

The fate of primary-dispersed *Mauritia flexuosa* L.f. fruit in different microhabitats in the Aripo Savanna Environmentally Sensitive Area, Trinidad, West Indies

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ABSTRACT

The fate of 1,500 *Mauritia flexuosa* L.f. fruit was observed between three distinct microhabitats of the Aripo Savanna Environmentally Sensitive Area, in Trinidad, by situating fruit stations and monitoring fruit fortnightly. Most fruit were used as a food source, with the most common fruit fate in all microhabitats being seeds remaining with the mesocarp partially or totally removed. Seed dispersal mainly occurred in the closed canopy of eastern forest margins and was negligible in island microhabitats (where stands of trees are surrounded by savanna). A lack of seed dispersers does not seem to be an immediate concern; however, ecological managers should closely monitor dispersers and their scatter-hoarding activities.

Key words: ecology, frugivores; Moriche Palm; post-seed dispersal; post-seed predation.

INTRODUCTION

In tropical rainforests, inter-species interactions are common and important for effective ecological functioning (Ghazoul and Sheil 2010, Lüttge 1997). Seed dispersal and seed predation are important biotic interactions that can determine the spatial distribution and population demography of many plant species in tropical rainforests (Beckman and Rogers 2013). Seed dispersal is broadly identified as the movement of seeds away from parents (Nathan and Muller-Landau 2000), whereas seed predation is the death of a seed as a result of the complete or partial consumption of the seed by some animal predator (Forget *et al.* 2005). Seeds are often (but not always) packaged in a fleshy pulp or mesocarp which acts as an enticement for animals to disperse the seeds (Ghazoul and Sheil 2010). The entire structure is commonly known as a fruit and animals eat just the fleshy mesocarp, just the seeds, or both (Vander Wall, Kuhn, and Gworek 2005). Different animals eat different parts of the fruit and disperse the seeds depending on the availability of food and the environmental conditions (Vander Wall, Kuhn, and Gworek 2005). Seed dispersal serves several important ecological functions for the plant, one of which is escaping seed predation/parasitism, which can lead to a very high or total loss of seeds that fall close to the parent (Beckman and Rogers 2013). Tropical trees with large seeds (> 10 g) (Jansen *et al.* 2002; Westoby, Leishman, and Lord 1996) tend to be at greater risk of predation or parasitism, as they are easier to find by seed predators and are thus more likely to benefit from dispersal away from the parent tree canopy (Vander Wall, Kuhn, and Gworek 2005). Tropical trees benefit from having large seeds because seedlings germinated from large seeds have more resources and are more likely to survive in closed canopy forests where competition for resources is highest. However, there is a trade-off in that larger seeds require larger seed dispersers to carry them away from the parent tree – even when the fleshy mesocarp is stripped from

the seeds (Westoby, Leishman, and Lord 1996). Primary dispersal (or the initial dispersal of large-seeded trees from the canopy) often happens through gravity pulling the seeds to the forest floor under the canopy of the parent tree. Additionally, terrestrial mammals commonly play the role of dispersers for large-seeded tree species in tropical forests once the seeds have reached the ground and are available to these mammals. Indeed, seed dispersers that can disperse large seeds are often limited to terrestrial mammals, such as large rodents, primates, or ungulates (Westoby, Leishman, and Lord 1996). The agouti (*Dasyprocta* sp.), a scatter-hoarding rodent, is a common disperser of medium-to-large seeds of tropical rainforest trees in the neotropics (Godó *et al.* 2022), including in Trinidad and Tobago (Rostant *et al.* 2021). Other terrestrial mammals that have been reported to disperse medium-to-large seeds in the neotropics are lappes (*Cuniculus paca* Linnaeus) (Mittelman *et al.* 2020), tapirs (*Tapirus terrestris* Linnaeus) (Virapongse *et al.* 2017), and primates (Hanya *et al.* 2011). Rats and smaller mammals have also been recorded dispersing larger seeds in some situations (Lim *et al.* 2020). Agouti and other rodent seed dispersers have been shown to be both dispersers and predators of tropical tree seeds (Jansen *et al.* 2002). During times of fruit abundance, they act as frugivores (fruit eaters) and feed on the fleshy mesocarp of the fruit, leaving the seeds intact and undispersed. At other times, when the fruit is no longer abundant, they may disperse the seeds away from the parent tree and cache them for future consumption (Mittelman *et al.* 2020). Some of the cached seeds are redispersed and may eventually be circulated hundreds of metres because of several different agoutis stealing from one another (Jansen *et al.* 2012).

To attract large mammals to disperse their seeds, plants must offer a reward. Scatter-hoarding is a model of seed dispersal through which an animal may act as a disperser

of a seed or fruit in one instance and as a predator of the same seed or fruit in another instance (Jansen *et al.* 2002). In this situation, the seeds themselves act as a food enticement to the disperser, where some seeds are sacrificed to allow others to be dispersed. Such scatter-hoarding relationships are relatively common between trees and vertebrate dispersers, particularly large-seeded tree species in both temperate and tropical forests (Forget *et al.* 2005; Vander Wall, Kuhn, and Gworek 2005). In some cases, dispersal via scatter-hoarding rodents is almost obligatory for the reproduction of the tree species (Connell 1971), such as in the relationship between the agouti and the tropical tree *Carapa guianensis* Aubl. (Forget *et al.* 2005). In other cases, the relationship seems to be more facultative with seed dispersal occurring in the absence of the scatter-hoarding partners but in a way that results in a more clumped distribution of seedlings (Westco *et al.* 2009).

The tropical palm *Mauritia flexuosa* Lf. has relatively large seeds (size: 2 to 4 cm diameter; dry weight: 4 to 16 g) (Virapongse *et al.* 2017; Khorsand Rosa, Barbosa, and Koptur 2014; Hernández-Valencia, Guitián, and González 2017) and is widespread in the Amazon basin and Guiana Shield regions of tropical America (Arneaud 2021). Dispersers of *Mauritia flexuosa* (*M. flexuosa*) seeds have been observed and recorded in Brazil, the Guianas, Venezuela, and Colombia (da Silva *et al.* 2011; Zona and Henderson 1989; Mendieta-Aguilar, Pacheco, and Roldans 2015; Jansen *et al.* 2002; Calderon 2002). The agouti (*Dasyprocta* sp.) is the most widespread species recorded dispersing seeds of *M. flexuosa* (da Silva *et al.* 2011; Mendieta-Aguilar, Pacheco, and Roldans 2015; Calderon 2002). Mendieta-Aguilar, Pacheco, and Roldan (2015) noted that the main dispersers of *M. flexuosa* in Laguna Azul, Beni, Bolivia were *D. punctata* and *C. paca*. However, they did not scatter-hoard or recache seeds due to the high abundance of fallen fruit. Agoutis can detect large numbers of de-fleshed (i.e. mesocarp removed) seeds and will pilfer them to eat and to re-cache for themselves (da Silva *et al.* 2011). This activity promotes the secondary movement of cached seeds and further increases dispersal distance (Jansen *et al.* 2012; Perea, Miguel, and Gil 2011). Additionally, Calderon (2002) recorded *D. leporina* removing *M. flexuosa* seeds from perimeter traps and Sherman traps that were set during seed removal studies in the southeast of Guárico State, Zaraza District, Venezuela.

Besides agoutis, other species have also been shown to disperse or predate *M. flexuosa* seeds or to eat the fleshy mesocarp of the fruit. In the Aripo Savannas Environmentally Sensitive Area (ASESA), ad-hoc trapping by motion-sensing camera traps baited with *M. flexuosa* fruit have recorded agoutis, galaps (turtles), and tegus (lizards) eating the flesh of the fruit, but only agouti was recorded predated the seeds. Remains of eaten *M. flexuosa* seeds (with the endosperms

destroyed) with teeth marks from agoutis and maybe rats have been observed in the ASESA. However, of Trinidad and Tobago's large terrestrial fauna likely only the agouti and the lappe frequently disperse *M. flexuosa* seeds (Arneaud, Farrell, and Oatham 2017).

Spatial distribution patterns of adult *M. flexuosa* on a landscape scale are likely determined by both the availability of dispersal vectors to transport seeds to potential establishment sites and the location of suitable microhabitats for germination and subsequent growth (Beckman and Rogers 2013). In ASESA, *M. flexuosa* trees tend to reveal clumped distributions in fire-dominated open canopy sites with high densities of individuals at the scale of one hectare. However, they reveal more dispersed distributions at closed canopy sites with significantly lower densities of individuals at the hectare scale (Arneaud, Farrell, and Oatham 2017). In open canopy sites, plentiful resources usually exist for seedling establishment and growth. In closed canopy sites, suitable habitats with gaps in the canopy are patchy and tend to be concentrated closer to the margin between the forest and savanna ecosystems (Arneaud, Farrell, and Oatham 2017). It has also been found that in open and closed habitats, *M. flexuosa* female trees show differences in fruit size and the number of fruit produced. They produce fewer but larger fruit in closed canopy habitats and smaller but more numerous fruit in open canopy habitats (Arneaud, Farrell, and Oatham 2017). In the open canopy environment, the uniform availability of light likely allows for a clumped distribution of *M. flexuosa* palms by allowing seedlings to establish themselves close to the parent trees. Moreover, seed dispersal presumably does not play as significant a role in determining the spatial patterning of adult trees in such a habitat. Conversely, in the closed canopy habitat, *M. flexuosa* seedlings are typically able to establish themselves. Nonetheless, they may be restricted based on the availability of seed dispersers to move the seeds into patches of suitable microhabitat.

This study investigates the differences in dispersal and predation patterns between the different microhabitats (i.e. open and closed margin environments) of the ASESA in Trinidad. The aim is to determine the probability of different fates for the fruit and seeds of *M. flexuosa* after primary dispersal in different microhabitats.

METHODOLOGY

The study site

The white-sand savanna habitats of the Aripo Savanna (Strict Nature Reserve) Environmentally Sensitive Area (10°35'30"N, 61°12'0"W) form the only remaining intact savannas in Trinidad (EMA 2007; John-Bejai *et al.* 2013). The ecosystem is a series of open, treeless areas of grass and sedge marshland within an extensive area of swamp forest.

Rainfall in the savannas is approximately 2,500 mm per annum, with a dry season of two to three months where the rainfall can fall below 50 mm for the month (TTMS 2016; Richardson 1963). The open savannas are characterised by an impermeable hardpan layer at a 20 to 30 cm depth that restricts primary productivity in the dry season because of drought and in the wet season because of waterlogging. *M. flexuosa* palms are located in the ecotone between the savannas and swamp forests. Palm marsh communities form where the impermeable hardpan layer is greater than 50 to 100 cm beneath the surface (Richardson 1963). The palm marsh forests can be classified into three microhabitats or margins: eastern, western, and palm islands (Figure 1). The western microhabitat of the savannas and the palm island microhabitat are classified as fire-impacted microhabitats (FIM) because fires are driven by trade winds that blow consistently in an east-to-west direction during the dry season. This leads to sparser vegetation in the western and island plots, resulting in reduced canopy coverage. The eastern microhabitats of the savannas are not exposed to substantial burning, as they are sheltered from trade wind-driven fires and are classified as non-fire-impacted microhabitats (NFIM), having dense vegetation with closed canopies (Arneaud, Farrell, and Oatham 2017).

Data collection

A map of the area was created using the QGIS Geographical Information System software (v3.16.12 LTR/PR). A stratified random sampling design was used to select 10 sample plots at random in the three different savanna microhabitats (eastern, western, and palm islands). These plots were positioned within five different patches of savanna (Fig. 1) and were located in the field using a portable global positioning system (GPSMAP v64s device, Garmin®, USA) with the datum set to WGS84. Circular quadrats (20 m in diameter; 314.29 m² in area) were then established for each plot. Within each plot, 10 fruit stations (i.e. white disposable polystyrene pour boats chosen for high visibility), each containing five fruit, were placed in the field. Two fruit stations were placed at the centre of the sample plot, while the other eight fruit stations were placed equidistantly along two 20-metre perpendicular transect lines, which crossed at the centre point (Arneaud 2020). The fruit stations were visited every 14 days (fortnightly) to record if any fruit/seeds were damaged, destroyed in situ, or removed. The data from the fortnightly visits were used to calculate the probability of four fates for fruit: i. untouched, ii. fleshy mesocarp damaged and/or removed, iii. mesocarp removed and endosperm consumed in situ (with remains evident), and iv. fruit completely removed (with no remains evident). The final category of 'fruit completely removed' is assumed to represent seed dispersal (i.e. the movement of the seed away

from the parent tree after primary dispersal). These fruit fate estimates were made from November 2012 to March 2013 and from October 2013 to January 2014 with a total of 1,500 fruit situated in 30 sample plots: 10 on island microhabitats, 10 on western microhabitats (open canopies), and 10 on eastern microhabitats (closed canopies). Only mature fruit at stage 4, as defined by Arneaud (2020) were used in this study. On average, it takes approximately 2 months for Stage 4 mesocarp to decompose, and approximately 1 year for the epicarp and endosperm to decompose. This timeframe assumes no post-harvest consumption by invertebrates or vertebrates, and that the fruit are not submersed. Most interactions with the fruit epicarp and mesocarp are expected to occur during the earlier stages of the study (Arneaud 2020).

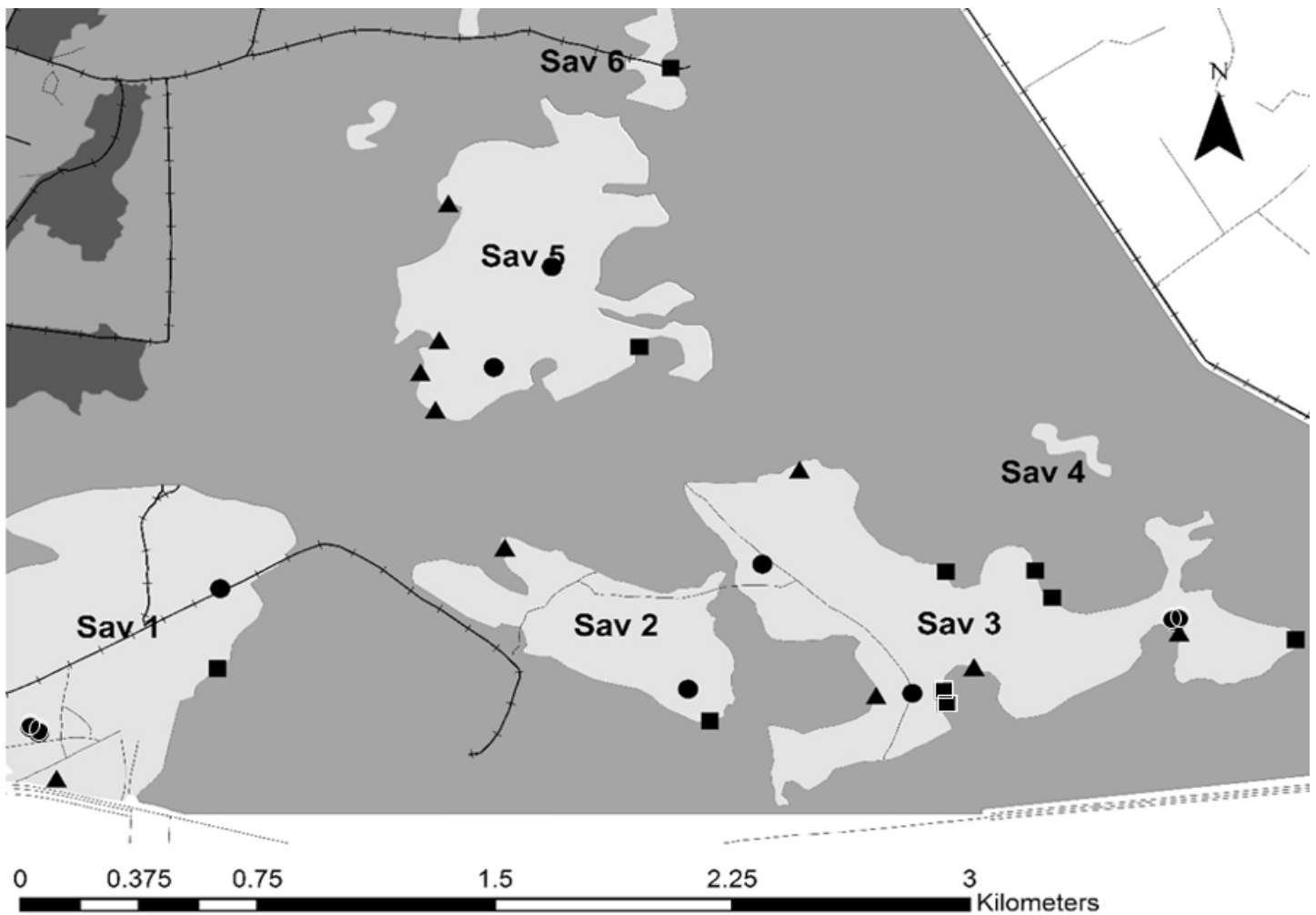
Data analyses

Data analysis was conducted in IBM SPSS Statistics v. 27.0.0 using the generalised linear model (GLiM) [GENLIN] (SPSS Software 2020). The reliability level (confidence interval) during these statistical tests was 95%.

The fate of fruit (i.e. the number of fruit untouched, mesocarp removed, mesocarp and endosperm removed, and whole fruit removed as the dependent variables) was tested using GLiM between the three microhabitats (as the independent variable). The analysis utilised a linear distribution and an identity-linked function. Fisher's least significant difference (LSD) tests were conducted whenever significant differences occurred during statistical analyses.

RESULTS

From the fruit fate plots, it was determined that 68% of the situated fruit revealed evidence of animal interference (Fig. 2). The majority of the fruit that revealed interference had all or part of the mesocarp removed. The fruit fate category that was least observed is the one where both the mesocarp and the endosperm were consumed (with fragments of both left in situ). There were no statistical differences in the number of untouched fruit between the three microhabitats (GLiM, $x^2 = 1.33$, $df = 2$, $P > 0.05$). There were statistical differences in the presence of fruit with the mesocarp removed between microhabitats (GLiM, $x^2 = 12.62$, $df = 2$, $P < 0.001$; Fisher's LSD test, $P < 0.05$, island and eastern microhabitats). Fruit that had their mesocarp removed were most common in the island microhabitats (33.20 ± 10.50 fruit) and least common within the eastern microhabitats (20.50 ± 6.48 fruit) (Fig. 2). There were statistical differences between fruit with the mesocarp and endosperm removed between microhabitats (GLiM, $x^2 = 16.52$, $df = 2$, $P < 0.001$; Fisher's LSD test, $P < 0.05$, island and eastern microhabitats). Fruit that were totally destroyed but with fragments (mesocarp and endosperm) left behind were most common in the eastern microhabitats (6.90 ± 2.18 fruit) and least common in the island microhabitats (1.10 ± 0.35



Legend

- Eastern_margins_(NFIMs)
- Island_margins_(FIMs)
- ▲ Western_margins_(FIMs)
- +— Roads in study area
- == Old Railway
- ~ Roads_Trinidad
- Quarry
- Savanna polygons
- Forest and Palm Marsh



Coordinate System: WGS 1984 UTM Zone 20N
 Projection: Transverse Mercator
 Datum: WGS 1984

Fig. 1. Sample site locations within Savannas 1–6 in the Aripo Savannas Environmentally Sensitive Area showing the three different microhabitats or margin environments. Map modified from Arneaud, Farrell, and Oatham (2017). FIMs -Fire-impacted microhabitats), NFIMs -Non-fire-impacted microhabitats.

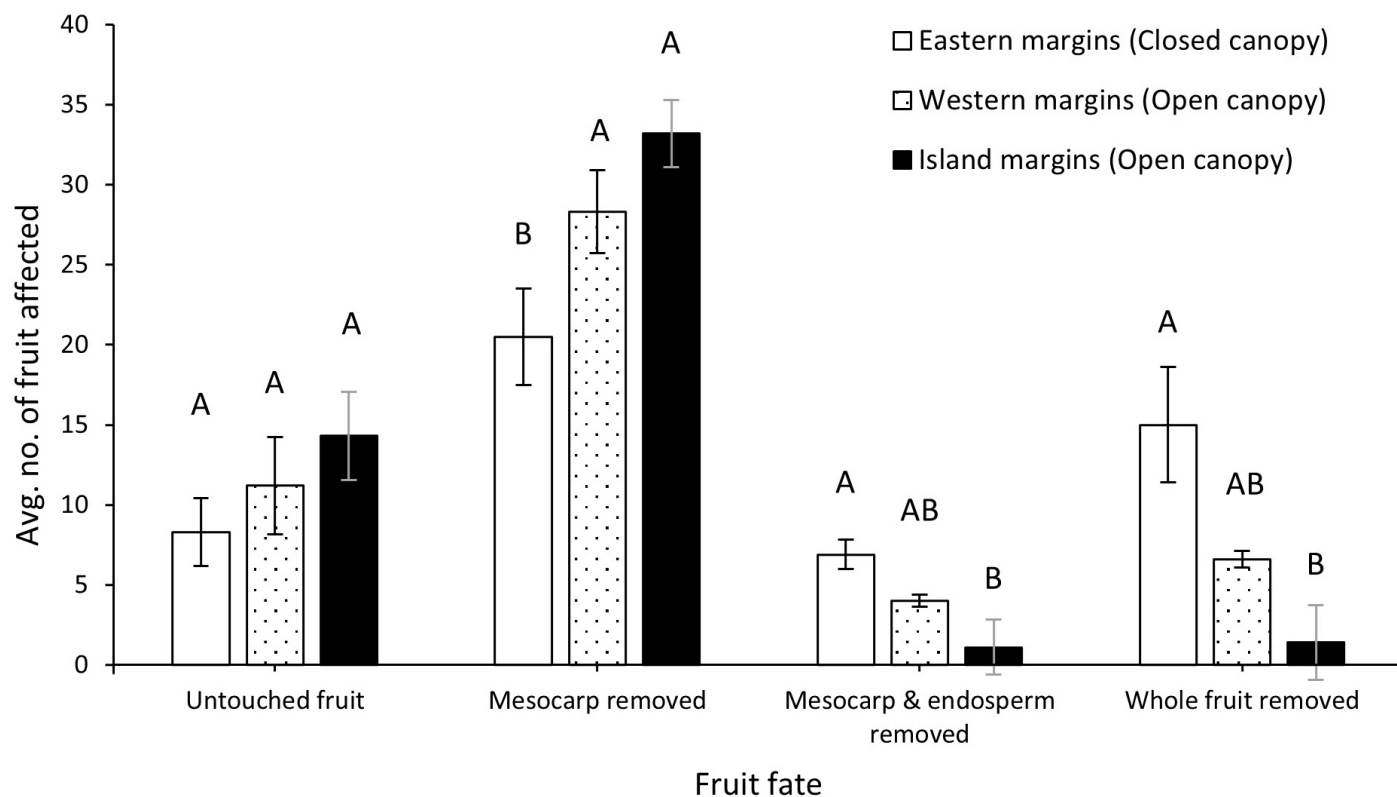


Fig. 2. Post-dispersal fates of *Mauritia flexuosa* fruit in the different microhabitats of the ASESAs. Within a fruit class, means that do not share a same letter are significantly different (Least Significant Difference Test, $p < 0.05$): bars represent the SE of the mean ($n = 10$).

fruit). There were statistical differences between whole fruit removed between the microhabitats (GLiM, $\chi^2 = 16.05$, $df = 2$, $P < 0.001$; Fisher's LSD test, $P < 0.05$, island and eastern microhabitats). Whole fruit that were removed were most common within the eastern microhabitats (15.00 ± 4.74 fruit) and least common within the island microhabitats (1.40 ± 0.44 fruit). Overall, most of the seeds were not dispersed, with 'mesocarp removed' being the most common fruit fate in all microhabitats. The dispersal of seeds occurred most often in the closed canopy eastern microhabitats and least often in the open canopy island margins (where dispersal was negligible). The open canopy western margins were intermediate between the two other margin types for all fruit fates (Figure 2).

DISCUSSION

Within the present study, differences in dispersal and predation between the different microhabitats (margin environments) of the ASESAs were observed. The most common fate of *M. flexuosa* fruit was to have the mesocarp (i.e. the fleshy part of the fruit) partially or totally stripped from the seeds and left under the parent tree. This was the most likely fate in all microhabitats: open, closed, or island.

In this study, it was not determined which animal

species was responsible for consuming the fruit mesocarp. Several species have been identified feeding on the mesocarp through use of camera traps in the past (Arneaud 2020), where only larger mammals are known to remove the whole fruit (Virapongse *et al.* 2017; Khorsand Rosa, Barbosa, and Koptur 2014). A possible reason for this pattern is that many smaller species have been reported to eat the mesocarp of *M. flexuosa* fruit in the ASESAs – from rodents to lizards and turtles (Arneaud 2020) – leading to greater utilisation of fruit mesocarps because there are greater numbers of animals that feed on the mesocarp alone. This suggests that *M. flexuosa* fruit is an important food source for many animal species, most of which are not dispersers of the seeds (Villalobos and Bagno 2011; Parolin, Wittmann, and Ferreira 2013). Known seed dispersers (e.g. agoutis and lappes) may also feed on mesocarps and leave the seeds when the supply of fruits is high and they are satiated on the mesocarps of the fruit alone (Mendieta-Aguilar, Pacheco, and Roldan 2015).

It seems that when seed dispersers are present and not satiated by the fleshy mesocarp, there is often evidence of seeds being used as a food source, sometimes with entire seeds or fruit being removed (Jansen *et al.* 2002). In the island microhabitats, very low rates of seed removal were observed. This indicates that large seed-dispersing

rodents, such as the agouti, were absent or that they were present but fully satiated by feeding on the fruit mesocarps alone. It cannot be determined which of these processes was dominant with the methodology used in this study, but this research does indicate that the dispersal of *M. flexuosa* seeds in the island habitats is very low, which is expected to result in a clumped distribution of seedlings and adult palms as fallen fruit/seeds remain beneath the parent tree (Beckman and Rogers 2013). It could be that seed predators and dispersers, like the agouti, are only present in the eastern or western habitats, as they do not cross the open savannas to the island habitats (Andreazzi, Pires, and Fernandez 2009).

The results indicate that seed dispersal does happen in the eastern and western microhabitats, which means that seedling and adult palms will be less clumped and more widely dispersed than in the island habitats (Beckman and Rogers 2013; Arneaud 2021). The total removal of fruit (probable dispersal) was observed predominantly in the closed eastern microhabitats (and to a lesser degree in the open western microhabitats). Seed dispersers were present in the western (open) and eastern (closed) microhabitats, and it seems that their satiation on fruit mesocarps alone was not achieved because the seeds were predated and/or dispersed (Jansen *et al.* 2002). Possible reasons for the lack of mesocarp satiation in eastern and western microhabitats could be that animals utilising fruit mesocarps in these microhabitats exist at a higher density than in island microhabitats. Therefore, more fruit mesocarp are consumed, leaving potential seed predators and dispersers hungry and inclined to utilise the seeds. Another possibility is that there is less fruit in the eastern and western habitats. Arneaud (2020) determined that the *M. flexuosa* produces less fruit in the closed canopy environment and that adult trees exist at lower densities, which could decrease the number of fruit available to animals and trigger predation and dispersal of seeds by the agouti population.

Considerable research has been conducted regarding the possible impacts of overhunting of seed dispersers and how this can negatively influence the dispersal and regeneration of tropical trees (Beckman and Rogers 2013; Federman *et al.* 2014). The results of this study indicate that a loss of seed dispersers through overhunting in the ASESAs is likely to impact the *M. flexuosa* in closed canopy sites rather than in open canopy sites. This is because dispersal is more common in closed canopy sites and more likely to be required for the establishment and survival of seedlings. It does not seem to be the case that current hunting pressures in and around the ASESAs are causing depression in the agouti population, as studies have shown healthy agouti numbers in the ASESAs (Rostant *et al.* 2021; Ganpat, Giordano, and Rostant 2021). Therefore, a lack

of seed dispersers may not be a problem for *M. flexuosa* population demographics at present – but should be closely monitored.

CONCLUSION

Utilisation of *M. flexuosa* fruit by animals in the ASESAs varies by microhabitat. The use of the mesocarp of the fallen fruit is most common in all microhabitats, and many different smaller animals likely utilise this as a food source. The utilisation of the *M. flexuosa* seeds was more common in eastern (closed canopy) microhabitats and scarcely occurred in island microhabitats. This indicates that seed dispersal within the ASESAs mainly occurs in forest margin habitats and not in island habitats. At present, a lack of seed dispersers does not seem to be an immediate concern; however, ecological managers should closely monitor dispersers and their scatter-hoarding activities.

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