

A Review of the Pollination Biology of *Mauritia flexuosa*

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1. Habit of
Mauritia flexuosa.

In a recent study (Khorsand Rosa & Koptur 2013), I demonstrated that the Amazonian palm, *Mauritia flexuosa*, a species previously thought to be beetle-pollinated, is actually wind-pollinated. This paper briefly reviews the study on *M. flexuosa* and discusses the academic and practical implications of these novel findings.

The dominant pollination system in the palm family has been a subject of debate for the past 150 years. Delpino (1870) was among the first to associate anemophily (wind-pollination) with palms. Drude (1889) and Kerner von Marilaun (1895) also assumed palms to be anemophilous. Cook (1943) considered anemophily in palms to be the rule. Meeuse (1972) considered the primitive pollination mode of palms to be anemophily, especially in dioecious groups (see Henderson [1986] for a complete historical review).

The wind-pollination paradigm held by many 19th century European botanists was likely fostered by knowledge of wind-pollination in the date palm (*Phoenix dactylifera*) (Johnson 1915). Early botanists believed that the large inflorescences with small flowers and copious amounts of pollen were “primitive” and that wind-pollination was consistent with evidence that the earliest seed plants (conifers) were pollinated “passively” (Raven et al. 1999). Certain floral traits characterize anemophilous flowering plants including small, unisexual flowers with reduced perianth parts and an absence of nectar (Faegri & van der Pijl 1979). Anemophily has perplexed botanists since the time of Darwin, as it was thought to be

inefficient and wasteful because of high pollen:ovule ratios and unpredictable wind aerodynamics (Niklas 1985, Ackerman 2000).

Although anemophily was the prevailing view of palms in the 19th and even into the 20th century, some observations from fieldwork in the Neotropics indicated entomophily (insect-pollination) (Wallace 1853, van der Pijl 1978) or a combination of both systems (Kerchove 1878, Coulter & Chamberlain 1915, Wettstein 1935). However, Henderson (1986) was responsible for shifting the predominant view away from anemophily and showing that insects are responsible for pollination in many palm species. Since his seminal paper, much progress has been made to understand pollination of palms. Barfod et al. (2011) conducted a thorough review of 60 studies focusing on palm pollination since 1986. The authors found the overwhelming majority of species to be animal-pollinated, with cantharophily, or beetle-pollination, as the most common mode. Ambophily, a combined system of wind- and animal-pollination, accounted for nine percent of the 77 species, while anemophily accounted for only seven percent.

2. *Buriti* fruits. Note scaly exocarp and beta-carotene-rich mesocarp.



The dioecious palm *Mauritia flexuosa* L. f. (Arecaceae: Calamoideae) is the most widespread palm in South America (Goulding & Smith 2007) and plays a pivotal role in Amazonian ecology, economy and culture (Fig. 1). In Roraima, Brazil, where the study was conducted, *M. flexuosa* grows in seasonally flooded habitats including lowland forest and savannas. This species provides critical food and nesting habitat for wildlife (Henry et al. 2000, Brightsmith 2005). The fruits, referred to as *buriti* in Brazil, constitute an important part of the Amazonian diet (Delgado et al. 2007) and have industrial and pharmaceutical applications (Schlemmer et al. 2007, Zanatta et al. 2008). *Buriti* fruits are typically one-seeded, globose to ellipsoid, and have a thin, scaly exocarp with bright yellow-orange fleshy mesocarp boasting the highest known levels of beta-carotene (Santos 2005) (Fig. 2).

Previously, *M. flexuosa* was associated with cantharophily. Storti (1993) observed curculionid, cucujid, and nitidulid beetles visiting pistillate and staminate inflorescences and found no pollen on Vaseline-covered microscope slides (a standard method of trapping wind-borne pollen) hung from pistillate inflorescences. Ervik (1993) also pointed to beetles as the primary pollinator of *M. flexuosa* and suggested that the wind may play a secondary role in pollination. However, recent work by Khorsand Rosa and Koptur (2013) provided strong evidence that the wind is the primary pollination vector of *M. flexuosa* and that beetles do not effectively pollinate the flowers.

I characterized floral morphology by conducting monthly phenological observations, testing for the presence of nectar and heat production (a characteristic of many beetle-pollinated plants) and recording flower opening time. To determine the pollination system, I conducted diurnal and nocturnal visitor observations in which visitor behavior and the number of landings were recorded. Floral visitors were collected from male and female inflorescences and analyzed for pollen content. Vaseline-covered microscope slides were hung from pistillate inflorescences and the number of pollen grains was counted 3–15 days later to understand if wind transports pollen between males and females. An exclusion experiment was also performed to determine the role of floral visitors and the wind in fruit set. In this type of experiment, closed, pistillate floral buds are covered in a



3. *Mauritia flexuosa* flowers. A. Pistillate flower. Note scaly gynoecium and six staminodes. B. Staminate flower in cluster of flower buds. Note flexed stamens and beetle foraging for pollen inside of flower.

mesh bag (excluding floral visitors but permeable to wind-borne pollen) or a paper bag (excluding floral visitors and wind-borne pollen). The proportion of fruit set in each treatment is compared with the control (pistillate inflorescences that were exposed to floral visitors and wind-borne pollen). Field observations and experiments were repeated in three habitats: undisturbed savanna-forest interface, undisturbed semideciduous forest and disturbed savanna. Disturbed savanna sites comprise native savanna converted into large-scale plantations of the exotic tree *Acacia mangium*.

I counted over 100,000 flowers on a single staminate inflorescence and up to 6000 flowers on a pistillate inflorescence. Female flowers (Fig. 3A) have six staminodes and are larger than male flowers (Fig. 3B), which have minute pistillodes. Stigmas are dry. Both sexes produce

floral fragrance, although the fragrance is stronger in males. Staminate flowers offer pollen as a reward; pistillate flowers offer no reward. No nectar was found in flowers of either sex. I found no evidence of thermogenesis.

Although a total of 20 insect taxa (belonging to seven families) was found visiting flowers, a large difference was found 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. Nitidulid and cucujid beetles comprised 53% of all landings on female flowers but only 12% of all landings on male flowers. I also observed chrysomelid beetles in female flowers at night, but they were absent in male flowers. Although bees (Africanized honey bees and native bees) and wasps collected pollen from male flowers, they rarely contacted the stigmas of female flowers. Weevils (Curculionidae) were frequently observed in male inflorescences but were not found in female counterparts. Finally, no pollen was found on visitors collected from female flowers. I concluded that insect-pollination was very unlikely.

The majority of slides (63%) suspended from female inflorescences contained *M. flexuosa* pollen. An individual slide had up to 117 pollen grains. In the exclusion experiment, fruit set differed significantly among treatments. Fruit set was highest in the control, followed by the visitor exclusion treatment; fruit set was lowest in the visitor + wind exclusion treatment. The results of this experiment pointed to wind-pollination.

Mauritia flexuosa demonstrates a suite of features conducive to anemophily: many unisexual flowers with a reduced perianth, lack of nectaries and thermogenesis, few ovules per flower, prodigious pollen production, synchronous flowering between sexes and high conspecific density. However, strong floral scent contradicts what we would expect for a wind-pollinated species, prompting me to ask the obvious question: why would an anemophilous species invest in floral fragrance? Given the presence of staminodes and pistillodes in the flowers of modern *M. flexuosa*, we may conclude that the ancestors were hermaphroditic. The hermaphroditic ancestor of *M. flexuosa* was presumably entomophilous, which is now considered to be the ancestral pollination mode in palms (Silberbauer-Gottsberger 1989). Unisexual

flowers and sexual dimorphism are believed to be a derived trait in palms (Tomlinson 1990). Khorsand Rosa and Koptur (2013) also raised the possibility that entomophilous ancestors used mimicry to attract floral visitors to unrewarding female flowers, as has been observed in the relatives of *M. flexuosa*, *Calamus castaneus* (McKey 2012) and *Mauritiella aculeata* (Listabarth 1999). The most parsimonious explanation, therefore, seems to be that floral fragrance in *M. flexuosa* has been carried over from an entomophilous ancestor and has not yet been lost.

Our knowledge of the evolution of anemophily in palms from presumed animal-pollinated ancestors is limited. Virtually nothing is known about the pollination systems of the one other species of *Mauritia*, *M. carana*. The only study of another species of the tribe Lepidocaryeae is Listabarth's (1999) study of *Mauritiella aculeata*, which he found to be pollinated primarily (but not exclusively) by meliponine bees. Both male and female flowers are fragrant in *Mauritiella aculeata*. The species is dioecious, although Listabarth (1999) occasionally found perfect flowers in staminate inflorescences. *Raphia taedigera*, a distant relative of *M. flexuosa*, is both wind and insect-pollinated (Myers 1984) and is monoecious.

Chamaedorea spp. (Listabarth 1993, Berry & Gorchov 2004), *Howea* spp. (Savolainen et al. 2006), *Juania australis* (Bernardello et al. 2001), *Mauritia flexuosa* (Khorsand Rosa & Koptur 2013), *Thrinax parviflora* (Read 1975), *Phoenix dactylifera* (Popenoe 1922) and other *Phoenix* spp. are wind-pollinated. They are a taxonomically heterogeneous assemblage of palms from diverse habitats, distributed around the world. Are they the only wind-pollinated palms? Is anemophily truly rare in the palm family, or does this generalization simply reflect the lack of field studies? Further research in the tropics is urgently needed to assess the frequency of anemophily in tropical palms.

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