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DIFFERENTIAL PHENOLOGICAL SHIFTS IN *Euterpe edulis* Mart. DURING AN EXTREMELY DRY YEAR ALONG AN ALTITUDINAL GRADIENT

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Abstract. Temporal variation in rainfall and temperature, which is likely to increase in frequency due to climate change, may cause changes not only in the endogenous rhythms of organisms, but also in their phenology. This is of great concern, because ecological mismatches caused by phenological shifts may affect not only individuals but entire communities, via disruption and cascade effects in diverse ecological processes. Here, we tested the sensitivity of the phenology of *Euterpe edulis* Mart. to a period of extreme drought, using phenological data for three populations occurring from 0 to 1,200 m a.s.l.. *Euterpe edulis* is a Neotropical palm that is ecologically important because of its abundance and diverse frugivorous interactions. Three phenophases (flowers, unripe fruit, and ripe fruit) were recorded monthly from June 2014 to May 2017. Additionally, seeds were collected in 2014 and 2015 to assess wet and dry mass variation. The intensity of the drought varied with altitude. The main differences between populations were earlier flowering, a longer fruit maturation period, and larger seeds at higher altitudes. In the year of the severe drought, there were marked decreases in the synchrony of flowering and unripe fruits in the high-altitude populations. All populations exhibited decreases in seed water content, but only the high-altitude populations had decreases in seed dry mass, probably due to the drought. Despite differences in the total annual rainfall, there was relatively similar exposure to the intense drought across the altitudinal range. Populations did however differ in their sensitivity to drought, and the high-altitude populations were not able to maintain synchrony in the flowering and unripe fruit phases. Extreme events in which both climatic and biotic responses were observed were thus related to distinct population thresholds to rainfall shifts in an endangered tropical keystone palm species.

Key words: Arecaceae; Atlantic rainforest; drought; long-term ecological research; phenology; southeastern Brazil.

INTRODUCTION

Plant phenology is related to climatic seasonality and is a major determinant of species ranges (Chuine & Beaubien 2001) and ecosystem productivity in different vegetation types (Chuine *et al.* 2000). Additionally, flowering and fruiting phenology may strongly affect the success of plant populations in a given locality via their reproductive success. In particular, the probability of seed germination and seedling establishment require favorable climatic conditions, which may not exist in all seasons (Primack 1987). Seasonal and interannual variation in rainfall are known to influence phenological events as well as other ecological processes, probably with more pronounced effects in drier areas (Schwartz *et al.* 2019) and lowlands, due to biotic attrition (Colwell *et al.* 2008). In tropical systems, phenological events are often more related to rainfall seasonality than to temperature and photoperiod (Cleland *et al.* 2007, Sakai & Kitajima 2019). Despite this, the relationship between environmental cues and phenological patterns in the tropics is not as straightforward as in temperate communities. This is reflected in the greater diversity of phenological patterns that is characteristic of tropical ecosystems (Sakai 2001, Morellato *et al.* 2016) due to the interaction of temperature, precipitation, and irradiance (van Schaik *et al.* 1993).

Monitoring phenology is perhaps the simplest way of tracking species' responses to climate change (Walther *et al.* 2002, Nicotra *et al.* 2010). Recently, climatic changes have been associated with phenological shifts that may have resulted in decreases in local abundance or even a higher probability of extinction of sensitive species (Llorens & Peñuelas 2005, Cleland *et al.* 2006, Allen *et al.* 2010, Foden *et al.* 2019). However, there is still a relative scarcity of research linking phenology and climate change in the tropics, since the majority of studies have been performed in temperate ecosystems (Walther *et al.* 2002). Intensifying weather extremes seem to be the most straightforward of climate change effects to observe (Jentsch *et al.* 2007). In any case, it is important to note that extreme events must be understood based on the intensity and rarity of climatic events that have a clear association with a well-defined ecological response (Smith 2011). Increasing annual climatic variation and extreme events could affect the onset of a phenological phase or even suspend it entirely (de Steven *et al.* 1987). On Barro Colorado Island, an extremely high annual rainfall caused some palm species to initiate flowering earlier than in other years. However, during the El Niño dry phase, flowering was severely depressed in one palm species and suspended in others (de Steven *et al.* 1987). Differential shifts in flowering phenology among species as a consequence of climate change may well affect community composition and ecosystem functioning, because they can introduce asynchronies into plant–plant relationships and disrupt relationships between plants and animals (Harrison 2000, Llorens & Peñuelas 2005, Forrest 2016, Morellato *et al.* 2016).

Palms are an important food resource for a wide assemblage of vertebrate frugivores (Galetti & Aleixo 1998), and in particular have been regarded as a "keystone resource" for frugivores in tropical forests (Terborg 1986). Studies of palm phenology are not very common in the literature (de Steven *et al.* 1987, Bruno *et al.* 2019). However, palms have been reported to produce more than 80 % of the total fruit-fall biomass on an Atlantic rainforest island, with only two species contributing more than 50 % of overall fruit biomass production (Genini *et al.* 2009). One of these is the endangered species juçara, *Euterpe edulis* Mart. (Arecales, Arecaceae) (Martinelli & Moraes 2013). Hence, phenological mismatches involving palms and their faunal pollinators flower and fruit consumers could have important effects across various trophic levels. *E. edulis* is a good model for understanding plant responses to future climatic changes, since it occurs in large parts of the Atlantic rainforest and Cerrado areas (Brazilian savanna-like vegetation) in different vegetation types, such as restingas and ombrophilous, semideciduous, and gallery forests, spanning a relatively large altitudinal variation for a tropical plant (Lorenzi *et al.* 2010). Altitude, indeed, seems to be an important factor affecting phenological patterns in *E. edulis* (Favreto 2010). Additionally, higher seed mass is generally, but not always, observed with increased elevation and moister habitats (Primack 1987, Qi *et al.* 2015, Sarukay & Takahashi 2017, Olejniczak *et al.* 2018). One study has considered the adaptive value of this larger seed size at higher elevations (Sarukay & Takahashi 2017). In addition, Primack (1987) proposed that the durations of fruit ripening and flowering should be associated with fruit size. Species with larger seeds will tend to require longer for fruit ripening and will thus flower earlier, as already observed in relation to altitudinal variation (Sarukay & Takahashi 2017).

Using phenological and seed mass data from three populations of *E. edulis*, occurring from 0–1,200 m a.s.l. in Atlantic rainforest, we aimed to test the following hypotheses: (1) low-altitude populations will show higher seasonality and synchrony of phenological phases due to a more marked dry season during the winter; (2) higher-altitude populations will show greater seed mass and earlier flowering than lowland areas; and (3) phenological events and seed mass in low-altitude populations will be more strongly affected by an extremely dry year than those in higher-altitude populations.

MATERIAL AND METHODS

Study species

Euterpe edulis Mart. (i.e., *"palmito Juçara"*) is a monoecious, single-stem, shade-tolerant, slow-growing subcanopy palm (Lorenzi *et al.* 2010). It can reach 20 m in height and 10–15 cm in diameter. It occurs primarily in forests along the Atlantic coast of Brazil, athough it can be found as far inland as Argentina and Paraguay (Henderson et al. 1995), growing on the crests or slopes of hills and flooded sites at up to 1,000 m elevation (Henderson *et al.* 1995). It produces large quantities of fruit (> 500 fruits per stipe) and forms high-density populations (100–500 individuals/ha) in well-preserved areas (Galetti & Aleixo 1998). In non-defaunated areas, 25 bird species and 15 mammal species have been recorded feeding on *E. edulis* fruits (Galetti & Aleixo 1998). This species is harvested for palm hearts for human consumption; these constitute one of the most abundant and valuable non-timber forest products in the Atlantic Forest (Fantini & Guris 2007). Many of the surviving populations are small and fragmented (Galetti & Aleixo 1998, Silva-Matos *et al.* 1999, Portela *et al.* 2010). Because *E. edulis* has a single apical meristem, harvesting of the palm heart results in plant death. Over-exploitation of palm hearts and habitat fragmentation have led to the species' current classification as vulnerable to extinction (Martinelli & Moraes 2013).

Study area

The study was carried out in the dense ombrophilous forest of the Atlantic Forest Biome in the state of Rio de Janeiro, at three different altitudes. The study sites were PO (Poço das Antas Biological Reserve; 0–100 m a.s.l.) in Silva Jardim, with an average annual temperature of 25.7 °C and rainfall of 1,995 mm (Pessoa & Oliveira 2006); and two sites in Serra dos Órgãos National Park (PARNASO): PRI (Primavera trail; 900 m a.s.l.) and RF (Rancho Frio trail; 1,200 m a.s.l.), both of which are in Teresópolis and have an annual average temperature of 17.8 °C and rainfall of 2,821 mm (Sattler *et al.* 2007) (Figure 1).

Reproductive phenology

In June 2014, 30 mature *E. edulis* individuals (with reproductive scars or old inflorescences/infructescences) were marked with aluminum tags at each study site (giving a total of 90) and monitored every month. Phenological observations were conducted monthly from June 2014 to May 2017, except in January and December 2015 and April, November, and December 2016 (PARNASO sites), and October and December 2016 and January 2017 (Poço das Antas site). The observations were made with binoculars, and the presence or absence of flowers, unripe fruits, and ripe fruits was recorded.

Seed mass

In early 2014, 30 mature plants were selected and tagged at each site, giving a total of 90 individuals. Thereafter, for the remainder of 2014 and 2015, all bunches containing ripe fruits were collected monthly, labelled according to source plant, and stored separately to avoid mixing of fruits. For each bunch, 100 fruits were randomly selected and subjected to removal of the pulp (or pericarp). Each seed was then numbered and weighed individually to determine its wet mass. The seeds were then stored in a kiln at 70 °C for 15 days, after which their dry mass was determined. The difference between the wet and dry masses was used to calculate the water content of each seed.

Environmental data

Monthly total precipitation and mean monthly temperature was obtained for all sites from the Instituto Nacional de Meteorologia (INMET), Brazil's national meteorological institute (http://www.inmet.gov.br/portal/). The data for the lowland site were obtained from Macaé weather station (22.37°S 41.81°W, 25 m a.s.l., World Meteorological Organization [WMO] station-86891) located 45 km from the Poço das Antas Biological Reserve. For the two montane sites, data from a weather station inside PARNASO were used (22.44°S 42.98°W, 991 m a.s.l., WMO-86888). Day-length data were obtained for all sites from The United States Naval

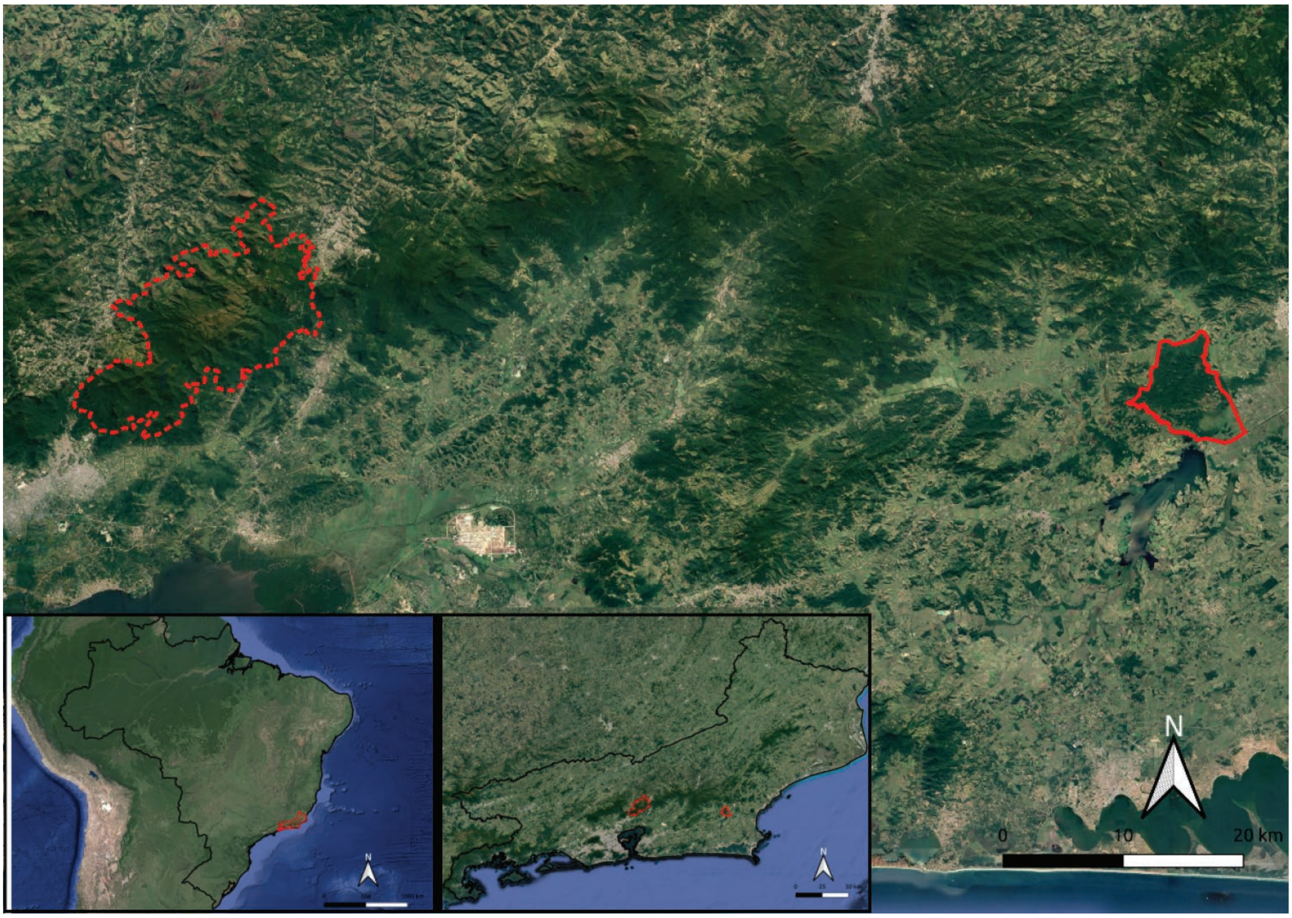

Figure 1. Map of the two conservation units where the study data were collected. Serra dos Órgãos National Park (where the 900 m a.s.l. and 1,200 m a.s.l. sites, PRI and RF, respectively, are located) is in the top left corner, delimited by a dashed red line, and Poço das Antas Biological Reserve (0–100 m, where the low-altitude site, PO, is located) is in the top right corner, delimited by a solid red line.

Observatory (USNO) website (https://www.usno.navy.mil/USNO).

Data analysis

The individual activity index was used to estimate the intraspecific synchrony of each population, indicating the proportion of the individuals sampled in each area that manifested a given phenological phase (Bencke & Morellato 2002). A phenological event was considered to be strongly synchronous when the percentage of individuals in that phase was > 60 %, weakly synchronous when it was 20–60 %, and asynchronous when it was < 20 % (Bencke & Morellato 2002).

Due to the intrinsic nature of phenological data, we used circular statistical methods. In this kind of analysis the year is regarded as a circle and the months are converted to angles, from 0° for January to 330° for December, at 30° intervals. The analyses were based on the phenological variables flowering, unripe fruit, and ripe fruit.

The Rayleigh *Z*-test was used to determine the significance of the mean angle (Zar 1996), hence testing for the presence of seasonality in a specific phenophase. The null hypothesis (H_0) states that the angles (or dates) are evenly distributed throughout the year, so there is no average direction, meaning no seasonality. If H_0 is rejected, the mean angle is significantly different between seasons and the pattern is seasonal. The intensity of concentration around the average angle, represented by *r*, can be considered a measure of the degree of seasonality. The vector *r* has no units and can range from 0 (when reproductive activity is evenly distributed throughout the year) to 1 (when reproductive activity is concentrated around a single date or time of year) (Morellato *et al.* 2000). The significant mean dates (indicating seasonal events) were compared among years and populations using the Watson–Williams *F*-test to determine whether the timing of two distinct phenological events differed significantly from each other.

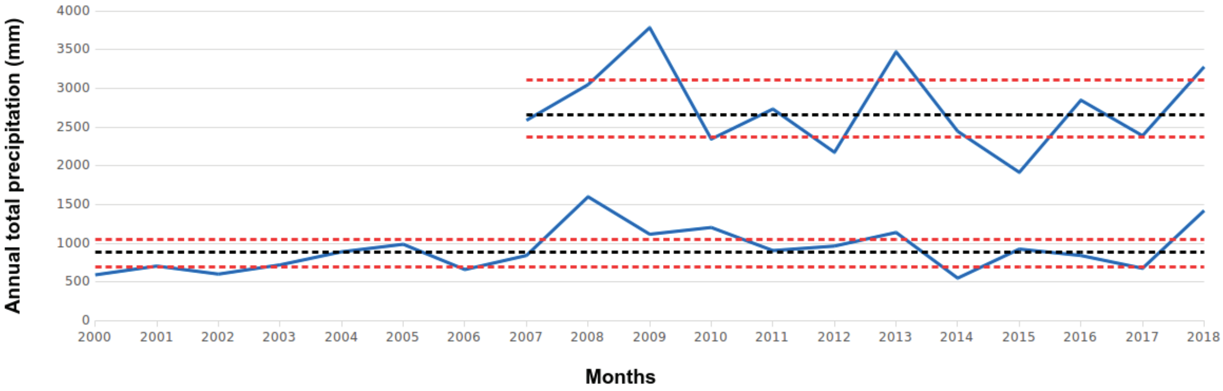

Figure 2. Historical precipitation series drawn from two weather stations. The solid blue line at the top is the series for Serra dos Orgaos National Park, for which the data were drawn from Teresopolis weather station (22.44°S 42.98°W, 991 m a.s.l., WMO-86888). The solid blue line at the bottom is the series for Poco das Antas Biological Reserve, for which the data were drawn from Macae weather station (22.37°S 41.81°W, 25 m a.s.l., WMO-86891). The black dashed lines represent the median rainfall in each series. The red dashed lines above and below the black dashed lines represent, respectively, the upper and lower quartiles of each series.

Spearman's correlation test was used to verify the relationships between the climatic factors considered (mean monthly temperature and monthly total precipitation) and phenophases during the study period. We tested whether variation in the timing of phenological events was related to immediate or delayed responses to local climatic conditions; that is, whether observed activity in a given month *t* was related to local climatic conditions during the same month or to those in earlier months *t*–1, *t*–2, *t*–3, *t*–4, or *t*–5. This relationship was tested for the entire three years of the study (June 2014 to May 2017) and for each year separately (from June to May for each interval).

Differences between 2014 and 2015 in seed dry mass and water content in each population were verified using notched box-plots. In this analytical method, notches are drawn in the sides of each plot. If there is an overlap between the notches from different plots, it is considered that there is no difference between their medians. If there is no overlapping of notches, it is considered highly likely that there is a difference between the plots (Chambers *et al.* 1983). All analyses were conducted in R v.2.15.1 (R Development Core Team 2012).

RESULTS

Rainfall variability

Overall, temporal variability in total monthly rainfall was similar between the lowland and montane forest sites, with a strong correspondence in the temporal distribution of monthly rainfall peaks over the study period. The lowland site, however, consistently had much less total monthly and annual rainfall than the montane sites (Figure 2). In 2014 it received 551 mm, which was dramatically lower than (62 % of) the 18-year historical record median of 891 mm. In the montane sites, however, the marked decrease in precipitation occurred in 2015, when they received an annual rainfall of 1917 mm, 72 % of the 12-year historical record median of 2662 mm. Ombrothermic charts for 2014–2017 show that both sites had a dry season (i.e., months when 2 × temperature > total rainfall). At the montane sites the dry season was one month long, occurring anytime between June and September, but at the lowland site it was 2–4 months long, occurring anytime between June and October.

Flowering

During the three years of the study, flowering was seasonal for all three populations (Table 1). At the lowland site, the mean flowering dates were in the middle of the wet season (November to February) and differed significantly from those of the montane sites, where flowering occurred earlier, at the end of the dry season (from June or August to September or October) (Table 2, Figure 3). Synchrony was clearly higher at the lowland site, with 70–80 % of individuals flowering together, whereas at the montane sites synchrony was weaker, with all values < 55 % (Figure 3). During 2015 there was a marked decrease in flowering

Table 1. Rayleigh test (Z, circular statistical analysis) for the occurrence of seasonality in *Euterpe edulis* phenology in the three study populations.

	2014-2015	2015-2016	2016-2017
Flower			
RF (1200m)	Z= 0.81; **p<0.001**	Z= 0.46; **p<0.05**	Z= 0.55; **p<0.001**
PRI (900m)	Z= 0.70; **p<0.001**	Z= 0.52; **p<0.001**	Z= 0.82; **p<0.001**
PO (0m)	Z= 0.67; **p<0.001**	Z= 0.54; **p<0.001**	Z= 0.65; **p<0.001**
Unripe Fruits			
RF (1200m)	Z= 0.06; p>0.05	Z= 0.27; **p<0.001**	Z= 0.13; **p<0.05**
PRI (900m)	Z= 0.06; p>0.05	Z= 0.11; p>0.05	Z= 0.15; **p<0.05**
PO (0m)	Z= 0.42; **p<0.001**	Z= 0.46; **p<0.001**	Z= 0.25; **p<0.01**
Ripe Fruits			
RF (1200m)	Z= 0.26; **p<0.05**	Z = 0.50; **p<0.001**	Z= 0.37; **p<0.001**
PRI (900m)	Z= 0.33; **p<0.01**	Z= 0.64; **p<0.001**	Z= 0.39; **p<0.001**
PO (0m)	Z= 0.76; **p<0.001**	Z= 0.55; **p<0.001**	Z= 0.37; **p<0.01**

Table 2. Watson–Williams test (F) for the comparisons of mean angles between the three study populations.

	2014-2015	2015-2016	2016-2017
Flower			
RF x PRI	F= 0.17; p>0.05	F= 0.07; p>0.1	F= 0.25; P<0.05
PO x PRI	F= 1.65; **p<0.001**	F= 1.35; **p< 0.001**	F= 1.85; **p<0.001**
RF x PO	F= 2.45; **p<0.001**	F= 0.86; **p<0.01**	F= 1.47; **p<0.001**
Unripe fruits			
RF x PRI	F= 0.11; p>0.1	F= 0.10; p>0.1	F= 0.08; p>0.1
PO x PRI	F= 0.57; **p<0.001**	F= 0.98; **p<0.001**	F= 0.49; **p<0.001**
RF x PO	F= 1.14; **p<0.001**	F= 1.44; **p<0.001**	F= 0.56; **p<0.001**
Ripe fruits			
RF x PRI	F= 0.27; **p<0.01**	F= 0.12; p>0.1	F= 0.09; p>0.1
PO x PRI	F= 0.42; **p<0.001**	F= 0.28; **p<0.01**	F= 0.18; **p<0.05**
RF x PO	F= 1.12; **p<0.001**	F= 0.30; **p<0.01**	F= 0.43; **p<0.001**

synchrony at the montane sites. The correlation analyses for each year individually and the entire study period showed that the flowering of all three populations was more frequently correlated with temperature than with rainfall (Tables 3 and 4). In contrast to the lowland population, for which there were positive correlations between flowering and temperature during the first two years of the study, the montane populations had consistently negative correlations with temperature (Table 3). Daylength was positively correlated with flowering in the lowland population in all three years, whereas in the montane populations, there was only a negative correlation in one year (2017) at PRI (900 m a.s.l.) (Table 3). For the entire study period, for both montane populations the lagged correlations between temperature and flowering were negative for t–0 up to t–2 months, for the lowland population they were positive (Table 4). The RF population (1,200 m a.s.l) also exhibited a negative correlation with temperature with a time lag of three months. There was thus an increase in the time lag and a reversal in the direction of the correlation, from negative to positive for the PRI population and positive to negative for the lowland population (Table 4). In general, flowering was negatively correlated with rainfall at the montane sites, except for a single positive correlation for t–5 for the PRI population, whereas flowering in the lowland population was consistently negatively

Table 3. Spearman correlation analysis of *Euterpe edulis* phenology and climatic variables during the study period for the three study populations.

	2014/2015	**2015/2016**	**2016/2017**
Temperature (°C)			
Flower			
RF (1200m)	$r_s = -0.59$; $\boldsymbol{p<0.05}$	$r_s = -0.65$; $\boldsymbol{p<0.05}$	$r_s = -0.68$; $\boldsymbol{p<0.05}$
PRI (900m)	$r_s = -0.75$; $\boldsymbol{p<0.05}$	$r_s = -0.61$; $\boldsymbol{p<0.05}$	$r_s = -0.83$; $\boldsymbol{p<0.001}$
PO (0m)	$r_s = 0.83$; $\boldsymbol{p<0.001}$	$r_s = 0.71$; $\boldsymbol{p<0.05}$	$r_s = 0.56$; $p>0.05$
Unripe Fruits			
RF (1200m)	$r_s = 0.50$; $p>0.05$	$r_s = -0.65$; $\boldsymbol{p<0.05}$	$r_s = -0.10$; $p>0.05$
PRI (900m)	$r_s = -0.05$; $p>0.05$	$r_s = -0.09$; $p>0.05$	$r_s = -0.02$; $p>0.05$
PO (0m)	$r_s = 0.12$; $p>0.05$	$r_s = 0.34$; $p>0.05$	$r_s = 0.80$; $\boldsymbol{p<0.05}$
Ripe Fruits			
RF (1200m)	$r_s = 0.54$; $p>0.05$	$r_s = -0.55$; $p>0.05$	$r_s = 0.66$; $\boldsymbol{p<0.05}$
PRI (900m)	$r_s = -0.57$; $\boldsymbol{p<0.05}$	$r_s = -0.69$; $\boldsymbol{p<0.05}$	$r_s = 0.44$; $p>0.05$
PO (0m)	$r_s = -0.77$; $\boldsymbol{p<0.05}$	$r_s = -0.40$; $p>0.05$	$r_s = -0.08$; $p>0.05$
Precipitation (mm)			
Flower			
RF (1200m)	$r_s = 0.03$; $p>0.05$	$r_s = -0.41$; $p>0.05$	$r_s = -0.64$; $\boldsymbol{p<0.05}$
PRI (900m)	$r_s = -0.22$; $p>0.05$	$r_s = -0.45$; $p>0.05$	$r_s = -0.69$; $\boldsymbol{p<0.05}$
PO (0m)	$r_s = -0.06$; $p>0.05$	$r_s = 0.28$; $p>0.05$	$r_s = 0.30$; $p>0.05$
Unripe Fruits			
RF (1200m)	$r_s = 0.32$; $p>0.05$	$r_s = -0.12$; $p>0.05$	$r_s = -0.26$; $p>0.05$
PRI (900m)	$r_s = 0.12$; $p>0.05$	$r_s = 0.06$; $p>0.05$	$r_s = -0.02$; $p>0.05$
PO (0m)	$r_s = 0.32$; $p>0.05$	$r_s = -0.49$; $p>0.05$	$r_s = 0.12$; $p>0.05$
Ripe Fruits			
RF (1200m)	$r_s = 0.66$; $\boldsymbol{p<0.05}$	$r_s = -0.03$; $p>0.05$	$r_s = 0.32$; $p>0.05$
PRI (900m)	$r_s = 0.08$; $p>0.05$	$r_s = -0.44$; $p>0.05$	$r_s = 0.30$; $p>0.05$
PO (0m)	$r_s = -0.14$; $p>0.05$	$r_s = -0.40$; $p>0.05$	$r_s = 0.07$; $p>0.05$
Daylength (hour)			
Flower			
RF (1200m)	$r_s = -0.20$; $p>0.05$	$r_s = -0.38$; $p>0.05$	$r_s = -0.48$; $p>0.05$
PRI (900m)	$r_s = -0.25$; $p>0.05$	$r_s = -0.50$; $p>0.05$	$r_s = -0.85$; $\boldsymbol{p<0.001}$
PO (0m)	$r_s = 0.85$; $\boldsymbol{p<0.001}$	$r_s = 0.85$; $\boldsymbol{p<0.001}$	$r_s = 0.88$; $\boldsymbol{p<0.001}$
Unripe Fruits			
RF (1200m)	$r_s = 0.76$; $\boldsymbol{p<0.05}$	$r_s = -0.40$; $p>0.05$	$r_s = 0.14$; $p>0.05$
PRI (900m)	$r_s = -0.11$; $p>0.05$	$r_s = -0.29$; $p>0.05$	$r_s = 0.30$; $p>0.05$
PO (0m)	$r_s = -0.40$; $p>0.05$	$r_s = -0.09$; $p>0.05$	$r_s = 0.80$; $\boldsymbol{p<0.001}$
Ripe Fruits			
RF (1200m)	$r_s = 0.69$; $\boldsymbol{p<0.05}$	$r_s = -0.39$; $p>0.05$	$r_s = 0.25$; $p>0.05$
PRI (900m)	$r_s = -0.30$; $p>0.05$	$r_s = -0.27$; $p>0.05$	$r_s = 0.12$; $p>0.05$
PO (0m)	$r_s = -0.41$; $p>0.05$	$r_s = -0.36$; $p>0.05$	$r_s = -0.28$; $p>0.05$

Table 4. Spearman correlation analysis of *Euterpe edulis* phenology and climatic variables across the entire study period (June 2014 to May 2017) for the three study populations. The variables *t*–0, *t*–1, *t*–2, *t*–3, *t*–4, and *t*–5 indicate the climatic variable for the same month, and one, two, three, four, and five months before the month of the phenological phase, respectively.

	t0	**t1**	**t2**	**t3**	**t4**	**t5**
			Temperature (°C)			
Flower						
RF (1200m)	rs = - 0.57; ***p<0.001***	rs = - 0.72; ***p<0.001***	rs = - 0.75; ***p<0.001***	rs = - 0.49; ***p<0.01***	rs = - 0.17; p>0.05	rs = - 0.17; p>0.05
PRI (900m)	rs = - 0.58; ***p<0.001***	rs = - 0.56; ***p<0.001***	rs = - 0.44; ***p<0.05***	rs = - 0.11; p>0.05	rs = 0.22; p>0.05	rs = 0.50; ***p<0.01***
PO (0m)	rs = 0.72; ***p<0.001***	rs = 0.62; ***p<0.001***	rs = 0.50; ***p<0.01***	rs = - 0.24; p>0.05	rs = - 0.58; ***p<0.001***	rs = - 0.79; ***´p<0.001***
Unripe Fruits						
RF (1200m)	rs = - 0.05; p>0.05	rs = - 0.30; p>0.05	rs = - 0.47; ***p<0.05***	rs = - 0.50; ***p<0.01***	rs = - 0.42; ***p<0.01***	rs = - 0.42; ***p<0.01***
PRI (900m)	rs = - 0.15; p>0.05	rs = - 0.22; p>0.05	rs = - 0.23; p>0.05	rs = - 0.18; p>0.05	rs = - 0.17; p>0.05	rs = - 0.10; p>0.05
PO (0m)	rs = 0.31; p>0.05	rs = 0.32; p>0.05	rs = 0.56; ***p<0.001***	rs = 0.74; ***p<0.001***	rs = 0.52; ***p<0.01***	rs = 0.13; p>0.05
Ripe Fruits						
RF (1200m)	rs = 0.11; p>0.05	rs = 0.08; p>0.05	rs = - 0.02; p>0.05	rs = - 0.17; p>0.05	rs = - 0.29; p>0.05	rs = - 0.29; p>0.05
PRI (900m)	rs = - 0.24; p>0.05	rs = - 0.23; p>0.05	rs = - 0.24; p>0.05	rs = - 0.19; p>0.05	rs = - 0.19; p>0.05	rs = 0.01; p>0.05
PO (0m)	rs = - 0.42; ***p<0.05***	rs = - 0.31; p>0.05	rs = - 0.42; ***p<0.05***	rs = - 0.26; p>0.05	rs = 0.05; p>0.05	rs = 0.26; p>0.05
			Precipitation (mm)			
Flower	t0	t1	t2	t3	t4	t5
RF (1200m)	rs = - 0.32; p>0.05	rs = - 0.41; ***p<0.05***	rs = - 0.47; ***p<0.01***	rs = - 0.42; ***p<0.05***	rs = - 0.07; p>0.05	rs = 0.10; p>0.05
PRI (900m)	rs = - 0.56; ***p<0.001***	rs = - 0.52; ***p<0.01***	rs = - 0.23; p>0.05	rs = - 0.03; p>0.05	rs = 0.11; p>0.05	rs = 0.34; ***p<0.05***
PO (0m)	rs = 0.27; p>0.05	rs = 0.06; p>0.05	rs = - 0.07; p>0.05	rs = - 0.14; p>0.05	rs = - 0.45; ***p<0.01***	rs = - 0.19; p>0.05
Unripe Fruits						
RF (1200m)	rs = 0.11; p>0.05	rs = 0.02; p>0.05	rs = - 0.11; p>0.05	rs = - 0.32; p>0.05	rs = - 0.30; p>0.05	rs = - 0.26; p>0.05
PRI (900m)	rs = 0.22; p>0.05	rs = 0.11; p>0.05	rs = - 0.02; p>0.05	rs = - 0.17; p>0.05	rs = - 0.23; p>0.05	rs = - 0.10; p>0.05
PO (0m)	rs = 0.06; p>0.05	rs = 0.40; ***p<0.05***	rs = 0.46; ***p<0.01***	rs = 0.27; p>0.05	rs = - 0.25; p>0.05	rs = - 0.51; ***p<0.01***
Ripe Fruits						
RF (1200m)	rs = 0.36; ***p<0.05***	rs = 0.28; p>0.05	rs = 0.06; p>0.05	rs = 0.11; p>0.05	rs = 0.16; p>0.05	rs = - 0.00; p>0.05
PRI (900m)	rs = 0.09; p>0.05	rs = 0.08; p>0.05	rs = 0.09; p>0.05	rs = 0.26; p>0.05	rs = 0.17; p>0.05	rs = 0.21; p>0.05
PO (0m)	rs = - 0.22; p>0.05	rs = - 0.10; p>0.05	rs = 0.13; p>0.05	rs = 0.14; p>0.05	rs = 0.25; p>0.05	rs = 0.08; p>0.05

correlated with rainfall, with a time lag of four months (Table 4).

Unripe fruit

During the study period, the unripe fruit phase was consistently seasonal in the lowland population (Table 1). This was also the case for the montane populations, with the exception of the 2014–2015 season for both populations and the 2015–2016 season for the PRI population (Table 1). At the lowland site, the duration of fruit maturation was shorter than at the montane sites, and we also observed a marked decrease in the length of the maturation period, with high synchrony in 2015–2017 (Figure 3). The mean unripe fruit date differed significantly between the lowland and montane sites, with periods of high synchrony beginning earlier at the high-altitude sites (Table 2, Figure 3). Synchrony was clearly higher at the lowland site, where 80–90 % of individuals had unripe fruits simultaneously, whereas at the montane sites synchrony was consistently < 30 % in 2015–2016 and 60–80 % in the 2014–2015 and 2016–2017 seasons (Figure 3). The correlation analyses for each year and the entire study period showed that the unripe fruit phase in all three populations was more frequently correlated with temperature than with rainfall, but not consistently so (Tables 3 and 4). Correlations were only observed for the entire study period. Daylength was positively correlated with the unripe fruit phase in the montane populations in the first year of the study, whereas this was the case for the lowland population in the last year (Table 3). For the lowland population there were positive correlations with temperature for *t*–2 to *t*–4, but for the RF population there were negative correlations for *t*–2 to *t*–5. No correlations were found for the PRI population (Table 4).

Ripe fruit

During the study period, the ripe fruit phase was consistently seasonal for all three populations (Table 1). At the lowland site, the mean ripe fruit dates occurred from the end of the dry season to the beginning of the wet season (July to October or November) and differed significantly from those in the montane forest, where the ripe fruit phase occurred from the end of the dry season to the middle of the wet season (October to February; Table 2, Figure 3). The montane populations exhibited a delayed ripe fruit phase in the last year: with the higher values observed in February. However, the synchrony was higher in that year (40–60 %). The synchrony was < 40 % for all three populations, and decreases in 2016 (Figure 3). The correlation analysis showed that the ripe fruit phase of all three populations was correlated only with temperature, with the exception that in the RF population there was also a positive correlation with precipitation in the same month (Table 3 and 4). There was also a positive correlation with daylength in this population, but only in the first year of the study (Table 3). Across the entire study period, the ripe fruit phase in the lowland population was negatively correlated with temperature in the same month and in *t*–2 (Table 4). The phase was also negatively correlated with temperature in the lowland and PRI populations in the 2014–2015 season, and in the latter in 2015–2016 as well. In contrast, this phase was positively correlated with temperature in the RF population in the 2016–2017 season.

Seed mass

Seed dry mass and water content were lower for the lowland population in both of the years in which they were recorded (Figure 4). There was a decrease in seed dry mass in the montane populations in 2015 relative to 2014, but not in the lowland population. There was also a decrease in seed water content in 2015 in all three populations (Figure 4).

DISCUSSION

Overall, in spite of differences in altitude, total annual rainfall, and the duration of the dry season among the three sites, the populations of *Euterpe edulis* were similar with respect to the existence of seasonality in their phenological phases. However, they differed with respect to the level of synchrony of these phases, mainly in terms of their flowering phenology; thus our first hypothesis is only partially supported. The study shows, however, that even among populations that are relatively close to each other (within 100 km) and in the same kind of forest (ombrophilous), phenological events can be unsynchronized and occur at different times of the year, with higher-altitude populations flowering earlier than lowland ones. We also observed a higher seed dry mass content in the higher-altitude populations, which, together with their earlier flowering, supports our second hypothesis. In

Figure 3. Phenological activity and rainfall throughout the three years of the study (June 2014 to April 2017). a–c) The percentage of individuals (activity index) in each month that were in the flowering, unripe fruit, and ripe fruit phases. Dotted blue line: RF population (1,200 m a.s.l.); solid red line: PRI population (900 m a.s.l.); dashed gray line: PO population (0–100 m a.s.l.). d) Rainfall data; solid red line: montane populations (PRI and RF) sites; dashed gray line: lowland population (PO) site.

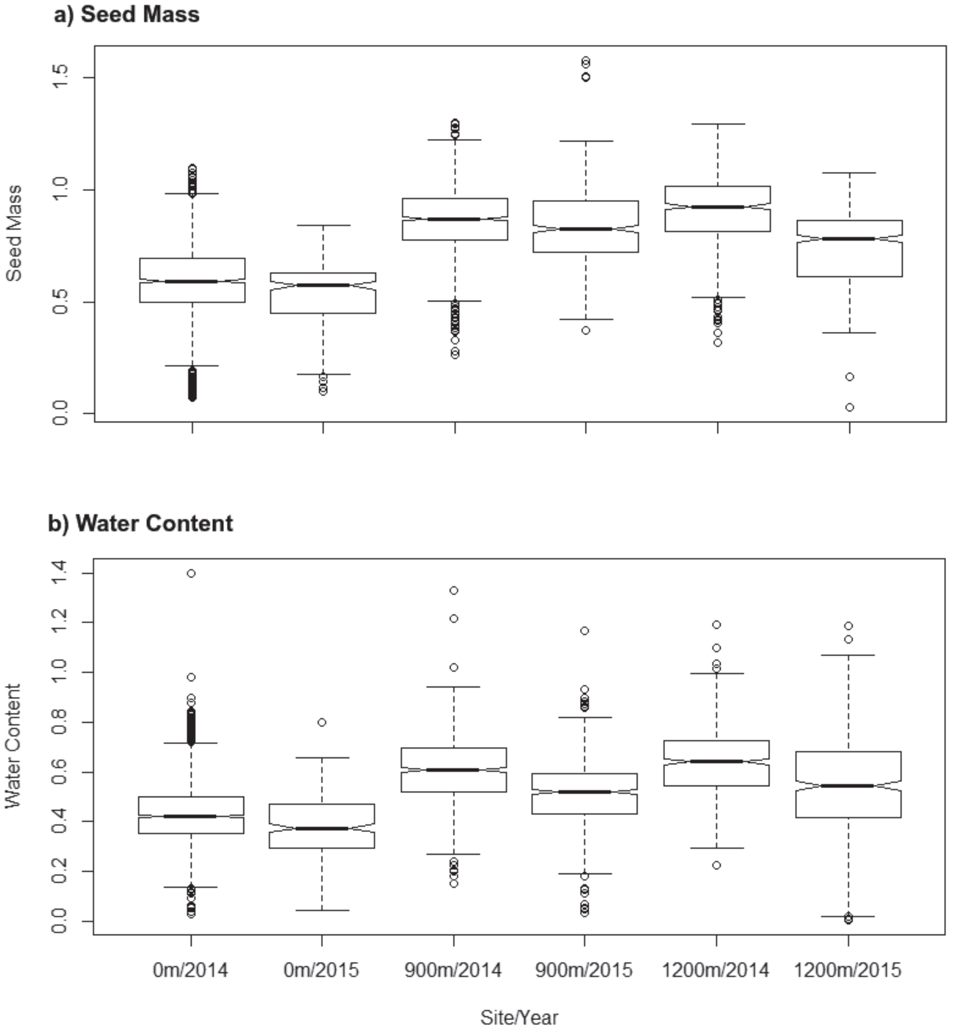

Figure 4. *Euterpe edulis* seed mass (g) and seed water content (g) for the three study populations in 2014 and 2015. The boxes represent 50 % of the observations, and the bars represent their range; notches surrounding the median represent median 95 % confidence intervals; o, extreme value; *, outlier. Non-overlapping notches indicates a significant difference at the 95 % confidence level.

contrast to the predictions of our third hypothesis, in the years of drought (which admittedly varied in intensity with altitude), the higher-altitude populations exhibited greater sensitivity (according to Foden *et al.* 2019) to climatic fluctuations, mainly in terms of decreased levels of flowering synchrony and seed dry mass.

In temperate regions there is a clear pattern of seasonality in phenological phases, which is mainly attributed to the more marked climatic changes among seasons due to the large differences in daylength and air temperature, which also decreases with increases in altitude (Sakai 2001). Our results indicate that despite marked differences in altitude, air temperature, and rainfall patterns, all three populations showed seasonal patterns in their phenological phases, with clear correlations with temperature (more so for the flowering phase than the other phenophases), and to a lesser extent with precipitation. These results contrast with those of Bruno et al. (2019) for *Syagrus* species in the Cerrado area of Brazil. In those species, the flowering and fruiting periods were aseasonal, despite a more marked and well-defined dry season than in our Atlantic rainforest sites. On the other hand, one might expect that altitudinal variation should cause different climatic factors to affect patterns of seasonality. Seasonality at higher altitudes should be more strongly related to the higher range of variation in air temperature among seasons, whereas at low altitudes it should be more strongly related to rainfall patterns.

Indeed, our lowland site was associated with a longer dry season and a lower annual rainfall. However, we found no clear differences among the populations in the magnitude or number of correlations between the phenological phases and monthly temperature or precipitation. However, at the lowland site, flowering was positively correlated with temperature with a time lag of up to two months, whereas flowering at the higher-altitude sites was negatively correlated with temperature, with a time lag of up to two (PRI) or three months (RF). A factor that increased the differentiation between the populations with respect to the main period of phenological events was the change in direction of the correlations with longer time lags, indicating the importance of altitude for variation in phenological traits. It is important to note, however, that despite possible differences in cues for flowering, it is widely recognized that flowering phenology is under strong phylogenetic constraints (Sakai 2001), which might partially explain the absence of variation in the seasonality of phenological phases in this species, which occurs across a relatively broad altitudinal range in the Atlantic Forest biome.

Earlier flowering in the montane populations resulted in a lack of synchrony in reproductive phenology between the three sites. Primack (1987) suggested that earlier flowering should be associated with higher seed mass, which we did observe in our higher-altitude populations, and the need for an extended maturation period for larger fruits. Low temperatures together with lower productivity are often observed with increases in altitude (Grubb 1977, Tanner *et al.* 1998, Malhi *et al.* 2017), and these might negatively affect metabolic rates and investment in fruit development, which is more strongly affected by endogenous factors than by environmental cues (Rathcke & Lacey 1985). This is corroborated by the longer duration of the unripe fruit phase in our higher-altitude populations. It is also important to note that we observed a sequential altitudinal pattern in the ripe fruit phase, with ripe fruit appearing earlier at the low-altitude site and later at the higher ones, with probable consequences for frugivorous fauna, as pointed out by Castro *et al.* (2007).

Interpopulation differences in phenological schedules might integrate a myriad of factors that can explain, in part, the great genetic differentiation observed among populations of *E. edulis* within the ombrophilous rainforest (Cardoso *et al.* 2000). Since the higher and lower populations occur in different environmental envelopes, these patterns are not unexpected, and could represent a rapid evolutionary response to environmental variation (Elzinga *et al.* 2007). However, evolution in plant phenology is also driven by biotic forces (Wolkovich *et al.* 2013). For example, selection for flowering time in some species may be driven to match the timing of specialist pollinators, but physiologically, such species often use environmental cues such as temperature and photoperiod to trigger flowering (Wolkovich *et al.* 2013). In addition, Wolkovich *et al.* (2013) predicted that abiotic drivers might dominate in high-altitude communities with short, variable growing seasons, while biotic factors might be dominant in shaping phenology in tropical systems where climatic variability is generally low.

Beyond the differences in phenological schedules between our *E. edulis* populations, we observed a probable strong effect of drought on the phenology of the higher-altitude populations. For both montane populations there was a reduction in flowering and unripe fruit activity, and also a delay in the ripe fruit phase, during a severe drought. Llorens and Peñuelas (2005) suggested that lower leaf net photosynthetic rates in drought-affected plants might explain alterations in plant phenology. This delay could hamper seed germination and seedling establishment. The existence of differential sensitivity to drier conditions between populations of the same species and between species indicates that climate change might well lead to changes in species distributions, species composition, and community structures. Phenological shifts due to extreme climatic events may disrupt biotic interactions, negatively affecting the reproductive success of plants under global climatic change (Peñuelas *et al.* 2004, Llorens & Peñuelas 2005, Foden *et al.* 2019). However, the vast majority of studies on shifts in phenology have focused on warming as the main component of climatic change, producing gradual phenological alterations. Less attention has been devoted to the fact that phenology is also responsive to other climatic changes, such as rainfall, at least in the majority of regions of the planet (Peñuelas *et al.* 2004). Here, we have found that changes in rainfall in a tropical forest region might alter the phenological patterns, investment in seed mass, and seed water content of a dominant palm species. Drier years caused a reduction in activity, a delay in phenological patterns, and a reduction in seed mass, but the three populations responded differently, mainly with respect to levels of flowering synchrony decreasing to different extents. On the other hand, seed water content was reduced in the same way for all three populations. Such a flexible reproductive strategy between populations of the same species could enhance the ecological range of this species and its potential to adapt to different environmental conditions and fluctuations. However, this complex intraspecific spatial phenological response to changes in rainfall is likely to lead to asynchronies in intra- and interspecific interactions, and could potentially lead to changes in population dynamics and the community.

The changes in seed dry mass between years that we observed in the montane populations were probably a result of the extreme reduction in rainfall between 2014 and 2015. The reduction in seed dry mass we observed in 2015 could have consequences for early plant development. It is thought that the amount of seed biomass determines the energy available for the seedling to undergo its initial development (Moles & Westoby 2004). Therefore, the reduced seed dry mass in 2015 may have affected seedling survival and growth rate (Picó & Retana 2000, Wolfe & Burns 2001), disadvantaging those seedlings in competitive situations (Westoby *et al.* 1996). Additionally, the seed water content was lower in 2015 in all three populations. This effect was strongest in the PRI population, whose seeds had 37 % of their relative water content in 2015, approaching the threshold of 35 %, below which seed viability decreases (Andrade 2001), but still well above the levels associated with complete loss of seed germination (18–24 %; Andrade 2001). However, *E. edulis* seeds show a relatively high germinability of 43 % under a water potential of –0.8 MPa (Braz *et al.* 2014). Hence, more studies are necessary to understand the consequences of drier years for the recruitment of new individuals and their impact on populations.

The exposure of the three populations to the intense drought was relatively similar across the altitudinal gradient, despite the differences in annual rainfall between the lowland and montane sites. These populations, however, differed in their sensitivity to decreases in rainfall, in that the high-altitude populations were not able to maintain their previous levels of synchrony between phenological phases such as those of flowering and unripe fruit. Montane populations of *E. edulis* are less used to variation (seasonality) in rainfall, and hence exhibit greater sensitivity to changes in that abiotic factor. Cardoso *et al.* (2000) highlighted the importance of *E. edulis* conservation efforts taking into account the geographical variation among populations. Additionally, we observed differences in phenological patterns between populations that could lead to differences in strategies for dealing with climatic changes. Thus, it is important to realize that climate change will often have contrasting effects on different populations or subpopulations of a species in different parts of its overall distribution (Foden *et al.* 2019). The differences we observed between our study populations could result in montane populations having poorer recruitment and consequently declining in density. Moreover, they could lead to disruptive consequences for interactions with animals, causing trophic cascade effects in communities located at higher altitudes.

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