Marked reproductive plasticity in response to contrasting fire regimes in a neotropical palm

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Abstract: The impact of fire on the stand structure of *Mauritia flexuosa* Linn f. was investigated in a tropical savanna-forest system by comparing savanna margins that are either protected from or regularly exposed to moderate to low intensity savanna fires. *Mauritia flexuosa* populations within different environments were sampled over two years to measure: stand density, size class distribution, operational sex ratio, and fecundity. It was found that the canopy was significantly more open in the fire-impacted margins. There were no significant differences in diameter at breast height, but non fire-impacted margins had significantly taller adult palms. The overall reproductive output was significantly higher in the fire-impacted margin and there was a marked trade-off in reproductive output, with palms in fire-impacted margins producing lighter fruit, but three times as many individual fruit. In all margins, stands formed an 'inverse-J' size class distribution, indicating a stable population structure. *Mauritia flexuosa* stands appear to have sufficient plasticity in reproductive output to sustain viable populations across a range of fire regimes.

Key words: Arecaceae, disturbance, fruit, *Mauritia flexuosa*, phenotypic plasticity, reproductive output, resilience, savannah.

Introduction

Disturbance plays a key role in the dynamics of tropical ecosystems, and fire is one of the key drivers of ecosystem processes in tropical savannas (Bond & Keeley 2005; Cochrane 2009; Montúfar *et al.* 2011). Understanding the ability of grasses and trees to coexist in tropical savannas, and the role of fire in this system, has been a key research question in recent years; in particular in the face of altered fire regimes due to human encroachment and Climate Change (Higgins *et al.* 2000; Moritz *et al.* 2012; Van Langevelde *et al.* 2003). Within tropical savanna assemblages, increasing fire rate or intensity tends to favour grasses over trees, while palms can be viewed as intermediary between grasses and dicotyledonous trees in terms of resilience to fire (Barot *et al.* 2005; McPherson &

Williams 1998; Souza & Martins 2004). Indeed the dominance of palms over dicotyledonous trees in certain savanna microhabitats is thought to be contingent on fire. *Mauritia flexuosa* Linn f. (Arecaceae) (common name: Moriche Palm) is abundant on the edges of neotropical savannas and provides a particularly useful model as it is common on both sheltered and fire-impacted savanna-forest margins. Here we use contrasting *M. flexuosa* stands to investigate the ability of palms to withstand frequent fires and to understand the traits that allow this species to dominate in fire-prone habitats and also persist at lower densities in habitats where fire is less frequent.

Mauritia flexuosa is one of the most common and widespread palms in the neotropics and plays a significant role in the economy as well as the ecology of many South America countries

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(Brightsmith & Bravo 2006; Delgado *et al.* 2007; Hada *et al.* 2013; Holm *et al.* 2008; Kahn & Granville 1992; Peters *et al.* 1989). Stand structure of *M. flexuosa* has been broadly categorized into two groups within the Amazonian region: floodplain stands and upland stands, neither of which has been described thoroughly (Gilmore *et al.* 2013; Kahn 1991). Floodplain stands are large and occur in riparian zones of the Peruvian Amazon, while upland stands are smaller, and scattered throughout upland forested areas associated with poorly drained depressions sharing similar abiotic conditions to floodplain stands (Gilmore *et al.* 2013). In South America, harvesting of fruit from female *M. flexuosa* trees is common, and sex ratios are known to be biased in many stands as a result of overexploitation. Harvesting is also thought to have severely degraded population size in some cases (Gragson 1995; Horn *et al.* 2012; Rosa 2013). This research represents the first detailed description of stand structure characteristics in an unexploited *M. flexuosa* populations and will act as a baseline for future management and preservation work.

Mauritia flexuosa is the dominant tree on the margins of the Aripo Savannas Environmentally Sensitive Area (ASESA); a protected savanna/forest ecosystem on the island of Trinidad, approximately 11° N of the equator. The ASESA is subject to frequent fires, which are thought to have become more frequent over the last 30 years (Bisramsingh & Oatham 2010; Bonadie & Bacon 1999). The ASESA is an ideal place to study the effects of fire on palm stands, as there are clearly defined fire-impacted areas and non fire-impacted areas due to the prevailing winds, which drive fires towards the western margins of the open savannas (termed fire-impacted or FIM in this study) while the eastern margins of the savannas are protected from fire by the unburnt forest stands (non fire-impacted or NFIM).

Although many palm species are considered resilient to fire and fire has been noted to increase palm density in certain cases (Barot *et al.* 2005; Montúfar *et al.* 2011; Souza & Martins 2004), changes in fire regimes have also been seen to reduce the stability of palm populations (Liddle *et al.* 2006). The effect of sporadic fires on the demographic and reproductive dynamics of *M. flexuosa* is not well studied (Bonadie & Bacon 1999). Rosa (2013) reported that *M. flexuosa* fruits are negatively affected by increasing fires in Brazil, as fire desiccates fruit and reduces overall productivity. On the other hand Rull & Montoya (2014) suggested that *M. flexuosa* palms were

promoted by humans 2000 years ago due to reduced fire return-times on the Grand Sabana in Venezuela. Indeed, *M. flexuosa* stands experiencing repeated exposure to fires increase in density dramatically (Montoya 2011) and the species is considered to be pyrophilous in nature (Hada *et al.* 2013; Latrubesse & Nelson 2001; Montoya & Rull 2011; Rull & Montoya 2014). Still, little is known about the long-term effects of repeated fire events on the density of wild arborescent palms.

Here we examine the stand structure and reproductive output of *M. flexuosa* and test the hypothesis that fires alter reproductive output and/or seedling establishment.

Methods

Data collection and study site

The hyperseasonal (edaphic) savanna ecosystems of the ASESA (10°35′30″ N, 61°12′0″ W) form the only remaining intact savannas in Trinidad (Bisramsingh & Oatham 2010; 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 2500 mm per annum with a dry season of 2–3 months where the rainfall can fall below 50 mm for the month (Richardson 1963; TTMS 2016). The open savannas in the ASESA are characterised by an impermeable hardpan layer at 20 to 30 cm depth that restricts primary productivity in the dry season because of drought and in the wet season because of waterlogging. *Mauritia flexuosa* is found on the ecotone between the savannas and swamp forest. 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 were classified into two environments or margins: Eastern and Western. The Western margins of the savannas were classed as fire-impacted margins (FIM) because fires are driven by trade winds that blow consistently east to west in the dry season. The Eastern margins of the savannas, which are not exposed to substantial burning because they are sheltered from trade-wind driven fires, are classed as non fire-impacted (NFIM) (Bisramsingh & Oatham 2010).

Sample site selection

Life history parameters of *M. flexuosa* from 20 different sites within the ASESA were measured over the period September 2012 to July 2015. We
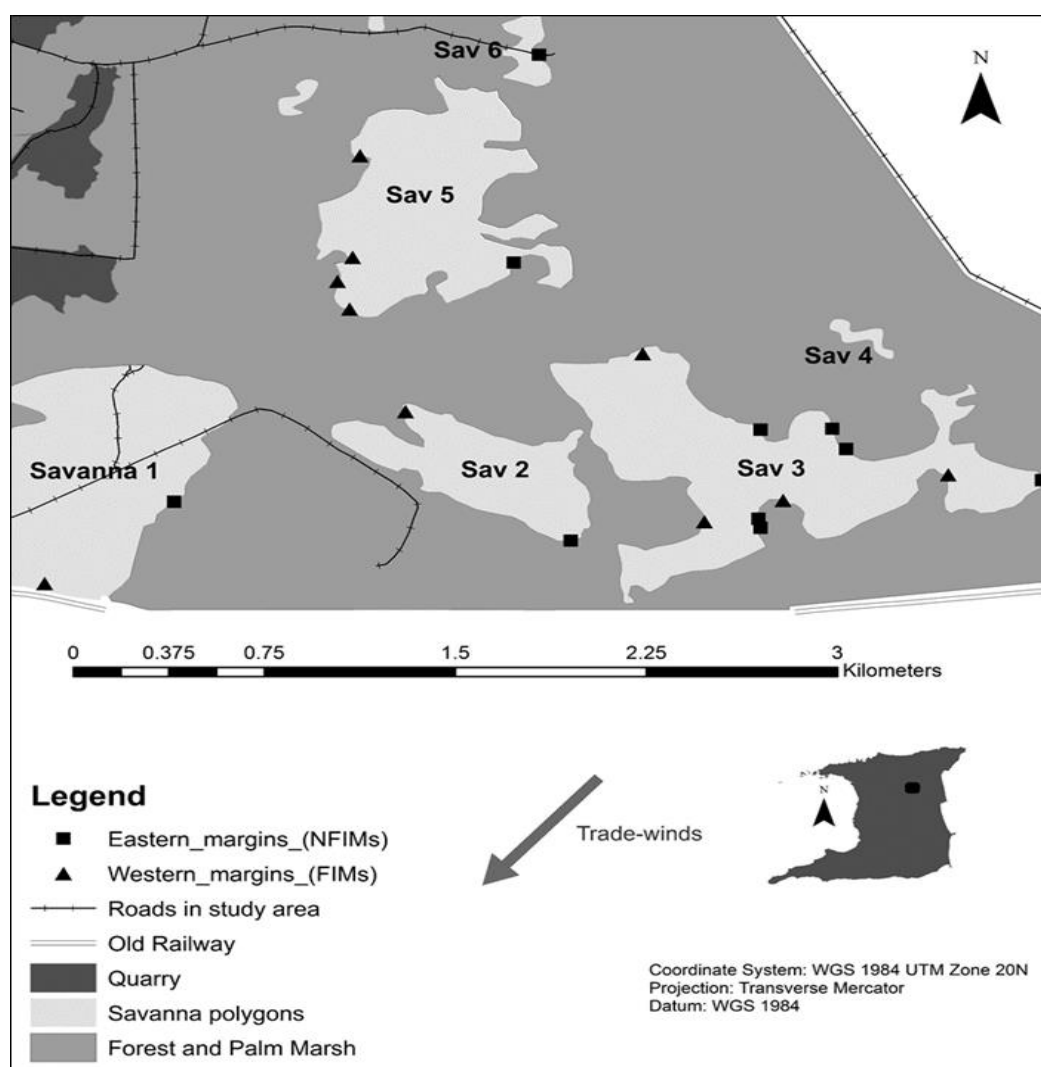
Fig. 1. Sample site locations within the Aripo Savannas Environmentally Sensitive Area showing fire-impacted and non fire-impacted stands. Modified from 1984 aerial photograph interpretation (ESRI 2012).

used a GIS map of the area and a stratified random experimental design to select 10 sample plots randomly in the two different savanna margins (NFIM and FIM). These plots were located within five different patches of savanna (Fig. 1) and were detected in the field using a Global Positioning System (GPS) device. Circular quadrants (20 m in diameter; 314 m² in area) were then established for each plot.

Palm density

To characterize stand structure, we estimated the density of *M. flexuosa* individuals by classifying palms into three major stage categories (seedlings, juveniles and adults). Categories were based on a size classification of height by Holm *et al.* (2008), then sub-classified into further stages according to their reproductive abilities (Table 1). The height boundaries of the stage classes were modified to cater for reproductive characteristics in the ASESA; particularly Total Height (TH) at reproduction. Seedling densities were estimated at each sample plot by counting the total number of individuals within two 3 x 20 m belt transects oriented N-S and E-W within sample plots (an area of 111 m² per plot). Juvenile and adult palm densities were estimated within the 20 m² diameter circular plots (an area of 314 m² per plot). Palm densities within the 20 sample plots were then used to calculate the average density of *M. flexuosa* in the two different margin environments in the ASESA.

Table 1. Observed sized class distribution based on total height.

Holm *et al.* 2008			This study		
Size Class	Growth stage	Height (m)	Size class	Growth stage	Height (m)
0	Seedling	<1	S0	New Seedling	<0.25
			S1	Established Seedling	0.25–0.5
			S2	Older Seedling	0.5–1.0
1	Young Juvenile	1–3	J3	Young Juvenile	1–3
2	Juvenile	3–6	J4	Juvenile 1	3–8
3	Juvenile	6–10			
4	Old Juvenile	10–20			
5	Adult	20–28	A5	Young Adult	8–12
6	Adult	>28	A6	Adult 1	12–22
			A7	Adult 2	>22

Canopy coverage, palm height, number of males and females, sex ratios and dbh

Canopy coverage was estimated from four cardinal points equidistant from the centre of each of the 20 sample sites using a spherical densiometer (model C, Robert E. Lemmon, Forest Densiometers, Oaklahoma USA). Height of seedlings was measured perpendicularly from the ground to the highest point on the leaf blade, while the height of juvenile and adult palms was estimated using a LaserAce Hypsometer (Measurement Device Limited UK) from ground level to the highest point reached by the leaves (Total Height or TH). The average height of adult trees was based on the means of 10 plots. The sex of mature fruiting *M. flexuosa* palms was recorded for each individual, non-fruiting individuals whose sex could not be ascertained were excluded from comparisons (as in Rosa 2013) as the number of unknown stems are expected to be high in dioecious palm species at any given time. Operational Sex ratios (OSRs) were averaged for each margin environment and were calculated by dividing the total number of males by the total number of sexually reproductive palms (Field *et al.* 2013). Diameter at breast height was measured using a dbh tape to the closest centimetre.

## Reproductive activity, fruit number and fruit mass

The total number of fruiting females and flowering males (reproductive activity) for each margin environment was recorded within the 20 permanent sample plots. This was done by counting the number of bunches on flowering males and flowering/fruiting females. Non-flowering and non-fruiting palms were omitted from this dataset.

Separate sampling plots were utilized to assess fruit number and mass because fewer than 50% of adult female palms were fruiting in the density plots. Ten randomly selected fruiting adult female palms were used in each margin environment, and fruits were harvested during the months of November 2012 to January 2013 (wet season first 10 palms) and July of 2015 (dry season 10 remaining palms); a total of 5 palms from each margin environment were harvested in each season. For each bunch or infructescence, the total number of fruits was counted and this figure was multiplied by the number of infructescences on the palm to estimate the total number of fruits per palm. In order to estimate the total fruit weight of each individual palm, a total of 50 fruits (15 from the top of the panicle, 20 from the middle and 20 from the base) from each bunch were transported to the laboratory and weighed. The average weight of one fruit was calculated. From these estimates, the 'fruit yield' per palm was estimated as fruit weight × fruit number.

Data analysis

Data analysis was conducted in Minitab 17 (Minitab Inc., Pennsylvania). One-way ANOVA was used to test whether margin environments differed in canopy coverage, TH and dbh. A two-way ANOVA was used to compare densities between stage classes and between different margin environments (all outliers more than two standard deviations were removed from this data set normalizing it without
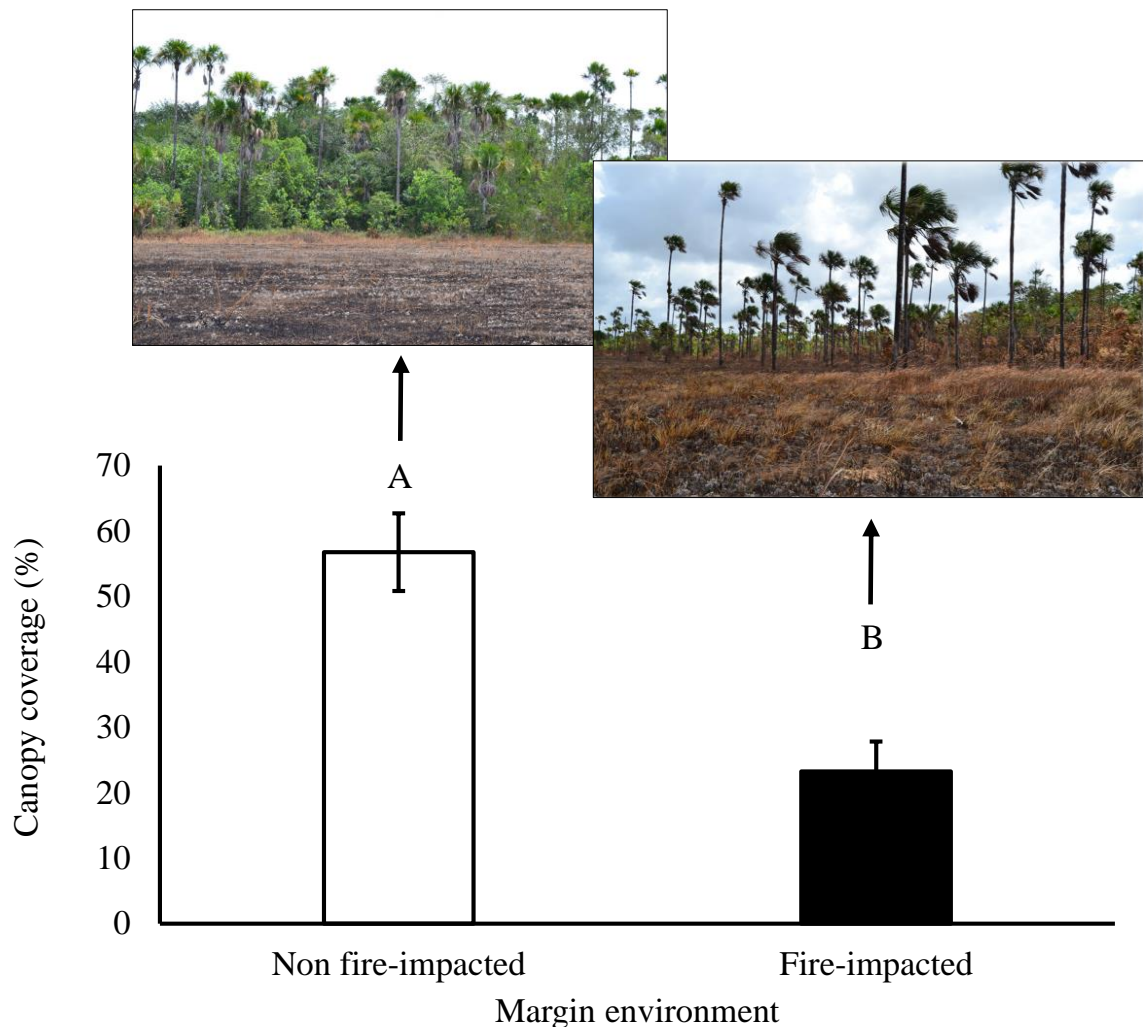
Fig. 2. Average canopy coverage (%) in fire-impacted and non fire-impacted stands of *Mauritia flexuosa.* Bars are means with SE, *n* = 10. Means that do not share a letter are significantly different (*P* < 0.005).

changing the result of the test). The number of males and females were analysed using a one-way ANOVA, while the OSRs (total number of males - total number of reproductive palms) were calculated using Chi-Square Goodness-Of-Fit tests. One-way ANOVA was carried out to investigate if any significant differences existed between margin environments for the average number of bunches (male and female). Once this was done, the average reproductive activity (the number of fruiting individuals) and the average reproductive output between margin environments were statistically tested using one-way ANOVAs (one outlier more than two standard deviations was removed from this dataset). Whenever significant differences existed within ANOVA tests, Pairwise Comparisons were performed using Tukey or Games-Howell

Simultaneous tests (for equal and unequal variances, respectively).

Results

Canopy coverage

Canopy coverage significantly differed among margin environments, where NFIM had a greater canopy coverage than FIM (Fig. 2; $F_{1,18}$ = 19.95, P = 0.001).

Palm density by stage of M. flexuosa

Palm density was highest on the NFIM at 170,118 palms per km² ± 50,127, while densities on FIM were 158,035 palms per km² ± 39,585; but the densities were not significantly different. The three
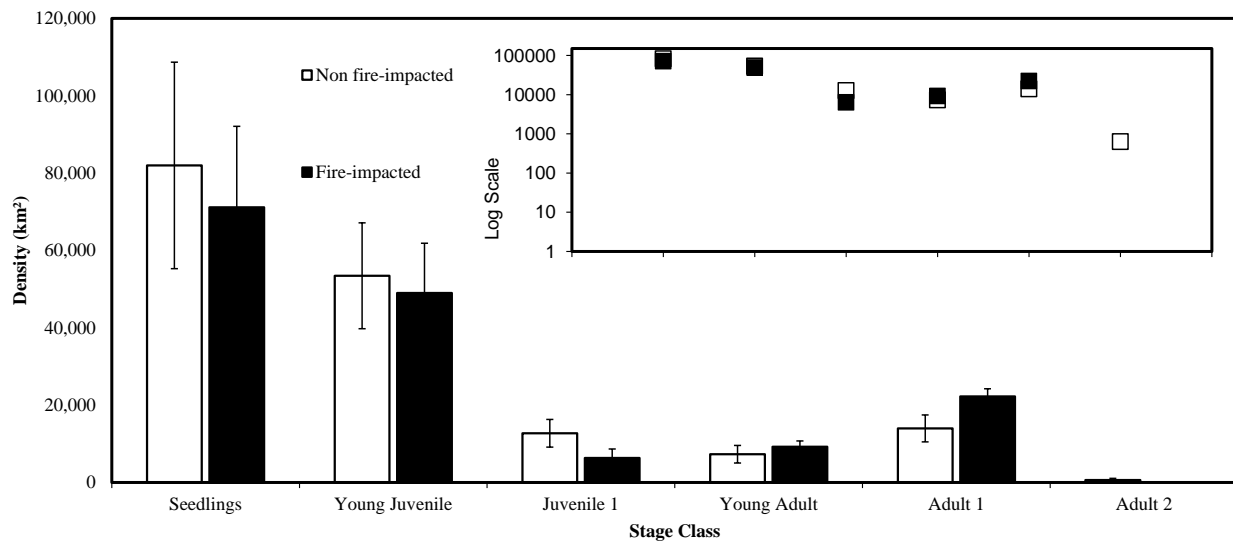
Fig. 3. Density (individuals/km^2) of *Mauritia flexuosa* palms of different stage classes in fire-impacted and non fire-impacted stands. Bars are means with SE, *n* = 10. Inset figure represents the log scale density of each margin.

Table 2. Total height (m) of *Mauritia flexuosa* trees in savanna margins that are fire-impacted (FIM) or non fire-impacted (NFIM). Data are means with SED between margins, *n*=10. *P* values are also given (see text for details).

Total height (m)	NFIM	FIM	SED	*P* value
Fruiting	16.20	13.84	0.96	0.020
Non-fruiting	14.60	13.03	0.75	0.050
Male	16.51	13.00	1.60	0.050
Female	15.66	14.40	1.41	>0.05
All	15.40	13.44	0.63	0.003

major classes; Seedlings, Juveniles and Adults showed no significant differences in density between margin environments (Fig. 3) and there was no interaction between stage and margin environment.

Average palm size on margins

There were significant differences in the average TH of all palms (fruiting, non-fruiting, male and female) between margin environments (Table 2; $F_{1,38}$ = 9.81, *P* = 0.003), with the NFIM having significantly taller palms than FIM. Within the subgroups, palms in the NFIM were taller in all cases, with significant differences for all subgroups apart from 'female'. There were no significant differences in dbh between margin environments;

dbh was 31.11 ± 1.5 on NFIM and 30.03 ± 1.1 on FIM.

Numbers of males and females and operational sex ratio

Overall, the male (44 individuals) to female (42 individuals) ratio was similar, however, 50% of individuals (87 out of 173) could not be categorized into a sex so this ratio should be treated with caution. There was no significant difference in the number of males across the two margins. There were significantly less females in the NFIM than in the FIM (Table 3; $F_{1,18}$ = 4.55, *P* = 0.047). However, overall no significant differences were found in the OSR between margin environments (Chi-square goodness-of-fit test, X^2 = 6.40, *df* = 11, *P* > 0.05).

Reproductive activity, fruit number and reproductive output

The number of inflorescences and infructescences did not differ significantly among margin environments, although there were more bunches per palm in the FIM (Table 3). Significant differences were seen in fruit weight (ANOVA $F_{1,17}$ = 11.14, *P* = 0.004), fruit number (ANOVA $F_{1,17}$ = 6.94, *P* = 0.017) and fruit yield - weight of fruits x number of fruits per female palm (ANOVA $F_{1,17}$ = 5.01, *P* = 0.039) (Table 3). There were significantly more fruit per palm on the FIM than on the NFIM, but the individual fruit were significantly lighter. The net result was that fruit yield per palm was

Table 3. Reproductive characteristics of *Mauritia flexuosa* stands in savanna margins that are fire-impacted (FIM) or non fire-impacted (NFIM), including: number of male and female trees per plot; number of bunches per tree (holding flowers for male trees; flowers and fruit for female trees); fruit fresh weight; and fruit yield (number × weight). All data are means ±SE, *n* = 10.

	NFIM		FIM		*P* value
	Male	Female	Male	Female	
Trees per plot	2.1 ± 0.7		2.1 ± 0.4		>0.05
		1.5 ± 0.4		3.4 ± 0.6	0.047
Bunches per tree	2.2 ± 0.7		2.1 ± 0.4		>0.05
		1.1 ± 0.4		2.1 ± 1.8	>0.05
Fruit number		816 ± 139		3171 ± 730	0.017
Fruit weight (g)		74 ± 4		51 ± 5	0.004
Fruit yield (kg)		62 ± 13		170 ± 44	0.039

significantly higher on the fire-impacted margins, with each palm producing approximately three times as much fruit mass on the FIM (170 kg ± 44.00) as on the NFIM (62 kg ± 13.00).

Discussion

Here we found that, *M. flexuosa* was equally abundant in fire and non fire-impacted savanna margins, but that stands exposed to fire exhibited distinct life-history traits, in particular a tendency to produce a large number of small fruit. We suggest that this plasticity in reproductive output contributes to the ability of *M. flexuosa* to outcompete both grasses and dicotyledonous trees on savanna-forest margins.

Variability and trade-offs in M. flexuosa *fruits*

Little is known about how habitat variability or disturbance affects reproductive traits in palms (Andreazzi *et al.* 2012; Rosa *et al.* 2014). Rosa *et al.* (2014) found marked variation in reproductive output when comparing *M. flexuosa* stands in forests and savanna-margins, but did not detect a trade-off between fruit number and fruit weight. In this study, we were able to identify a consistent pattern between margin environments; where FIM had significantly higher fruit yield, producing a greater number of small fruit. The fruit yield on NFIM were similar to those measured by Rosa *et al.* (2014) (≃40–50 kg per palm), while the higher output in fire-impacted stands (≃170 kg per palm) was higher than seen in any of their sites. The mechanism that allows *M. flexuosa* to vary fruit size and number in different micro-environments is not

clear. Rosa *et al.* (2014) found correlations between reproductive output and both resource availability (i.e. soil moisture and soil organic matter) and palm vitality (i.e. height and dbh), but correlations were not seen in all cases and the authors did not mention a correlation with reproductive characteristics. They suggested pollination and fruit-set may be key drivers of variation in reproductive output. Fire will impact on many abiotic and biotic factors that may influence reproductive output; notably FIM have an open canopy which may allow better access to light and pollen compared to NFIM. This suggestion is consistent with the observation of Rosa *et al.* (2014) that in disturbed/deforested sites *M. flexuosa* stands had a higher fruit yield and lower fruit weight. Barot *et al.* (2005) describes similar plasticity in the palm *Attalea speciosa* Mart. ex Spreng, where frequent burning results in monodominant stands partly due to an increase in the reproductive output in the burnt stands (compared to stands in closed forest areas). Overall these results support the suggestion that *A. speciosa* and *M. flexuosa* palms have an ability to increase reproductive output in disturbed habitats (Andreazzi *et al.* 2012; Barot *et al.* 2005; Campos *et al.* 2017; Rosa *et al.* 2014).

In the Amazon Basin, palm density in ecosystems under the impact of human exploitation ranges from 5,500 to 24,600 adult palms per km² for gallery, basin and valley landscapes (Gurgel-Gonçalves *et al.* 2004; Gurgel-Gonçalves *et al.* 2006; Hada *et al.* 2013; Horn *et al.* 2012; Kahn & Granville 1992; Kahn & Mejia 1990). In the ASESA, Adult density within margin environments was calculated as 27,788 per km² ± 5,239, with fire

having no significant impact. One possible reason for *M. flexuosa* densities on the margins of the ASESA being high, is that the populations have never been harvested or exploited by humans and are more likely to represent population responses to environmental variation.

The most striking difference between the margins was the much greater fruit number found in the fire-impacted stands. This is all the more intriguing as although the number of fruits produced in the FIM is greater than in the NFIM, the seedling density is similar. Within both FIM and NFIM there was a high mortality in the Young Juveniles stage likely due to the competition for resources (Tilman 1994) and overcrowding (Barot *et al.* 1999). Two different mechanisms that reduce survival of seedlings into the Juvenile 1 stage may be operating in each margin environment; low light penetration to the forest floor in NFIM (Salm *et al.* 2005; Walters & Reich 2000; Wenger 1984) and exposure to fires in FIM (Rull & Montoya 2014). Larger fruits in the more stable and buffered microclimate of NFIM (Table 3) will allow higher rates of seedling establishment and survival but a slow rate of growth. This means few individuals reach the next size class and they accumulate from year to year in the Young Juvenile stage where eventually overcrowding is the main cause of mortality. Palms in FIM have a higher fruit number which would allow seedling populations to be constantly replenished and maintain a high density despite high mortality during sporadic fires. It is unlikely the phenotypic difference in fruit mass and number between the FIM and NFIM is genetically based, as gene flow between palms in FIM and NFIM occurs readily (Federman *et al.* 2013); thus fruit size in *M. flexuosa* palms appears to respond plastically to environmental variation.

There are significant gaps in our understanding of how fire impacts on palm populations (Higgins *et al.* 2000; Montúfar *et al.* 2011). Stand structure of *M. flexuosa* within the different environments did not vary significantly and individuals formed a typical "inverse-J" size class distribution. Inverse-J size class distributions, where seedling densities are considerably higher than that of juvenile and adults, are typical of population growth-curves for neotropical palm species (Boom 1986; Haugaasen & Peres 2006; Resende *et al.* 2012; Rosa *et al.* 2014; Sampaio *et al.* 2008). Higgins *et al.* (2000) suggests that a major role of fire in palm demographics is to limit tree recruitment while adult mortality may remain low. Our results for *M. flexuosa* are consistent with a low adult mortality, but the large number of seedlings and juveniles in fire-impacted stands suggests this species has escaped from the possible recruitment restriction posed by fire. Souza & Martins (2004) found similar results for *Attalea* species, with long-term stage structure resilient to fire. Souza & Martins (2004) further observed a temporary increase in the number of immature plants in the months following a fire, which would further increase resilience in these stands. It should be noted however, that other palm species that were resilient to one fire regime were nonetheless shown to be vulnerable to encroachment by grasses when the fire regime is altered (Liddle *et al.* 2006).

Sex ratio

Differences in number of individuals of a given sex in a population is of great importance to palm population stability (Delgado *et al.* 2007; Holm *et al.* 2008). We did not detect a significant difference in the ratio of males to females between margins and the overall sex ratio was balanced. Untouched *M. flexuosa* stands existing within the Americas portray similar features (Gilmore *et al.* 2013; Oyama 1990; Rosa 2013), while exploited populations are sex biased (Rosa 2013). Male palms produced more inflorescences than females during our study, which is expected as they do not required as great a resource commitment as female inflorescences (Bazzaz *et al.* 1987; Oyama 1990).

Sporadic fires impact height in M. flexuosa

Sexual dimorphism in height is common in palms (Friedman & Barrett 2009; Granville 1992; Rich 1986). The height of males and females in this study were similar to Rosa (2013) findings. She found that male *M. flexuosa* palms were taller than female palms in three different habitats in Roraima, Brazil. Mature palms within the NFIM were taller than those within the FIMs. This may be related to the closed canopy seen on NFIM. Tallness is the trait associated with habitats that have a closed canopy because intense competition for light between trees means having to grow tall to overtop their neighbours (Adams *et al.* 2007). Similar results were observed by Rosa *et al.* (2014) where *M. flexuosa* palms found in the forests were much taller (≃23 m) than those found in undisturbed margins (≃15 m) and disturbed savannas (≃14 m). This indicates that in closed canopy areas, palms continue to grow upwards, before reproducing, illustrating a shade-avoidance response (Granville 1992). This phenomenon does make size-stage based demographic comparisons

between margins more difficult, e.g. some short 'juvenile' palms were seen to be reproductive in areas of low canopy closure; potentially transitioning them into the sub-adult stage, nonetheless height remains the most convenient means of classifying individuals in palm stands.

Mauritia flexuosa *as a pyrophilous species*

The absence of any negative impact of fire on *M. flexuosa* stand structure is consistent with the view of *M. flexuosa* as a *pyrophilous* species. Montoya & Rull (2011) noted that the increase in *M. flexuosa* stands and the increase in fire occurrence appeared simultaneously in the pollen record in the Grand Sabana, while Rull (1999) referred to *M. flexuosa* palms as a colonizer species that reacts rapidly to fire disturbance. In both margin environments in the ASESA, *M. flexuosa* appears to form stable populations indicating it can survive in more competitive environments where fire is restricted, although the possibility remains that NFIM populations may require immigration from FIM populations to remain stable in a source-sink metapopulation relationship.

Conclusion

Demographic parameters in both fire-impacted and non-fire impacted margin populations were within the range of those measured in the South American mainland, and there was no evidence that either population is unstable. Fire-impacted stands retained high densities of Seedlings and Young Juveniles, together with a higher total reproductive yield. This indicates that although current fire regimes do influence life-histories properties they do not negatively impact *M. flexuosa* population stability. Phenotypic plasticity in response to habitat variability was observed, with palm height, fruit number and fruit mass differing between margin environments. *Mauritia flexuosa* populations appear to be resilient to the current fire regime in this tropical savanna system, nonetheless the significant impact of fire on reproductive output suggests that careful management of fire may be required to maintain healthy stands.

Acknowledgements

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