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NEW FINDINGS ON THE POLLINATION BIOLOGY OF *MAURITIA FLEXUOSA* (ARECACEAE) IN RORAIMA, BRAZIL: LINKING DIOECY, WIND, AND HABITAT[1]

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- *Premise of the study:* Despite the ecological, economic, and cultural importance of the palm *Mauritia flexuosa* in Amazonia, knowledge of its reproductive biology is scarce. Previous observations of this species suggested beetles as the probable pollinator, but experimental work to confirm this hypothesis was lacking.
- *Methods:* We investigated the floral biology and pollination of *M. flexuosa* in undisturbed forest, undisturbed savanna/forest ecotone, and fragmented savanna within plantations of the exotic tree, *Acacia mangium*, in northern Brazilian Amazonia. In each habitat, we examined floral biology, combined floral visitor observations with laboratory analyses, and performed anemophily and exclusion experiments.
- *Key results:* Fruit set was significantly greater in the visitor exclusion treatment than in the wind + visitor exclusion treatment and significantly lower in the wind + visitor exclusion treatment than the open control, but there was no difference in fruit set between the visitor exclusion treatment and the control. We found no significant difference in pollen dispersal among the three habitats. The presence of *A. mangium* appears to have no immediate effect on pollination of *M. flexuosa*, although it may indirectly affect other aspects of this native's reproductive ecology.
- *Conclusions:* Floral visitors of *M. flexuosa* are not pollinators. This dioecious palm depends on wind as its primary pollen vector. Wind pollination is not necessarily most effective in open habitats. These findings are important because they re-evaluate traditional assumptions of wind pollination and can improve management strategies of this natural resource in the Amazon.

Key words: Amazon; anemophily; Arecaceae; dioecy; habitat; palm ecology; pollination; reproductive biology.

- *Premissa do estudo:* Apesar da importância ecológica, econômica e cultural da palmeira *Mauritia flexuosa* na Amazônia, o conhecimento sobre sua biologia reprodutiva é escasso. Observações anteriores desta espécie sugerem besouros como prováveis polinizadores, mas faltam trabalhos experimentais para confirmar esta hipótese.
- *Métodos:* Nós investigamos a biologia floral e polinização de *M. flexuosa* em floresta não-perturbada, ecótono (savana/floresta) não-perturbado, e savana fragmentada por plantações da árvore exótica *Acacia mangium*, no norte da Amazônia brasileira. Em cada habitat, examinamos a biologia floral, combinamos observações dos visitantes florais com análises de laboratório, e realizamos experimentos de anemofilia e exclusão.
- *Resultados chaves:* Produção de fruto foi significativamente maior no tratamento de exclusão de visitantes em relação ao tratamento de exclusão de visitante + vento, e significativamente menor no tratamento de exclusão de visitante + vento em relação ao controle, mas não houve diferença significativa entre o tratamento de exclusão de visitante e o controle. Não encontramos diferença significativa na dispersão de pólen entre os três habitats. A presença de *A. mangium* indica não ter efeito imediato na polinização de *M. flexuosa*, embora possa afetar indiretamente outros aspectos da ecologia reprodutiva desta espécie nativa.
- *Conclusões:* Visitantes florais de *M. flexuosa* não são polinizadores. Esta palmeira dióica depende do vento como seu vetor primário. Polinização por vento não é necesariamente mais efetiva em habitats abertos. Estes resultados são importantes porque reavaliam as idéias tradicionais da polinizacão pelo vento, e podem melhorar o manejo deste recurso natural na Amazônia.

Palavras chaves: Amazônia; anemofilia; Arecaceae; dióica; ecologia de palmeiras; habitat; polinização; biologia reprodutiva.

Pollination is a fundamental and critical process of plant reproduction and ecosystem function (Waser and Ollerton, 2006) and has helped shape plant diversity (Torezan-Silingardi, 2012). Understanding the pollination systems of plants is important from both scientific and practical standpoints. However, relatively little is known about the evolution of wind pollination in

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flowering plants and the interactions among floral form, mating system, and pollination (Sargent and Otto, 2004; Thomson and Wilson, 2008; Friedman and Barrett, 2009). Describing reproductive transitions, such as those in breeding systems, morphology, and pollination, elucidates the evolutionary forces that have shaped angiosperm reproduction (Specht and Bartlett, 2009; Barrett, 2010a).

From an applied perspective, understanding pollination of plants in agricultural and nontimber forest product (NTFP) systems is necessary to develop practical and sustainable harvesting methods (Klein et al., 2007; Tscharntke et al., 2012). Understanding pollination of wild, harvested plants has profound implications for conservation strategies and land management (de Marco Jr. and Monteiro Coelho, 2004; Hoehn et al., 2010). Results from field observations and experiments of these plants can therefore not only elucidate evolutionary patterns, but also may help land managers, harvesters, and policymakers protect and sustainably use these natural resources.

There is a dearth of information on the effects of habitat type and disturbance on pollination (Hadley and Betts, 2012). Although certain pollination systems are commonly associated with specific habitat types, these patterns may vary among species and habitats. Few studies have synthesized how disturbance, particularly the presence of exotic species, affects the pollination and other ecological interactions of native species (Pyšek et al., 2012). Quantifying the effects of exotic species on reproductive processes of native plants is crucial to develop effective land management and prevent loss of native biodiversity (Stokes et al., 2006; Lindsay et al., 2011).

Although the dioecious palm *Mauritia flexuosa* plays a central role in Amazonian ecosystems and economies (Goulding and Smith, 2007), little is known about its reproductive ecology. *Mauritia flexuosa* can be considered a foundation species given the broad consequences it has on associated biota and ecosystem structure (Ellison et al., 2005), such as providing critical food and habitat for wildlife (Henry et al., 2000; Brightsmith, 2005). The fruit is an important part of the diet of Amazonian peoples (Henderson, 1995) and is central to indigenous culture (Mejia, 1988; Horn et al., 2012). Unmatched beta-carotene levels of the fruit highlight the pharmaceutical and industrial applications of this palm (Santos, 2005; Silva et al., 2009; Zanatta et al., 2010). Overharvesting, including the felling of female trees, is a problem in many parts of the Amazon (Holm et al., 2008; Brokamp et al., 2011). Hence, understanding the floral biology and pollination system of this foundation species can improve the way *M. flexuosa* is managed, with important consequences for its ecological processes.

The goal of this research was to investigate the floral biology and pollination system of *Mauritia flexuosa* in three distinct habitats: undisturbed forest, undisturbed forest–savanna ecotone, and disturbed savanna (within plantations of the exotic tree, *Acacia mangium*). Cantharophily was previously concluded to be the primary pollination system of *M. flexuosa* (Ervik, 1993; Storti, 1993), although pollinators were not distinguished from floral visitors. Ervik (1993) also noted wind-borne pollen for this species, but did not point to wind as the primary vector. We described floral morphology, observed and examined floral visitors, and performed anemophily and exclusion experiments to determine whether this species depends on animal vectors for its pollination. We also asked how habitat might affect plant–pollinator interactions and whether sexes of this species show height dimorphism, which might play a role in pollen transfer. We tested three specific hypotheses: (1) *M. flexuosa* is likely to be insect-pollinated, specifically by beetles; (2) wind plays a secondary role in pollination, although less so in the forest habitat than in the other habitats; and (3) habitat disturbance negatively affects native floral visitor abundance.

MATERIALS AND METHODS

Study species—*Mauritia flexuosa* L. f. (Arecaceae, Calamoideae) is the most widespread palm in South America and is restricted to seasonally wet habitats (Goulding and Smith, 2007). This dioecious palm tolerates continuous flooding, typically forming monodominant stands along streams and rivers and in swamps. Fruits are globose to ellipsoid, scaly, 4–6 cm long with 3–5 cm diameter, and usually one-seeded. The thin, scaly exocarp is light orange to dark red, and the fleshy mesocarp is bright yellow-orange. Different morphotypes are identified based on the size, color, and fresh mass of the fruit (Barbosa et al., 2010).

Study area—Fieldwork was conducted in Roraima, Brazil, northern Amazonia (Fig. 1), from March 2009 to March 2011. The climate of this region is considered tropical wet-dry, "Aw" (Köppen, 1936). Average annual rainfall is 1614 mm, with a mean monthly temperature of 27.8 ± 0.6°C (Barbosa et al. in press). Roraima has two distinct seasons: a rainy season (May through August), and a dry season (December through March).

Field observations and experiments were done at six sites representing three habitats: (1) undisturbed, lowland savanna–forest ecotone (hereafter referred to as "ecotone"); (2) undisturbed, lowland semideciduous forest ("forest"); and (3) former lowland savanna converted to plantations ("disturbed savanna") of *Acacia mangium* Willd., a potentially invasive tree (Aguiar Jr., 2010). The four native, undisturbed sites are located at Maracá Ecological Reserve (3°21′21″N, 61°25′47″W), a federally protected reserve consisting of the world's third-largest riverine island (830 km^2), on the Uraricoera River. The two disturbed savanna sites are located at Núcleo Jacitara, (3°12′53″N, 60°49′53″W), a 9.16-km^2 piece of fragmented, native savanna, of which 3.34 km^2 are dense monocultures of *Acacia mangium*. *Mauritia flexuosa* occurs naturally within the disturbed sites, and free-roaming cattle and unmanaged Africanized honey bees characterize the area.

Sampling methods—In each *M. flexuosa* population, we tagged all individuals within a 200 × 20 m transect for sampling. Sample size varied among habitats given natural variability of plant distribution within sites and habitats (forest sites: $N = 45$, $N = 57$; ecotone sites: $N = 64$, $N = 80$; disturbed savanna sites: $N = 70$, $N = 58$). We climbed study individuals using a custom-made system that is an adaptation of the two-cable prusik system known as a peia, that is used by coconut harvesters in northeastern Brazil (L. Noblick, Montgomery Botanical Center, personal communication).

Floral biology—Monthly monitoring of inflorescences of all sample individuals in all six sites ($N = 374$) was conducted to describe phenology and quantify the duration of anthesis (R. Khorsand Rosa, unpublished manuscript). Flower opening time of males and females was investigated by climbing individuals ($N = 15$) and observing floral opening patterns. We also noted floral scent, touched stigmas to verify wetness, and tested for the presence of nectar using microcapillary tubes and a hand-held refractometer (Bellingham and Stanley Ltd., Tunbridge Wells, Kent, UK) at various times of the day and night, from 0600 to 0200 hours. We randomly selected one inflorescence per individual and counted the number of flowers (male individuals: $N = 12$; female: $N = 13$). Staminate flowers bearing pollen were collected, and pollen was extracted via acetolysis (Kearns and Inouye, 1993) to create pollen-reference slides. Prepared pollen was measured.

Since observing inflorescences for several consecutive days while suspended high up a palm trunk was not feasible, we cut preanthesis male and female inflorescences ($N = 6$), stored them in sugar water, and monitored the duration of individual flowers during several days.

Visitor observations—We conducted 81 ten-min observation periods during each flowering season (September through November) of 2009 and 2010 in all habitats: 29 observations on 16 male individuals and 53 observations on 18 female individuals. Unscalable individuals (those that contained Africanized honey bee nests, termite mounds, or irregular trunks) were not used in the study. Most diurnal and all nocturnal observations were made while the observer was

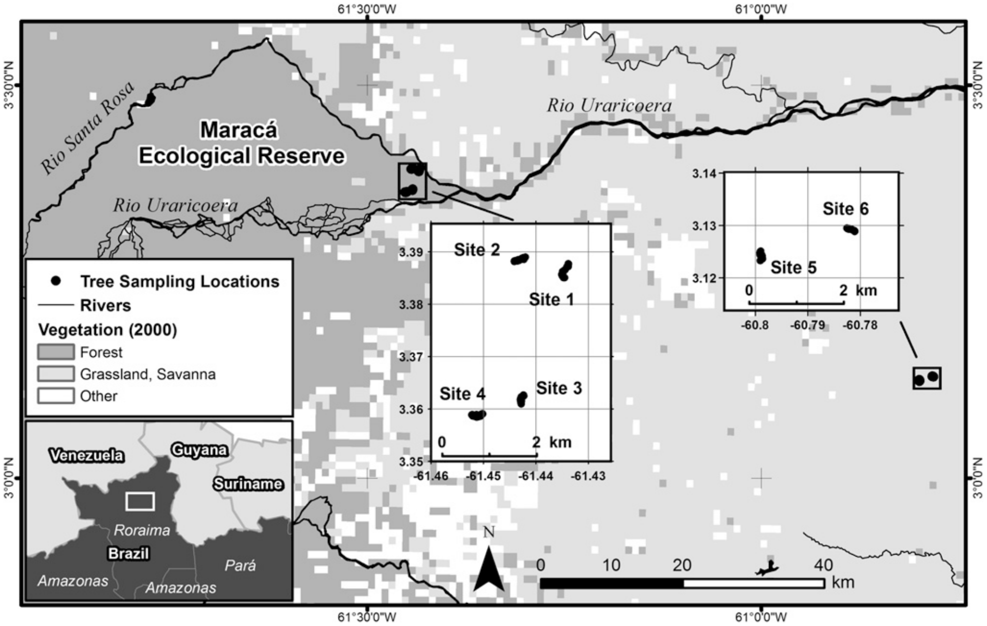

Fig. 1. Map of study area in Roraima, Brazil. Sites 1 and 2 comprise savanna ecotone habitat; sites 3 and 4 comprise forest habitat; and sites 5 and 6 comprise disturbed savanna habitat. Sites 1 through 4 are located at Maracá Ecological Reserve (MER). Sites 5 and 6 are located at Núcleo Jacitara, within *Acacia mangium* plantations. Forest vegetation category includes primary and secondary forest. Given coarse resolution of vegetation cover (1 km), savanna enclaves on MER appear as forest. Dark clumps represent sampled trees in each site. Source: Global Land Cover 2000 by the Global Vegetation Monitoring Unit of the Joint Research Center.

in the palm and less than 1 m from the inflorescence; a few diurnal observations were made from the ground using binoculars. Nocturnal observations were made using a headlamps covered in red cellophane. Since inflorescences are typically at least 1 m long, we focused our observations on a specific 40–50-cm-long portion of the inflorescence. During each observation, we noted the visitor type present, counted the number of landings of each visitor type, and recorded behavior including: visitation duration, visitation to multiple flowers within an inflorescence, and contact with the floral sexual part. We also inspected female flowers for damage made by beetles and signs of oviposition such as eggs or larvae.

The relative number of landings by each floral visitor family was calculated as the proportion of the family's total landings relative to the total number of landings by all visitors. We also calculated the proportion of landings that resulted in contact with the stigmas or anthers. Proportions were calculated for male and female palms, separately.

Visitors were collected, and in the laboratory, we verified the pollen content on visitors' bodies. Vials with the stored visitors were also centrifuged, and slides of the pellet were scanned for the distinctive, spiny pollen grains of *M. flexuosa* with a light microscope. Floral visitors were identified to family or species by Dr. M. L. Barbosa and Dr. C. Ruy Fonseca (National Insitute for Research in Amazonia [INPA], Manaus, Brazil), and Dr. S. J. R. da Silva (Integrated Museum of Roraima [MIRR], Boa Vista, Brazil). Voucher specimens were deposited in the insect collection of INPA, Manaus, Brazil.

Anemophily experiment—To determine whether *M. flexuosa* pollen is transported by wind, we hung petrolatum-covered slides from female inflorescences in all habitats. Microscope slides were sterilized prior to use. A total of 19 slides were hung in the three habitats (ecotone: $N = 6$; forest: $N = 9$; disturbed savanna: $N = 4$) on rainless days of similar cloud cover during the 2010 flowering season (September through November). Slides were removed from female trees 3–15 d later, and pollen grains were counted under the light microscope. A one-way ANOVA was conducted on double square-root transformed pollen count data to evaluate whether the mean number of pollen grains differed significantly among habitats, followed by Tukey's honest significant difference (HSD) pairwise comparisons.

Bagging experiment—To determine the pollination system of *M. flexuosa*, we performed a bagging exclusion experiment in each habitat, consisting of two treatments and a control: (1) a portion of the female inflorescence was enclosed in a fine mesh (0.5 mm) bag to exclude visitors but not wind-borne pollen, (2) a portion of the female inflorescence was enclosed in a resin-infused paper bag (Pollen-tector, Des Moines, Iowa) to exclude visitors and wind-borne pollen, and (3) control, no bag used, the female inflorescence was open to ambient pollination. We placed each bag on a separate branch of the inflorescence. Unequal sample sizes of females and treatments resulted as a result of the difficulty of climbing these tall palms and fastening bags to inflorescences: 10 females received the mesh treatment ($N = 15$; 1–2 bags per individual), eight females received the paper treatment ($N = 8$; 1 bag per individual), and nine females received the control ($N = 14$; 1–2 tagged, unbagged branches per individual). Before bagging flowers, we confirmed that all flowers were closed buds, pollen-free, and no visitors were present. Mesh bags were closed with hook-and-loop tape (Velcro) sewn onto bag lining and reinforced with wiring; paper bags were first closed with string to ensure a tight fit around the inflorescence branch, then reinforced with wiring. Bags were removed 1–2 mo later, and fruit set was compared with that of the controls. Fruit set was the proportion of fruits to flower scars on the bagged area of the inflorescence.

Fruit set data were arcsine square-root transformed and analyzed using a mixed model ANOVA, using treatment as a fixed factor and habitat as a random factor. Least significant difference post hoc tests were performed.

Sex ratios and sexual dimorphism in height—We tested the hypothesis that males may be taller than females (Friedman and Barrett, 2009) by measuring height of all sample individuals using a clinometer (Suunto Instrument, Vantaa, Finland). Sex ratios were also calculated for each habitat. A test of independence was performed to determine whether a relationship existed between sex and habitat type, and a χ^2 goodness-of-fit test was used to determine whether the male to female ratio in each habitat deviated significantly from the expected 1 : 1. We conducted an independent samples t test on log-transformed height data to determine whether height differed significantly between sexes. To determine whether height differed significantly among habitats, we performed a one-way ANOVA, followed by pairwise comparisons. Nonflowering individuals (of undetermined sex) were removed from analyses.

Minimum distance between flowering conspecifics—The minimum distance between sexes theoretically demonstrates how far wind-dispersed pollen must travel for effective pollination. For each female in bloom, we measured the distance to the closest male in bloom. For females in preanthesis floral development stage, we measured the distance to the closest male in a similar floral development stage, given that males and females flower synchronously. The mean minimum distance between flowering females and males was compared among habitats using a one-way ANOVA on log-transformed data, followed by Tukey's HSD pairwise comparisons. A Holm's sequential Bonferroni correction was performed on all pairwise comparisons to control for type I error. All statistical analyses were performed in IBM SPSS Statistics version 19 (SPSS, Chicago, Illinois, USA).

RESULTS

Floral morphology and phenology—The inflorescences of *Mauritia flexuosa* are axillary, solitary, and interfoliar. We counted over 100 000 flowers on a single staminate inflorescence (mean ± SE = 49 938.0 ± 397.3), and up to 6000 flowers on a pistillate inflorescence (2464.1 ± 23.4). Staminate flowers are borne in dyads, arranged tightly in clusters (18 to 40 flowers per cluster). Pistillate flowers are borne in solitary dyads or triads. Male flowers are smaller (approximately 0.5 × 0.8 cm) than female flowers (1.1 × 1.5 cm), containing three coriaceous petals, six stamens, and a minute pistillode. Female flowers have three coriaceous petals, six staminodes, and a triovulate, scaly gynoecium. The stigmas are dry.

Both staminate and pistillate flowers produce a sweet scent, stronger in males than in females. Knudsen et al. (2001) found 44 volatile compounds present in flowers of *M. flexuosa*, particularly fatty acid derivatives. No difference was detected in the intensity of fragrance between night or day. Staminate flowers produce copious amounts of dry pollen; pollen grains are round and echinulate (mean ± SE = 61.07 µm, ± 0.57). Pistillate flowers offer no apparent reward. Neither sex produces nectar or resin in the flowers nor undergoes thermogenesis. Resin is present, however, on developing fruit (Khorsand Rosa, 2011).

Flowering of *M. flexuosa* in Roraima occurs between the wet and dry seasons (September through November), although variation in precipitation may influence this pattern. Males and females flower in synchrony and do not produce significantly different numbers of inflorescences. Individual flowers did not open at a specific time: both staminate and pistillate flowers opened continuously, with an individual flower lasting a maximum of 5 d and a single inflorescence less than 1 wk.

Visitor watches—We observed insects from a total of 20 taxa visiting flowers, representing seven insect families. Of these 20 visitor types, 13 visited both staminate and pistillate flowers. Four families accounted for 91% of all landings in male flowers and 84% of all landings in female flowers: Curculionidae (Coleoptera), Nitidulidae (Coleoptera), Apidae (Hymenoptera), and Vespidae (Hymenoptera). However, we observed a large difference in the importance of family visitation rates to each sex, measured as the proportion of landings by that family relative to the total number of landings by all families (Fig. 2A, 2B). The most abundant visitors to pistillate flowers were nitidulid and cucujid beetles, comprising 53% of all landings; these two families only accounted for 12% of all landings in staminate flowers. We also observed chrysomelid beetles in female flowers, but not in male flowers.

Some insect visitors had a relatively high proportion of landings to both staminate and pistillate flowers, but their behavior suggested they are unlikely to be pollinators (Table 1). Diurnal honey bees (*Apis mellifera*, Apidae), native *Trigona* bees (Apidae, Meliponinae), and wasps (Vespidae) actively collected pollen from male flowers, but rarely entered female flowers and contacted the stigmas. Rather, they landed on the vegetative axes of female inflorescences and foraged around the calyx of the flowers for resin or prey. Weevils were constantly observed in male inflorescences during the day; none were found in female inflorescences during the day.

Although nocturnal visitation rates were higher than diurnal rates, the most abundant floral visitors in female flowers were not those we had observed visiting male flowers. Nocturnal visitors to female inflorescences included beetles in the families Chrysomelidae, Nitidulidae, and Cucujidae, as well as Heteroptera (Thaumastocoridae, Xylastodorinae). At night, chrysomelids landed frequently on female flowers, but were not found in male flowers. Nitidulids and cucujids spent up to 5 min at a time in female flowers and were also observed in male flowers, though much less frequently than in female flowers. Heteropterans visited female flowers at night, although they spent less than 1 min per landing, moving very quickly within the same inflorescence. We did not observe heteropterans on male inflorescences. We also saw ants on male and female inflorescences, comprising the major part of "other" in our classification. However, ants rarely entered female flowers.

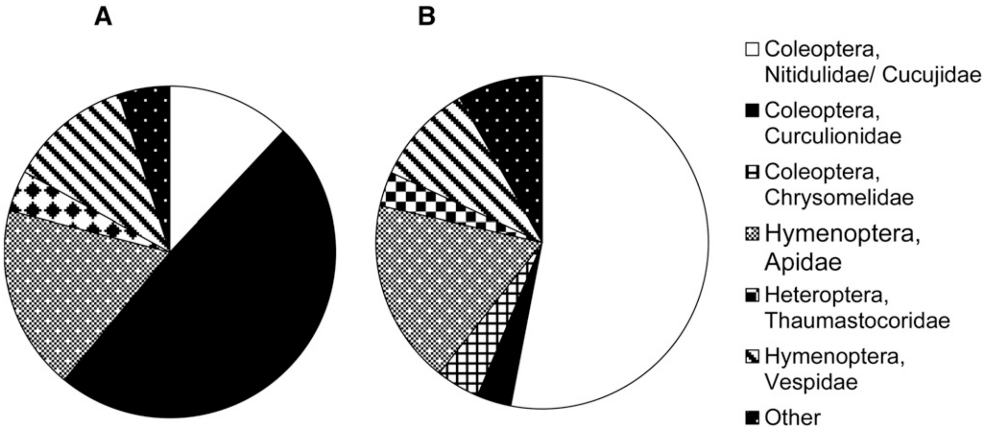

Fig. 2. Proportion of landings by each insect family on *Mauritia flexuosa* inflorescences, expressed as the total number of landings by a particular family relative to the total number of landings by all families, and where "other" constitutes unidentified visitors. A, Male inflorescences; B, female inflorescences.

Table 1. The mean number of landings (±SE) by floral visitor family to male and female inflorescences of *Mauritia flexuosa* in three habitats of Roraima, Brazil, and the proportion of visits in which visitor contacted the sexual floral part (stamen or stigma). Nitidulidae and Cucujidae are lumped together because we were unable to differentiate them during field observations. Other/undetermined includes unidentified dipterans, ants, and one unidentified coleopteran.

	Male inflorescence		Female inflorescence	
Insect family	Mean number of landings (±SE)	Proportion contacting anthers	Mean number of landings (±SE)	Proportion contacting stigmas
Apidae	—	0.76	4.23, 1.35	0.14
Chrysomelidae	—	—	2.80, 0.92	0.80
Curculionidae	62.75, 18.18	0.88	1.60, 0.60	0.40
Nitidulidae/Cucujidae	60.00, 40.00	1.00	26.89, 13.87	0.89
Thaumastocoridae	4.63, 1.67	0.14	1.75, 0.70	0.38
Vespidae	7.00, 2.16	0.50	4.00, 1.49	0.09
Other/undetermined	2.53, 1.08	0.69	1.15, 0.46	0.21

***Laboratory analyses of floral visitors*—**We collected 133 individuals. Individuals of the following families were found to have *Mauritia flexuosa* pollen on their bodies: Curculionidae, Apidae, Vespidae, and Diptera (family undetermined). Although weevil individuals (Curculionidae) collected from male flowers carried up to 10 pollen grains on their bodies, weevils collected from female flowers carried no pollen grains. Honey bees and native bees (Apidae, Meliponinae, *Partamona* sp. and *Plebeia* sp.) collected from male flowers carried up to 100 pollen grains in hairs and corbiculae. Pollen was also found on flies (Diptera), although fewer than 20 grains on a single individual. No pollen was found on visitors (nitidulids, cucujids, and chrysomelids) collected from female inflorescences or in alcohol in which female floral visitors were stored.

***Anemophily experiment*—**Twelve of the 19 microscope slides (63%) that had been suspended from female inflorescences contained *M. flexuosa* pollen. The number of pollen grains per slide in each habitat ranged from zero to 117 grains. There was no significant difference in mean number of pollen grains on slides among the three habitats ($F_{2,\,16} = 3.73$, $P = 0.05$).

***Bagging experiment*—**Fruit set was highest in the control (mean ± SE = 0.31 ± 0.04), followed by the mesh bag treatment (0.20 ± 0.06); fruit set was lowest in the paper bag treatment (0.04 ± 0.03) (Fig. 3). Only treatment had a significant effect on fruit set ($F_{2,\,33.66} = 7.53$, $P = 0.002$); we found no significant effect of habitat on fruit set. Pairwise comparisons showed a significant difference in fruit set between the mesh bag treatment (visitor exclusion) and the paper bag treatment (wind + visitor exclusion) ($P = 0.019$) and between the paper bag treatment and the control (open pollination) ($P < 0.001$), but not between the mesh bag treatment and the control ($P = 0.10$). We noticed dry, undeveloped (presumably aborted) fruits in some of the paper bags, but did not include them in "fruit set".

***Sex ratios and height*—**Females significantly outnumbered males across all habitats ($\chi^2 = 9.47$, $P = 0.002$), although the sex ratio deviated significantly from the expected 1 : 1 only in the ecotone habitat ($\chi^2 = 7.91$, $P = 0.005$). We did not find a significant relationship between habitat and sex ($\chi^2 = 1.40$, $P > 0.05$). Across all habitats, males were slightly taller than females (18.70 ± 0.54 m vs. 18.23 ± 0.46 m), although these means were not significantly different from each other ($t = 0.636$, df = 303, $P = 0.71$). For both sexes, height was greatest in the forest, followed by the ecotone, and shortest in the disturbed savanna (Fig. 4). Height significantly differed between males ($F_{2,\,122} = 93.83$, $P < 0.001$) and between females ($F_{2,\,177} = 117.30$, $P < 0.001$) among the three habitats. All pairwise comparisons between habitats were significant in the analysis of each sex.

***Neighborhood size*—**Male–female interindividual distances ranged from 1 to 50 m: smallest in the forest habitat (mean ± SE = 7.32 m ± 0.71), followed by the ecotone habitat (11.28 m ± 1.32), and largest in the disturbed savanna habitat (11.89 m ± 0.90). However, these means did not differ significantly among habitats ($F_{2,\,151} = 2.781$, $P = 0.07$).

DISCUSSION

Previously, palms (Arecaceae) were thought to be wind-pollinated (Delpino, 1870). Henderson (1986) challenged this paradigm, providing evidence of insect pollination in many palm species. Beetles have been shown to be the most important pollinators of palms (Barfod et al., 2011). Indeed, the only two published studies on the pollination of *Mauritia flexuosa* hypothesize beetles to be the probable pollinators (Ervik, 1993; Storti, 1993). For effective pollination to occur in a dioecious species, a floral visitor should theoretically visit male inflorescences at a relatively similar frequency to female inflorescences. A pollinating visitor should also carry conspecific pollen on its body. Our results do not satisfy these expectations.

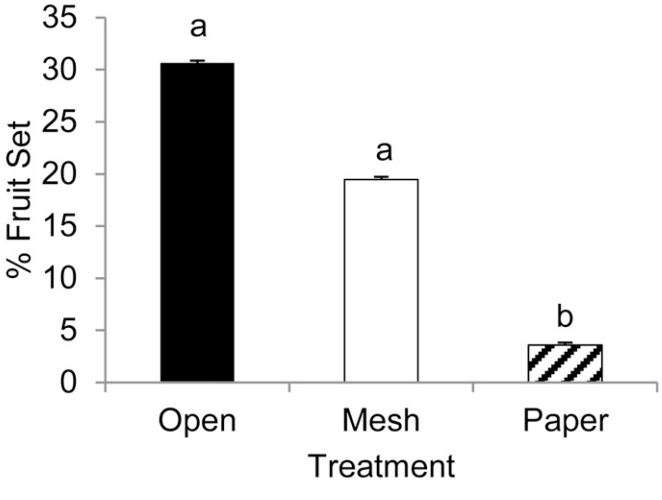

Fig. 3. Percentage fruit set (±SE) of *Mauritia flexuosa*, expressed as the proportion of fruits to flower scars, for each treatment and control, where different letters indicate significant differences at α = 0.05.

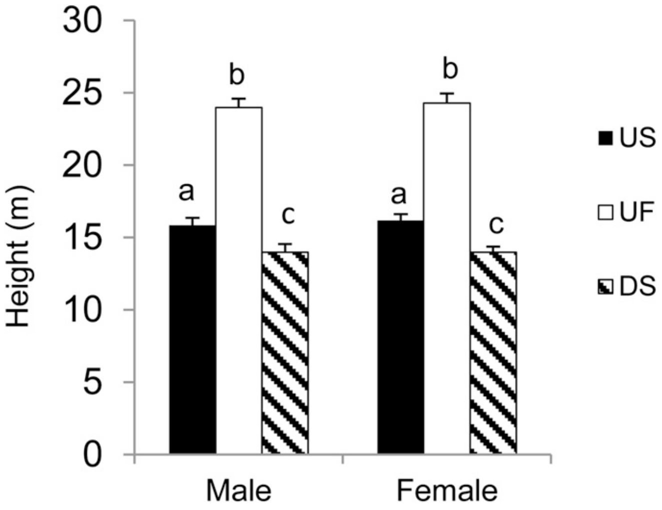

Fig. 4. Height (±SE) of *Mauritia flexuosa* males and females by habitat, where US is undisturbed savanna ecotone, UF is undisturbed forest, and DS is disturbed savanna, and where different letters indicate significant differences within a sex at α = 0.05.

Although native stingless bees and feral Africanized honey bees frequently landed on flowers, the behavior of both types of bees strongly suggests that they are not effective pollinators of *M. flexuosa*. Similar observations have been made on other dioecious species such as *Carica*, *Solanum*, and *Clusia*, in which *Trigona* bees visit flowers but do not pollinate (Baker, 1976; Anderson and Symon, 1987; Renner and Feil, 1993). *Trigona* discriminates between floral morphs, ultimately acting as a predator of floral resources and not a pollinator (Janzen, 1975). Ants are also an unlikely pollinator of this species and are known to hinder pollination processes in most plants as a result of their antibiotic secretions (Beattie et al., 1984).

If *M. flexuosa* is a wind-pollinated species, we would expect no significant difference in fruit set between the control and visitor exclusion treatment and a significant difference in fruit set between the control and the wind + visitor exclusion. Our results agree with both of these expectations, providing support for wind-pollination of this species in our study sites. Furthermore, the fact that the majority of slides suspended from female inflorescences contained pollen also supports anemophily. Berry and Gorchov (2004) found similar results in an exclusion experiment of the dioecious palm, *Chamaedorea radicalis*, and concluded wind to be the primary pollen vector.

The presence of fruit in the paper bag treatment, though less than 4%, raises the possibility of apomixis, specifically agamospermy, in which embryos develop independent of fertilization (Raven et al., 1999). It is unlikely that fruits set inside of bags as a result of contamination; we checked closed flowers and bags for the presence of pollen prior to bagging. Henderson (1995) also suggested that *M. flexuosa* may be facultatively apomictic because he observed isolated pistillate plants producing viable seeds. The possibility of apomixis has been raised in other dioecious palms including the date palm, *Phoenix dactylifera* (Abdallah et al., 2001), and *Chamaedorea radicalis* (Berry and Gorchov, 2004). Facultative apomixis offers dioecious plants a flexible alternative when pollination does not occur (Allem, 2003).

Wind pollination is a derived condition that has arisen on multiple occasions in independent lineages of land plants (Barrett, 2010b). The predominant view for roughly the past 140 years, articulated by Darwin (1876), is that wind pollination is inefficient, given high pollen to ovule ratios and unpredictable wind aerodynamics (Niklas, 1985; Ackerman, 2000; but see Hall and Walter, 2011). Experimental evidence, however, does not support this charge (Friedman and Barrett 2009). Several features typically associated with anemophily are present in *Mauritia flexuosa*, including many flowers, small petals, absence of nectaries, few ovules per flower, prodigious pollen production, unisexual flowers, synchronous flowering, and high conspecific density. There is a strong association between dioecy and wind pollination (Bawa, 1980), confirmed by Chazdon et al. (2003), who found a significant correlation between unisexual flowers and wind pollination, and that wind pollination was more common in canopy species than understory species. In our forest sites, *M. flexuosa* can be considered a canopy species, and its inflorescences have full access to the wind.

Many exceptions exist for the constructed pollination "syndromes" (Ollerton et al., 2009), such as the wind-pollination syndrome. The spiny, relatively large pollen grains of *M. flexuosa* do not contradict anemophily. Sannier et al. (2009) found no significant association between pollen ornamentation and pollination mechanism in palms. Contrary to popular misconception, Wodehouse (1935) found no significant difference in mean pollen size among wind-pollinated species and animal-pollinated species. Wind pollination may be more common in tropical flowering plants than previously thought (Renner and Feil, 1993; Renner and Ricklefs, 1995).

An obvious question remains, however. Why should an anemophilous plant invest in floral fragrance? The presence of staminodes and pistillodes suggests that ancestors were hermaphroditic (Anderson et al., 2000), and perhaps entomophilous, the original pollination mode in palms (Silberbauer-Gottsberger, 1989). Unisexual flowers and sexual dimorphism are believed to be a derived trait in palms (Tomlinson, 1990). It is also possible that entomophilous ancestors used mimicry to attract floral visitors to rewardless female flowers, similar to that observed in the relative of *M. flexuosa*, *Calamus castaneus* (Kidyoo and McKey, 2012). Thus, floral fragrance may be a carry-over from an entomophilous ancestor and has not been selected against because the cost of producing floral scent in this species is, perhaps, minimal. Ambophily, employing both wind and insects for pollination (Culley et al., 2002), may be an intermediate state in the transition from entomophily to anemophily, although we found no evidence of this mechanism in our study.

Wind pollination has traditionally been associated with open, dry habitats (Culley et al., 2002) and thought to be rare in tropical lowland forests (Regal, 1982; but see Chazdon et al., 2003). Our results do not support the claim that pollen grains are more easily dispersed in open areas than forest. Our finding suggests that, in this species, pollen dispersal by the wind is equally effective in the forest as in the savanna. These results suggest that although wind speed and duration may differ among habitats, these differences do not significantly affect the outcome of pollen transport.

The height of *M. flexuosa* in the forest may facilitate wind pollination. Individuals in the forest were significantly taller than individuals in either of the savanna habitats. Light limitation is the obvious explanation for this finding, although height may also reflect differences in age. However, it is possible that a height–habitat relationship has also evolved in this species to optimize pollination success. Tree-scale canopy heterogeneity has been shown to affect turbulence characteristics, increasing seed dispersal above the canopy (Bohrer et al., 2008). Although pollen may behave differently than seeds in wind currents, it seems reasonable to expect that wind within and above the canopy is capable of dispersing pollen. Other examples of other tropical forest, wind-pollinated trees include *Shorea robusta* (Dipterocarpaceae) (Atluri et al., 2004) and *Agathis australis* (Araucariaceae) (Ecroyd, 1982).

Assuming abundant resources, males tend to be larger than females (Charnov, 1982). Logically, males invest fewer resources in reproductive function and development than females and should be competitively superior in growth (Darwin, 1877; Lloyd and Webb, 1977). However, sexual dimorphism in size may also relate to pollination mechanisms. Male-biased sex allocation is common in anemophilous species (Burd and Allen, 1988; McKone et al., 1998; Hesse and Pannell, 2011). Large males should disperse pollen more effectively than short males because of the interaction between wind aerodynamics and height (Levin and Kerster, 1974; Rosenberg et al., 1983; Niklas, 1985). Similarly, short females should capture pollen more effectively than tall females. An increase in size has been shown to be associated with an increase in maleness, while a decrease in size has been shown to be associated with an increase in femaleness (Bickel and Freeman, 1993; Paquin and Aarssen, 2004). The relationship between sexual system, pollination mechanism, and architectural effects warrants further investigation.

Sex ratio also relates to pollination, as equal male to female ratio increases the probability of successful outcrossing (Anderson et al., 2006). A significant deviation from the expected equal sex ratio only occurred in the ecotone habitat, where 26% of the population's sex remained undetermined. Sex ratios in this species may be equal, theoretically increasing the probability of successful pollination between sexes by the wind. The lack of relationship between sex and habitat also supports our conclusion that wind pollination is important in all three habitats.

Neighborhood size has been proposed as a factor influencing reproductive assurance in wind-pollinated species (Knapp et al., 2001). On the basis of the fact that the majority of females in our study had access to pollen less than 12 m away, we conclude that spacing in our sites was amply sufficient for wind pollination to occur. The tendency of this species to establish in inundated areas may promote closer proximity between sexes. Pollen in the anemophilous, tropical tree, *Cecropia obtusifolia*, has been shown to travel up to 40 km (Kaufman et al., 1998), and pollen transport by wind in *Phoenix dactylifera* has been shown to exceed 200 m (Almehdi et al., 2005). Given that less than 2% of all flowering females in our study did not produce fruit suggests that pollen limitation in this species is low, consistent with the prediction that pollen limitation will be uncommon in anemophilous species (Friedman and Barrett, 2009).

Little is known about the evolution of anemophily in Arecaceae from presumed zoophilous ancestors. The few palms known to depend on wind for pollination include *Attalea phalerata* (Anderson et al., 1988), various species of *Chamaedorea* (Listabarth, 1993; Otero-Arnaiz and Oyama, 2001; Berry and Gorchov, 2004), *Howea* (Savolainen et al., 2006), *Thrinax parviflora* (Read, 1975), and *Phoenix dacytylifera* (Popenoe, 1922). Listabarth (1993) used the term "insect-induced pollination" in *Chamaedorea pinnatifrons*, whereby insects dislodge wind-transferred pollen and function to aid the wind-pollination system. We did not test for insect-induced pollination in *M. flexuosa* because the dry pollen dislodges easily in large quantities by wind. Virtually nothing is known about the pollination systems of the taxonomically closest relatives of *Mauritia*, *Lepidocaryum*, and *Mauritiella,* or the other species of *Mauritia*, *M. carana* Wallace ex Archer. In the distantly related *Raphia taedigera*, Myers (1984) indicated both wind and insect pollination. Additional studies are needed to better understand the pollination transitions in the evolution of Arecaceae.

Results from field observations, laboratory analyses, and field experiments do not support our stated hypotheses, leading us to draw the following conclusions: (1) *Mauritia flexuosa* is wind-pollinated, (2) habitat and disturbance did not affect the number of pollen grains transferred by wind, and (3) although native floral visitor abundance was lower in the disturbed sites relative to the undisturbed sites, this difference seems irrelevant to anemophilous *M. flexuosa*. Disturbance may not have immediate consequences on fruit set of abiotically pollinated species, contrary to many biotically pollinated species (Ricketts et al., 2008). However, gene flow may be reduced in fragmented populations, and the presence of the exotic tree (*A. mangium)* may have indirect effects on the reproductive biology of *M. flexuosa* and other native plants. We hope that our work encourages others to investigate the possibility of wind pollination in tropical plants. Results from such studies can elucidate evolutionary transitions in pollination systems and improve conservation and natural resource management practices.

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