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ORIGINAL ARTICLE

Reproductive phenology variation of the multiple inflorescence-palm tree *Wettinia maynensis* in relation to climate, in a Piedmont forest in western Amazonia

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Abstract

Key message ***Wettinia maynensis*'* phenology is influenced by temperature and the relative humidity, suggesting that the reproductive phenology can change in extreme climate event contexts, even in very humid unseasonal forests.**

Abstract *Wettinia maynensis* is a piedmont palm tree whose ecology, phenology and responses to climate are yet unknown. In order to examine the reproductive biology of this species, we observed the flowering and fruiting performance of 101 adult palms in the Colonso Chalupas Biological Reserve in the Ecuadorian Piedmont, located between the Andean mountains and the Amazon. All individuals were monitored every 1 or 2 months during 2.3 years (2015–2018). The inflorescences are infrafoliar with usually one central, large, pistillate and several lateral, centrifugally smaller, staminate inflorescences. Flowering took place throughout the year although staminate and pistillate inflorescences showed low synchrony towards the end of the year, 40% and 32%, respectively. Staminate inflorescences showed a negative strong relationship with relative humidity and a positive one with temperature. The infructescences exhibited high synchrony (80%) for almost 6 months. Compared to other species of the genus, *W. maynensis* presented the lowest ratio of male/female inflorescences, the higher production of infructescences but lower number of fruits per year. Infructescences production per palm was between cero and 7, and the time elapsed between the fruit formation and its dehiscence was about 5–8 months. Some palms were observed with simultaneously active pistillate and staminate inflorescences (21–22 palms), therefore geitonogamy is not discarded. *Wettinia maynensis* inflorescences production and its correlation with relative humidity, hence with temperature, highlights that crucial changes could occur in the reproductive phenology of this species under future climate change scenarios affecting the population dynamics and then the community of Andean–Amazon piedmont forests.

Keywords Andean–Amazon piedmont · Relative humidity · Flowers production · Synchrony · Infrutescences

Introduction

Palms, distributed in tropical and subtropical regions of the world (Dransfield et al. 2008), are considered key species for ecosystems in terms of structure and composition of forests and are relevant in the cultural and social relationships among people given their multiple uses as food, in construction, for hunting and even for medicine (Cámara-Leret et al. 2017). Despite their importance studies in phenological patterns and other reproductive aspects of palms population are scarce (Barfod et al. 2011). Those studies are important to understand plant reproduction, regeneration, the fruit development process and dispersion, enabling us to determine seed collection strategies and fruit availability for evaluating the management and conservation status of the resource (Talora and Morellato 2000; Guilherme et al. 2015; Garcia and Barbedo 2016).

Ecuador harbors 141 palm species out of which people use 105 in some way (Moraes et al. 2015). The convergence of the Andean and Amazon region, known as piedmont forest, borders the western area of the Amazon basin. In Ecuador Valencia and Montúfar (2013) recognize these Amazon foothills covering areas that go from 400 up to 1000 m.asl.

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which are especially rainy (> 4000 mm/year) and without clear seasonality. This confluence makes the area of singular species richness and at least 19 palm species are registered (Valencia and Montúfar 2013). However, the piedmont forest has been submitted to intense anthropogenic pressure since the colonization that has led the transformation to pastures for cattle and cultivation areas. Thus it is one of the most threatened ecosystems in the country (Ministerio del Ambiente de Ecuador 2012).

The genus *Wettinia* with 20 palm-tree species has apparently evolved responding to adaptive convergence pressures, as a result there are now some species associated to the Western Andes and others associated with the Eastern Andes–Amazon (Bacon et al. 2016). Although the genus has been poorly studied, we know that these species have multiple inflorescences, which is recognized in other plants as a strategy to prolong the flowering period (Fisher and Moore 1977).

Wettinia maynensis spruce is a medium tall palm reaching close to 20 m of height (Navarro et al. 2010; Villa-Muñoz et al. 2016). This palm is relatively abundant in the Andean-piedmont and western Amazon from Colombia, Ecuador and Peru (Navarro et al. 2010) between 200 and the 1600 to 2000 m.asl (Villa-Muñoz et al. 2016) and high precipitation. It is monoecious, with multiple staminate and pistillate inflorescences in the same plant. Fruits resemble an inverted pyramid of about 2.6–3.2 cm of length, with brown hairs and obovoid seeds of 2.2–2.4 cm in length (Galeano and Bernal 2010). The palm is locally known as *palma canela*, or *killi* (kichwa name). It is mainly used as part of the agroforestry systems; when the farmers prepare the land for coffee cultivation they do not cut these palms and use them as shade (Peñuela et al. 2016) or in provisional constructions. In the lowlands they are used to manufacture machetes, lances and blowguns (Villa-Muñoz et al. 2016). In Colombia, the trunks are used as poles and the leaves are used for transitory huts. Like many other palms with big fruits, it is apparently consumed by several medium and large mammals.

Three studies on *Wettinia* are reported in Colombia, one about pollination of *Wettinia quinaria* (O. F. Cook and Doyle) Burret (Núñez et al. 2005) and two on population structure and demography, and the reproductive biology of *Wettinia kalbreyeri* (Burret) R. Bernal (Lara Vásquez et al. 2012; Lara et al. 2017). *W. kalbreyeri* did not show relationship between climate and phenology, nor synchrony of flowering. *W. quinaria* instead, showed a peak of flowering in the less rainy months in a place where the rainfall exceeds 7000 mm of precipitation (Núñez et al. 2005), nonetheless, the association with climate variables was not explored.

Given the restriction in the distribution of *W. maynensis* for the piedmont and western Amazon and considering the high precipitation into the area, we aimed to study the morphology of the reproductive components of the species, the phenology of flowering and fruiting and its relations with climate. Thus, we wanted to answer the following questions: are there differences in the production of inflorescences of different sexes of *W. maynensis* along the year? Does the fruit productivity changes along the year? Is there any influence of climate variables on the flower or fruit production of *W. maynensis*?

Methods

Study area

The study was carried out in the buffer area at Los Monos trail at 750 m.asl. (0°55′51.25″S 77°52′59.55″W) (Fig. 1) in The Colonso Chalupas Biological Reserve (CCBR). The CCBR was created in 2014 and has 93,246 ha that serve as a bridge between two other reserve areas, Antisana in the North east and Llanganates in the South. Their main goal is to conserve as many of the ecosystems located in the piedmont as possible, as well as to serve as a biological corridor among the Andean and Amazonian regions. The reserve holds species of most genera of the Iriarteae group, including the genus *Dictyocaryum, Iriartea y Socratea* and *Wettinia* (Lozano et al. 2011; Lozano 2012).

The area is classified as evergreen piedmont forest from the north-central eastern Andean chain, from 400 to 1200 m. asl (Ministerio del Ambiente de Ecuador 2012), with various strata and trees with heights between 15 and 35 m. The landscape, although it is variable, is dominated by sharp hills with steep slopes (van der Hoek et al. 2018). Climatological data was obtained from Ikiam automated station located at 550 m.asl and less than 3 km from the study site (Fig. 2). The annual average rainfall in the area during the study 2016–2017 was 4571 mm, with minimum 180.1 mm and maximum 745.3 mm monthly, rainfall is high all over the year; any month is below 200 mm. The average temperature is 22.8 °C and the relative humidity is 91.7% (Laboratorio de cambio global-Ikiam 2018). Soils are usually acidic and well drained classified as Acrudoxic Ultic Hapludults (Ministerio de Agricultura y Ganadería 2015).

Structure and morphology

To determine the morphology of reproductive structures of the *W. maynensis* palms, we permanently marked 101 individuals with aluminum tags in a half-hectare area. We measured the diameter at breast height (DBH), estimated their height and counted the number of leaves of the crown on all of them. In order to characterize the morphology of the reproductive structures, we climbed 18 palms and collected 20 inflorescences and 7 infructescences. We analyzed 10 pistillate and 10 staminate inflorescences and counted

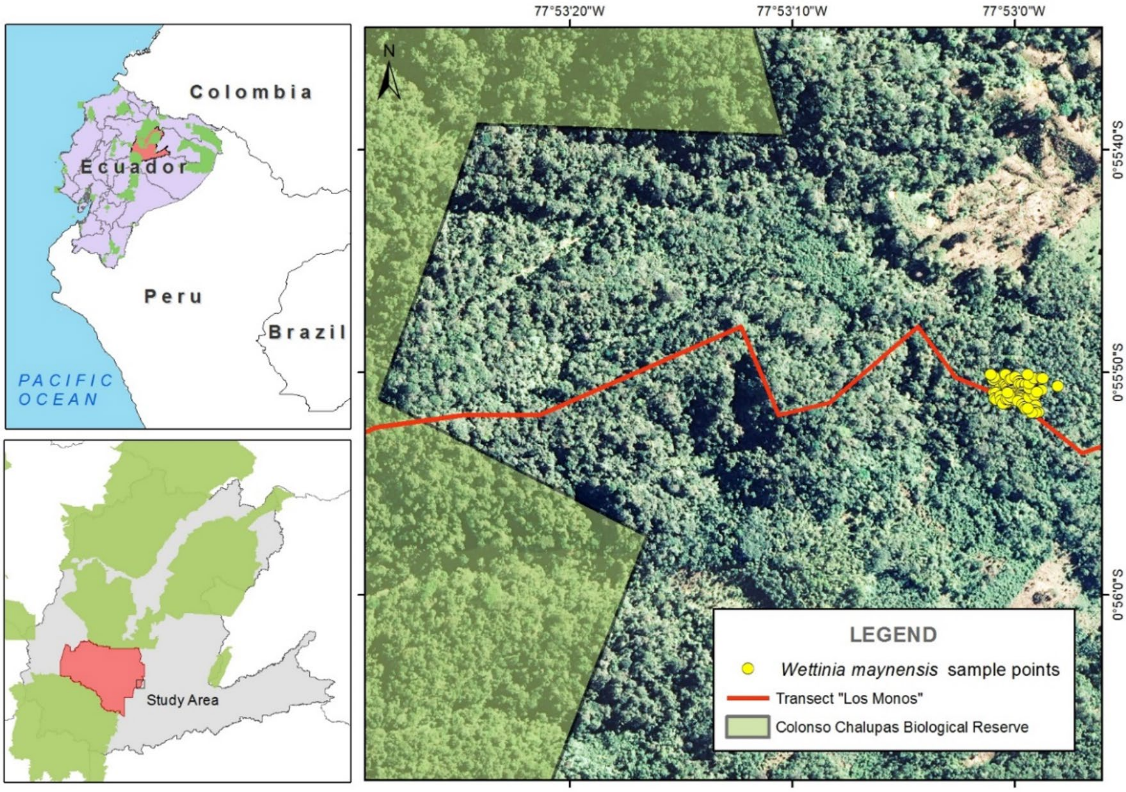

Fig. 1 Study area at the buffer zone of the Colonso Chalupas Biological Reserve, Napo, Ecuador

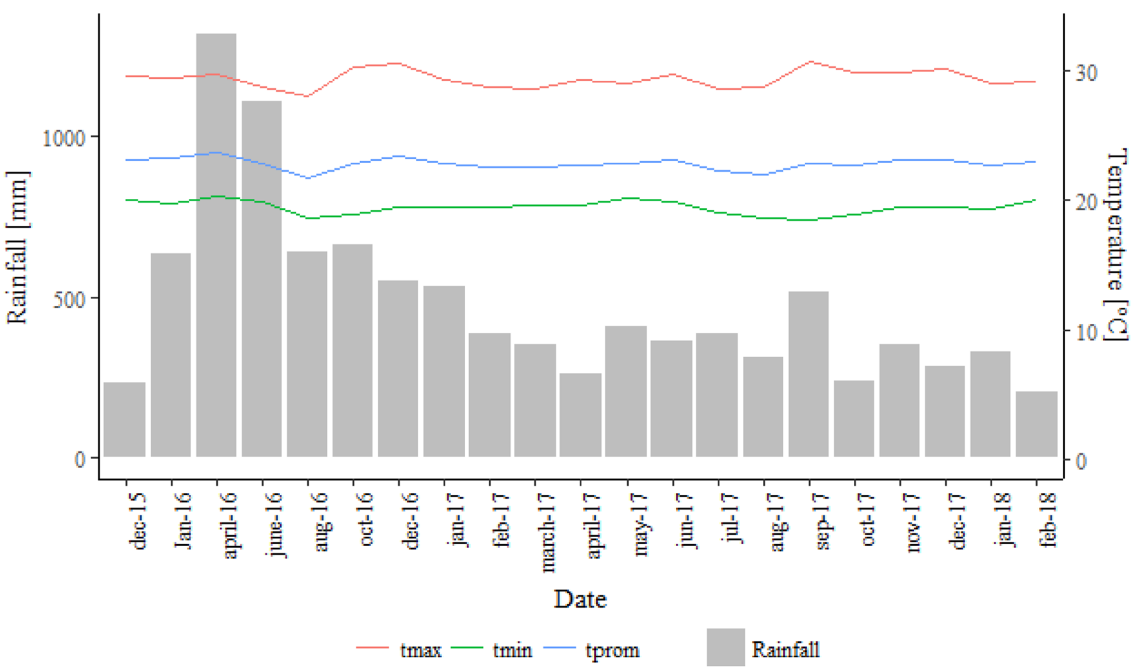

Fig. 2 Rainfall and temperature (t_{max}: maximum, t_{min}: minimum, t_{prom}: average)

the number of branches on each one, measuring the length of the inflorescences, racemes and branches, and counting the number of flowers per branch, and the total number of flowers per inflorescence. The seven collected infructescences were measured, weighed and the number of fruits was counted. These infructescences were used to determine the reproductive efficiency of this species that was assessed as the number of fruits with developed seeds and the number of fruits without seeds (abortions) divided by the total number of produced fruits (Nuñez Avellaneda 2014). The number of buds per node per palm was carefully counted to a sample of 20 palms.

Flowering and fruiting phenology

We monitored 101 adult palms with reproductive structures, in 21 observations from November 2015 to February 2018 (2.3 years). Given the slope of the area and the size of the palms all individuals were clearly observed with binoculars. The following phenological stages were registered: (1) the number of inflorescences with staminate flowers; (2) the number inflorescence with pistillate flowers; (3) the number of infructescences; (4) the number of leaves per individual. We also assessed synchrony by recording the relative frequency of palms with pistillate or staminate inflorescences following (Bencke and Morellato 2002): (a) no synchrony, when less than 20% of individuals were in the same phase; (b) low synchrony, when 20–60% of the individuals were on the same phase; and (c) high synchrony, when more than 60% of the individuals were in the same phase.

Climate and phenology relationship

Monthly precipitation, maxima, minima, daily temperatures, and maxima, minima, relative humidity data was obtained from the automatic climatic station from the Universidad Regional Amazónica Ikiam (Laboratorio de cambio global-Ikiam 2018), which is the closest station to the study area. To determine an association between the flowering or fruiting stages of phenology with climate, we used the dates from measurement to measurement, for rainfall the accumulative precipitation between measurement dates, for temperature and relative humidity the average of all days between measurements.

Results

Structure and morphology

The average DBH of the 101 individuals measured was 14.7 cm (SD ± 2.1 cm), varying from 11.1 to 25.8 cm; the average height was 9.6 m (SD ± 1.7 m) with a 6.0 m minimum and 14.0 m maximum. Palms presented on average seven leaves (rank 5–10 leaves).

Wettinia maynensis produced bunches of staminate, pistillate or both types of inflorescences simultaneously and close to each other (Fig. 3). We observed a maximum of five staminate and four pistillate inflorescences per palm. The number of branches was similar in staminate and pistillate inflorescences, six on average, as well as the number of bracts covering them. The opening of the staminate inflorescences was 4 h approximately during the morning, usually around 0900–1300 h.

The 101 palms of *W. maynenis* produced 1081 inflorescences (578 staminate and 503 pistillates) for the total study period; the average between 2016 and 2017 for the number of staminate was 269 ± 84 and the number of pistillate inflorescences was 235 ± 24. The number of flowers was different between sexes; staminate almost tripled the pistillate flowers per bunch (Table 1). Fruit bunches of different ages can be found on the same palm tree as well as fully matured fruit bunches. The brown hairy fruits of the species make it difficult to classify them as green/ripe fruits, thus we subjectively considered the size of fruits and how close they are to other fruits in the same bunch as the main difference: small fruits (less than 3 cm) and very close to each other as immature, and those well separated and bigger as mature. We observed 1–7 bunches per individual, and an average of 824 (SD 254) fruits per bunch, but it was highly variable as the average amount of fruits per palm ranged from 446 to 1120. However, in all cases reproductive efficiency was very high as we obtained an average value of 96% (SD 0.042, $n = 7$).

Fruits measured.

Phenology

We found that, all through the year, the palms displayed both staminate and pistillate inflorescences, even though the number of inflorescences per palm was highly variable. During the study period, 1.9% of the palms showed only pistillate inflorescences, 5.7% only staminate inflorescences, but the majority (92.4%) showed both pistillate and staminate inflorescences. The annual average in 2016 and 2017 was 2.2 and 2.5 staminate and 2.6 and 1.7 pistillate inflorescences per palm. In 2017 we registered the maximum number of staminate and pistillate inflorescences per palm. The number of pistillate and staminate inflorescences and, infructescences per observation are shown in Fig. 4 Only six palms showed four staminate inflorescences simultaneously along the study period but the maximum of pistillate inflorescences was two in 27 palm trees.

Low synchrony of flowering was found in November 2015 and January 2016 for both staminate (40%) and pistillate (32%) inflorescences; and also between October to December 2016 for staminate inflorescences. High

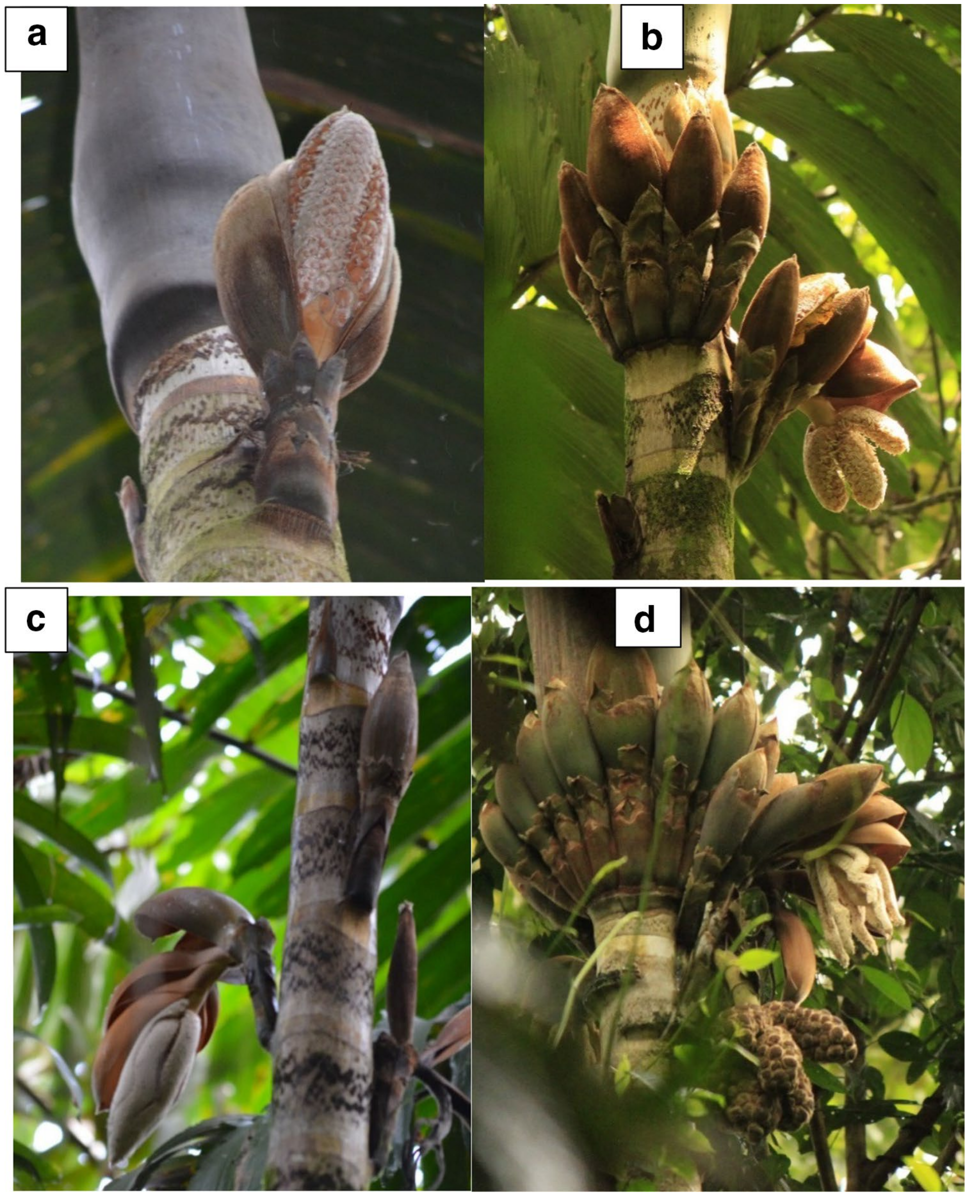

Fig. 3 Pistillate (**a, b**) and staminate (**c, d**) inflorescences of *Wettinia maynensis* in the Colonso Chalupas Biological Reserve, Ecuador

Table 1 Morphology of reproductive parts of *Wettinia maynensis*, based on 10 staminate and 10 pistillate inflorescences

Inflorescences	# of branches	# flowers	Length (cm)	# of bractea	Length bractea (cm)	Length pedunculus (cm)
Pistillate						
Average ± Std	6 ± 2	819 ± 273	14.79 ± 4.10	3 ± 1	30.15 ± 6.03	32.45 ± 8.3
Rank	4–9	334–1174	9.0–21.6	3–4	21.8–39.8	20.0–43.5
Staminate						
Average ± Std	6 ± 1	2181 ± 798	23.2 ± 4.6	4 ± 1	25.8 ± 3.6	23.3 ± 3.4
Rank	4–8	1172–3460	16.7–30.3	3–5	22.3–32.9	20–30.2

synchrony (closes to 80% of the individuals) was found in infructescences from January to June 2016, December to May 2017. We observed palms with simultaneously active staminate and pistillate inflorescences, 21 palms in December 2016 and 22 palms in November and December 2017. The proportion of staminate inflorescences was, in general, higher than pistillate inflorescences with

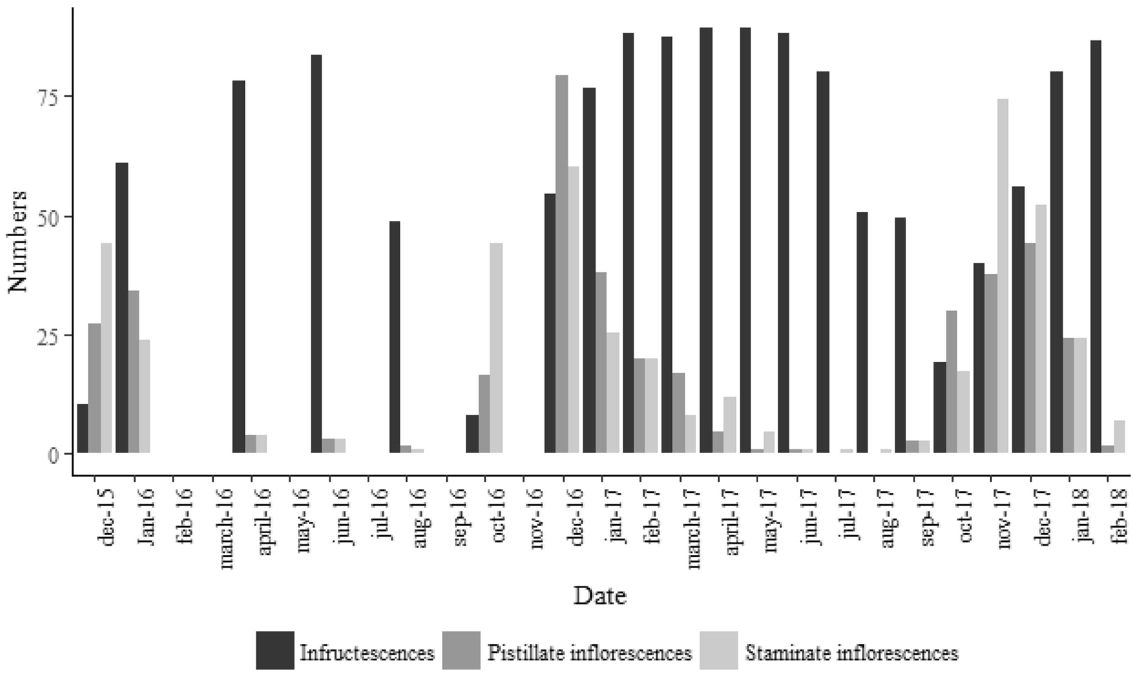

Fig. 4 Percentage of palms of *W. maynensis* with staminate (light gray), pistillate (dark gray) inflorescences and palms with infructescences (black) observed from November 2015 to February 2018 (2.3 years)

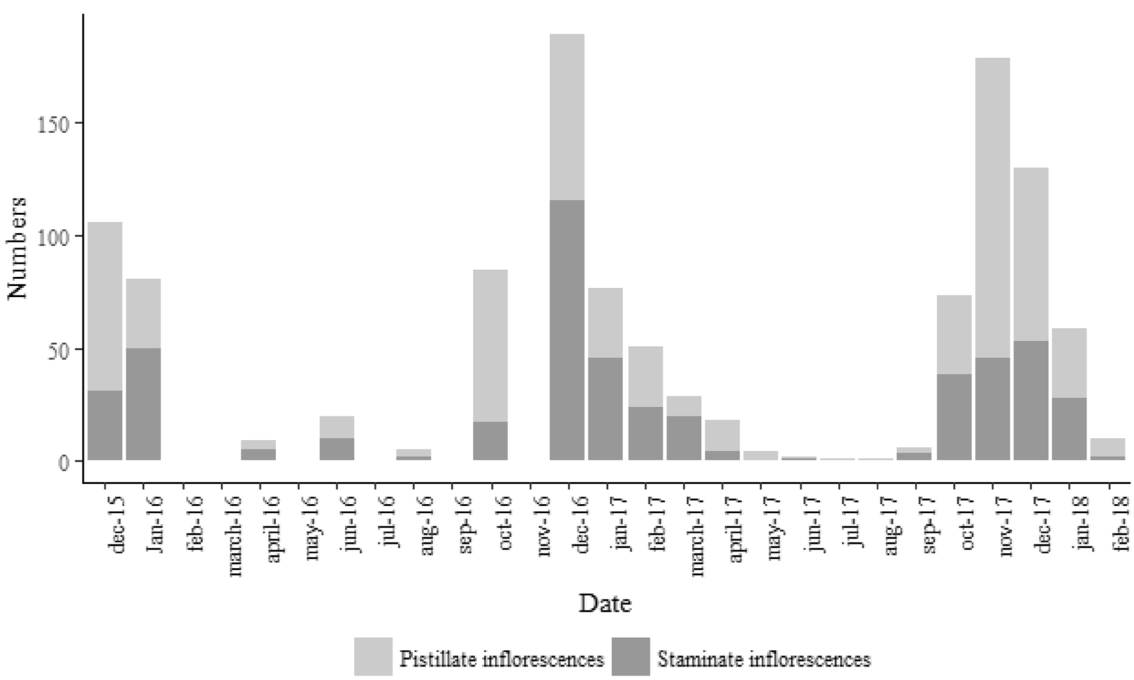

Fig. 5 Proportion of pistillate and staminate inflorescences of *Wettinia maynensis* in the Colonso Chalupas Biological Reserve, observed from November 2015 to February 2018 (2.3 years)

exceptions in January, April and December 2016, as well as March, September and October 2017 (Fig. 5).

Most of the infructescences observed stay between 5 and 8 months in the palm and the average was 6.73. It was common to observe palms with one infructescence in 1 month and in the next 2 or 3 months the number of infructescences increased to three or more. We also observed lots of fruits on the forest floor in September and a high density of seedlings covering it in November 2017 and 2018 (Fig. 6).

Climate vs. phenology

A significant positive correlation was found between number of staminate inflorescences with average and minimum temperature and minimum relative humidity (Table 2), which in turn is related to the strong negative relationship found between these inflorescences and average humidity. Pistillate inflorescences did not show any correlation with any climate

Fig. 6 Fruits, seeds and seedlings of *Wettinia maynensis* in the Colonso Chalupas Biological Reserve, Ecuador

Table 2 Pearson correlation between reproductive parts of *Wettinia maynensis* and the climate variables: data of temperature and relative humidity consider the average of days between measurements, rainfall is the cumulative precipitation

Inflorescences	Temperature			Relative humidity			Rainfall
	Average	Maximum	Minimum	Average	Maximum	Minimum	
Pearson correlation							
Staminate	**0.96**	**− 0.82**	**0.85**	**− 0.97**	**− 0.97**	**0.66**	− 0.34
Pistillate	0.09	0.16	0.05	0.01	− 0.01	− 0.09	0.06
Infructescences	0.15	− 0.33	0.44	− 0.09	− 0.15	0.57	− 0.01
Determination coefficient							
Staminate	**0.92**	**0.68**	**0.72**	**0.95**	**0.93**	**0.44**	0.11
Pistillate	0.01	0.03	0.00	0.00	0.00	0.01	0.00
Infructescences	0.02	0.11	0.19	0.01	0.02	0.32	0.00

Bold numbers are significant values

variable indicating that the mechanisms of triggering flowering are different between sexes. No correlations were found between peaks of staminate or pistillate inflorescences or fruits and the rainfall.

Discussion

This study is the first report about the reproductive phenology of *W. maynensis*. Three other species of *Wettinia* species have been studied, all in Colombia (Núñez et al. 2005; Lara Vásquez et al. 2012; Núñez Avellaneda 2014; Lara et al. 2017). The data of *W. maynensis*, diameter and number of leaves (14.7 cm DBH, 7 leaves), were between the averages reported by Galeano and Bernal (2010) and Navarro et al. (2010) in Colombia.

Are there differences in the production of inflorescences of different sexes of W. maynensis throughout the year? Does the fruit productivity changes throughout the year?

In relation to the inflorescences' production, the 101 palms of *W. maynensis* produced 504 inflorescences 53.46% staminate vs 46,53% pistillate, which is similar to *W. quinaria* in Gulf of Tribugá (Biogeographical region of Chocó, Colombia), where 73 individuals produced 308 inflorescences: 238 staminate (77.27%)/65 pistillate (21.10%) and five (1.6%) androgynous per year, but more than *W. kalbreyeri* in Colombia, where 100 individuals produced 125 inflorescences: 96 staminate (76.8%)/28 (22.4%) pistillate and one androgynous per year (Lara et al. 2017). In all cases a higher number of staminate than pistillate inflorescences are produced. Interestingly, in *W. maynensis* the proportion between staminate/pistillate inflorescences was not as marked as in the other two species, and the number of palms that could present geitonogamy was higher, with a maximum of 22 in 2017. The opening of the staminate inflorescences was 4 h approximately during the morning, usually around 0009–1300 hours, which it could be considered fast, in relation to the reported for *W. kalbreyeri* between the 24:00–8:00 h (Lara Vásquez 2011).

The ratio staminate/pistillate shown by different species of *Wettinia* is remarkable (Table 3). The species *W. quinaria* and *W. kalbreyery*, both with a much higher number of pistillate inflorescences, are younger phylogenetically than *W. praemorsa* and *W. maynensis*, which are in the Eastern clade in the phylogenetics of the palm tribe Iriarteeae (Bacon et al. 2016). It seems that the derived character is towards a closer proportion of staminate/pistillate inflorescences. This character could be related to pollination, suggesting that the oldest the origin of the species of *Wettinia*, the more specialized pollinators and less necessity of having a closer ratio between staminate/pistillate.

Regarding the variability of reproductive phenology, Galeano and Bernal (2010) mention that *W. maynensis*, under similar conditions in Colombia, has inflorescences in November and December and fruits in June and December. Nevertheless, long time studies are not available still. Villa-Muñoz et al. (2016) remark that in Yasuni, eastern Ecuador, *W. maynensis* produces inflorescences and fruits throughout the year, with peaks between May and July during the rainy season. Though, we also found fruits throughout the year, we found high synchrony between January to June and December to May in 2016, and 2017, respectively, but these felt down in August to October during the dry season. Our findings are contrary to what has been found by Lara Vásquez (2011) in *W. kalbreyeri* in Colombia where a low synchrony of fruits was reported.

Synchrony of both staminate and pistillate inflorescences was low (Fig. 4), whereas in Colombia *W. kalbreyeri* and *W. quinaria* did not show synchrony (Lara et al. 2017; Núñez et al. 2005). Asynchrony has been interpreted as a mechanism to permanently promote the presence of floral visitors, thus a little synchrony could suggest that the actual production of inflorescences is enough to maintain the pollinators for all the inflorescences in the area studied. The high reproductive efficiency found could support this interpretation.

Table 3 Reproductive characters of four *Wettinia* species including the staminate/pistillate ratio

No.	Palm species	Clade (following Bacon et al. 2016)	Buds by node	Flowering time	Fruit time	The staminate: pistillate inflorescence ratio	The staminate: pistillate flower ratio	Reference
1	*W. quinaria*	Western	1–15	All year	NA	3.6:1	13:1	Núñez et al. (2005)
2	*W. kalbreyeri*	Western	1–13	All year	9.2	3.43:1	3.38:1	Lara et al. (2017)
3	*W. praemorsa*	Eastern	1–12	All year	NA	4:1		Núñez Avellaneda (2014)
4	*W. maynensis*	Eastern	1–18	All year	5–8 months	1.2:1	2.74:1	This study

NA not available

Is there any influence of climate variables in the reproductive phenology of W. maynensis?

In other palm species, flowering has been associated with rainfall or temperature (Cifuentes et al. 2013; Guilherme et al. 2015; Urrego et al. 2016; Mendes et al. 2017). Some palm species show synchrony in fructification or flowering in different periods of the year. Synchrony in flowering has been reported in various palm species and it may be associated to dry season such as in *Bactris gasipaes* Kunth in Manaos (Ferreira and Santos 1992), *Butia purpurascens* (Glassman) in the Brazilian cerrado (Guilherme et al. 2015), or to the wet season and high temperatures in *Butia eriospphata* (Mart. ex Drude) Becc. in Santa Catarina southern Brazil (Garcia and Barbedo 2016) or *Euterpe edulis* Mart. in the northeast of Sao Paulo state (Genini et al. 2009).

The same differences could be found in fructification; some species do not show synchrony, whereas others show a relationship with dry or wet seasons; v.gr. *B gasipaes* has a peak at the end of the rainy season (Garcia and Barbedo 2016) and *Euterpe oleraceae* Mart. has a peak in the dry season (Galetti et al. 1999). However, in Colombia, *W. kalbreyeri*, did not show any correlation with those variables (Lara et al. 2017) and in *W. quinaria* this relationship has not been explored. While, *W. maynensis* exhibited a strong relationship with relative humidity and temperature (Table 2). We found a high negative correlation between staminate inflorescences with average and maxima relative humidity as well as a strong and positive relationship with average temperature, in these three cases the r^2 explained more than 90% of this relationship. The relationship is reasonable given that relative humidity is inversely related to the air temperature. In the current scenarios of climate change, temperature shows to be an important driver of changes in phenology (Chambers et al. 2013; Urrego et al. 2016). In the case of *W. maynensis*, the increase of temperature and subsequent decrease of relative humidity, due to more severe and frequent droughts, could increase the production of staminate inflorescences, probably raising the staminate/pistillate ratio. In this way, the palms could reduce the energy invested in producing pistillate flowers under difficult climate conditions, consequently the production of fruits. This situation could diminish the production of seedlings. Another possibility is an explosion of staminate flowers attracting more pollinators, ensuring pollination when the humidity is enough to invest resources in producing pistillate flowers. In any case, there will be an alteration of the population dynamics of the species.

On the other hand, interesting questions arise about the evolution of the species when examining the ratio of staminate/pistillate flowers, the length of the fruits in the palm-trunk and duration of the opening of flowers which seem to be variables that had evolved differentially in the species of the genus, that deserve to be studied. The ratio between male/female flowers is partly interpreted as an optimization in the allocation of resources (Parra and Vargas 2007), therefore could be interpreted as the unnecessary production of more staminate flowers if the pollination is highly successful or perhaps there are more grains of pollen per flower, something that must be further explored.

In general, *W. maynensis* inflorescences production suggested a complex ecology and reproductive biology, that is associated with climate variables (relative humidity, temperature), which highlights that changes in regional climate could lead to impacts on this palm population and hence the species.

Author contribution statement Study conception and design: MCP, LAN, SA. Acquisition of data: MCP, MB, SA. Analysis and interpretation of data: MCP, MB, LAN. Drafting of manuscript: MCP, LAN.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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