate in increased fruit production, as we studied only relatively weakly invaded non-weeded forests (Florens et al., 2012). Trees at our study site therefore likely face weaker competition from alien plants compared to most other native forest remnants on Mauritius, which are much more invaded (Florens et al., 2016; Page & d'Argent, 1997). Our results also imply that the foraging habitat quality for flying foxes is expected to further degrade as the invasion by alien plants continues to increase (Florens, Baider, Seegoolam, et al., 2017; Florens et al., 2016). Additionally, alien plant invasion in native forest is known to cause substantial (about 50%) reduction in the density of larger trees (trunk diameter of ≥ 10 cm) within about 70 years (Florens, Baider, Seegoolam, et al., 2017). This indicates that alien plant invasion deteriorates the foraging habitat quality of *P. niger*, not only by reducing the quantity of fruits produced per tree, but also through reduced tree density. The control of invasive alien plants in native habitats can thus halt this degradation and promote improvement. These results hold promise in informing management decisions to alleviate the worsening human-wildlife conflict between fruit-growers and flying foxes, which has recently led to several mass-culling events. Indeed, improved native foraging habitat quality should help reduce the exploitation of commercial fruits by flying foxes.

The importance of controlling invasive alien plants to restore native forests has been recognized for a long time (Vaughan & Wiehe, 1937). Yet, less than 3% of native forests on Mauritius have been cleared of alien plants due to the significant costs attached to this type of management action (Hammond et al., 2015; Republic of Mauritius, 2015). The finding that flying foxes forage more often on larger native trees can be taken advantage of by conservation managers when resources to control alien plants may be insufficient to weed whole forest areas. In such situations, managers may selectively remove alien plants from around the taller and large-crowned fleshy fruited species preferred by flying foxes. Selective weeding in specifically targeted areas would in this manner substantially improve foraging habitat quality of flying foxes without incurring the full costs of weeding entire swaths of native forests. This may be particularly valuable while more powerful and low-cost weed control methods are developed.

Finally, our finding that flying foxes feed predominantly on ripe fruits containing mature seeds underlines their instrumental role as seed dispersers. Flying foxes may therefore accelerate habitat restoration by dispersing seeds into weeded areas, thereby perpetuating a virtuous cycle through reinforcing their mutualistic interaction with fleshy-fruited native trees. This is particularly important because fruits of more than 50% of native woody plants on Mauritius are known to be eaten by flying foxes. Thus, flying foxes have the potential to disseminate the seeds of a wide diversity of endemic and threatened woody flora (Baider et al., 2010; Florens, Baider, Marday, et al., 2017). These include keystone species like figs, structural ecosystem engineers like emergent Sapotaceae that shape and maintain forest biodiversity, and species of high conservation priority (Baider & Florens, 2013).

Conclusion

Pteropus niger is now the last native species on Mauritius capable of disseminating large-seeded species, following the extinction of two other *Pteropus* species and other larger

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vertebrates that included fruits in their diet (Cheke & Hume, 2008). Our results strongly underline the interplay between native forest health and flying fox foraging behaviour, emphasizing the necessity of flying foxes for the maintenance of the native forest biodiversity of Mauritius. Based on these findings, we encourage decision makers to include invasive alien species control as part of the management strategy to pre-empt and alleviate human-wildlife conflict associated with flying foxes feeding on commercial fruits. This will concurrently improve the outlook for many other native species that rely on these unique forest ecosystems.

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Supplementary information

Table A. Description of the most parsimonious (*ΔAICc<4)* GLMMs explaining native fruit production and flying fox foraging intensity in weeded and non-weeded forests and of focal trees with different characteristics (including diameter at breast height, height, crown size and distances from forest edges) and GLMMs explaining the preference of flying foxes regarding native fruit size and ripeness. Models are ranked in ascending order of *AICc*. The number of parameters (*K*), *AICc* weight (*Wt*), and cumulative weight (*Cum. Wt*) are given for each model.

| Native fruit production	K	AICc	ΔAICc	AICc Wt	Cum. Wt
fruits ~ crown + species*weeding	7	784.52	0.00	0.51	0.51
fruits ~ crown + distance + species*weeding	8	784.63	0.11	0.49	1.00
Flying fox foraging intensity					
ejecta ~ crown + species*weeding	7	1579.55	0.00	0.70	0.70
ejecta ~ crown + distance + species*weeding	8	1581.23	1.68	0.30	1.00
Fruit size and ripeness preference					
fruit condition ~ ripeness + size	3	356.01	0.00	0.69	0.69
fruit condition ~ ripeness * size	4	357.98	1.97	0.26	0.95
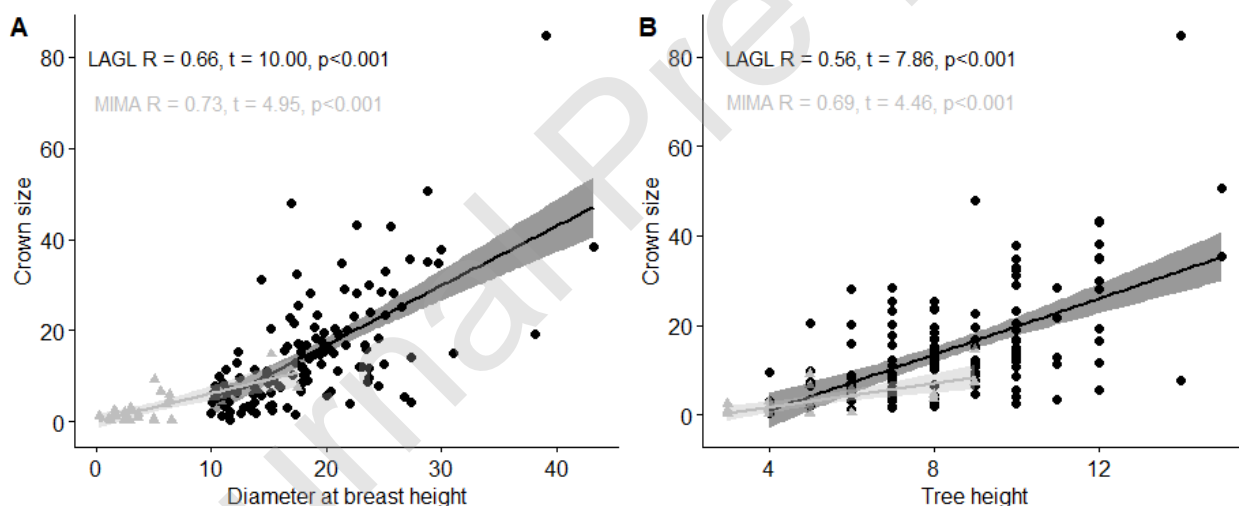
Figure A. Relationship between tree crown size and A) diameter at breast height and B) tree height, based on Pearson's correlation coefficients, of two Mauritian native canopy trees *Labourdonnaisia glauca* (LAGL; black circle) and *Mimusops maxima* (MIMA; grey triangle sampled at Mt Camizard.