Distinct seeds in contrasting habitats: Morphological and reproductive responses in Butia eriospatha to new environmental conditions

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ABSTRACT

Distinct environments drive particular responses in the reproduction pattern of plants and may have ecological and evolutionary consequences for local populations. Currently, populations of the palm Butia eriospatha are found in forests and open grasslands in southern Brazil, providing opportunities to investigate how this species responds to recent habitat transformations. We assessed phenology and fruit morphology in two geographically close populations of B. eriospatha under contrasting environmental conditions – forest and open grassland – to address the following questions: 1) Are there phenotypic differences between populations of B. eriospatha occurring in contrasting habitats? 2) What ecological and evolutionary consequences could those differences impose on local populations? Greater variation was observed within the forest population. The grassland population showed lighter endocarps on average, reflecting a greater proportion of pulp per fruit, but smaller seeds, which may suggest plasticity, local adaptation, or both after the habitat transformation. Reproductive status is dependent on individuals’ sizes in the forest environment but not for the open grassland population. Additionally, the average production of infructescences per individual is lower in the forest environment. Our findings indicate that the transformation of B. eriospatha’s habitat has promoted important phenotypic changes. We emphasize the importance of forest environments in promoting dispersal selectivity, which may increase population fitness through time.

1. Introduction

Local environmental conditions are critical in determining how plant populations perform and adapt through time (Anderson et al., 2012). Distinct habitats with contrasting environmental conditions may be associated with different population patterns in phenology (Duchoslav, 2009), reproduction (Seguí et al., 2018), and fruit morphology (Munthali et al., 2012; Mkwezalamba et al., 2015), among other traits (Guerrero et al., 2018). Such changes in population performance arise from natural selection, where phenotypes with the highest fitness prevail, from individual plasticity (Jacobs and Lesmeister, 2012; Michel et al., 2014), or from both. As a result, distinct ecological responses, and therefore evolutionary consequences, may be expected (Gram and Sork, 2001). In addition, responses in other organisms interacting with the plant, e.g., seed dispersers or predators, are also expected to vary depending on the number of interactions involved in each particular environment (Fragoso et al., 2003; Beckman and Muller-Landau, 2011).

Natural ecosystems have been drastically transformed since the rise of modern agriculture around the world (Foley et al., 2005; Laurance et al., 2014; Newbold et al., 2015). Over the past century, humans have driven landscape transformation across many Central and South American ecosystems, generally from forested to non-forested systems (Pacheco et al., 2011; Ribeiro et al., 2009), yet some biomes in this region are naturally open and constrained by abiotic factors (e.g. Cerrado and Pampa). During the transformation process, some tree and palm species have been retained or even planted in these new, open environments. The reasons for this are not well documented for all the ecosystems where it has happened. Nevertheless, pieces of evidence suggest that cultural importance and human use, both economic and non-economic, have generally played roles in this process (Bondar, 1964; Harvey and Haber, 1999; Pulido and Caballero, 2006; Harvey...
et al., 2011; Santos and Mitja, 2011; Silva et al., 2012). Anecdotal evidence, such as chainsaws and axes being damaged by the fibrous palm stems, also help to explain the maintenance of this group of plants in open landscapes. Despite the large-scale transformation of the South American landscape, some fragmented forests have been left behind or were less exploited (Ribeiro et al., 2009; Vibrans et al., 2012). These remaining fragments vary in size, form, connectivity, and in terms of current disturbances, but still are valuable sites for comparison with more intensively modified environments such as open grasslands when the same species is present under both conditions.

Several palms are currently found in contrasting environments in Brazilian biomes as a consequence of anthropogenic interventions, e.g., Mauritia flexuosa (Rull and Montoya, 2014); Attalea speciosa (Barot et al., 2005; Silva et al., 2012; Tucker Lima et al., 2018); A. dubia (Meiga and Christianini, 2015); A. phalerata (Sopchaki, 2014; Tucker Lima et al., 2018). This represents an opportunity for the investigation of responses, risks and adaptive potential that emerge from habitat differentiation (Barot et al., 2005; Meiga and Christianini, 2015), especially for species with urgent needs for conservation and management strategies. This is the case for Butia eriospatha (Martius ex. Drude) Beccari, a remarkable palm species that occurs in the Southern Plateau of Brazil. This species is associated with the Araucaria Forest, a type of forest formation in the Atlantic Forest biome that has experienced massive transformation in the past century (Ribeiro et al., 2009).

Butia eriospatha is a monoecious palm with seasonal reproduction and predominantly allogamous with potential for self-fertilization when solitary despite protandrous inflorescences (Nazareno and Reis, 2012). In general, adult individuals grow to 6 m and typically occur in clusters (Reitz, 1974). B. eriospatha is currently found in two contrasting habitats, Araucaria Forest fragments and open grasslands. Its ripe fruits are globose and yellowish with a sweet and fleshy mesocarp – containing one to three seeds inside the endocarp (Lorenzi et al., 2010) – highly appreciated by local communities for food (Bourscheid, 2011). Butia eriospatha is considered critically endangered by the national environmental ministry in Brazil (MMA, 2014) and is listed as vulnerable on the IUCN Red List (Noblick, 1998). It is at high risk of local extirpation due to demographic restrictions caused by cattle predation and illegal poaching of adult individuals for sale as ornamental plants (Nazareno and Reis, 2013a, b), leading to a call for more studies regarding the species’ ecology. Despite previous efforts in characterizing the species’ morphology, ecology and neutral genetic diversity, no study has considered populations of B. eriospatha in natural forest environments. Therefore, understanding the differences between forest and open grassland populations of B. eriospatha is critically important to clarify the possible impacts of habitat transformation on the ecology and evolution of this species.

Phenotypic differences observed in natural populations can be characterized by fruit morphological descriptors (Franco and Hidalgo, 2003). Fruit and seed size variability, within and among populations are an important component in the adaptation and evolution of trees in tropical and sub-tropical ecosystems. This is especially true for species dependent on zoochoric dispersal (Howe, 1986; Wheelwright, 1993), including most palm species (Zona and Henderson, 1989). Dispersal is one of the most important factors in determining spatial distribution in palms (Eiserhardt et al., 2011) and may be intimately related to the process of natural selection in this taxon (e.g., Galetti et al., 2013). Butia eriospatha is an important food source for animals that eat its fruits (Nazareno and Reis, 2012), suggesting dependence on vertebrates for dispersal. Traits related to phenology and reproduction in palms are greatly affected by the environment (Amadeu et al., 2016; Tucker Lima et al., 2018), and divergent conditions may lead to differentiation among populations.

In spite of its use potential and ecological importance, little is known about existing variation in fruit morphology, reproductive status and infructescence production among and within wild B. eriospatha populations, particularly with regard to those in the Araucaria Forest.
Therefore, the aim of this study is primarily to describe how *B. eriospatha* occurring in two contrasting environments (Araucaria Forest and open grassland) vary in terms of fruit morphology, reproductive patterns and infructescence production. Secondly, we test the hypothesis of phenotypic differences between grassland and forest environments. Finally, we discuss possible ecological and evolutionary consequences of phenotypical differences in *B. eriospatha* found between contrasting environments.

2. Material and methods

2.1. Study site and populations

Two wild populations of *B. eriospatha*, located on a private property (−27°12′10″; 50°36′31″) in Southern Brazil, were selected for this study (Fig. 1). This region has a maritime climate (Cfb) according to Köppen's classification, with annual average temperatures between 16°C and 17°C and precipitation between 1,600 mm and 1,700 mm (Alvares et al., 2014). This area is characterized by plateau areas under the influence of the Araucaria Forest, where *B. eriospatha* shows a broad but discontinuous distribution, generally found in altitudes between 800 m and 900 m (Bourscheid, 2011). According to the property owner, the adult individuals of *B. eriospatha* are more than 100 years old and were used for decades for crina vegetal production (palm fibers produced from leaves for multiple purposes, such as mattress and cushion manufacturing).

One of the selected populations (GRA) occurs in a landscape of open grassland where all trees except *B. eriospatha* were removed more than 60 years ago for timber production and livestock has been raised in this area for more than 100 years (property owner, personal communication). The maintenance of *B. eriospatha* is likely associated with the crina vegetal production, the appreciation for its fruits, and the use of leaves and fruits to feed the livestock. In this population, all *B. eriospatha* individuals are exposed to direct sunlight. Management practices including frequent mowing and occasional burning has been applied to this area, which maintains the open character of the landscape (Fig. 1).

The other population (FOR) is situated in a fragment of Araucaria Forest, where *B. eriospatha* individuals grow beneath the canopies of larger trees, such as *Araucaria angustifolia* and *Podocarpus lambertii*. Systematic, low-impact timber harvesting has been practiced in this forest fragment within the past century but left little impact on the forested landscape of the fragment (Fig. 1). This area does not receive any other management interventions besides the constant presence of cattle.

We established one permanent plot in each environment for observations (220 m × 220 m in FOR; and 220 m × 260 m in GRA). All *B. eriospatha* individuals (sample units) within each plot were measured for diameter at breast height (DBH) and total height, and were classified as adults, according to Nazareno and Reis (2013a). The two plots are approximately 2 km apart and, since there appears to be low genetic differentiation between the two populations (based on neutral nuclear markers; R. Candido-Ribeiro, unpublished data), we assume they formed a single population in the forest environment prior to human landscape transformation. Additionally, no major differences are expected in climatic conditions between them.

2.2. Morphological descriptors of fruits

We sampled fruit from 32 to 22 randomly selected reproductive individuals (sample units) within the GRA and FOR plots, respectively. Due to the low number of individuals bearing mature fruit in the FOR plot, we also sampled eight individuals just outside the plot but still within the same forest fragment, totaling 30 sampled individuals for this population. We collected 40 mature fruits from each sampled individual (single infructescences) in the GRA population and 31–40 mature fruits per individual in the FOR population, producing a total of 2,448 fruits from 62 different individuals.

Fruits were assessed for the following morphological variables: i) fresh fruit mass (g); ii) pyrene (endocarp + seeds) mass (g); iii) maximum fruit diameter (cm); and iv) fruit length (cm). Fruit and pyrene mass (obtained immediately after pulp removal) were assessed with a semi-analytical weighing scale. The maximum diameter and the length of fruits were measured with a digital caliper. We also estimated the pulp mass (g) and the proportion of pulp per fruit using the following equations: \( P_0 = P_f - S_v \), and \( P_r = \left( \frac{P_f}{P_i} \right) \), where \( P_f \) is the pulp mass for the jth fruit from the ith individual, \( P_r \) is the fresh fruit mass, \( S \) is the pyrene mass and \( P_r \) is the proportion of pulp per fruit.

After averaging the measurements of fruits for each sampled individual, we used descriptive statistics to describe variation within each population. We also visualized the data sets for each morphological variable in box plots for a better interpretation of how each trait varied within and among individuals within populations (Supplementary material S1).

In order to test the differences in fruit morphology between the two environments we fitted a mixed effect model for each descriptor (dependent variable) using the *lme* function implemented in the package nlme (Pinheiro et al., 2018) in R software – v. 3.3.0 (R Core Team, 2016). For each model, habitat (forest and grassland) was considered a fixed effect and the fruits were nested within each reproductive individual to be counted as a random effect with a nested structure (random intercept). This approach was used to control for non-independence among the measured fruits within each individual (Harrison et al., 2018). Likelihood ratio tests were performed between full and reduced models to test the significance of the estimated coefficients for the fixed effect and consequently the significance of the difference between FOR and GRA.

We used non-parametric approach to compare DBH and height between the two habitats using 95% confidence intervals constructed with bootstrapped samples (1,000 samples for 95%). The bootstraps were constructed using standard functions (resampling) in R software – v. 3.3.0 (R Core Team, 2016). If the confidence intervals from the two populations overlapped, the means were not considered significantly different.

Relationships among all morphological descriptors of fruits within populations were analyzed using Spearman correlation implemented in the package "Hmisc" (Harrell, 2019) in R software – v. 3.3.0 (R Core Team, 2016). The relationships were depicted in scatterplots with trendlines and visually compared to assess possible differences between the two populations.

2.3. Reproductive status

In order to identify and quantify reproductive individuals, all *B. eriospatha* individuals (sample units) within each plot were monitored over one reproductive season (October 2015 to March 2016). An individual was considered reproductive if any reproductive structure – male/female inflorescence or infructescence – was observed during the season. A generalized linear model using logistic regression and following a binomial distribution was used to test the hypothesis of positive association between individual size and reproductive status in each population, and to verify if the populations diverge in terms of size-related reproductive patterns. We used the model equation:

\[
g(\mu) = \beta_0 + \beta_1 X, \quad \text{where } g(\mu) \text{ is the logit function } (\ln \left( \frac{\mu}{1-\mu} \right)), \quad \mu \text{ is the predicted reproductive status given the growth variable } X \text{ (either height or DBH) and } \beta_0 \text{ and } \beta_1 \text{ are the estimated intercept of the model and the estimated coefficient of the variable } X, \text{ respectively.}
\]

The growth variables used to fit the models (height and DBH) were fitted separately to verify which of the variables best predicts reproductive status of individuals. For this, we used the “nle” package (Pinheiro et al., 2018) in R software – v. 3.3.0 (R Core Team, 2016).
models were compared based on the Akaike Information Criterion (AIC) (Burnham and Anderson, 2002). A log-likelihood ratio test was performed to test the fitted model against a reduced model (without the explanatory variable) and to obtain the significance of the coefficients.

2.4. Number of infructescences through time

The difference between the two environments concerning timing and number of infructescences per individual was also tested. We examined randomly selected reproductive individuals (sample units) five times from October 2015 to March 2016 in the FOR (NP = 38) and in the GRA (NP = 34) plots, respectively. The first and the second observation were performed approximately three months apart from each other and the third last observations were performed approximately every two weeks. The total number of infructescences on assessed individuals (Ni) and the average number of infructescences per individual (ΣNi) in each population were obtained for each observation time. We modeled the number of infructescences per individual in relation to time by fitting a Generalized Linear Mixed Model, using a Poisson regression (Supplementary material S2 for detailed information).

3. Results

3.1. Population and fruit descriptors

We observed 109 adult individuals in the GRA plot (19.1 ind ha\(^{-1}\)), 101 of which were reproductive (17.7 ind ha\(^{-1}\)), and 209 in the FOR plot (43.2 ind ha\(^{-1}\)), 58 of which were reproductive (12.0 ind ha\(^{-1}\)). The maximum number of infructescences observed (including both ripe and unripe fruits) during the assessments was 108 in GRA (across 34 individuals), ranging from one to six infructescences per individual, and with a maximum average of 3.18. This value was greater (p < 0.05) than the maximum average number of infructescences per individual observed in the FOR population (1.97; in 38 individuals), which ranged from one to four and totaled a maximum of 75 infructescences during the assessments (Table 1). When all the individuals within the plots were considered, no significant difference was observed for height between the two populations (p > 0.05). However, for the mean DBH, FOR presented a significantly higher value (p < 0.05) (Table 1).

We observed significant differences (p < 0.05) between the GRA and FOR populations for two of the six studied morphological fruit descriptors. The GRA population showed the greatest mean value for the proportion of pulp per fruit (0.78, p < 0.001) (Table 2); and the mean value of pyrene mass (endocarp + seeds) was significantly greater in the FOR population (1.88 g, p = 0.015) (Table 2). The FOR population also showed the widest range for most fruit descriptors. However, the coefficient of variation (CV) was similar between the populations for most of the descriptors, with exception for the pulp mass and the proportion of pulp per fruit (Table 2). The average size (height and DBH) of sampled individuals was not significantly different between the two populations (p > 0.05). Variance in the evaluated descriptors was high both within and among reproductive individuals of each population (Supplementary material S1).

### Table 1
Population descriptors for the sampled *B. eriospatha* grassland (GRA) and forest (FOR) populations.

<table>
<thead>
<tr>
<th>Population descriptors</th>
<th>FOR</th>
<th>GRA</th>
</tr>
</thead>
<tbody>
<tr>
<td>N (ind ha(^{-1}))</td>
<td>43.2</td>
<td>19.1</td>
</tr>
<tr>
<td>H (m) (\text{ns}^a)</td>
<td>5.78</td>
<td>5.65</td>
</tr>
<tr>
<td>DBH (cm) (\text{ns}^a)</td>
<td>33.37</td>
<td>31.92</td>
</tr>
<tr>
<td>N(_{120}) (ind ha(^{-1}))</td>
<td>12.0</td>
<td>17.7</td>
</tr>
<tr>
<td>N(_{28})/N (\text{ns}^a)</td>
<td>0.28</td>
<td>0.92</td>
</tr>
<tr>
<td>N(_{1})</td>
<td>38</td>
<td>34</td>
</tr>
<tr>
<td>N(_{1}) (\text{ns}^a)</td>
<td>75</td>
<td>108</td>
</tr>
<tr>
<td>N(<em>{1}/N</em>{120}) (\text{ns}^a)</td>
<td>1.97</td>
<td>3.18</td>
</tr>
</tbody>
</table>

\(N\): number of individuals per hectare (ind ha\(^{-1}\)); \(H\): average height (m) of individuals within the plot. \(\text{DBH}\): average DBH (cm) of individuals within the plot. \(N_{120}\): number of sampled individuals for fruit morphology. \(N_{28}/N\): proportion of reproductive individuals within the plot. \(N_{1}/N\): number of assessed individuals for phenology. \(N_{1}\): maximum number of infructescences on the assessed individuals. \(N_{1}/N_{120}\): average number of infructescences per assessed individual. \(\text{ns}^a\): p ≤ 0.05. ns: p > 0.05.

### Table 2
Differences between grassland (GRA) and forest (FOR) *B. eriospatha* populations for the measured fruit morphological descriptors. \(p\)-values were extracted from the likelihood ratio tests between full and reduced models.

<table>
<thead>
<tr>
<th>Populations</th>
<th>FOR</th>
<th>GRA</th>
</tr>
</thead>
<tbody>
<tr>
<td>N(_{1})</td>
<td>38</td>
<td>32</td>
</tr>
<tr>
<td>N(_{120})</td>
<td>1.168</td>
<td>1.280</td>
</tr>
<tr>
<td>N(_{28}/N)</td>
<td>31–40</td>
<td>40</td>
</tr>
<tr>
<td>H (m) (\text{ns}^a)</td>
<td>5.49</td>
<td>6.25</td>
</tr>
<tr>
<td>DBH (cm) (\text{ns}^a)</td>
<td>32.14</td>
<td>34.7</td>
</tr>
<tr>
<td>Fruit descriptors</td>
<td>Mean ± SD</td>
<td>Range (min. - max.)</td>
</tr>
<tr>
<td>Fresh fruit mass (g) (\text{ns} (p = 0.308))</td>
<td>6.55 ± 1.92</td>
<td>3.158–13.50</td>
</tr>
<tr>
<td>Pyrene mass (g) (\text{ns} (p = 0.015))</td>
<td>1.88 ± 0.45</td>
<td>1.257–3.11</td>
</tr>
<tr>
<td>Max. diameter of fruits (cm) (\text{ns} (p = 0.124))</td>
<td>2.25 ± 0.24</td>
<td>1.68–3.05</td>
</tr>
<tr>
<td>Fruit length (cm) (\text{ns} (p = 0.187))</td>
<td>2.05 ± 0.19</td>
<td>1.69–2.38</td>
</tr>
<tr>
<td>Pulp mass (g) (\text{ns} (p = 0.005))</td>
<td>4.66 ± 1.67</td>
<td>1.90–11.32</td>
</tr>
<tr>
<td>Proportion of pulp per fruit (*** (p &lt; 0.001))</td>
<td>0.70 ± 0.06</td>
<td>0.59–0.84</td>
</tr>
</tbody>
</table>

\(N_{1}\): number of individuals sampled for fruit morphology. \(N_{120}\): number of sampled fruits. \(N_{28}/N\): number of sampled fruits per individual. \(H\): average height (m) of sampled individuals. \(\text{DBH}\): average DBH (cm) of sampled individuals. SD: Standard deviation. ***: p ≤ 0.001. \(\text{ns}^a\): p ≤ 0.05. ns: p > 0.05. CV: coefficient of variation.
p = 0.004), contrasting with a non-significant correlation in the FOR population ($r_s = -0.31; p = 0.094$; Fig. 2). The correlation of the proportion of pulp per fruit with the pulp mass was positive and significant in FOR ($r_s = 0.50; p = 0.005$), while non-significant in GRA ($r_s = 0.16; p < 0.368$). The correlation between fresh fruit mass and pulp mass for the GRA population ($r_s = 0.97; p < 0.001$) and for the FOR population ($r_s = 0.96; p < 0.001$), in addition to the correlation between fresh fruit mass and maximum fruit diameter for GRA population ($r_s = 0.93; p < 0.001$) and FOR population ($r_s = 0.92; p < 0.001$) were the strongest positive correlations observed (Fig. 2).

### 3.3. Reproductive status

A positive and significant association between size (both height and DBH) and reproductive status of individuals was observed in the FOR population ($p < 0.001$ and $p < 0.05$, respectively). However, height ($\Delta AIC = 0.0$) was found to be a better predictor of reproductive status over DBH ($\Delta AIC = 15.5$) in this population (Fig. 3A and B). No significant association between individual size (height or DBH) and reproductive status was observed in the GRA population ($p = 0.519$ and $p = 0.506$, respectively), indicating that all classes of height or DBH present a similar proportion of reproductive individuals when *B. eriospatha* is in an open grassland environment (Fig. 3C and D).

![Fig. 2. Scatterplots with the Spearman correlations ($r_s$) among all the measured fruit morphological descriptors in *B. eriospatha*. Trendlines were added to facilitate the visualization of each association. $p$-values for the correlations are depicted within each graph. FOR: forest population. GRA: grassland population.](image-url)
3.4. Number of infructescences through time

A significant difference between the two populations was observed for the mean number of infructescences ($p < 0.05$) at most observation times (Fig. 1 – Supplementary material S2). The largest difference was observed when the populations reached their maximum production of infructescences per individual i.e., between 89 and 108 days of assessment ≈ January 2016 (Fig. 1, Supplementary material S2). The difference between FOR and GRA for the number of infructescences produced through time was confirmed to be highly significant ($p < 0.001$) after the log-likelihood ratio test between the full and the reduced models (Supplementary material S2).

4. Discussion

This is the first attempt to report and compare the variation in fruit morphology, reproductive status and production of infructescences in two populations of B. eriospatha that currently occur in different environments, forest and open grassland. Despite the short distance between the two populations (≈ 2 km), we detected significant differences across two important fruit morphological descriptors, reproductive patterns, production of fruits, and demographic parameters. These differences have likely been triggered by differences in local environmental conditions resulting from the transformation of the landscape. Local adaptation or extirpation due to evolutionary forces are expected through time (disregarding the effect of cattle predation). Here we discuss how differences between the habitats may be playing a role in local adaptation of B. eriospatha populations.

4.1. Population and fruit descriptors

The two studied populations presented a remarkable difference in census size. The FOR population has more than twice the total number of individuals per hectare when compared to the GRA population (43.2 ind ha$^{-1}$ and 19.1 ind ha$^{-1}$, respectively) and is comparable to what was found by Nazareno and Reis (2013a) in three other grassland populations studied in the same region (39, 58 and 40 ind ha$^{-1}$). The same authors also studied another grassland population with a similar number of individuals to our grassland population (16 ind ha$^{-1}$). Since the FOR and GRA populations are close to each other, it is assumed they once formed a single population, before the transformation of the landscape which occurred at least 60 years ago. Therefore, the observed difference in census size between the two populations, together with the fact that fallen and dying palms were seen in the grassland area (personal observation), suggests that the landscape change may also have affected the demographic dynamic of the species in addition to fruit morphology and reproductive patterns. Nevertheless, long term demographic studies with more populations are necessary to confirm this pattern. Another study of four open grassland populations of B. eriospatha estimated a reduction up to 50% in effective population size over the next 40 years (Nazareno and Reis, 2013a), owing to mortality and low seedling recruitment, which aligns with the observed difference between FOR and GRA in our study.

The FOR and GRA populations differed significantly in two of the evaluated fruit traits. While GRA showed fruits with heavier pyrenes (endocarp + seeds), which reflected a lower proportion of pulp. FOR presented the broadest range of values for most of the studied traits. This suggests that, with the transformation of the landscape, GRA was submitted to distinct selective pressures (e.g., light and water availability), pushing the
population to express different phenotypes (with smaller seeds and more pulp per fruit), but using the preexisting genetic variation from the original environment (forest).

A possible explanation for the observed differences in fruits and pyrenes between FOR and GRA is the cross-pollination rate, as significant increases in pulp yield per fruit is characteristic of self-pollinated individuals of *B. odorata* (Eloy, 2013). This suggests that when geitonogamy takes place – a form of self-pollination observed in open grassland populations of *B. eriospatha* (Nazareno and Reis, 2012) – pyrenes, and consequently the seeds, exhibit a reduced size, which in turn, is associated with higher proportion of pulp per fruit. Similarly, heavier pyrenes in the FOR population, and thus larger seeds, suggest more outcrossing in this environment. Larger seeds of *Mauritia flexuosa* – a palm species native from northern South America – were also observed in forested environments when compared to disturbed savannas in northern Brazil (Rosa et al., 2014).

Differences between populations have been observed in fruit descriptors of other species of the genus *Butia* (*B. odorata*, Rivas and Barilani, 2004; *B. capitata*, Silva, 2008) but some differences may represent variation between reproductive seasons (Silva, 2008). The possible explanations for these differences were not thoroughly discussed by the authors; nevertheless, there is an argument for environmental and genetic causes.

### 4.2. Reproductive patterns

The proportion of reproductive individuals was nearly threefold higher in GRA than FOR (0.92 and 0.28, respectively). This proportion in GRA was similar to that observed in previously-studied open grassland populations (Nazareno and Reis, 2013a). The average number of infructescences per reproductive individual was higher in GRA (3.18) than in the FOR population (1.97) and similar to the number of inflorescences observed in another grassland population of *B. eriospatha* studied in the same region (3.15 in 2010 and 2.93 in 2011, Nazareno and Reis, 2012). However, the values presented in this study are the number of inflorescences and therefore, might overestimate the number of infructescences per individual. In other *Butia* species, average number of infructescences varies substantially (Rosa et al., 1998; Soares, 2013; Amadeu et al., 2016).

The high environmental heterogeneity common in forested environments (e.g., light, water, wind, moisture and soil nutrient availability), alongside higher inter- and intraspecific competition, are possible explanations for the FOR population’s low proportion of reproductive individuals showing fewer infructescences. Palms occurring in the understory of forest environments may show accelerated growth and higher reproductive rates in light gaps produced by falls or the death of larger trees (Ash, 1988). For populations of *Astrocaryum mexicanum*, a palm that occurs under the canopy of tropical rainforests in Mexico and Central America, the influx of light into the forest produced by gaps likely plays a fundamental role in the reproductive status of adult individuals (Piñero and Sarukhán, 1982). After studying the relationship of growth rates and reproductive status in *Geonoma macrostachys* – an understory palm – with the presence of canopy gaps, Svenning (2002) posited that fine-scale spatial and temporal variation in the opening of canopies of tropical trees plays a key role in the ecology of shade-tolerant understory plant populations. Since *B. eriospatha* individuals occurring in forest environments do not occupy the upper canopy and are therefore under the influence of gap dynamics, light availability is possibly one of the main determining factors in the reproductive potential of individuals.

In the forest environment, taller and thicker *B. eriospatha* individuals are more likely to have a reproductive structure than shorter and thinner ones, and height is a better predictor of reproduction than DBH. Significant associations between size and reproductive status were also observed in other palms in their natural habitats, e.g., *A. mexicanum* (Piñero and Sarukhán, 1982), *B. catarinensis* (Rosa et al., 1998), and *Acromia aculeata* (Scarioni et al., 1995). In our study, this pattern was not observed in open grassland environment, where almost all individuals were reproductive. In the GRA population, the reproductive status of individuals had no relation to their sizes. No correlation was found between DBH and reproductive status of *B. eriospatha* individuals in another open grassland population studied by Nazareno and Reis (2012). This reinforces the claim that light may be a determining factor in the reproduction of *B. eriospatha*, and that the transformation of the landscape, producing open habitats, may have changed the mechanisms involved in the selection of which individuals will reproduce in the population. Complementary studies in *B. eriospatha* involving multiple populations in both environments are necessary to validate if this pattern persists throughout the species natural range after the habitat transformation.

Another possible factor acting upon the flowering of *B. eriospatha* individuals under forest cover may be a reproductive fluctuation mechanism from one season to the next. Rosa et al. (1998) observed a fluctuation in the reproductive and non-reproductive state of individuals in a population of *B. catarinensis* on the southern coast of Brazil, suggesting the possibility of individuals alternating their reproductive state through time. A large variation in number of reproductive individuals among reproductive events was also observed in *Euterpe edulis* (Silva, 2011) and *A. mexicanum* (Piñero and Sarukhán, 1982), both understory palm species. Despite the evidence, long-term studies following the reproductive phenology of wild populations of *B. eriospatha* are necessary to confirm the occurrence of reproductive state fluctuation in forest environments and whether this mechanism occurs in open grassland populations.

### 4.3. Possible evolutionary consequences

Larger seeds may represent both a selective advantage and disadvantage for palm trees and could be understood as a trade-off between survival and dispersal (Howe, 1986). Larger seeds of the palm *Euterpe edulis*, for instance, show a higher potential of germination, and seedlings generated from larger seeds show higher total biomass values, indicating a greater potential of survival (Pizzo et al., 2006). A reduction in seed size of the palm *E. edulis* may even decrease the average fitness of a population (Galetti et al., 2013). Furthermore, while studying seed size in different groups of tropical tree species, Foster (1986) suggested that larger seeds could either increase the ability of seedlings to persist in an environment with low light intensity beneath a canopy cover, or even accelerate the initial vegetative growth of seedlings to reach strata with available light. On the other hand, an increase in seed size may imply a reduction in the number of seeds produced by the population as a whole, since more energy is allocated to producing larger seeds (Foster, 1986). This pattern is observed in the FOR population where the number of reproductive individuals and the number of infructescences per plant were significantly lower than in the GRA population, but the pyrenes (and, by inference, seeds) were larger. This reduction in reproductive potential in the FOR population may represent a selective pressure, resulting in fewer fruits and seeds produced by the population, but with seedlings generated by more capable and well-adapted individuals, which tends to increase the adaptive value of the population as a whole (Moore, 2001). A reduction in the total number of fruits produced by a population may also increase the selectivity of dispersers in finding the most rewarding individuals (Howe, 1986).

From another adaptive perspective, fruit characteristics in some groups of plants have been found to be associated with variation in seed dispersal rates (Herrera, 1988). Brewer (2001) observed that for the palm *A. mexicanum*, smaller seeds might be less predated and dispersed at longer distances, which contrasts with the adaptive advantages conferred by larger seeds described above. The same trade-off was observed for other tropical trees in previous studies (Howe, 1986). Therefore, the larger seeds of *B. eriospatha* observed in the forest
environment may increase the species’ chance of persisting in this type of environment, since it potentially confers better germination and greater seedling survival in the population. In contrast, a higher number of smaller seeds, observed in the open grassland environment, possibly represents a greater chance for dispersing across longer distances with a lower probability of predation. Hence, there seems to be a compensatory adaptive mechanism in *B. eriospatha* populations once the forest habitat is converted to open grasslands habitats, where germination and survival after germination may be reduced, but production of seeds and their dispersal could be more effective. While seeds are more exposed to predation in open environments, colonization of new areas and avoidance of density-dependent mortality near parents could be considered plausible advantages of a longer dispersal (Howe and Miriti, 2000).

Considering that fruit productivity in palms can be highly influenced by the environment (Freitas et al., 2016), the observed smaller variations in fruits of the GRA population may be related to the homogeneity of conditions in the open grassland habitat e.g., in light availability. Differences in fruit productivity due to differences in light availability have been observed in other understory palms (Martínez-Ramos et al., 2016; Amadeu et al., 2016). Moreover, other environmental factors may influence patterns in fruit production of palms (e.g., Rosa et al., 2014; Schindwein et al., 2017; Tucker Lima et al., 2018), suggesting that habitat transformation may lead to important changes in the reproductive mechanisms and fruit traits in this group of plants.

If a different selective pressure has taken place during the past years since the transformation of the landscape and at least one new generation was formed in the GRA population, an adaptive genetic component could be involved in the phenotypic variation observed between *B. eriospatha* populations. High heritability values for traits related to fruit production have been found in other palms (Passos et al., 2007; Oloye et al., 2009; Neto et al. 2013) and are expected in *B. eriospatha*. However, future experiments are necessary to verify the genetic control of each studied trait and determine which portion of the variation could be attributed to the adaptive genetic component.

5. Conclusions

Our study empirically demonstrated that the transformation of *B. eriospatha* habitat in one population from Araucaria Forest to open grassland more than 60 years ago might have caused shifts in local phenotypic variation of traits related to its reproduction and fruit morphology. These findings suggest not only possible changes in patterns of fruit production, but also of seedling survival and seed dispersal, possibly affecting ecological interactions with other organisms. If this is true for other populations, over generations, differences in conditions between remaining environments where of *B. eriospatha* occurs (e.g., forest and open areas) may act as selective drivers of local adaptation and subsequent population differentiation, speciation, or extinction. Given the uncertain evolutionary trajectory of this critically threatened species, further studies aiming to describe and confirm the evolutionary consequences of these phenotypic changes in local populations of *B. eriospatha* associated with specific habitats are crucial.

Author contributions

RCR and MSR conceived the study and designed the sampling method. RCR, MBL, TM, APB, NCFC and MPH collected the data. RCR analyzed the data. RCR wrote the manuscript. MBL, TM, APB, NCFC, MPH and MSR edited the text. All the authors have approved the final version of the manuscript.

Declarations of interest

None.

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Appendix A. Supplementary data

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References


