



Insects or Wind? New findings on the pollination system of *Euterpe edulis* (Arecaceae)

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Abstract

The palm *Euterpe edulis* is an important palm species for the extraction of palm heart, a highly profitable consumable product. Due to its importance, much research has been conducted around the ecology of this palm species. Nevertheless, information available on its reproductive ecology is quality-deficient and fragmented, resulting in misleading views of the pollination and reproductive ecology of *E. edulis*. Here we conduct the first thorough study assessing the relative dependence on animal pollination of *E. edulis* in Argentina, and conduct parallel detailed observations on floral visitors. Also, we integrate our results with those available for the species in the literature. Here we found that *E. edulis* has an ambophilic pollination system. However, in our study system, there was a predominance of wind pollination over insect pollination and the species can also set seeds in the absence of pollen. Also, our study shows in great detail the large diversity of insects visiting *E. edulis*, indicating the generalist pollination system of the species, where Hymenoptera and Diptera stand out in richness and frequency of visits. The palm represents a key resource for a wide diversity of insect visitors, but the palm does not rely on their efficiency to act as pollinators. The varied levels of reproductive dependence on animal versus wind pollination of *E. edulis* may be shaped by climatic and landscape conditions. Such alternative versatile strategies allow the species to guarantee the reproductive success under different ecological contexts.

Keywords Ambophily · Euterpeinae · Meliponini · Pollination service · Reproductive dependence · Seed germination · Seed set

Introduction

Palms are distributed in tropical and subtropical regions around the world (Eiserhardt et al. 2011) and represent socio-economic and ecological keystone resources (Bates 1988; Zona and Henderson 1989; Reis et al. 2000;

Sosnowska and Balslev 2009; Galetti et al. 2013; Dislich et al. 2017). *Euterpe* Mart. is a neotropical palm genus composed of seven species (Henderson and Galeano 1996) and most of them have economic and cultural importance due to the medicinal and commercial uses of their products (Barroso et al. 2010; Corrêa Martins et al. 2014; Trevisan et al. 2015). For example, *Euterpe oleracea* Mart. and *Euterpe edulis* Mart. palms provide highly priced edible palm hearts,

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and also fruits for the production of beverages such as "Açaí" juice, cosmetics, construction and ornamental purposes, among others (Trevisan et al. 2015; Garcia et al. in press). *Euterpe* palms also have ecological importance since most of them produce large quantities of fruits rich in nutrients (Ferreira et al. 2016). Fruits of some species are available for several months and represent vital food resources for birds, mammals and other wild animals (Zona and Henderson 1989; Galetti et al. 1999; Castro et al. 2007; Zago da Silva and dos Reis 2018). Similarly, their inflorescences produce large quantity of flowers that are important source of pollen and nectar for a large diversity of insects (Küchmeister et al. 1997; Mantovani and Morelato 2000; Wendt et al. 2011; Campbell et al. 2018).

In particular, *E. edulis* was for many years the most important palm species for the extraction of palm heart, which is a highly profitable consumable product. Because the palm heart is the apical meristem, its harvest implies the killing of the palm. As a result, the harvest of palm hearts from wild populations has resulted in the destruction of several million *E. edulis* palms over the past decades (Henderson and Galeano 1996; Chediack and Baqueiro 2003). Moreover, unlike *E. oleracea* and *E. precatoria* Mart., which are extensively cultivated (Aranguren et al. 2014; Campbell et al. 2018), *E. edulis* is not cultivated and their products are obtained through the management of natural populations (Reis et al. 2000). Due to the continued expansion of the agricultural and forestry frontiers, the commercial demands generated by the price of palm heart and the few incentives for an adequate management, *E. edulis* populations are threatened in several areas of the Atlantic Forest in Brazil and Argentina, where some populations were locally extinct (Orlande et al. 1996; Galetti and Fernández 1998; Reis et al. 2000; Chediack and Baqueiro 2003; Montagna et al. 2018). Currently, it is considered a key species to favor the conservation by use, i.e. as the conservation of any resource, motivated by perceptions of its utility (Barrance et al. 2009; Villagra et al. 2019; García et al. in press).

Euterpe edulis is a monoecious species and its floral phenology shows an accentuated protandry with no overlap between male and female flowers within a plant (Reis et al. 1993; Henderson and Galeano 1996). Each palm produces between one and two inflorescences with more than 40,000 flowers per reproductive season (Mantovani and Morelato 2000; Wendt et al. 2011). Although both floral types are small and inconspicuous, they emit sweet odor and produce nectar, stigmatic exudates and pollen as rewards (Mantovani and Morelato 2000; Dorneles et al. 2013). These floral traits, along with the temporal and spatial separation of male and female functions, suggest altogether high sexual reproductive dependence on animal pollination. Up to now, the established knowledge about the pollination and breeding system of this palm species comes from a preliminary study

conducted with only four palms (Reis et al. 1993) in a forest fragment in Brazil. Reis et al. (1993) showed that *E. edulis* can produce seeds both asexually by apomixis and sexually by wind and insect pollination (i.e., ambophily), suggesting *Trigona spinipes* Fabricius (Meliponini) as the main pollinator. However, two more recent studies conducted with five individuals each, suggest the species is self-compatible but not apomictic (Wendt et al. 2011; Dorneles et al. 2013). Particularly, Dorneles et al. (2013) showed that pollen can be transported by wind; however, their findings do not necessarily imply the occurrence of anemophily. In palms, insect pollination is the predominant, most common pollination system whereas wind pollination is rare and considered a derived trait (Henderson 1986). However, the combination of both pollination agents, ambophily, has been found in some monoecious palms (e.g., Listabarth, 1992; Culley et al. 2002; Rios et al. 2014), including *E. edulis* (Reis et al. 1993). While ambophily is not considered a frequent pollination system throughout angiosperms, it might be more common than previously thought (Culley et al. 2002). Ambophily represents a generalist pollination strategy that may ensure successful pollination under varied and/or changing ecological scenarios (Culley et al. 2002). Finally, genetic studies on *E. edulis* have shown a predominantly exogamous breeding system and high genetic diversity within most studied populations (Carvalho et al. 2017).

In addition to the somewhat inconsistent results of these previous studies to determine the reproductive system of this key species, observations of floral visitors have been conducted with poor accuracy. Due to the high height of their inflorescences (8–18 m), previous attempts to observe and identify effective pollinators on this palm species have been made with poor resolution, as interactions were registered mostly at the level of insect orders and only a few insects have been identified at the species level (Reis et al. 1993; Mantovani and Morelato 2000; Wendt et al. 2011). Identifications at the order level indicate that individuals of Hymenoptera, Diptera and Coleoptera visit both, male and female flowers (Mantovani and Morelato 2000; Wendt et al. 2011; Dorneles et al. 2013), implying all of them have the potential to be effective pollinators. More recently, Santos et al. (2018) conducted observations on flowers of 11 *E. edulis* palms, but limiting the sampling to two mornings only. They identified 13 species of floral visitors, suggesting *Apis mellifera* L., *Plebeia droryana* (Friese), and Euglossini spp. as potential pollinators of *E. edulis* as they contacted reproductive structures of both male and female flowers (Santos et al. 2018).

Despite these previous attempts to assess the reproductive ecology of *E. edulis*, there is still fundamentally contradictory information and poor-quality data about the reproductive dependence on animal pollinators of this key species. In this study we conduct the first comprehensive

evaluation of the level of dependence on animal pollination for sexual preproduction of *E. edulis* and the consequences of sexual and asexual reproduction on their progeny vigor. Based on the floral traits of male and female flowers together with evidence of seed set after insect and wind pollination, as previously described, we hypothesize that *E. edulis* has an ambophyllous pollination system (wind and animal pollination). To test this hypothesis, here we determine (a) the identity and diversity of floral visitors and effective pollinators, (b) the level of reproductive dependence on wind and animal pollination, (c) and the effect of sexual vs. asexual reproduction and animal vs. wind pollination on seed set and progeny performance. Finally, we conduct a systematic literature search to compare our results on the reproductive biology of this palm with previous studies.

Material and methods

Study area

The study was conducted at Iguazú National Park (INP), north of Misiones province, NE Argentina (Fig. 1). The park comprises 65,000 ha of semi deciduous subtropical forests known as Alto Paraná Atlantic Forest (Galindo-Leal and Camara 2003). The INP is connected with other conservation areas, which together represent one of the largest remnants of continuous forest from the whole Atlantic Forest (Ribeiro et al. 2009).

The Alto Paraná Atlantic Forest constitutes the southernmost and western portion of the eco-region complex of the Atlantic Forest, holding the largest extension of remaining forests between Argentina, Brazil and Paraguay countries (Galindo-Leal and Camara 2003). The mean annual temperature ranges from 16 to 22 °C and rainfall between 1900 and 2100 mm, which is evenly distributed along the year (Ligier 1999). *Euterpe edulis* is endemic to the Atlantic forest, distributed from the state of Bahia, Brazil, to the state

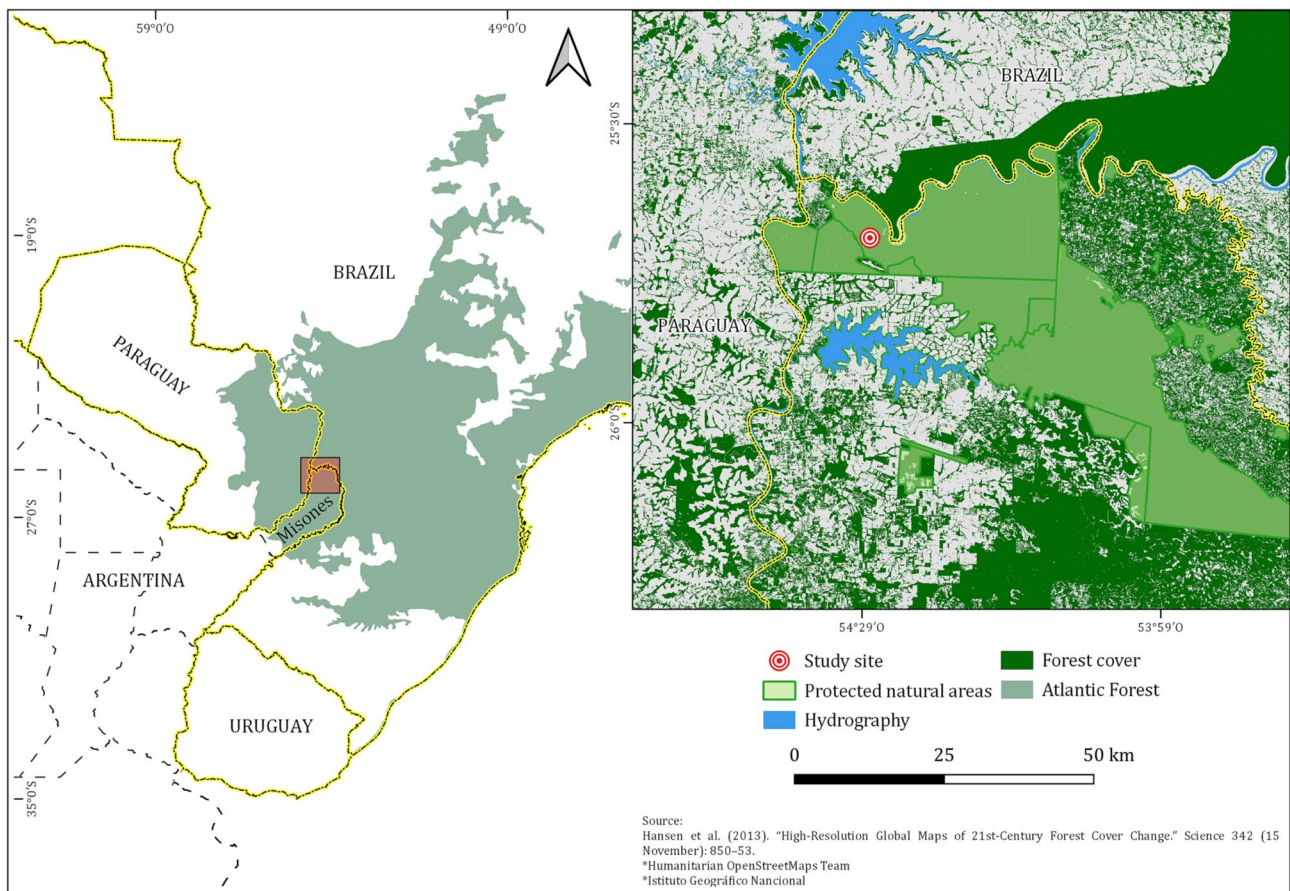


Fig. 1 Study site in the province of Misiones in northern Argentina, South America

of Misiones, in the northeast of Argentina and southeastern Paraguay (Henderson and Galeano 1996). In Argentina it is locally called “Palmito”, so patches of forests dominated by Palmitos are so-called “Palmitales”. Within the Alto Parana Atlantic Forest, and in particular in the INP, the *palmitales* grow in the highest parts of the landscape where temperatures rarely drop below 0 °C (Gatti et al., 2008), soils are red, deep and well-drained. *Palmitales* are forests of high specific richness (between 50 and 70 tree species per ha.), where *E. edulis* is the dominant species for having the highest density of individuals (Placci et al. 1992). *Euterpe edulis* occupies the intermediate stratum in the forest canopy (Srrur et al. 2007). We selected a *palmital* of 1 km² located near National Route N° 12 close to the main public access of the INP (Fig. 1).

Euterpe edulis has panicle-like inflorescences formed by an average of 128 rachillae of 26–58 cm long that extend from a common peduncle (Reis et al. 1993; Henderson and Galeano 1996). Each rachillae has between 53 and 162 female flowers and more than twice as many male flowers (Mantovani and Morellato 2000). Flowers are arranged in triads, two basal males and one female. The floral phenology per inflorescence lasts about 20–30 days. Male flowers open first and this phase lasts 7–17 days, followed by a period of approximately 6 days without flowers, and then the female phase begins for another 6–9 days (Mantovani and Morellato 2000; Wendt et al. 2011). Male and female flowers live one and three days, respectively (Mantovani and Morellato 2000; Wendt et al. 2011). Overlap between male and female flowers can only occur when there are two inflorescences in the same palm, but it is infrequent (approximately 6% of palms; Reis et al. 1993; Wendt et al. 2011). Despite the asynchronicity observed in male and female phases at the individual level, there is high overlap of male and female individuals at the population level. Following Reis et al. (1993), individuals with male and female phases occur in an approximate ratio of 1:1 (e.g., 35 and 30 individuals in male and female phase, respectively).

Pollination treatments

To conduct pollination treatments on flowers and observation of floral visitors, we designed and constructed a chair with a special system that allows attaching the chair to the palm stem with two tensioned belts such as cargo truck tightening device. We climbed the chair with the help of stairs and placed the chair near the inflorescence, once seated we were able to observe all floral visitors in detail and conduct pollination treatments (Fig. 2a, b).

During the flowering period of *E. edulis* in 2013 (September and December), a total of 22 palms were selected to evaluate the pollination system and sexual reproductive dependence on animal pollination. We conducted

four pollination treatments in each palm. Three rachillae of the same inflorescence were assigned to each treatment and female flowers within each pollination treatment were counted. Pollination treatments were: (a) Open-pollination: rachillae were marked with a flagging tag and left exposed to pollinators; (b) Apomixis: male flowers of the rachillae were removed previous to bagging the female buds with voile to prevent the entry of pollen (Fig. 2c); (c) Wind pollination: rachillae were bagged with mosquitoes net bags to prevent the access of pollinators but allowing the movement of pollen by wind (Fig. 2c); (d) Pollination by small bees: inflorescences were covered with a coarse mesh stuff that allows the entry of small bees of the genus *Tetragonisca*, *Plebeia* (3–5 mm Meliponini) and Halictidae, but prevents the entry of larger bees such as *Apis mellifera*, bumblebees (10–12 mm), and some Euglossini among others (Fig. 2c). It is important to highlight that seed production by apomixis can potentially occur in all pollination treatments. As *E. edulis* is uniovulated, seed production (seed set) was determined as the proportion of female flowers that develop into mature seeds (# of mature seeds/# of female flowers). We estimated the potential contribution of asexual seed production to total seed production as: (seed set by apomixis/seed set by open pollination) × 100. Moreover, we estimated the potential contribution of wind pollination to seed production as: (seed set by wind / seed set by open pollination) × 100, and the potential contribution of pollinators as: 1 – (seed set by wind / seed set by open pollination) × 100 (Klein et al. 2007). We also estimated the potential contribution of apomixis to seed production in the absence of pollinators as: (seed set by apomixis/seed set by wind pollination) × 100. Finally, we assessed the potential contribution of small bees to seed production as: (seed set by small bees/seed set by open pollination) × 100. In all cases we refer to *potential* contribution to seed production because under natural conditions the relative contribution of each agent can vary depending on environmental and ecological factors (Roldán and Ashworth 2018). For example, if both wind and animal pollination are abundant, seed production by apomixis may be negligible.

Floral visitors and pollinators

To determine the identity, abundance and role of floral visitors, we conducted direct observations with video recordings and also captured floral visitors with hand nets for taxonomical identifications (Fig. 2b, d). With the use of video cameras (Sony full HD) we recorded floral visitations on one inflorescence per palm in 31 extra palms that were not used for pollination treatments: 17 palms in female phase and 14 in male phase. In total we recorded 34.17 h of video (morning: 11.29 h; midday: 11.52 h, and afternoon: 11.36 h). The handycam was left filming between 1 and 1.3 h per palm across 12 consecutive days. To fix and place the rachillae at



Fig. 2 Field work and pictures of filming output: **a** L.A. conducting pollination treatments, **b** F.Z. collecting insects in inflorescences, **c** rachillae bagged with mosquitoes net bags, for wind pollination treatment (1), rachillae bagged with a voile stuff for apomixis treatment (2) and inflorescences bagged with a coarse mesh stuff that allows the entry of small bees but exclude larger ones (3), **d** aluminum frame fixed to the camera, **e** pictures taken from filming's output showing stingless bees (circles), one wasp of genus *Polibya* spp. (left arrow) and one halictid bee (right arrow). *Plebeia droryana* (upper circle) sucking sugar exudates on the stigmatic lobes on the apex of the female flowers, and *Tetragonisca fiebrigi* standing on the light-blue

cardboard background (left circle) and the same specie landing on a female flower (right circle), **f** Dipterans (circles), and an halictid bee (arrow). *Lucilia* spp (Diptera, Calliphoridae) is shown in the upper-left circle, and Muscini fly (Diptera, Muscidae) in the upper-right circle. A Syrphidae spp. is observed in the middle circle, and one Sarcophagidae fly is observed in the lower circle. The halictid bee (black arrow) sucking nectar from nectaries of the female flowers. **g** One Sarcophagidae fly (upper circle) and one halictid bee (arrow), both "hugging" the flower from the apex to take nectar from female flowers. Credits: Fernando Zamudio

the same distance to focus the camera we used an aluminum frame (20×20 cm) joined at the base with the camera placed at a fixed distance of 30 cm from the frame (Fig. 2d). This system allowed us to keep focus of the 10–15 rachillae held to the frame, thus having a great level of detail of each

insect visiting the flowers. To increase the contrast, we used a light-blue board as a background of the frame. The videos were analyzed and the following information was obtained: number of individuals per species visiting each floral morph, the time spent by each insect species in the rachillae and,

type of behavior (e.g., collection of pollen or nectar, type of movement and mating, among others, Fig. 2e–g). The activity, behavior and feeding guilds of floral visitors were classified using the categories proposed by Listabarth et al. (2001).

All captured insects were kept in 70% alcohol and then mounted for their taxonomic identification. Collected insects were deposited at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) and at the entomological collection of the Museo de La Plata, Argentina (MLP). The simultaneous combined sampling of filming and capturing insects on the same inflorescences allowed us to have detailed identifications of floral visitor species: those unique to each floral morph and those shared between floral morphs. A floral visitor species contacting fertile whorls of both floral morphs in a similar frequency was considered an effective pollinator. A floral visitor species without contacting floral fertile whorls or visiting mostly one floral morph was considered an *actual* floral visitor. We show insect-floral interactions as the percentage of relative abundance of each insect species by floral morph during 34.17 h, i.e. (# individuals sp. one visiting male (or female) flowers/# total individuals sp. one visiting both floral morphs) \times 100.

Seed quality

We measured seed quality by assessing the seed germination percentage. In March 2014 we collected mature seeds from the 12 palms where we had conducted pollination treatments. Seeds were conserved in paper bags at room temperature until germination assays were made in April 2014. Seeds were sown in plastic trays (15 \times 20 cm) with homogeneous sterilized vermiculite substrate in greenhouse with natural light. Between one and two trays per mother plant with 3–5 seeds each were used per pollination treatment. A total of 580 seeds from all pollination treatments were watered every 3–5 days and germination was controlled every 10–15 days. Seeds were considered germinated when radicle was 2 mm long (Oliveira et al. 2003). We computed the proportion of germinated seeds for each pollination treatment after 110 days.

Synthesizing sexual reproduction in *E. edulis*

To summarize and integrate the accumulated knowledge generated up to now about the reproductive biology of *E. edulis*, we conducted an extensive literature search using the following keyword combination: “*Euterpe edulis*” AND (pollinat* OR seed* OR fruit*). We searched through multidisciplinary online databases (ISI Web of Knowledge,

SCOPUS, and Google Scholar) comprising the period between 1900 and 2020.

Data analysis

We analyzed the effect of pollination treatment on seed set and proportion of seed germination using generalized linear mixed models with binomial distribution of errors (*glmer* function from the lme4 package, Bates et al. 2015). Pollination treatment was the fixed factor with four levels (open, apomixis, wind and small bees) and palm was the random factor. The significance of the fixed factor was assessed by likelihood ratio test (L ratio), comparing two models, one with the fixed effect and the other without it (null model). When significant effects were found we used multi comparisons of means (*glht* function from the multcomp package, Hothorn et al. 2008). To evaluate the assumption of homogeneity of variances we estimated overdispersion by calculating the parameter of scale, $\hat{c} = \Sigma(\text{Pearson residuals}^2) / \text{degrees of freedom}$. Overdispersion ($\hat{c} > 3$) was not observed in the explanatory models of the two response variables. All analyses were performed in R environment (Team 2017, version 3.4.0). We use igraph package (Csardi and Nepuz 2016) in R environment for elaborate Fig. 3.

Results

Seed set and germination

All four pollination treatments yielded seeds in low proportions, ranging from 2.7 to 10%. The apomixis treatment was the only one showing significantly lower seed set than the rest of the treatments ($Z \geq 3.67$; $P \leq 0.001$, Fig. 3a). No differences were observed in seed set among open, small bees and wind pollination treatments (Fig. 3a). The highest seed set was observed in the open-pollination treatment, followed by wind and small bees’ treatments (Fig. 3a; for mean values see Table 1). From wind to open pollination there was an increase of 26% in seed set, which is attributed to insect pollination. From the total seed set obtained by open pollination (10%), 27% corresponded to apomixis, which imply that most (73%) of that 10% of open-pollinated seeds was set by sexual reproduction (animal and wind pollination). The contribution of wind to open-pollinated seed set was 74%. Moreover, in the absence of pollinators, the contribution of wind to successful set seeds was much more important (64%) than apomixis (36%). Finally, small bees and wind were equally successful in setting seeds (Table 1). Although no systematic observations were made on the ability of small bees to cross the mesh used in this treatment, *Tetragonisca fiebrigi* (Schwarz) individuals

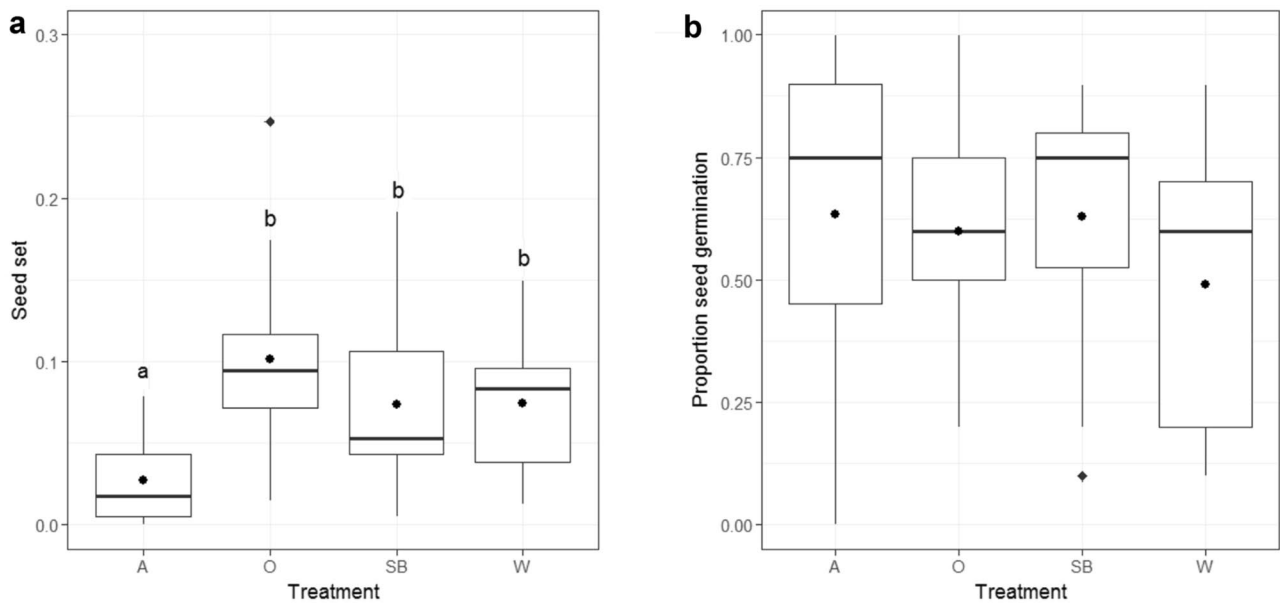


Fig. 3 **a** Seed set (number of mature seeds / number of female flowers) and **b** proportion of seed germination by each pollination treatment in *Euterpe edulis*: A Apomixis, O open-pollination, SB small bees, W wind pollination. The bottom of each box is the 25th percentile and the top is the 75th percentile, horizontal lines inside the

boxes correspond to the median and points to the mean. The vertical lines outwards from boxes represent 95% confidence interval of the median. Different letters above the boxes show significant differences among treatments after post hoc contrasts. Diamonds are outliers

Table 1 Seed set (%) under different pollination treatments in studies carried out through the north–south (left to right columns, respectively) distribution of the palm *Euterpe edulis*: open pollination, manual self and cross pollination, Apomixis in absence of pollen, and wind pollination

Pollination treatments	Wendt et al. (2011)	Reis et al. (1993) Mean ± SD	This work mean ± SD	Dorneles et al. 2013 *	Overall mean ± SD	CV (%)
# Palms (N)	5–6	3–4	22	5		
Open pollination	8.5	70.2 ± 16.13	10 ± 5.1	48	34.17 ± 30.18	88.31
Self-pollination	10.1	–	–	45	27.55 ± 24.67	89.56
Cross-pollination	13.1	47.8 ± 13.90	–	80	46.96 ± 47.30	100.7
Apomixis	0	3.7 ± 4.29	2.7 ± 2.0	0	1.6 ± 1.89	118.2
Wind pollination	–	28 ± 17.13	7.4 ± 4.3	Indirectly**	17.7 ± 14.56	82.3
Wind contribution***	–	40	74			
Small bees	–	–	7.4 ± 5.0	–		

CV coefficient of variation per pollination treatment through the studies (standard deviation/mean) × 100

*In that studies were introduced managed colonies of stingless bees (85 colonies of nine species)

**Wind pollination was evaluated through the arrangement of eight slides with liquid glycerin at 1 m from the palm

***Contribution of wind pollination to total seed set was estimated as: (seed set by wind pollination/seed set by open pollination) × 100

(Apidae: Meliponini) were seen several times within them, suggesting that the mesh used was not an obstacle to small bees. After 25 and 33 days of sowing the seeds, 1.9% and 11.9% of them germinated, respectively. The germination peak was recorded for all treatments 50 days (42.2%) after the seeds were sown. Mean (± SD) seed germination percentage varied from 49 ± 30, 60 ± 25, 63 ± 28 and 63 ± 37, in seeds produced by wind, open, small bees,

and apomixis pollination treatments, respectively, and differences were not statistically significant among pollination treatments ($X^2 = 7.25, P = 0.07$; Fig. 3b).

Floral visitors and pollinators

A total of 3267 insect individuals belonging to seven orders, and 147 species and morphospecies were observed visiting the flowers of *E. edulis*. We identified 36 species and

they visited more frequently and in higher richness female flowers (Fig. 4).

We classified as pollinators only to those species represented by more than five individuals that visited and effectively contacted fertile whorls of male and female flowers in a similar frequency (between 40 and 60% each floral morph). The most prominent insect pollinators were the meliponines *Plebeia droryana*, *P. emerinaoides* (Silvestri), *Trigona spinipes*, and *Leurotrigona muelleri*. Specifically, *Plebeia droryana* was the most abundant species. Moreover, there were several taxa (morphospecies) that visited in similar frequency both floral morphs. However, because we were unable to determine whether the same species visited both floral morphs, they can only be considered *potential* pollinators. Such is the case of bees from the genus *Habralictus* spp., *Hylaeus* spp., (Hymenoptera), flies from the families, Tephritidae, Ulidiidae and tribu Muscini, and beetles of the genus *Chauliognathus* (Hentz) (Coleoptera) (Fig. 4, Table s1, supplementary file). Finally, although *Celetes* sp. (Coleoptera) and species of Formicidae have visited in similar frequency male and female flowers, they were not considered *potential* pollinators because they did not contact floral fertile organs (see section Activity and behavior). *Celetes* sp. is a small weevil that appeared in great abundance and it is likely it was subsampled because of the small size (≤ 1.5 mm).

Activity, behavior and feeding guilds of floral visitors

Most floral visitors were nectarivorous (Table s1, supplementary file). Nectar is contained in a septal nectary at the outer base of the female and male flowers. Usually, bees and vespids species visited several flowers in the same trip and spent only a few seconds in each one. These insects made contact with floral fertile organs in two ways; (a) with their mouthparts and some part of their head (clypeus and frons) when they suck sugar exudates on the stigmatic lobes, and, (b) with the ventral part of their body (thorax and abdomen) when they "hug" the female flower from the apex to take nectar. Also, some small bees and dipterans sometimes took nectar from female flowers without touching the stigma as they enter from the sides of the flower (Fig. s1 d, supplementary file). Such behavior was also observed in other insects like the small cucurlicionids of genus *Celetes* Schoenherr and ants. The time spent in each flower varied among species according to their foraging strategies (Fig. s2, supplementary file). The activity of floral visitors depended on the environmental temperature and capacity of defensiveness of the species. In very hot days (greater than 28 °C) the activity was high and negative interactions between insects were observed. Meliponini bees, wasps and even some Diptera (e.g. Tephritidae) frightened other insects with flush flights and even making contact. Halictid species had a different

behavior; they stayed more than two minutes within the filming frame (Fig. s2, supplementary file), walking around the rachillae and spending long time at the same flower. On the other hand, Coleoptera and Tephritidae (Diptera) species spent a long time traversing the rachillae searching resources. Species of *Chauliognathus* Hentz mainly fed on pollen but they also took nectar and made contact with the stigmatic lobes with their abdomen when "hugging" the flowers. In contrast, very small Curculionids (nearly three times smaller than flowers) apparently consumed tissues or other resources on the surface of the rachillae and flowers and generally did not make contact with the fertile parts of the female flowers. Species of *Chauliognathus* and *Celetes* (Coleoptera) also used the flowers as mating site (Table s1, supplementary file).

Synthesizing the reproductive biology of *E. edulis* across studies

The literature search yielded 42 studies that were subsequently examined for information and data on the reproductive biology of *E. edulis*. The vast majority of these studies evaluated different aspects of the species (genetic diversity, seed dispersal, seed predation, recruitment, etc.) and only three of them provided comparable pollination treatments to determine the relative contribution of different pollination vectors to successful seed set (Reis et al. 1993; Wendt et al. 2011; Dorneles et al. 2013). All of the previous studies were conducted in different parts of Brazil and showed a good geographic representation of *E. edulis* populations across its distribution.

Reis et al. (1993), was the first work on the reproductive ecology of *E. edulis*, conducted in a group of plants located on the edge of a fragment of river forest in São Paulo State. They used observation towers and stairs to access the flowers and made non-systematic observations, recording the frequency of visits and the behavior of the floral visitors of three palm individuals. Wendt et al. (2011) conducted the study in the Augusto Ruschi Reservation, a 4000 ha of continuous primary forest in Espírito Santo State. They used five to six individuals of each palm morph for the reproductive experiments and insect flower visits were observed directly or with binoculars. Scaffolds were used to allow visual proximity to the inflorescences. The most recent work was carried out in a 9 ha area of secondary forest mixed with an agroforestry system (1 ha) in Florianópolis city, in the state of Santa Catarina (Dorneles et al. 2013). In this work, the data on flower visitors were mostly focused on social insects (Dorneles et al. 2013). They worked with five palm individuals and used ladders and scaffolding between tall palm trees to make observations (Table 1).

We observed a large variability in seed set among studies for all pollination treatments (Table 1). Studies in Table 1

were ordered following a north–south gradient of distribution of *E. edulis*. Studies carried out by Wendt et al. (2011) and Dorneles et al. (2013) correspond to the northern and southern distribution extremes, respectively. Apomixis and wind pollination treatments showed the most and less variable seed set through the studies, respectively (see CVs values in Table 1). Notably, seed production by apomixis occurred only at the most central sites along the distribution, and mean values were rather similar. Seed production by wind pollination was more than three times higher in Reis et al. (1993) than in this study. Seed production by open pollination showed a great variability but no geographical pattern was observed. Results from Reis et al. (1993) show wind pollination provided 40% of total seed production (Table 1). Finally, differences in seed set after manual self and cross pollination were also variable between studies. In Wendt et al. (2011) seed set by manual self and cross-pollination were more similar than in Dorneles et al. (2013), which would indicate variation in the compatibility system of this palm among populations, changing from self-compatible to partially self-compatible, respectively.

Discussion

The detailed assessment of the reproductive ecology of highly used and ecologically important plant species represents a fundamental endeavor in conservation biology research. The generation of seeds by sexual reproduction represents an essential event for the long-term sustainability of plant populations. Seeds represent the most important independent diploid dispersal phase of plants, and when sexually produced, they provide an opportunity to increase genetic diversity and thus the potential to adapt to new environments (Wilcock and Neiland 2002). Here, we evaluate with great detailing and for the first time the reproductive ecology of *E. edulis* palm in Argentina. Our findings show that *E. edulis* has an ambophilic pollination system, implying that it may produce seeds by both wind and insect pollination. Such pollination system is relatively common among monoecious palms (e.g., Listabarth 1992; Culley et al. 2002; Rios et al. 2014).

In our study system, however, we found a prevalence of wind pollination, which produced 74% of the overall total seed set (from the net 10% of open pollination). Male flowers of *E. edulis* display a large quantity of very small and light pollen, which is easily transported by the wind especially on sunny days when the anthers dry quickly and the pollen is released (Mantovani and Morellato 2000; Dorneles et al. 2013). In line with this, we observed very similar values of seed set in both small bees and wind pollination treatments, suggesting that pollination by small bees may be irrelevant. While we did observe small bees visiting flowers

in the pollination treatment used to exclude large bees, we cannot exclude a sampling artifact if the mesh used in this treatment hindered floral visitation by small bees. If this is the case, we may be underestimating the functional role of these small insects. Interestingly, insects may also indirectly contribute to wind pollination. When visiting inflorescences, insects can create pollen clouds which are subsequently airborne and mobilized by the wind (Schulze-Albuquerque et al. 2020). Thus, what is the relative importance of animal pollination in the sexual reproduction of *E. edulis* at the southernmost west limit of its distribution in Argentina? While we did estimate the *potential* seed set by different pollination vectors, there are several external factors and changing conditions that may modify these estimations (Roldán and Ashworth 2018). In particular, if climatic and landscape conditions (spatial fragmentation and isolation) are unfavorable for pollen movement by wind, pollinators may become particularly important.

Low wind speed and high relative humidity and precipitations may difficult pollen release and transportation by the wind (Culley et al. 2002). Some of these climatic conditions are common during the flowering period of *E. edulis* in the Atlantic forest of Misiones (September–January). In September, at the beginning of its flowering, mean rainfall is intermediate with 160 mm, but it increases to 240 mm in October, which is usually the rainiest month in the region. From November to January, precipitations remain stable with near 180 mm (Gatti et al. 2008). Under such environmental conditions, pollination by insects may be the only way to achieve sexual reproduction in this palm. Moreover, the characteristics of *E. edulis* populations and the surrounding forest where *E. edulis* grow may also have implications for the relative importance of wind versus insect pollination within and between populations. Most *E. edulis* palms have an intermediate canopy position within the forest, thus wind pollen transfer may be mainly favored in dense populations with available conspecifics nearby within the same stratum. However, under such conditions, pollen transportation by wind to other more distant or isolated palm populations would be more difficult. In that case, longer pollen dispersal distances may be conducted by insect pollinators, particularly from some bee species that are able to fly moderate distances throughout the forest roof (see Santos et al. 2018). In contrast, long-distance pollen dispersal by wind might only be achieved by taller palms that grow over the forest canopy or by palms growing in forest gaps. Any of these latter possibilities can have an important role in boosting wind-pollen dispersal at long distances and increasing male reproductive success, as observed in other wind-pollinated species (Friedman and Barrett 2009). Unisexual flowers and male-biased sex allocation commonly occur in wind-pollinated species, which is particularly associated to increased plant size. Larger plants are more effective at dispersing pollen to

their neighbors, while smaller plants may perform better at capturing pollen and thereby increasing female reproductive success (Friedman and Barrett 2009). In short, the contribution of wind versus insect pollination to seed production in *E. edulis* may vary in time, space, and between different sized palms and be closely linked to both, climatic and environmental conditions.

In monoecious species, pollinators must contact fertile organs of both floral sexual morphs to accomplish effective pollination. Thus, floral visitors that either visit only one floral morph or that visit both floral morphs but are unable to contact the fertile whorls, cannot achieve pollination. Here, we observed a large number of floral visitor species that were not pollinators but still assiduously visited the flowers (e.g., some meliponine species such as *Oxytrigona tataira* and weevils like *Celetes* sp.). This high diversity of non-pollinator species visiting *E. edulis* is sustained by the abundant floral resources mostly offered by the female flowers. The higher insect diversity visiting female flowers may be related to the more concentrated nectar, which is also secreted for a longer period of time during the day compared to male flowers (Dorneles et al. 2013). Based in our observations, small bees of the tribe Meliponini, like *Plebeia droryana*, *P. emerinoidea*, *Trigona spinipes*, and *Leurotrigona muelleri* are the most important insect pollinators, since they contacted fertile floral organs, were abundant, and visited rather equitably male and female flowers of *E. edulis*. Thus, these stingless bee species may be responsible for the increase in seed set observed from the wind to the open pollination treatments. Bees from the Meliponini tribe have been described as the most frequent floral visitors in previous studies. However, their role as pollinators was not clear since visitation frequency per species to both floral morphs was never quantified (Reis et al. 1993; Mantovani and Morelato 2000; Wendt et al. 2011; Santos et al. 2018; but see Dorneles et al. 2013 only by Apini social bees).

Euterpe edulis may produce seeds asexually by apomixis (Reis et al. 1993, this study), which represent a reproductive assurance mechanism in the absence of pollen and/or pollination vectors. Nevertheless, the potential seed set obtained by apomixis does not imply that it actually occurs, as it is usually a facultative reproductive strategy (Koltunow and Grossniklaus 2003). Apomictic seed production may be more frequent in isolated individual palms or under heavy rainy conditions that preclude wind pollination and severely restrict insect activity. In line with these arguments, recent genetic studies on the species support the idea of low apomixis levels. The high levels of genetic diversity (measured as expected heterocigosity; $H_e = 0.57-0.86$) and low levels of inbreeding coefficients ($F_{IS} = 0.00-0.30$) observed in adults and progeny of *E. edulis* across 57 different sites (Carvalho et al. 2017), suggest that clonality and inbreed matings, either through

apomixis, self-pollination or even mating among close relatives are infrequent. Interestingly, the germination capability of seeds was comparable regardless of how seeds are being produced (sexual, asexual, biotic, or abiotically). Such results imply that the mating patterns (i.e., the relative amount of exogamous versus endogamous crosses) are also comparable between wind and insect pollination. Moreover, when apomixis occurs, the progeny reflects the fitness of the maternal plant, which appears to be overall genetically diverse (Carvalho et al. 2017).

Our and previous studies are conclusive in showing that *E. edulis* is a generalist species that attracts a large number and diversity of floral visitors from Hymenoptera, Diptera, and Coleoptera orders mainly (Reis et al. 1993; Mantovani and Morelato 2000; Wendt et al. 2011; Dorneles et al. 2013). Here we also observed some species of Lepidoptera, Hemiptera and Orthoptera. Probably due to the higher sampling effort made in this study, we observed the highest diversity, with 148 taxa, compared to 8–18 species observed in previous studies (Reis et al. 1993; Wendt et al. 2011; Dorneles et al. 2013; Santos et al. 2018). Our results suggest that this palm represent an important food resource for insect populations but insects are not necessarily essential for the sexual reproduction of the palms. Each palm produces hundreds of thousand flowers across 5 months, offering an abundant and lengthy source of pollen and nectar. Moreover, the flowering onset of *E. edulis* in the early spring would constitute one of the first massive blooms in the forest representing the main staple food source (see Placci et al. 1994) for most wild and managed colonies of stingless bees after the winter scarcity period in the surroundings of the *palmitales*. Not only for meliponines, their flowers are key resources for more than a hundred insect species, many of which are important pollinators of many other wild and cultivated plant species (Singer and Cocucci 1999; Li et al. 2008). Similarly, wasps and flies visiting *E. edulis* may be also important natural enemies of several pests in cultivars and orchards (Santana Junior et al. 2012; Glinos et al. 2019). These facts highlight the relevant ecological role of *E. edulis* by sustaining not only a high diversity of vertebrates that eat their fruits (Terborgh 1986; Castro et al. 2007; Reis and Kageyama 2000; Zago da Silva and dos Reis 2018), but also a broad assemblage of invertebrates that feed from their floral rewards, providing important ecosystem services such as pollination, pest control and honey production, among others (Zamudio et al. 2010; Ingram et al. 2012; Zamudio and Alvarez 2016).

When integrating results from previous studies, we observed that seed set values were highly variable for each pollination treatment across studies. The contribution of wind pollination to seed set was significantly higher in this study compared to the study of Reis et al. (1993) conducted in Brazil. These contrasting results may indicate

a wide spatial variability in the relative contribution of wind versus animal pollination agents. Notably, although ambophilous species seem to be more common than previously thought (Cox and Grubb 1991; Culley et al. 2002), only a few attempts have been devoted to assess the spatial and temporal variability of the contribution of each pollination vector to progeny production (but see Galindo da Costa et al. 2018).

Variability in seed production by open pollination treatments may be a consequence of the low sampling effort accomplished in previous studies (3–5 palms per study), implying low statistical power to obtain robust estimates of mean values per study site. Moreover, variability in open seed set through the studies may reflect variations in the climatic conditions of the studied season (wind speed, relative humidity) and/or particular environmental conditions as conspecific density (see Santos et al. 2018). These factors may affect the availability of pollen, pollinators and the efficiency of wind as pollen vector. To disentangle the effect of these factors on seed set, future studies should measure pollen limitation through climatically different seasons, and pollen limitation under different conspecific densities. It is an interesting challenge, since pollen limitation in ambophilic species should not only consider limitation by pollen and pollinators, but also by wind. Seed set by asexual mode was low and similar in the two study sites where it occurred (Reis et al. 1993 and this study). Even though apomixis was registered only in two sites within the distribution of this palm, the low quantity of palms sampled in the other two sites where it was tested but not detected, does not allow to discard its occurrence. Indeed, from the twenty-two palms sampled in this study, two of them did not produce any apomictic seeds.

Our findings shed light on the reproductive system of *E. edulis* and underline its key ecological role as a main resource for a large diversity of nectarivorous and pollenivorous insects from the Atlantic Forest. Likewise, the comparison with other studies allowed us to elucidate a generalist and resilient pollination system that enable this palm to produce highly fit progeny under a wide diversity of environmental and ecological conditions.

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Author contributions Idea: FZ, LA, GG and NH worked together on the idea. Experimental design: FZ, LA mainly; GG and NH made general contributions. Execution: FZ was in charge of logistics and field work. FZ, LJA and LA performed the first insect sampling and the application of pollination treatments. GG and NH performed the fruit harvest and the seed germination experiment. Data analysis: FZ and LA performed all analysis. Taxonomic identification of insects: LJA identified all taxa with the exception of Diptera that were identified by PM. Preparation of the writing: FZ, LA and RA wrote the work. Review of the writing: All authors. The language correction was in charge of RA.

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Declarations

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

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