

Landscape change alters reproductive phenology and sex expression in *Attalea* palms (Arecaceae) of southwestern Amazonia

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Abstract As deforestation and land-use/land-cover change advance in tropical forest regions, an understanding of how plants adjust phenology and reproductive dynamics to altered landscapes can provide insights into plasticity, productivity, and population persistence. We compared the reproductive phenology, sex expression, and flower and fruit production of two monoecious Amazonian palms, *Attalea phalerata* and *Attalea speciosa*, in old-growth forest and as remnant trees growing in actively grazed pastures.

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Using 2 years of phenology data collected from natural populations near Vila Extrema, Rondônia, and eastern Acre, Brazil, we compared flowering and fruiting in the two habitats and tested for effects of palm height, crown size, and light availability on inflorescence and sex expression. Forest conversion to pasture stimulated greater overall flowering and fruiting in individual Attalea palms. As a population, remnant pasture palms continuously bore flowers and fruits year-round, while forest palms flowered seasonally in isolated peaks with consecutive months of inactivity. Crown size and greater light exposure affected flowering and fruiting dynamics in A. phalerata and A. speciosa, respectively, and increased light availability shifted A. speciosa sex expression towards greater female investment, primarily through regulation of sex determination and bud abortion. Removal of tropical forest does not always lead to the downfall of remnant tree populations, and under favorable conditions, such as abandonment of cropland and pasture, higher levels of reproduction can facilitate recovery of future generations. Tree species with flexible sex expression may be particularly resilient in the face of land-use and land-cover change.

Keywords Attalea phalerata · Attalea speciosa · Flowering · Remnant trees · Reproductive biology · Tropical rain forest

Introduction

Human migration, agricultural expansion, unsustainable logging, urban growth, and advancing infrastructure have spurred the loss of almost half of the world's original forest cover (Abramovitz and Mattoon 1999; Williams 2008). Forest conversion not only fragments the vast forested landscapes that once covered our planet, it also leaves behind scattered trees and spatially disjointed plant populations. Currently, more than 70% of the world's remaining forests are within 1 km of a forest edge (Haddad et al. 2015). When felling tropical forest for agriculture, land-owners often retain trees that provide tangible benefits, such as shade, food, or building materials (Harvey and Haber 1999; Pulido and Caballero 2006). Sometimes, trees are left standing due to the difficulty of felling, or to comply with legal stipulations that prohibit harvest of protected species (e.g., Brazil nut: Bertholletia excelsa). These remnant trees encounter a new set of biotic and abiotic conditions that potentially alter reproductive biology and have far-reaching consequences for future tree populations.

While Janzen (1986) described remnant trees as "the living dead" with no productive future, more recent studies highlight potential ecological value of isolated trees in converted landscapes. Remnant trees can improve soil quality (Wick et al. 2000), enhance nutrient cycling (Harvey and Haber 1999), provide critical habitat for fauna (Harvey and Haber 1999; Manning et al. 2006), facilitate long-distance pollen and seed dispersal in fragmented landscapes (Aldrich and Hamrick 1998; White et al. 2002; Lander et al. 2010), increase genetic connectivity among plant populations (Manning et al. 2006; Breed et al. 2011), help conserve biodiversity (Fischer et al. 2010, Robinson et al. 2013), and accelerate forest recovery (Nepstad et al. 1991; Schlawin and Zahawi 2008; Sandor and Chazdon 2014).

Deforestation is a double-edged sword for many trees. Those left standing in converted or disturbed forest habitats sometimes experience elevated reproductive activity (Cascante et al. 2002; Aldrich and Hamrick 1998), as they benefit from increased exposure to sunlight and reduced resource competition (Chazdon 1986; Schroth et al. 2004). Conversely, changes in the landscape can elicit resource limitations and disrupt pollination systems, which impair flower and fruit production (Levin 2009; Rymer et al. 2013). Limited evidence of the impacts of fragmentation and isolation on plant reproductive phenology suggests that shifts in flowering phenology, triggered by environmental changes can prompt a mismatch between pollinators and flower anthesis (Xiao et al. 2016). For insect-pollinated species, lower visitation rates and decreased out-crossing can constrain genetic diversity (Rocha and Aguilar 2001; but see Dick 2001), reduce progeny fitness (Cascante et al. 2002; Lander et al. 2010), and compromise fruit set (Rocha and Aguilar 2001; McKechnie and Sargent 2013).

To examine the effects of forest conversion on plant reproductive biology, we studied flowering and fruiting phenology, sex expression, and productivity of two closely related palm species, Attalea phalerata Mart. ex Spreng. and Attalea speciosa Mart. ex Spreng. While multiple studies have been conducted on palm phenology in tropical America (Desteven et al. 1987; Otero-Arnaiz and Oyama 2001; Castro et al. 2007; Adler and Lambert 2008; Rojas-Robles and Stiles 2009; Urrego et al. 2016), little attention has been given to phenological differentiation in disturbed environments (Montufar et al. 2011). Both A. phalerata and A. speciosa are prevalent in deforested landscapes of contemporary Amazonia, especially in pastures where they persist long after forest clearing. When converting forest to cropland or pasture, farmers frequently spare large palms, in particular, to provide shade and fodder for cattle, and because silicacontaining palm stems quickly ruin chainsaws and dull axes, providing a strong disincentive for their removal. The abundance of these two species in forest as well as pasture make them prime candidates for studying the impacts of landscape change on reproductive phenology.

Monoecious Attalea palms are a particularly interesting case study due to labile sex expression in several species, where palms alternate between entirely pistillate and entirely staminate inflorescences on the same plant over time (Henderson 2002). This pattern was coined "temporal dioecism" by Cruden and Hermann-Parker in 1977 and has been identified in at least 37 plant families (Cruden 1988). Besides Attalea, few palm genera predominantly alternate between exclusively male and female inflorescences, including Wettinia (Lara et al. 2017), Caryota and Arenga (Nadot et al. 2016), Wallichia and Lepidorrhachis (Baker and Hutton 2006), Marojejya (Marcus 2010), and Elaeis (Adam et al. 2011). Factors shown to influence sex expression in plants, include temperature (Thomas 1956; Freeman et al. 1980), soil moisture (Freeman et al. 1981), drought/water deficit (Adam et al. 2011; Opedal et al. 2016), sunlight (Charnov and Bull 1977; Freeman et al. 1980; Varga and Kytöviita 2016), vapor pressure deficit (Henson 2000), photoperiod (Mann 1942; Freeman et al. 1980), plant size (Bierzychudek 1984; Fox 1993; Klinkhamer et al. 1997), reproductive history (Cunningham 1997), herbivory (Cobb et al. 2002), hormones (Korpelainen 1998; Yamasaki et al. 2005), and genetic make-up (Werren and Beukeboom 1998; Adam et al. 2011). Environmental stress usually favors maleness (Freeman et al. 1980; Korpelainen 1998), although not always (Lloyd and Bawa 1984; Buide et al. 2018).

In this paper, we compare and contrast the reproductive biology of Attalea palms in two drastically different ecological contexts, or habitats-old-growth tropical forest and cattle pasture-and ask: (1) Does reproductive phenology in A. phalerata and A. speciosa differ between forest and pasture? and (2) What effects do environment, palm size, and light availability have on Attalea phenology and sex expression? Over 24 and 18 months, we monitored the flowering and fruiting in A. phalerata and A. speciosa, respectively, in old-growth forests and actively grazed pastures of southwestern Amazonia and tested for associations between reproductive output (flowering and fruiting) and habitat, palm height, crown size (i.e., number of leaves), and sunlight exposure.

Materials and methods

Study area

The study area stretches from the western tip of Rondônia (9°47'S, 66°24'W) to eastern Acre, Brazil (10°00'S, 67°58'W). Across this mostly flat landscape, tropical rainforest is frequently interrupted by agriculture, creating a mosaic landscape with patches of pasture, cropland, abandoned fields, and humid, moist tropical forest (Holdridge 1978). Extensive areas of pasture predominate along principal roadways.

The rainy season extends from October to April with a pronounced dry season between May and September, when monthly precipitation falls below 100 mm (http://www.acrebioclima.pro.br). Average yearly rainfall is 1600–2000 mm, and mean annual temperature is 25 °C (ZEE 2002). Cold fronts pass through the region each year during the early dry season, bringing bursts of cooler temperatures in the low teens (°C).

Study species

Attalea phalerata is an arborescent, lower canopy palm up to 20 m tall with a thick stem (25–40 cm in diameter) that grows in forests throughout the southern and western periphery of the Amazon region, including Brazil, Bolivia, and Peru, as well as in drier forests and savannas of the *planalto* in Brazil, Bolivia, and Paraguay (Henderson et al. 1995). This species persists in pastures and deforested areas throughout eastern Acre and northern Bolivia and frequently dominates regenerating secondary forests (Henderson 1995). Attalea phalerata is primarily pollinated by nitidulid weevils from the genus *Mystrops* (Fava et al. 2011), although due to the powdery nature of *A. phalerata* pollen, we also suspect wind pollination (*cf.* Rios et al. 2014).

Attalea speciosa is an arborescent, upper canopy palm up to 30 m tall with a thick stem (25–41 cm in diameter) occurring in the Amazon regions of Guyana, Suriname, Brazil and Bolivia (Henderson et al. 1995). Besides occurring at high densities in old-growth forests, this species flourishes in cleared forest areas, such as pastures and abandoned agricultural fields, often forming dense monodominant stands (Anderson 1983; Henderson et al. 1995). It is particularly abundant in transition zones between tropical forest and other drier vegetation types. Pollination of *A. speciosa* is by nitidulid weevils (*Mystrops* sp.) and wind (Anderson et al. 1988). Within our study area, *A. phalerata* and *A. speciosa* have distinct, non-overlapping distributions.

Site selection

We observed flowering and fruiting phenology of palms in three pasture and three forested sites with *A. phalerata* along principal roadways within 300 km of Rio Branco, Acre, Brazil, and three pasture and three forested sites with *A. speciosa* along a 35 km stretch of Federal Highway BR-364 in Extrema, Rondônia, Brazil. All pasture sites were actively grazed by cattle and had been cleared of forest 15–30 year earlier. Oldgrowth forest sites were largely intact with some signs of light disturbance typical of the region (i.e., smallscale timber extraction and hunting). Each pasture site was paired with a forest site so that all pairs were within 2 km of each other. Land-owners reported no use of chemical fertilizers or herbicides for pasture management.

Data collection

At each study site, we selected 12 reproductive palms for monthly phenology observations (n = 72 palms per species). All selected palms presented evidence of past reproduction and leaf crowns were fully visible from the ground. In pastures, palms stood within a roughly 1 ha area. In old-growth forest, where adult palms are typically more dispersed, individuals were scattered over 2–5 ha.

We monitored phenology of both Attalea species through two flowering peaks: January 2006-December 2007 for A. phalerata and January 2006–July 2007 for A. speciosa. At monthly intervals, we observed flowering and fruiting from the ground using binoculars. For each palm we recorded reproductive phase and inflorescence sex: peduncular bracts (closed inflorescence buds), inflorescences in anthesis (open flowers) and post-anthesis inflorescence structures. We noted the azimuth of each reproductive structure using a compass and followed it through flowering and fruiting phenophases (cf. Anderson et al. 1988). Inflorescence sex was easily identified due to distinct morphology of male and female flowers. The majority of Attalea species produce exclusively male and exclusively female inflorescences on the same plant, but in some cases we observed bisexual androgynous inflorescences with both male and female flowers (Henderson 2002). Because A. phalerata observations through July 2007 yielded surprisingly few inflorescences, we extended observations until December 2007 to capture a second flowering cycle at two pasture and two forest sites.

During our initial site visits, we also recorded the number of leaves on each palm and measured palm height (to top of the leaf crown) using a tangent height gauge. To assess leaf production rates we marked the youngest fully expanded leaf on a sub-sample of palms with red paint (*A. phalerata:* n = 33; *A. speciosa:* n = 37) and tallied the number of newly expanded leaves 1 year later. As a proxy for light availability, we

ranked crown light exposure each month on a scale of zero to five by dividing the crown into five sections—four vertical faces plus the top—and then counting the number of sections that receive direct sunlight when the sun is directly overhead (Bechtold 2003).

Data analysis

For comparisons between pasture and forest, we calculated the number of flowering and fruiting events per year per palm (*cf.* Newstrom et al. 1994), referred to as flowering and fruiting frequency, and graphed inflorescence and infructescence intensity (i.e., proportion of palms in flower or fruit each month) over the study period. For analysis purposes, the occasional bisexual inflorescence was grouped together with pistillate inflorescence counts due to their active female function (i.e., fruit generation).

Circular statistics

We used circular statistics to determine seasonality of flowering and fruiting and compare across habitats and between staminate and pistillate phenophases. Circular analyses provide an intuitive approach to display phenological data and test hypotheses related to seasonality, synchrony, and phenophase differences between groups (Morellato et al. 2010; Cortés-Flores et al. 2017; Cardoso et al. 2018). To calculate circular statistic parameters, we converted months to 30° intervals around a circle, starting with January (0°-30°) successively through December (330°-360°) (Morellato et al. 2010). The mid-point of each interval represents the month in which flowering or fruiting January = 15° , February = 45° , was observed: March = 75° , and so on (Williams-Linera and Alvarez-Aquino 2016). Rather than the proportion of palms in flower each month, circular histograms reflect relative frequency of phenological events for each month of the year, displayed as a rose diagram. Phenological variables analyzed include staminate flowering, pistillate flowering, total flowering (pistillate plus staminate), and mature infructescence. Circular statistics were calculated using R version 3.4.2 (R Core Team 2017) with the package Circular 0.4–93 (Agostinelli and Lund 2017). Circular parameters reported are: (1) mean angle a, or mean date of each phenophase and (2) resultant vector length r, or the concentration of phenological events around the mean angle that varies between 0 and 1, representing degree of synchrony with values closer to 1 indicating greater concentration of phenological activity around a single date (Morellato et al. 2000). To test for seasonality, we applied Rao's Spacing test (Batschelet 1981). We used Wallraff's test of angular dispersion around the mean to test for phenological differences within and between habitats, inflorescence sex, and species (Wallraff 1979).

Modeling flowering and fruiting patterns

To determine effects of habitat, palm height, crown size (i.e., number of leaves), and illumination on Attalea phenology we examined five response variables: infructescence, pistillate and staminate inflorescence, total inflorescence, and proportion of female inflorescences. All continuous predictors (i.e., palm height, crown size, and illumination) were scaled and centered (i.e., for each measure we subtracted the mean and divided by the standard deviation). For each model, we verified that predictor variables were not multicolinear by examining variance inflation factors (i.e., VIF < 5), all Poisson models were not overdispersed (dispersion parameter \sim 1), and graphically assessed linear models to ensure they met assumptions of normally distributed residuals and homoscedasticity. When these criteria were not met, we modified modeling procedures by removing multicolinear variables (i.e., VIP > 5), using a quasi-Poisson error distribution to account for overdispersion, and applying a zero-inflated model in the presence of an abundance of zeroes in the data. For all models, we determined significance of predictor variables using likelihood ratio tests.

For *A. phalerata* we modeled infructescence and pistillate inflorescence using a generalized linear model (GLM) and assumed a Poisson error distribution, but for staminate inflorescence, we used a zeroinflated Poisson model due to the abundance of zeroes. Additionally, for staminate inflorescence we removed the illumination predictor variable as it was multicolinear with other predictors. For total inflorescence, we used a quasi-Poisson GLM, and to assess the proportion of female inflorescences we applied a linear model.

For *A. speciosa* we modeled infructescence, pistillate and staminate inflorescence, and total inflorescence using a GLM with a Poisson error distribution. Additionally, for all four response variables, we removed the habitat predictor variable as it was multicolinear with our other predictors. Lastly, for proportion of female inflorescences we used a linear model and likewise removed the habitat predictor variable due to multicolinearity.

We used R version 3.4.2 (R Core Team 2017) for statistical analyses, the *car* package (Fox and Weisberg 2011) to determine variance inflation factors, the *pscl* package (Jackman 2017) to develop zero-inflated models, and the *lmtest* package (Zeileis and Hothorn 2002) for likelihood ratio tests.

Results

Flowering and fruiting phenology

Attalea phalerata and A. speciosa inflorescence and infructescence production varied in magnitude between forest and pasture (Table 1). Nonetheless, each species displayed similar seasonal patterns in terms of peak and low reproduction periods that generally matched across habitats (Figs. 1, 2). In terms of annual leaf production, A. phalerata produced more leaves in pasture ($\bar{x} = 8.7 \pm 0.16$ SE) than in forest ($\bar{x} = 7.9 \pm 0.14$ SE, P = 0.025), while A. speciosa showed no difference in leaf production between habitats (pasture: $\bar{x} = 6.2 \pm 0.38$ SE; forest: $\bar{x} = 6.0 \pm 0.41$ SE, P = 0.4874).

Attalea phalerata

Regardless of habitat, *A. phalerata* flowering peaked in September toward the end of the dry season (Figs. 1, 3a). In forest, *A. phalerata* palms considerably reduced or suspended inflorescence during the rainy season and reinitiated flowering at the onset of the dry season (May–June), while pasture palms flowered continuously throughout the year (Fig. 1). During the first year, staminate and pistillate flowering followed similar seasonal patterns, but in 2007 pistillate flowering peaked 2 months earlier (July) than staminate (September) (Fig. 1). In pasture, pistillate inflorescence peaks in April and July 2007 contrasted sharply with 2006 when pistillate flowering peaked in October (Fig. 3c, d).

On average, A. *phalerata* infructescences ripened over 6 months in forest (\pm 0.17 SE) and 7 months in

Species	Phenological phase	Habitat	Year	Mean number of events (\pm SE)
Attalea phalerata	Infructescence	Pasture	2006	1.7 ± 0.2
			2007	2.3 ± 0.4
		Forest	2006	0.5 ± 0.1
			2007	0.2 ± 0.1
	Pistillate inflorescence	Pasture	2006	1.7 ± 0.4
			2007	2.6 ± 0.5
		Forest	2006	0.3 ± 0.1
			2007	0.6 ± 0.1
	Staminate inflorescence	Pasture	2006	3.0 ± 0.5
			2007	2.6 ± 0.5
		Forest	2006	1.3 ± 0.2
			2007	2.8 ± 0.3
Attalea speciosa	Infructescence	Pasture	2006-2007	1.1 ± 0.1
		Forest	2006-2007	0.4 ± 0.1
	Pistillate inflorescence	Pasture	2006-2007	1.6 ± 0.2
		Forest	2006-2007	0.7 ± 0.1
	Staminate inflorescence	Pasture	2006-2007	2.4 ± 0.2
		Forest	2006–2007	2.1 ± 0.2

Table 1 Comparison of Attalea phalerata and Attalea speciosa inflorescence and infructescence production (mean number of reproductive events \pm SE) in forest and pasture during 2006 and 2007 in Acre and Rondônia, Brazil

Attalea phalerata statistics were aggregated over 12-months and A. speciosa over 18-months

pasture (± 0.08 SE). The greatest availability of mature fruit coincided with the wettest months of the year (February–May). In old-growth forest, ripe *A. phalerata* fruits were available 5–6 months out of the year, while in pasture, we encountered mature fruits year-round (Fig. 1). Fruit set was remarkably successful, independent of habitat: only 8% (n = 2) and 3% (n = 3) of pistillate inflorescences aborted prior to fruit ripening in forest and pasture, respectively.

Attalea speciosa

Attalea speciosa flowering peaked during the wet season, and staminate and pistillate phenology closely overlapped throughout the study (Fig. 2). Most *A. speciosa* inflorescences opened between March and May (Fig. 3b). Flowering in pastures peaked 2 months earlier than in forest, and while pasture palms displayed pistillate and staminate inflorescences year-round, forest palms halted pistillate inflorescence for 2 months at the end of the dry season (Fig. 2).

Attalea speciosa fruits developed over 8 months in both forest (\pm 0.08 SE) and pasture (\pm 0.39 SE), such

that ripe fruits were most abundant during the late dry and early wet seasons (September–January; Fig. 2). In forest, we encountered few, if any, mature infructescences from February to May, but pastures displayed mature fruits year-round (Fig. 2). Merely 6% (n = 3) and 1% (n = 1) of *A. speciosa* pistillate inflorescences failed to develop mature fruit in forest and pasture, respectively.

Rao's spacing test indicated significant seasonality for flowering and fruiting phenophases in both *Attalea* species (Table 2). Resultant vector length r (i.e., concentration of flowering and fruiting events) was generally greater in forest and lower in pasture (Table 2), pointing to more pronounced seasonality in forest. Results also showed higher synchrony of staminate than pistillate flowering in *A. phalerata*, whereas in *A. speciosa*, the opposite was true: staminate was less aggregated over the year than pistillate flowering (Table 2).

Wallraff's test revealed differences in phenology between habitats and between inflorescence sexes in both *Attalea* species, except for three cases: (1) overall staminate vs. pistillate phenology in *A. speciosa*, (2)



Fig. 1 Monthly rainfall (mm; INMET 2008), proportion of *Attalea phalerata* palms flowering in forest and pasture, split into staminate (dark gray square) and pistillate (light gray

square) inflorescence, and proportion of *A. phalerata* palms with ripe fruit in forest (black square) and pasture (light gray square) from January 2006 to December 2007 in eastern Acre, Brazil

staminate vs. pistillate phenology for *A. speciosa* palms in pasture, and (3) staminate vs. pistillate flowering of *A. phalerata* palms in forest (Table 3). Flowering peaks for *A. phalerata* were consistently and significantly different from those in *A. speciosa* (Fig. 3a, b).

Sex expression

Individual *A. phalerata* and *A. speciosa* palms displayed gender plasticity both between and within flowering seasons, switching back and forth between male and female inflorescences during the two-year **Fig. 2** Monthly rainfall (mm; field-collected data), proportion of *Attalea speciosa* palms flowering in forest and pasture, split into staminate (dark gray square) and pistillate (light gray square) inflorescence, and proportion of *A. speciosa* palms with ripe fruit in forest (black square) and pasture (light gray square) from January 2006 to June 2007 in western Rondônia, Brazil



study period. Over the entire observation period, both *Attalea* species produced more staminate than pistillate inflorescences, regardless of habitat (Table 4). Average annual staminate-to-pistillate inflorescence ratios per palm in forest and pasture were 5.0:1.0 and 1.4:1.0, respectively, for *A. phalerata*; and 2.5:1.0 and 1.3:1.0, respectively, for *A. speciosa*. In *A. phalerata*, we observed bisexual inflorescences on only one individual growing in pasture. *Attalea speciosa*

produced bisexual inflorescences in both habitats and across study sites (n = 11 palms).

Pistillate flowering in *A. phalerata* was rare among forest palms in 2006: only 21% of individuals produced pistillate inflorescences. In contrast, 54% of forest palms produced pistillate inflorescences in 2007. Sixty-four percent of pasture palms produced pistillate inflorescences in 2006 and 79% in 2007. In *A. speciosa*, 51% of forest palms and 58% of pasture palms produced at least one pistillate inflorescence Fig. 3 Circular plots (phenograms) of overall flowering (staminate and pistillate inflorescence) for a Attalea phalerata and b Attalea speciosa, recorded over 24 months in eastern Acre and 18 months in western Rondônia, Brazil, respectively, plus phenograms of Attalea phalerata pistillate inflorescence in pasture during c 2006 and d 2007 in eastern Acre, Brazil



during the first 6 months of 2006. During the first half of 2007, 61% of forest palms and 78% of pasture palms produced pistillate inflorescences.

Impacts of habitat, palm height, crown size, and light availability on *Attalea* flowering and fruiting

Models revealed clear differences in predictor variables for flowering and fruiting between the two *Attalea* species. Full details on model type, VIF and parameter estimates, and statistics are summarized in Tables 5 and 6.

Attalea phalerata

In *A. phalerata*, habitat was a significant predictor for infructescence ($\chi^2 = 9.283$; df = 1; P = 0.002), pistillate ($\chi^2 = 7.774$; df = 1; P = 0.005), staminate ($\chi^2 = 11.028$; df = 1; P = 0.004), and total

inflorescence ($\chi^2 = 10.235$; df = 1; P = 0.031). For these response variables, forest showed lower amounts of infructescence and inflorescence compared to pasture (Fig. 4). Crown size significantly predicted pistillate ($\chi^2 = 9.656$; df = 1; P = 0.002), staminate $(\chi^2 = 9.022; df = 1; P = 0.011)$, and total inflorescence ($\chi^2 = 15.029$; df = 1; P = 0.009). Palms with a greater number of leaves had more inflorescences compared to palms with fewer leaves (Fig. 4b-d). Lastly, palm height significantly predicted pistillate $(\chi^2 = 4.765; df = 1; P = 0.029)$ and staminate inflorescence ($\chi^2 = 6.135$; df = 1; P = 0.047); shorter palms produced a greater number of pistillate inflorescences compared to taller palms, whereas the opposite was true for staminate inflorescences (Fig. 4b, c). Contrary to expectations, light availability was not a significant predictor of flowering or fruiting in A. phalerata, and none of the tested variables significantly predicted proportion of female inflorescence (Table 5).

Phenological variable	Observations (N)	Mean angle (Month ^a)	Mean resultant vector length (<i>r</i>)	Rao's spacing test <i>P</i> value
Attalea phalerata				
Forest fruiting	24	88.8 (Mar)	0.7216	< 0.001
All fruiting	147	137.7 (May)	0.4406	< 0.001
Pasture fruiting	123	147.2 (May)	0.3866	< 0.001
Pasture and pistillate flowering	125	196.4 (Jul)	0.1170	< 0.001
Pistillate flowering	152	202.1 (Jul)	0.1716	< 0.001
Pasture flowering	303	208.3 (Jul)	0.2094	< 0.001
All flowering	447	215.7 (Aug)	0.2996	< 0.001
Pasture and staminate flowering	178	216.6 (Aug)	0.2799	< 0.001
Staminate flowering	295	222.7 (Aug)	0.3717	< 0.001
Forest and pistillate flowering	27	228.3 (Aug)	0.4284	< 0.001
Forest flowering	144	231.2 (Aug)	0.4929	< 0.001
Forest and staminate flowering	117	231.9 (Aug)	0.5137	< 0.001
Attalea speciosa				
Forest and pistillate flowering	52	111.9 (Apr)	0.6735	< 0.001
Forest flowering	205	120.2 (May)	0.5188	< 0.001
Forest and staminate flowering	152	123.4 (May)	0.4655	< 0.001
Pistillate flowering	166	133.7 (May)	0.4296	< 0.001
All flowering	489	136.3 (May)	0.3819	< 0.001
Staminate flowering	323	137.6 (May)	0.3574	< 0.001
Pasture and pistillate flowering	114	143.7 (May)	0.3387	< 0.001
Pasture flowering	284	147.9 (May)	0.2918	< 0.001
Pasture and staminate flowering	171	150.3 (June)	0.2654	< 0.001
Pasture fruiting	82	197.6 (Jul)	0.1368	< 0.001
All fruiting	113	203.0 (Jul)	0.2139	< 0.001
Forest fruiting	31	217.3 (Aug)	0.4376	< 0.001

 Table 2 Results of circular analyses characterizing Attalea

 phalerata and Attalea speciosa flowering and fruiting events in

 different habitats (forest vs. pasture) and for different

inflorescence sexes (staminate vs. pistillate) in eastern Acre and western Rondônia, Brazil

^aFor circular analyses, we converted months to 30° intervals around a circle, starting with January (0°–30°) successively through December (330°–360°) (Morellato et al. 2010). In this study we used the midpoint of each interval to represent phenology observation months (e.g., 15° = January, 45° = February, 75° = March, and so on)

Attalea speciosa

In *A. speciosa*, light availability (i.e., illumination) was a significant predictor for infructescence $(\chi^2 = 6.660; df = 1; P = 0.010)$, pistillate

inflorescence ($\chi^2 = 12.288$; df = 1; P < 0.001), staminate inflorescence ($\chi^2 = 5.635$; df = 1; P = 0.018), total inflorescence ($\chi^2 = 15.276$; df = 1; P < 0.001), and proportion of female inflorescence ($\chi^2 = 3.868$; df = 1; P = 0.049). Greater exposure to sunlight

	Attalea phalerata	Attalea speciosa
Forest \times pasture (all flowering)	< 0.0001	0.0020
Staminate \times pistillate	0.0002	0.3070
Ripe fruit: forest × pasture	0.0188	0.0356
Forest: staminate \times pistillate	0.1774	0.0271
Pasture: staminate \times pistillate	0.0353	0.8347
Staminate: forest × pasture	0.0004	0.0492
Pistillate: forest \times pasture	0.0309	0.0055

Table 3 Comparisons of reproductive phenology across habitats (forest vs. pasture) and inflorescence sex (staminate vs. pistillate) for *Attalea phalerata* and *Attalea speciosa*, based on the Wallraff test (z) for common concentration around the mean

Bolded values denote statistically significant differences in timing of phenophases

Table 4 Number and proportion of staminate inflorescences and pistillate inflorescences followed through time in pastures and oldgrowth forest for *Attalea phalerata* and *A. speciosa* in eastern Acre and western Rondônia, Brazil, respectively

	Old-growth forest		Pasture	Pasture		
	Staminate (%)	Pistillate (%)	Staminate (%)	Pistillate (%)		
Attalea phalerata (Jan 2006–Dec 2007)	117 (82)	26 (18)	178 (59)	125 (41)		
<i>Attalea speciosa</i> (Jan 2006–Jun 2007)	153 (75)	52 (25)	171 (60)	113 (40)		

meant more infructescences and inflorescences as well as greater proportions of female inflorescences (Fig. 5). Crown size significantly predicted total inflorescence ($\chi^2 = 4.321$; df = 1; P = 0.038): palms with more leaves produced more inflorescences compared to palms with fewer leaves (Fig. 5d). Palm height was not a significant predictor for flowering or fruiting in this species.

Discussion

Reproductive phenology across the landscape

Landscape change and forest conversion to pasture have a significant impact on *Attalea* phenology and reproduction. Circular analyses and modeling results underscored the impact of habitat differences on both reproductive phenology and levels of inflorescence and infructescence production. We expected similar timing of flowering and fruiting between forest and pasture, since the principal cues that trigger phenological patterns in the tropics-photoperiod, irradiance, temperature, and rainfall (Rathcke and Lacey 1985; Borchert et al. 2004; Stevenson et al. 2008)—showed little variation between the two habitats. Timing of flowering peaks in forest and pasture was generally similar, although A. speciosa flowering peaked 2 months earlier in pasture (Fig. 2). Phenological triggers can be mediated by the microenvironment, which differed substantially between the two habitats. While rainfall was generally consistent across study sites, quicker saturation of exposed pasture soils might explain A. speciosa's earlier flowering peak in pasture, since this species normally peaks during the wet season (cf. Anderson et al. 1991). Likewise, closed canopy forest dries out more slowly than open pasture at the end of the rainy season, and thus A. phalerata, which peaks during the dry season, experiences dry conditions in pasture before it would in forest, stimulating an earlier uptick in flowering among pasture palms (Fig. 1). Athayde and Morellato (2014) also found that isolated trees growing along an exposed forest edge started flowering earlier than trees

Response	Model type	Error distribution	Dispersion parameter	Predictor variable	Variance inflation factor	Estimate (SE)	$\chi^2 (df = 1)$	P value
Infructescence	Generalized linear model	Poisson	1.2	Habitat	3.2	- 1.24 (0.42)	9.283	0.002
				Height	1.3	- 0.10 (0.11)	0.794	0.373
				Number of leaves	1.1	0.14 (0.08)	3.320	0.068
				Illumination	3.2	0.15 (0.20)	0.552	0.457
Pistillate inflorescence	Generalized linear model	Poisson	1.6	Habitat	3.4	- 1.09 (0.40)	7.774	0.005
				Height	1.3	- 0.23 (0.10)	4.765	0.029
				Number of leaves	1.1	0.23 (0.07)	9.656	0.002
				Illumination	3.6	0.08 (0.20)	0.165	0.684
Staminate inflorescence	Zero-inflated model	Poisson	NA	Habitat	2.4	- 0.51 (0.16)	11.028	0.004
				Height	1.4	0.20 (0.08)	6.135	0.047
				Number of leaves	1.3	0.18 (0.06)	9.022	0.011
Total inflorescence	Generalized linear model	Quasi- Poisson	2.2	Habitat	3.9	- 0.69 (0.33)	10.235	0.031
				Height	1.3	0.06 (0.10)	0.877	0.529
				Number of leaves	1.1	0.18 (0.07)	15.029	0.009
				Illumination	3.8	0.04 (0.16)	0.119	0.817
Proportion female inflorescence	Linear model	Normal	NA	Habitat	3.7	- 0.07 (0.18)	0.015	0.695
				Height	1.5	- 0.10 (0.06)	0.273	0.091
				Number of leaves	1.1	- 0.01 (0.05)	0.003	0.851
				Illumination	3.5	0.06 (0.09)	0.053	0.456

 Table 5
 Model details and statistics for Attalea phalerata infructescence, pistillate, staminate and total inflorescence, and proportion female inflorescence

Illumination was not included in the staminate inflorescence model due to its higher variance inflation factor (see Materials and methods). Estimates for infructescence, pistillate, staminate and total inflorescence are on the log scale. Bolded terms denote significance ($\alpha = 0.05$)

of the same species located in the forest interior. Furthermore, the earlier peak in *A. phalerata* pistillate flowering across habitats in 2007 (Fig. 3c, d) may reflect an atypical early start of the dry season in April. Normally, the dry season begins in June.

Significant differences for all phenophase comparisons between forest and pasture, in terms of

 Table 6
 Model details and statistics for Attalea speciosa infructescence, pistillate, staminate and total inflorescence, and proportion female inflorescence

Response	Model type	Error distribution	Dispersion parameter	Predictor variable	Variance inflation factor	Estimate (SE)	$\begin{array}{c} \chi^2 \\ (df=1) \end{array}$	P value
Infructescence	Generalized linear model	Poisson	1.1	Illumination	1.5	0.39 (0.16)	6.660	0.010
				Height	1.6	- 0.21 (0.13)	2.605	0.107
				Number of leaves	1.2	0.22 (0.11)	3.806	0.051
Pistillate inflorescence	Generalized linear model	Poisson	0.91	Illumination	1.5	0.42 (0.12)	12.288	< 0.001
				Height	1.6	- 0.05 (0.10)	0.204	0.651
				Number of leaves	1.2	0.17 (0.09)	3.564	0.059
Staminate inflorescence	Generalized linear model	Poisson	0.99	Illumination	1.4	0.17 (0.07)	5.635	0.018
				Height	1.5	0.10 (0.07)	2.036	0.154
				Number of leaves	1.2	0.08 (0.06)	1.387	0.239
Total inflorescence	Generalized linear model	Poisson	0.77	Illumination	1.5	0.24 (0.06)	15.276	< 0.001
				Height	1.5	0.05 (0.06)	0.665	0.415
				Number of leaves	1.2	0.11 (0.05)	4.321	0.038
Proportion female inflorescence	Linear model	Normal	NA	Illumination	1.5	0.08 (0.04)	3.868	0.049
				Height	1.6	-0.004 (0.04)	0.014	0.904
				Number of leaves	1.2	0.05 (0.04)	2.457	0.117

Habitat was not included for all responses due to its higher variance inflation factor (see Materials and methods). Estimates for infructescence, pistillate, staminate and total inflorescence are on the log scale. Bolded terms denote significance ($\alpha = 0.05$)

concentration and dispersion around the mean (Table 2) primarily reflected the continuous versus seasonal flowering patterns in pasture and forest, respectively. Athayde and Morellato (2014) also observed longer flowering periods for trees growing in pastures compared with those inside *cerrado* forest in southeastern Brazil. Extended duration of flowering and fruiting in pastures implies a lack of seasonal deficiencies in key resources (Rathcke and Lacey 1985).

Pasture palms out-produced forest palms

Many species, including palms, suffer negative impacts of deforestation due to specific life history characteristics, such as susceptibility to higher light levels and drier soils. Potential mismatches between pollinators and flowering periods can further impair fruit set and compromise future generations (Burd 1994; Rocha and Aguilar 2001; Grogan et al. 2010). McKechnie and Sargent (2013) emphasized cattle pastures as particularly detrimental to plant reproductive success through reduced fruit set, yet evidence of



Fig. 4 Significant predictors of **a** infructescence, and **b** pistillate, **c** staminate, and **d** total inflorescence for *Attalea phalerata*. Red bars (**a**) and gray shaded ribbons (**b**-**d**) denote 95% confidence intervals, while red points (**a**) and solid, dashed or

dotted lines (**b-d**) denote mean predictions. The size of points in (**b**, **c**) show palm height (i.e., larger dots represent larger palms), and in (**d**) open circles denote pasture and solid squares denote forest habitat. (Color figure online)



Fig. 5 Significant predictors of a infructescence, b pistillate, c staminate, d total inflorescence, and e proportion female inflorescence for *Attalea speciosa*. Gray shaded ribbons denote

95% confidence intervals, while solid lines denote mean predictions. Point and line colors in \mathbf{d} denote illumination. (Color figure online)

elevated reproduction in remnant trees also exists (White and Boshier 2000; Cascante et al. 2002; Herrerias-Diego et al. 2006; Athayde and Morellato 2014). In terms of reproduction, A. phalerata and A. speciosa displayed advantages as scattered remnant trees compared to trees growing in old-growth forest, even 15-30 year after forest conversion to pasture. Continuous flowering paved the way for the greater inflorescence and infructescence in pastures. The overwhelming success of Attalea to set fruit regardless of habitat indicated highly successful pollination in both habitats. For both study species, pollination can proceed via wind in the absence of beetle pollinators, offering an advantage in open areas, such as pastures (Anderson et al. 1988). At the eastern end of the Amazon Basin, A. speciosa allocated nearly 100% more resources toward reproductive structures in pasture than in forest (Anderson et al. 1991), and in Costa Rica, isolated Pachira quinata trees growing in agricultural fields produced more flowers than trees of the same species in continuous forest (Fuchs et al. 2003). In our study, A. phalerata palms annually produced more than four times as many pistillate inflorescences in pasture than in forest, and A. speciosa produced more than twice as many. On the other hand, we noted virtually no difference in staminate flowering between forest and pasture during the second year of observations. Since pistillate flowers and fruits are more resource intensive, they likely exhibit a tighter relationship with environmental conditions.

In palms, selective abortion of developing inflorescence buds regulates flowering patterns long before peduncular bracts become visible on the plant (Tomlinson 1990). Because inflorescence production is sequential with each new leaf harboring a single bud, bud abortions leave gaps between flowering events. On average, Attalea palms produced 6-8 new leaves annually, but in forest only 2-3 inflorescence buds developed to anthesis. In pasture 4-5 buds bore flowers. The lower inflorescence-to-leaf ratio in forest reflects higher bud abortion rates, suggesting greater resource limitation. Anderson et al. (1991) found particularly high inflorescence-to-leaf ratios of 1:1 for an A. speciosa pasture population in Eastern Amazonia. In Elaeis guineensis palms, defoliation, high levels of shading, and moisture stress elicit high bud abortion rates (Hartley 1977). Even though we expected greater moisture stress in pastures, ample sunlight and reduced competition from other vegetation promoted favorable conditions for bud development (Anderson et al. 1991), while shadier conditions in forest likely contributed to higher rates of bud abortion and fewer inflorescences. Substantially lower inflorescence production in 2006—particularly in terms of pistillate inflorescence (Table 1)—may be attributed to a severe drought that afflicted the region in 2005.

Habitat, palm height, crown size, and light availability linked to flowering and fruiting

Habitat, palm height, crown size, and light availability played decisive roles in inflorescence and infructescence production, but the influence of each factor depended on species and inflorescence sex. For example, palm height was not associated with *A. speciosa* flowering or fruiting, but it was a significant predictor of inflorescence in *A. phalerata.* Shorter palms produced more pistillate inflorescences, and taller palms produced more staminate inflorescences. Increased height may convey an advantage for staminate flowers in wind-pollinated species like *A. phalerata*, as taller palms can disperse pollen more effectively due to higher wind speeds and less intervening vegetation (Friedman and Barrett 2009).

In A. speciosa light, not height, helped predict infructescence and inflorescence production. A direct relationship between flowering and light intensity is common in palms and other plant species (Piñero and Sarukhán 1982; Burgess et al. 2006; Varga and Kytöviita 2016). Since mature A. speciosa palms extend into the forest canopy, they are better adapted to take advantage of increased illumination (Bazzaz and Carlson 1982; Chazdon et al. 1996) and respond readily to increased sunlight by greater investment in reproduction. Attalea phalerata, on the other hand usually remains beneath the canopy. Consequently, this species' physiology is likely less responsive to increased sunlight (Poorter 1999). Indeed, illumination had no significant impact on infructescence nor inflorescence frequencies in A. phalerata. On average, A. phalerata palms were five meters shorter than A. speciosa.

Influence of crown size on inflorescence also varied by species. While number of leaves was a poor predictor of flowering and fruiting in *A. speciosa, A. phalerata* palms with larger crowns exhibited greater inflorescence frequencies, suggesting that the number of leaves helps regulate flowering patterns. As a subcanopy palm, *A. phalerata* must rely on crown size rather than light exposure to increase photosynthesis and gather resources for reproduction. For another understory palm, *Astrocaryum mexicanum*, palms with more leaves reproduced more frequently (Piñero and Sarukhán 1982). Annual inflorescence production in *Attalea butyracea* in Colombia was also positively related to number of expanded leaves (Olivares and Galeano 2013). Thus, while in *A. speciosa*, gains in photosynthesis were principally attained through increased light exposure, plant size (crown size and height) played a more predominant role in *A. phalerata* reproductive output.

Sex expression and male dominance

In *A. phalerata* and *A. speciosa*, male function predominated at both individual and population levels, regardless of habitat (i.e., 60–80% of all inflorescences were male). Other *Attalea* species exhibit similar proportions of male inflorescences: *A. speciosa*, 80% (Anderson et al. 1991), *A. funifera*, 80% (Voeks 1988), *A. colenda*, 67–74% (Feil 1996), and *A. microcarpa*, 72% (Kuchmeister et al. 1993). Male-biased sex ratios prevail among dioecious and monoecious plant populations (Solomon 1985; Otero-Arnaiz and Oyama 2001; Lazaro and Mendez 2007; Queenborough et al. 2007), as well as within sexually labile individuals (Korpelainen 1998).

Among monoecious species, sex expression is considered adaptive to optimize male and female resource allocation according to fluctuating or patchy resources and external conditions (Charnov and Bull 1977). According to Environmental Sex Determination (ESD), favorable conditions tend to increase femaleness, while environmental stress favors maleness (Charnov and Bull 1977; Freeman et al. 1981; Korpelainen 1998). In our study, stronger male bias among palms growing in the forest compared to pasture suggests resource limitation in forest. One obvious difference between the two environments was access to sunlight. While we found no significant effect of light availability on sex expression in A. phalerata, increased illumination led to a significant shift towards higher proportions of pistillate inflorescences in A. speciosa. Several other palm species also amplify female flower production with increased light (Voeks 1988, 2002; Scariot et al. 1995; Cunningham 1997; Barot et al. 2005; Berry and Gorchov 2006; Andreazzi et al. 2012), supporting the idea that female function is relatively more sensitive to resource availability than male function (Voeks 1987).

Plant size is also commonly cited as driving gender switching (Bierzychudek 1984; Clay 1993; Zhang et al. 2014). The size advantage model (Charnov 1982; Vega-Frutis et al. 2014) predicts that larger individuals are more likely to display female flowers. Of course, ecological context is key when considering the impacts of ontogeny on sex expression: interactions between plant size and environment directly affect resource status. Previous Attalea studies implicate the role of environment and plant size on inflorescence sex determination (Voeks 1988; Anderson 1983; Feil 1996, Barot et al. 2005). Voeks (1988) observed a transition from male to female with increased height in Attalea funifera, ascribing the shift to greater access to sunlight. Anderson et al. (1991) and Feil (1996) also reported greater numbers of staminate inflorescences during early reproductive years in A. speciosa and A. colenda, and a subsequent decline in the ratio of staminate-to-pistillate inflorescences as palms grew upwards. We found evidence of size-related sex changes in A. phalerata, but instead of increased female investment with height, taller palms produced fewer pistillate and more staminate inflorescences. This unexpected increase in male inflorescence with height may be related to efficiency gains in pollen dispersal. Plastic sex allocation offers flexibility to alter gender expression to match neighborhood conditions (e.g., closed versus open vegetation), thereby optimizing fitness (Friedman and Barrett 2009; Millerón et al. 2012).

Hidden mechanisms control sex determination

Linking the sequential patterns of male and female inflorescence to specific biotic or abiotic factors is complex, since environmental stress and resource availability regulate patterns over different phases of reproduction during (1) inflorescence sex differentiation, (2) bud development, and (3) fruit ripening (Lloyd 1979). In the case of *Attalea*, inflorescence sex determination and bud abortion were the underlying mechanisms controlling sex expression and operated along a continuum from bud initiation to anthesis. Inflorescence sex determination in our study species occurred well before expansion of the associated spear leaf, up to 3-4 year prior to flowering (Anderson 1983; Tucker Lima 2010), making it difficult to pinpoint drivers of sex expression. Sex differentiation may also depend on feed-back signals from developing fruit or past environment conditions, such as drought (Jones 1997; Legros et al. 2009). Even for the muchstudied African oil palm (Elaeis guineensis), which also produces unisexual male and female inflorescences, the exact timing of sex determination remains elusive (Jones 1997; Adam et al. 2011). To complicate things further, Hartley (1977) presented evidence that, under stress, female inflorescence buds in E. guineensis are preferentially aborted. If true, present-day phenological observations offer a distorted view of initial sex differentiation patterns and mask the early operation of internal and external factors that determine inflorescence sex.

Conclusions

Our aim in this paper was to assess the consequences of forest clearing on the reproductive biology of remnant tree populations by comparing *A. phalerata* and *A. speciosa* phenology in old-growth tropical forest and actively grazed pasture. Results illustrate that forest conversion to pasture does not always precipitate the demise of remnant trees and may even stimulate flowering and fruiting. The underlying mechanisms that direct changes in phenology vary from one species to another, depending on life history and biotic and abiotic conditions. Although *A. phalerata* and *A. speciosa* are closely related and exhibited similar responses to landscape change, flowering and fruiting in these two species were driven by different factors.

Unmeasured variables, such as soil quality, moisture availability, grazing intensity, and finer scale climatic variables likely also influenced *Attalea* phenology. A more extensive phenological history and environmental context would help improve our understanding of the dynamics of sex expression, as plants react to the balance of available resources. Besides abiotic environmental factors, Adam et al. (2011) also cited metabolic factors (e.g., carbon reserves), hormone status, and genetic composition as influencing a plant's decision to produce male or female inflorescences. The extent to which environment can trump or interact with these factors deserves further study.

Reproductive phenology is an excellent lens through which to gauge plant species' responses to landscape change (Laurance et al. 2003). Surely not all tree species can withstand landscape change, as some will be more or less susceptible to the environmental, physiological, and genetic stresses imposed by deforestation and fragmentation. In the case of Attalea, adaptation to pasture conditions and the capacity to enhance reproduction through extended phenophases and changes in sex expression place these species in an advantageous position for population recovery if bottlenecks to seedling growth and establishment are removed. Attalea regeneration from seed is generally negligible in pastures due to cattle grazing (herbivory) and parched conditions (Anthelme et al. 2011; Mitja and Ferraz 2001). The absence of post-seedling and juvenile size classes in pastures attest to these harsh circumstances (Sanin et al. 2013; Athayde and Morellato 2014). Still, if grazing, weeding, and burning interventions are mitigated, the continued and elevated reproductive success of remnant Attalea palms may spur recovery and subsequent forest regeneration.

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