



Effects of ecological and anthropogenic factors on population demography of the harvested *Butia capitata* palm in the Brazilian *Cerrado*

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Abstract

Plant population response to ecological and anthropogenic factors provides essential information for conservation and management, mainly for species occurring in ecosystems under intense and rapid land use changes, like the *Cerrado*. We assessed the effects of land use and management upon the distribution of size and on the frequency of life stages of *Butia capitata*, an intensively harvested fruit palm, endemic to a southeastern portion of the Brazilian *Cerrado*. Most populations had a reverse-J size-class distribution, indicating good recruitment in the landscape even under fruit harvesting pressure and extensive cattle ranching. Regeneration was null or scarce in areas under more intense land use and management pressure, such as found on large, industrial farms. Soil fertility and texture were associated with seedling frequency, soil texture with sapling frequency, and precipitation with juvenile frequency. These factors must be taken into account for the enrichment, introduction and restoration of populations, actions demanded by traditional populations and family farmers who harvest the valuable fruits of *B. capitata*. Populations in areas with intense land use and inadequate management practices may be doomed to plummet. In contrast, in areas managed by traditional peoples and family farmers, characterized by low intensity of fruit harvesting and low frequency of cattle, populations should persist. Supporting traditional peoples and family farmers' livelihoods and promoting changes in the management of areas where the species occurs may contribute to in situ conservation of the *Cerrado's* biodiversity in multiple-use landscapes.

Keywords NTFP · Savanna palm ecology · Life stage abundance · Population structure · Management

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Introduction

Environmental gradients impose physiological constraints on the occurrence and abundance of organisms on different scales (Austin 2002; Barry and Elith 2006), and these organisms are also constrained by anthropogenic effects in disturbed areas (Newbold et al. 2015). Land-use change caused by human activities is one of the main drivers of biodiversity loss, increasing the loss, fragmentation and degradation of native vegetation, which affect demographic rates and population viability through their effects on landscape conditions and resource availability (Selwood et al. 2015). Understanding how plant populations respond to these effects in deforested and degraded ecosystems is, therefore, fundamental for conservation and management strategies (Host et al. 1996; Nicholls 1989). This is particularly important, because anthropogenic effects are quickly reshaping the natural conditions in tropical ecosystems.

Knowing how plants respond to ecological and anthropogenic pressures is even more important in ecosystems covering a limited area that is preserved and subject to intense and rapid land changes, as in the *Cerrado*. This biodiversity hotspot harbors more than 12,000 plant species, 4200 of which are endemic (Forzza et al. 2010). It faces a high deforestation rate (0.69% a year) and rapid land use change, which has resulted in the loss of half of its native vegetation cover (IBGE 2015). Only 3% of the *Cerrado* is protected by conservation units where human activity is not allowed (CNUC/MMA, 2017). Most of the remaining native areas are highly fragmented and immersed in a matrix of agriculture, pasture, mining, plantation forests and urban development. Plant populations in these areas are exposed to anthropogenic pressures, such as the harvest of plant parts and cattle ranching, which is common in savannas, and may face increased mortality and reduced recruitment to the next size classes or life stages (Gaoue and Ticktin 2007; Avocevou-Ayisso et al. 2009; Giroldo and Scariot 2015). If regeneration failure lasts long enough, populations may not persist, eroding biodiversity at the landscape level (Tilman et al. 1994).

Due to the urgency of conservation initiatives and the unavailability of long-term data for most species and areas, it is important to extract as much information as possible from static data to reconstruct the trajectory of populations affected by anthropogenic and ecological changes (Doak and Morris 1999; Souza et al. 2010). Size class distributions (SCD) can provide an initial assessment of populations status (Bhuyan et al. 2003; Wiegand et al. 2000), because theoretically they result from a dynamic process of recruitment, growth and mortality that may reach a steady state when these processes are held constant for long enough (Wright et al. 2003), such conditions may not, however, be achieved in disturbed systems. Detailed size distribution analysis allows the detection of specific moments in the past trajectory of the population when recruitment across size classes was affected. In addition, life stages record contributes to incorporating information on survival, growth and fecundity, functions of individual variation in size, stage and/or age, which is possible as a tighter size-age correlation is stronger in perennial plants (Chu and Adler 2014).

Understanding population structure, regeneration, and the ecological and anthropogenic effects determining life-stage abundances can contribute to conservation and management actions, especially for non-timber forest species (NTFP) that provide products to rural communities (Ticktin 2004). The close connection between demographic responses and population viability provides a critical indication of extinction risk probability in response to human pressures (Selwood et al. 2015). In this study, we investigate the status of *Butia capitata* (here in after *Butia*) populations and ecological and anthropogenic gradients associated with the species' demography. This endemic

palm, restricted to the southeastern portion of *Cerrado* (Henderson et al. 1995), is a major non-timber forest product and contributes to the income, livelihood, and welfare of rural communities (Lima et al. 2010; Carvalho 2007). The sustainable use of this species may contribute to conservation strategies through biodiversity use, because the commercialization of its valuable fruits may foster conservation instead of the promotion of other land uses, such as agriculture and cattle ranching.

We assessed the population structure of *Butia* at 14 sites spanning throughout the species distribution in the *Cerrado* of Brazil. We asked the following questions: (1) Is there evidence of recruitment changes in populations subjected to different land use and management? We compared the size-class distributions of populations under different land uses and management practices to search for possible recruitment gaps, which may be detected in unbalanced size-class distributions. (2) Which ecological and anthropogenic variables are most associated with life stage abundance? We assessed the relative importance of ecological and anthropogenic variables for life stage by comparing several competing hypotheses, to identify the most important models and ecological and anthropogenic variables associated with life stage abundance. We posited that anthropogenic disturbances, mainly cattle ranching, would affect population structure, as they are associated with the frequency of life stages, negatively affecting smaller sized plants.

Methods

Species and study areas

Butia capitata (Arecaceae) known as *coquinho-azedo*, is a monoecious palm, growing up to 10 m in height, solitary, erect and slightly inclined. It is endemic to a well-defined region in northern and northwestern Minas Gerais, southwestern Bahia and northeastern Goiás states in Brazil (Lima et al. 2010). Although, in old literature, the species has been misidentified as occurring also in Paraguay, Argentina, Uruguay and southern Brazil, another species (*B. odorata*) occurs in these regions (Henderson et al. 1995). Populations have clumped distributions at all life stages. Seeds have dormancy and low germination rate, but do not form a permanent seed bank (Silva 2008). Fruits are widely used for the preparation of beverages, popsicles, and ice cream and are also consumed directly. Kernels are used for manufacturing edible oil and leaves are used for roofing and craftwork (Lima et al. 2010). Throughout the fruiting season, from June to January, fruits are harvested from wild populations and sold directly to food industries, cooperatives, restaurants, farm markets, and along main highways (A. Scariot, pers. obs). The demand for fruits and pulp far exceeds the production.

The *cerrado* sensu stricto vegetation predominates in the areas sampled. The climates are Aw, with dry winter, and Cwa, with dry winter and hot summer in the Köppen system. (Alvares et al. 2013). Precipitation varies from 760 to 1260 mm/year (INMET 2012), falling mainly during the summer, from October to March. Main soils are oxisols (57%) and inceptisols (43%) (IBGE and Embrapa 2001). Mean monthly temperatures vary from 19 to 25.4 °C, being colder in the dry season, from May to September, when precipitation is minimal to null.

Population sampling

Most populations of *Butia* are small, with a few scattered individuals and, with a few exceptions the sampled populations did not exceed 1–2 ha in size. Following extensive field observations, in the rainy season, early in 2011, we sampled 14 populations across an area covering 92,500 km², with different land use or management, separated by fences and located up to 380 km apart. The study sites were immersed in different landscape matrices and subjected to diverse ecological and anthropogenic conditions (Fig. 1, Suppl. Mat. 1). We sampled closely located populations only when land use and management were different between areas occupied by populations.

At four sites (C7H7F0, C6H6F0, C6H3F0b and C3H4F9) subject to an ongoing population dynamics study of *Butia*, we sampled all plants in 9–25 randomly placed 200 m² plots, and seedlings in a 25 m² subplot in the corner of each plot. At all other sites we sampled one large plot, 0.3–15 ha in size, and sampled seedlings either the whole area or in subplots randomly spread over the plot (Table 1). We recorded the height of all individuals from soil level to the insertion of the spear leaf in each plot, except for seedlings, which were sampled in subplots. We classified plants into life stages based on height, leaf morphology, stem, and reproductive structures. Seedlings and saplings do not have a visible aerial stem, to which sizes we attributed 1.0 and 5.0 cm, respectively. Seedlings have 1–5 entire, lanceolate eophylls, not presenting pinnate leaves. Saplings have pinnate leaves, with crown shaft without sheaths or remains of petioles. Juveniles have all leaves pinnate, with remains

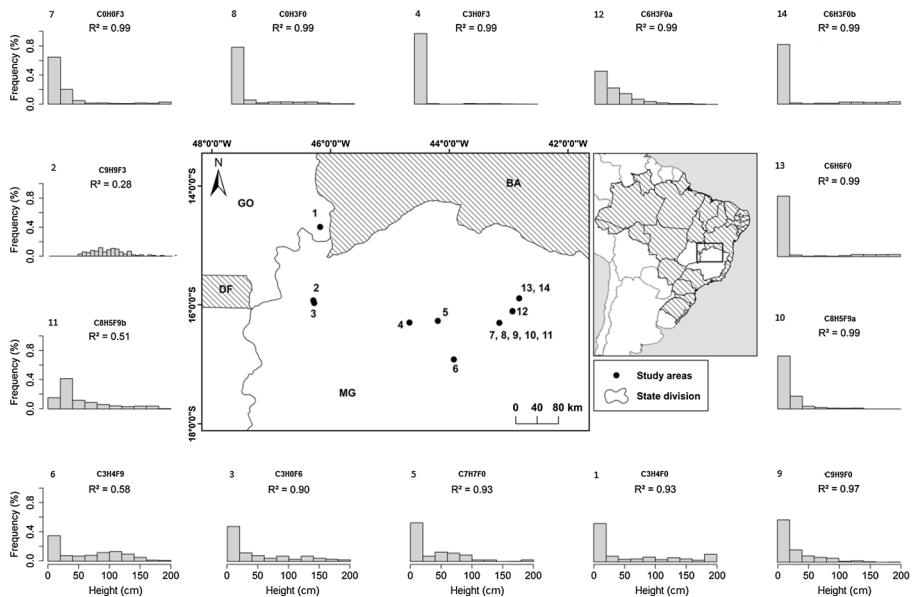


Fig. 1 Location of the 14 populations of *Butia capitata* studied in Cerrado, with acronyms named after cattle ranching (C), fruit harvest (H) and fire (F) indexes. Indexes summarize severity, duration and area of the perturbation. For example, a population named C8H5 means that it has cattle and fruit harvest indexes equal to 8 and 5, respectively. See Table 1 for correspondence of map numbers and population acronyms on Table 1. Histograms (high in classes of 20 cm) are ordered clockwise, beginning at the top left, following the negative exponential fitting

Table 1 Location and description of study sites—main characteristics of the 14 populations of *Battia capitata* studied in the Cerrado

Map number	Population code	Matrix	Altitude (m)	Latitude	Longitude	Sampled area (ha)	Sampled area (ha) (seed-lings)	Seedling (ind/ha)	Sapling (ind/ha)	Juvenile (ind/ha)	Adult (ind/ha)	<i>b</i> ± SE
1	C3H4F0	Pasture	760	- 14°41'21.86"	- 46°10'34.74"	0.3	0.11	433	57	177	397	0.08 ± 0.01*
2	C9H9F3	Pasture	570	- 15°55'14.80"	- 46°17'11.41"	15	0.15	0	0	0	7	0.002 ± 0.001*
3	C3H0F6	Cerrado	560	- 15°58'16.89"	- 46°16'32.67"	0.3	0.15	200	0	180	70	0.05 ± 0.01*
4	C3H0F3	Pasture	660	- 16°17'41.83"	- 44°40'16.38"	0.3	0.1	2250	230	127	50	0.25 ± 0.04*
5	C7H7F0	Cerrado	790	- 16°15'56.35"	- 44°11'47.71"	0.36	0.045	600	17	111	530	0.05 ± 0.01*
6	C3H4F9	Cerrado	980	- 16°54'53.22"	- 43°55'23.78"	0.5	0.0625	160	24	118	274	0.01 ± 0.005*
7	C0H0F3	Cerrado	995	- 16°17'59.32"	- 43°09'23.89"	0.675	0.1	190	49	455	77	0.06 ± 0.001*
8	C0H3F0	Pasture	955	- 16°17'47.75"	- 43°08'32.10"	0.45	0.1	949	67	371	247	0.12 ± 0.01*
9	C9H9F0	Pasture	930	- 16°17'17.60"	- 43°09'51.28"	0.39	0.39	41	87	982	203	0.05 ± 0.005*
10	C8H5F9a	Pasture	965	- 16°17'36.36"	- 43°09'59.90"	0.675	0.1	210	30	178	25	0.07 ± 0.002*
11	C8H5F9b	Pasture	965	- 16°17'36.36"	- 43°09'59.90"	0.3	0.1	10	3	437	157	0.01 ± 0.006
12	C6H3F0a	Pasture	790	- 16°06'24.64"	- 42°56'03.04"	0.4625	0.375	188	26	497	115	0.03 ± 0.001*
13	C6H6F0	Cerrado	920	- 15°53'34.59"	- 42°49'22.80"	0.18	0.0225	3244	11	211	539	0.18 ± 0.03*
14	C6H3F0b	Cerrado	880	- 15°53'34.59"	- 42°49'22.80"	0.32	0.04	1825	9	125	350	0.20 ± 0.05*

Population code summarizes the values attributed to cattle (C), fruit harvest (H), and fire (F) and are followed by score attributed (0–9), which is the sum of 0–3 scores for each of the three effects analyzed (severity, duration and area of the disturbance). Slope of the theoretical curve (b) with standard error (SE) summarizes the shape of the size distributions. Estimates followed by an asterisk indicate that the 95% confidence interval does not include 0. All Cerrado areas are of *cerrado sensu stricto*



of sheaths and stem, without exposed stem, and lack reproductive structures. Adults have all leaves pinnate, with remains of sheaths and petioles, with or without exposed stem, with reproductive structures or evidence of previous reproduction.

Ecological and anthropogenic variables

We collected three soil samples 0–30 cm deep at each site, homogenized and analyzed for nutrients and particles (Suppl. Mat. 1 and 2). We used mean annual precipitation for a 10 years period (2001–2010) from three weather stations close to the sampled populations (INMET 2012). In each population, we used the line intercept method (Canfield 1941) to sample vegetation cover in a line 100 m long and one meter above soil level (Floyd and Anderson 1987). We took three measures of terrain slope with a clinometer and used the mean in analyses.

We obtained fruit harvesting and cattle ranching information from landowners and from our field observations, and fire events from satellite images. Deforestation and vegetation thinning are proportional to cattle ranching, because cattle number and time spent by cattle are higher in pastures and null or close to null in areas with *Cerrado* vegetation. Cattle feed on inflorescences, young fruit bunches, leaves, and seedlings of *Butia* and can trample seedlings. Harvest involves the removal of most fruits during the peak of the fruiting season. To determine the frequency of fire we counted and summed fire scars in each site for the 10 years prior to the field sampling using LandSat 5.0 images composition R4G5B3. For the seedlings, we summed fire scars from the 2 years previous to field sampling, a time interval during which fire may inhibit fruit production and kill seedlings. For sapling, juvenile and adult, we used the sum of fire events for the last 10 years prior to field sampling, since for at least 8 years are needed for *Cerrado* plants to evade the fire-resistance threshold (Hoffmann et al. 2012). We used a modified interaction matrix (Leopold et al. 1971) to estimate the anthropogenic factors (Suppl. Mat. 2). Based on field observations and information from landowners, we assigned scores of 0–3 for the intensity, extent and duration of the impact of cattle and fruit harvest on each population. We assigned the highest score to the population with the highest frequency of fires, and proportional scores to the fire frequency for the others populations. As a result, every population scored 0–9 for cattle (named CAT—cattle grazing) and fruit harvest (HAR—fruit harvest) and fire (FIRE—fire) indexes, with 0 indicating no effect and 9 the highest effect.

Statistical analyses

Population structure

We assessed the homogeneity of life stage frequencies within populations, as well as differences among populations, with Chi square tests. Plant height is an appropriate variable to assess the structure of *Butia* populations because it is closely related to the onset of the reproductive phase, the maximum reproductive capacity, and longevity. Hence, the distribution of height classes is related to population balance through the recruitment of individuals in subsequent classes (Wright et al. 2003). We analyzed size distributions to search for evidence of changes in population structure and to predict the direction of population change with the fit of negative exponential distribution to make inferences about the population's continuous recruitment (Schumann et al. 2010; Souza et al. 2010). We tested the fit of the exponential distribution ($y = ae^{-bx}$) in all populations, the distribution

that describes populations with abundant regeneration (Condit et al. 1998). In this equation, y is the relative frequency of individuals in size class i , x_i is the midpoint of size class i , a is the intercept and b the slope, aka the rate parameter. We fit the observed distribution to the theoretical curve using nonlinear regression, with the function *nls* in base package of R. The slope of the theoretical curve (b) summarizes the shape of the size distributions, and we used it to search for structure differences between populations. Steeper negative slopes indicate a predominance of smaller individuals, with decreasing slope values indicating increased proportion of larger individuals. We re-sampled the estimated values of b 10,000 times with non-parametric bootstrap, with replacement, to obtain the mean b with 95% confidence (Crawley 2007) using the *boot* package of R (Canty and Ripley 2011). The frequency distribution of re-sampled values was used as a benchmark to rank populations according to the probability of randomly finding the estimated values.

Ecological and anthropogenic factors associated with life stages

To assess the effects of ecological and anthropogenic factors on the frequencies of life stages of *Butia*, we fit Generalized Linear Models (GLM) using the information-theoretic approach to translate biological hypotheses into statistical models (Burnham and Anderson 2002; Cade 2015). We treated *Butia* populations as independent observations following the data analysis protocol proposed by Zuur et al. (2010). A priori, we tested for collinearity between pairs of variables with a correlation matrix and graphs in the *cor* and *pairs* functions of the R environment, and used only those uncorrelated; when two were correlated we used the one that was easier to interpret. To account for the large number of soil variables and their non-independence, we used a Principal Component Analysis (PCA) to generate summary variables representing soil particle size (clay, silt and sand—TX), and fertility (FERT1 and FERT2). This technique is commonly applied to a set of variables to determine which variables form coherent subsets of the set and to visualize this change in a few original dimensions (Tabachnick and Fidell 2001). The scores generated by these analyses were then used as synthetic explanatory variables of the habitat with effect on plant frequency (Suppl. Mat. 2).

The population response variables, frequency of seedlings, saplings, juveniles, and adults are life stages and indicate potential regeneration, pre-established regeneration, established regeneration, and the reproductive capacity of the population, respectively. With the mathematical models, which represent hypotheses about the relationship between the response variables and habitat structure and management, we followed the multiple models approach to select the most plausible ones (Burnham and Anderson 2002). This approach argues in favor of judging each model according to the evidence, estimated by the Akaike Information Criterion (AIC) according to information theory (Anderson 2007). AIC indicates model plausibility based on its likelihood and number of parameters. To account for over-dispersion, we adopted the correction for small samples (AICc) proposed by Burnham and Anderson (2002) and the model with the lowest AICc as a benchmark to assess the relevance of other competing models. For this, we used the simple difference between the values of competing models AICc ($\Delta AICc = AICc_1 - AICc_2$) and the Akaike weight (wAICc) (Burnham and Anderson 2002). The wAIC indicates support for the model, i.e., the number of times the data set with the same information structure will be best explained by the model in question (Anderson 2007). Because the residual deviance was greater than the degrees of freedom, and the visual inspection of the Q–Q plot also indicated over-dispersion, we used binomial models to correct the standard errors. To

estimate the ability of the model to describe the variation in the response variable and the association level with the predictor variables, we calculated the ratio of the explained deviance by total deviance (Nagelkerke 1991). Using the subsets of candidate models, we estimated the averaged standardized coefficients (β) for each variable, its relative importance and significance. Model coefficients were standardized to avoid issues due to multicollinearity between predictor variables by multiplying the unstandardized coefficient in the model by the partial standard deviation of the variable (Cade 2015). The relative importance of each variable was measured as the ratio of the absolute values of model-averaged standardized estimates for variables (Bring 1994; Cade 2015). We used the MASS and MuMIn packages of R (R Development Core Team 2015) to obtain the models, coefficients and relative importance of each variable in the models set (Barton 2018; Ripley 2015). We assessed 128 models for seedlings and 64 models for each of the other life stages. Population C3H4F9 was not included in these analyses because its plots were very heterogeneous.

Results

Habitat characterization

Vegetation cover ranged from 9% to 53%, but with values between 21% and 38% for most populations. The average slope varied from 0° to 22°, but most slopes from most areas varied from 3° to 5.6°. The scores summarizing the anthropogenic disturbance parameters highlight a gradient to which populations are subject. Populations span from those with no fruit harvest and no cattle grazing, others with intermediate scores for one or both parameters, to those subject to intense fruit harvest and/or cattle grazing pressure (Suppl. Mat 1).

Soils are sandy, acidic, poor in nutrients, with high aluminum toxicity, low base saturation and sum of bases, and with little organic carbon and organic matter. The first score of the Principal Component Analysis (PCA) with soil texture explained 86% of total variance. Sand concentration (− 0.62) is the major source of variation in this component, followed by clay (0.56) and silt (0.54) (Suppl. Mat. 2). Areas have relatively heterogeneous soil texture, without defined groups of areas sharing similar grain fractions (Suppl. Mat. 2). Two principal components were required to summarize 77% of the observed variation in soil fertility variables. Potential acidity (− 0.48), aluminum concentration (− 0.47) and base saturation percentage (0.45) are the largest sources of variation in the first score of the PCA, and the sum of bases and cation exchange capacity extract the maximum variability not retained in the first linear combination. As with soil texture, no classes of soil fertility can be distinguished among areas (Suppl. Mat. 2).

Population structure

Life stage frequencies varied across populations ($\chi^2=92632.4$, $df=5239$, $p<0.001$; Suppl. Mat. 1). Seedling was the most abundant life stage (0–3224 ind ha^{−1}; median=205 ind ha^{−1}), with lower frequencies (0–41 ind ha^{−1}) in intensively managed areas (C9H9F3, C8H5F9b and C9H9F0). Sapling is the least abundant stage (0–230 ind ha^{−1}; median=25 ind ha^{−1}), except in two populations (Fig. 2).

The size class distribution of most populations was a reverse-J shape (Fig. 1). In all but two populations, the first size class (0–20 cm) formed mainly by seedlings predominates. All but three populations had high fit to the reverse-J model ($r^2 < 70\%$) (Fig. 1).

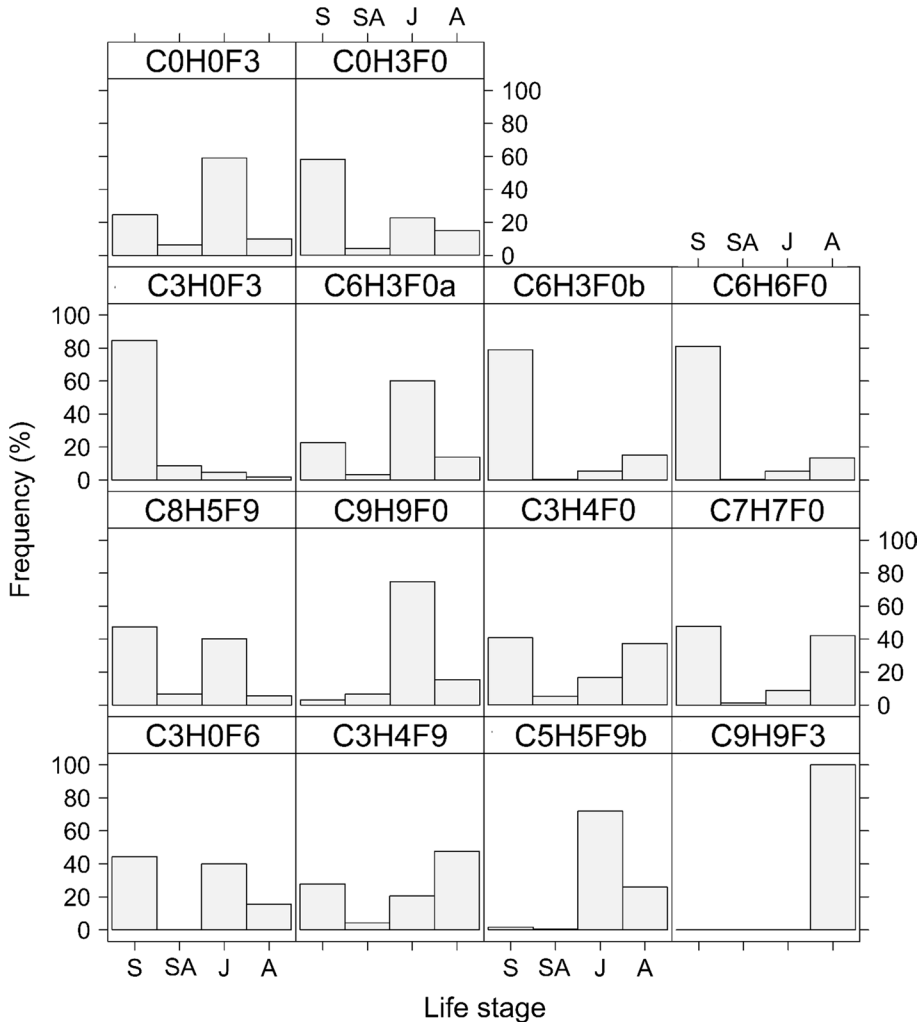


Fig. 2 Proportion of individuals in each life stage of the 14 populations of *Butia capitata* studied in *Cerrado*

Three groups can be identified based on bootstrap re-sampling: four populations with *b* smaller than the first quantile (numbers 2, 6, 11 and 12), seven with *b* between the first and third quantiles (1, 3, 5, 7, 8, 9 and 10), and three populations with *b* larger than the third quantile (4, 13 and 14) (Fig. 1, Table 1). The highest values of *b* highlight the abrupt decline between the 0–20 and 20–40 cm size classes in three populations, where small individuals predominate (Fig. 1). This information may be useful to assess the recruitment success between these size classes and compare population status, although it is not possible to set a value for balanced populations.

Ecological and anthropogenic factors and life stages

For all life stages, no single model had all the support (Table 2). Thus, we based our inference on the plausible models ($AICw_i > 0.1$), by computing model standardized averaged estimates and the relative importance for variables of the top models (Table 2). The deviance explained by the most plausible models indicates that seedling frequency is associated with the variables measured, with the percentage of deviance explained between 55.2 and 58.2%. Sapling and juvenile frequencies were reasonably associated with the variables measured, with models explaining 23.6–40.6% and 20.7–24.6% of deviance, respectively (Table 2). Adult frequency had weak association with the variables measured, with 29.4% of total deviance explained by the single model that competes with the hypothesis that the observed variation is random (intercept only) (Table 2).

The most plausible model {AD+CAT+TX} positively associates seedling with adult conspecific abundance and sand fraction, and negatively with cattle ranching (Table 2). The model {AD+CAT+FERT1+TX} represents another possible explanation for seedling frequency (Table 2), and includes the positive association with acidity, aluminum concentration, CEC and phosphorus, and negative with base saturation. Texture (TX) is the most important variable, contributing to the explained deviance of seedling frequency in all plausible models (Table 2), followed by FERT1 (0.38%) and CAT (0.28%), AD being close to null. Because TX is a linear combination of soil texture parameters, its interpretation rests on sand fraction (Suppl. Mat. 2). The same happens with FERT1, which summarizes soil potential acidity, aluminum concentration, and base saturation. Parameters estimated by the averaged model were accurate only for TX and FERT1 (Table 2). The confidence intervals did not overlap zero, supporting positive trends of soil sand fraction (TX), potential acidity and aluminum concentration, and negative trend for base saturation. TX and FERT1 are present in all plausible models, and are important variables associated with seedling frequency.

The best model {VC+FERT1+TX} suggests that sapling frequency is positively associated with sand fraction and negatively with plant soil cover and fire, and, unlike seedling abundance, is negatively associated with acidity, aluminum concentration, CEC and phosphorus, and positively associated with base saturation (Table 2). Most of relative explanation relies on TX, present in all models, followed by FERT1 (0.38%), FIRE (0.08%) and VC (0.05) (Table 2).

The most plausible model {PREC} suggests that juvenile frequency is negatively associated with the mean annual precipitation (Table 2). Potential competing models {PREC+SLOPE} and {PREC+FIRE} suggest negative association with mean annual precipitation, site slope and fire and positive with soil texture. Parameters estimated by the averaged model were accurate only for mean annual precipitation, present in all three models, highlighting its negative association with juvenile frequency; estimates for texture (0.40%), site slope (0.18%) and fire (0.17%) were not accurate (Table 2).

Table 2 Top-ranked binomial generalized linear models of the association between life stages of *Buitia capitata* with environmental and anthropogenic variables and model averaged standardized estimates (β) with the relative importance of variables for each life stage

Life stage	Top-ranked binomial generalized linear models				Model averaged standardized estimates (β) of explanatory variables and the relative importance (in parenthesis)								
	Model	AICc	Δ AICc _i	w _i	Explanation (%)	FERT1	TX	CAT	AD	VC	PREC	SLOPE	FIRE
Seed-ling	AD+CAT+TX	189.5	0.00	0.622	55.25%	-0.3967 (0.3770)	-1.052016 (1.0)	-0.28764 (0.2876)	0.004561 (0.004)				
	AD+CAT+FERT1+TX	190.5	1	0.378	58.23%								
	VC+FERT1+TX	118.5	0	0.276	40.63%	0.56183 (0.3871)	-1.45125 (1.0)			-0.07785 (0.053)			-0.12368 (0.085)
Sapling	VC+FIRE+FERT1+TX	118.5	0.05	0.27	42.18%								
	VC+FIRE+TX	118.8	0.36	0.23	27%								
	VC+TX	118.9	0.41	0.225	23.65%								
Juve-nile	PREC	176.4	0	0.351	20.72%		0.120424 (0.4038)				-0.2982 (1.0)	-0.05517 (0.1850)	-0.05062 (0.1697)
	PREC+SLOPE	177.6	1.22	0.191	24.65%								
	PREC+FIRE	177.9	1.54	0.162	23.05%								
Adult	INTERCEPT	178	1.61	0.157	0								
	SLOPE+TX	178.2	1.86	0.139	21.44%							0.08103 (0.5652)	-0.14334 (1.0)
	INTERCEPT	182.6	0.00	0.296									
SLOPE	SLOPE	182.8	0.19	0.268	10.87%								
	SLOPE+FIRE	183.1	0.56	0.223	29.42%								
	FIRE	183.2	0.66	0.213	16.82								

Estimates in bold indicate that the 95% interval did not includes 0. TX summarizes soil particle size (clay, silt and sand); FERT1 summarizes soil fertility variables; CAT summarizes cattle grazing index, FIRE summarizes fire occurrence

Discussion

Population structure under different human disturbances

The reverse-J shape of size distributions and the positive skewness coefficient of the *Butia* populations reflect a predominance of smaller size classes, indicating active regeneration in most populations. Reverse-J size distributions have been found in many tropical species subjected to the harvest of plant parts (e.g. Giroldo and Scariot 2015; Schumann et al. 2010), including neotropical palms (Sampaio et al. 2008; Isaza et al. 2016). The abundant regeneration of small size individuals supports the debate about the persistence of populations, based on the premise that self-regenerating populations have size distributions with a monotonic decline (Condit et al. 1998; Leak 1965). The monotonic decline results from the balance between continued recruitment to subsequent size classes determined by growth, and mortality remaining constant along the size distribution (Wiegand et al. 2000), a premise not always fully filled in natural populations (Wright et al. 2003).

Harvest of plant parts, cattle ranching and fire are important anthropogenic effects affecting plant populations in savannas (Mandle et al. 2012; Schumann et al. 2010; Peres et al. 2003). The harvest of reproductive structures may hinder natural regeneration and determine the shape of the size distribution (Sullivan et al. 1995; Peres et al. 2003), but species occurring in high abundances, with high fertility rates, tend to be less impacted by fruit harvest (Bernal 1998; Guédjè et al. 2007; Tickin 2004). In the study area, *Butia* populations have a high relative frequency of individuals in the first size class, consisting mainly of seedlings, indicating the success of seed germination and early survival. The low impact of present levels of fruit harvesting on natural regeneration is favored by the concentration of harvesting in areas near harvesters' residences, low harvest frequency, harvest of fruit bunches with almost mature fruits only, and the *Butia* population's asynchronous fruit maturation (Silva and Scariot 2013). Harvesting intensity may also be determined by market demand (Arnold and Pérez 2001), but difficulties accessing the markets, transportation, and distance to some populations contribute to keeping harvesting pressure null or at low levels in some areas, not preventing regeneration. Present fruit harvesting levels of *Butia* populations are consistent with the biodiversity conservation strategy founded on use.

In the *Cerrado*, most pastures are renewed at intervals of a few years, and this renewal generally includes the cutting of herbs and shrubs followed by the use of fire. High frequency and intensity of pasture renewal may not allow enough time for the establishment of new seedlings and transition into higher plant size, leading to populations dominated mainly by tall individuals, that were already present in the area (biological inertia, sensu Summerfield 1972). Populations doomed to extinction, because of recruitment failure, seem viable because of the presence of old, tall individuals, but may not persist if land use and management do not change. The successful establishment of new individuals in the population may be impaired by the long permanence of plants in the seedling stage. In slow-growth palms, this permanence may last several years (McPherson and Williams 1998), as observed in *Butia* (Lima et al. 2010), increasing the risk of death by physical damage (e.g. Scariot 2000), cattle herbivory, and management practices. Ceasing some management practices or changing land use may be enough to allow population recovery. High fruit harvesting and cattle grazing (C3H4F9) in the past may account for the low frequency of plants in small size classes, except for the first size class that has recovered since fruit harvesting decreased and cattle ranching ceased in the site (Fig. 1). Similarly,

in areas where cattle ranching and fruit harvesting were recently discontinued, there was enough time for producing increased frequency of seedlings (Fig. 2). However, ceasing cattle ranching in these areas resulted in increased biomass abundance of *Melinis minutiflora* P. Beauv., an aggressive invasive African grass known to form a closed canopy, which reduces the seedling recruitment of native species (Hoffmann and Haridasan 2008). In a later visit to population dynamics sites, we observed that most *Butia* seedlings in these areas were under a dense canopy of this grass, unable to overcome this barrier, possibly staying in this life stage until they die. Long-lived species, with frequent reproduction and high fertility rate, highlight the importance that adults have for population maintenance and growth (Alvarez-Buylla et al. 1996). However, the high relative frequency of seedlings may not be enough to ensure persistence of populations with few adults (e.g. C3H0F3) (Lima et al. 2010), which makes the importance of invasive species in suppressing regeneration more marked (Sinasson et al. 2017).

In the landscape, most populations have a reverse-J size distribution and high frequency of seedlings, and most of the current land uses and management practices do not prevent continuous regeneration and passage between life stages. Low relative frequency of saplings results mainly from the short duration spent in this life stage, but seedling proportion lower than sapling frequency characterizes populations under intense land use and management.

Models of the relationship between plant abundance and habitat structure

The models selected highlight the association of life stage frequency with ecological variables instead of with anthropogenic variables, except for one *Butia* population occurring in a site subjected to frequent soil plowing (C9H9F3). Seedling frequency is negatively associated with soil fertility and soil texture, saplings and juveniles are negatively associated with soil texture and rainfall, respectively, suggesting that the models are more general and applicable to other situations (Guisan and Zimmermann 2000). The models demonstrate the need to consider the combined influence of ecological gradient variables to understand (1) the relative contribution of each variable to the frequency pattern of each life stage, (2) the relationship of population structure and habitat (3), and the niche description of the species; information desirable both to management and conservation (Chatfield et al. 2010).

The dynamics of regeneration seems to be more related to the heterogeneity within the population than to large-scale restrictions (Gomez-Aparicio et al. 2005). The two models for seedlings were consistent with our ecological knowledge, which attributes a large contribution to soil variables in the explanation of the abundance of tropical plant species (Clark et al. 1998; Stevens et al. 2004; Brenes-Arguedas et al. 2008). Both models considered demographic (conspecific adult abundance) and anthropogenic variables associated with the ecological variables, and, as expected, the abundance of conspecific adults and cattle should affect the regeneration of the population positively and negatively, respectively. These variables were, however, not retained in the averaged model, suggesting that the relationship of these variables with the regeneration of *Butia* is not too straightforward and should be further tested. The effect of cattle grazing on natural regeneration is usually negative, causing physical damage by herbivory and trampling, reducing reproduction and increasing plant mortality, with higher impacts associated with high cattle stock densities (Ribeiro et al. 2015). In other cases, cattle may promote seedling establishment (Oosterheld and Sala 1990), reducing the biomass of potentially competing exotic grasses

(Hoffmann and Haridasan 2008), increasing the germination of seeds with dormancy (Silvertown 1980), promoting safe sites for germination (Oosterheld and Sala 1990), and dispersing propagules. In most *Cerrado* areas, cattle are raised in low densities, not exceeding one animal/ha (IBGE 2006), and in some areas they are removed during the flowering and fruiting periods, not to impair fruit production of *Butia* (Silva 2008). It is likely that cattle cause physical damage to smaller plants of *Butia*, by trampling and browsing, and, as observed in juveniles and adults, by browsing leaves, inflorescences, and young infructescences in the dry season when there is a shortage of fodder for cattle. Soil fertility and especially soil texture were the most important variables and the only significant ones in the averaged model to explain the seedling frequency in the study areas. High seedling frequency is associated with sandy, acidic, alic soils with low base saturation, suggesting site specificity for seed germination and establishment.

Of the four variables in the four competing plausible models for sapling frequency, only soil texture is retained, suggesting a positive association with sandy soils. Soil fertility, vegetation cover and fire did not succeed in being linked to the observed variation in sapling abundance, suggesting that saplings, unlike seedlings, are associated with soils with higher base saturation, less acidic and less alic. This difference in nutritional requirements may reduce the successful transition from seedling to sapling and it is consistent with the association found between habitat structure and savanna palm tree life stages, whose spatial distribution pattern depends on patches with specific fertility (Barot et al. 1999). This association highlights the environment as a key factor producing different spatial patterns resulting from different mortality patterns within populations (Barot et al. 1999). The lack of negative association of fire with seedling and sapling frequencies suggest that *Butia* does not follow the main pattern of mortality caused by fire events which is otherwise predominant for the *Cerrado* plants, where plants with diameter < 5.0 cm represent more than 90% of the plants killed by fire (Medeiros and Miranda 2005).

The most plausible model for juveniles is negatively related with precipitation, the only variable retained in the averaged model, slope, soil texture and fire emerge as complementary effects. No model related adult frequency with habitat structure. Weak links of adult frequency and measured habitat characteristics imply that our sampling did not detect possible associations, probably because adults occur in patches that are suitable for previous life stages, with heterogeneous habitat causing different mortality patterns within populations (Barot et al. 1999).

Implications for conservation and management

Most populations of *Butia* are self-regenerating, and persisting in the landscape even under fruit harvesting pressure, extensive cattle ranching, and eventual fires. In populations with scarce regeneration, changes in land use and management are needed to create conditions for active population regeneration. However, the removal of anthropogenic pressure does not always provide a direct positive effect on regeneration, and possible gains for recruitment should be evaluated with caution. The initial gains in seedling abundance may not always result in successful recruitment where cattle grazing has ceased, since the aggressive regrowth of invasive exotic grasses, abundant in the *Cerrado*, can constrain seedling transition to higher sizes. Frequent plowing or thinning of herbaceous vegetation, practices more frequent on large, industrial farms, makes regeneration null or scarce, dooming populations to local extinction. Understanding the simultaneous effects of multiple stressors is

fundamental to for the application of appropriate interventions for conservation (Mandle and Ticktin 2012).

Soil fertility and texture influence seedling frequency importantly, soil texture affects sapling abundance, and, together with precipitation, which is important for juvenile abundance, are important aspects to be observed in enrichment, introduction and restoration initiatives with *Butia*. These actions are much demanded by traditional populations and family farmers, due to the abundant market and high value of *Butia* fruits. Cattle removal from areas with *Butia* populations during its reproductive period will safeguard plants from leaf and immature fruit herbivory, as is already practiced by traditional peoples and family farmers.

In contrast to the management of industrial farms, the present management and land uses practiced by most traditional peoples and family farmers is characterized by low-intensity fruit harvesting and low-intensity cattle ranching. This shows that self-regenerating populations of *Butia* may persist even in areas with multiple uses. This approach may ensure that traditional livelihood of people and family farmers are maintained and may contribute to a strategy of in situ conservation under sustainable management. Public programs aimed at promoting the enrichment of disturbed areas with *Butia* can contribute to income generation, ecological restoration and the expansion of this palm in areas from which it has been removed.

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