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PAPER

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# Cattle affect regeneration of the palm species *Attalea princeps* in a Bolivian forest–savanna mosaic

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## Abstract

*Attalea princeps* is an important palm species that shapes the forest–savanna mosaic in Beni, Bolivia, as it dominates the two principal forest landscape elements (forest islands and gallery forest), and provides a vital microhabitat, food, and nesting source for numerous plant and animal species. The forest–savanna mosaic is used for extensive grazing, and the palm population is declining on the forest islands due to a low regeneration rate, which threatens the maintenance of this landscape. We therefore examined the (a)biotic factors that influence the population structure of *Attalea* in the centers and edges of forest islands and gallery forests. Ninety-one 0.1-ha plots were established, and 500 palm adults and 3,700 juveniles were measured for their size, health condition, and fire damage. For each plot, habitat characteristics, such as landscape position, grazing pressure, and soil conditions, were measured. *Attalea* population density was significantly lower on the forest islands than in the gallery forests, especially in the juvenile life stage. A structural equation model showed that juvenile density is positively related to the health condition of juveniles and amount of fruits present, where the amount of fruits is positively affected by the condition of adults. Juvenile density is negatively influenced by grazing, affecting the health condition of the juvenile, as well as organic matter and phosphate availability in the soil. Therefore, it is recommended to decrease the grazing pressure by decreasing livestock densities, fencing off vulnerable forest islands, or by rotating cattle.

Abstract in Spanish is available with online material.

KEYWORDS

Beni savanna, Bolivia, landscape mosaic, Llanos de Moxos, Motacú palm

## 1 | INTRODUCTION

A landscape mosaic promotes a high beta biodiversity as different ecological communities occur in different patches (Watt, 1947). Species within and between patches interact with each other and are influenced by abiotic factors (Loreau, 2010; Naeem, Duffy, & Zavaleta, 2012). Landscapes and species are also influenced by human activity and with the high human population pressure in the Anthropocene these alterations become more visible than ever (Brook, Bradshaw, Koh, & Sodhi, 2006; Hansen et al., 2005).

The Beni savanna in Bolivia is a forest–savanna mosaic and has been identified as a center of plant diversity and endemism (Mayle, Langstroth, Fisher, & Meir, 2007). This dynamic ecoregion is a complex mosaic of rivers and lakes, seasonally flooded treeless grasslands, savanna, herbaceous wetlands, riverine gallery forest, and forest islands (Ibisch, Beck, Gerkmann, & Carretero, 2003). Riverine gallery forest borders rivers on raised fluvial deposits (Lombardo, 2014) and forest islands are small (<50 m width), round-shaped patches of trees on elevated areas in a treeless savanna landscape, formed by anthropogenic influences or termite mounds (Denevan, 1966; Erickson, 1995; Lombardo et al., 2013). These patches are modified by environmental drivers such as human-induced and natural fires in the dry season, and inundation in the wet season (Berkunsky et al., 2016).

The Beni savanna ecoregion is a threatened Amazonian savanna due to a rapid decline in biodiversity caused by large-scale cattle ranching, habitat degradation, and conversion of natural grassland (de Carvalho & Mustin, 2017; Mayle et al., 2007). For the past 12,000 years, the Beni savanna has been influenced by human activity (Erickson, 2000; Haase & Beck, 1989; Lombardo et al., 2013; Navarro & Maldonado, 2002) as the savanna was inhabited by a dense population of pre-Columbian Paleo-Indians who constructed earth mounds for agriculture and habitation, and dug canals and fishing ponds (Denevan, 1966; Erickson, 2000). Nowadays, the main human impacts are protracted and uncontrolled cattle grazing, burning of savanna by farmers to ensure fresh grass sprout for cattle, natural grassland conversion, and forest destruction for cattle ranching infrastructure (Berkunsky et al., 2016; Killeen, 1991; Killeen et al., 2003; Mayle et al., 2007).

The two principal forest landscape elements in the Beni savanna, forest islands and gallery forest, are dominated and maintained by the palm species *Attalea princeps*, hereafter referred to as *Attalea* (Yamashita & de Barros, 1997). *Attalea* is an important species in the Beni savanna, as it provides and shapes a specific microhabitat and a food source for numerous plant, mammal, and bird species (Alvez-Valles et al., 2018; Corrêa, Fischer, & dos Santos, 2012; Rios & Pacheco, 2006). For example, *Attalea* has been identified as the most important factor for the survival of the critically endangered endemic Blue-throated Macaw (*Ara glaucogularis*) (BirdLife International 2015; Hesse & Duffield, 2000). In the Beni savanna, three factors are likely to have strong impacts on the life cycle and regeneration of *Attalea*: landscape mosaic, disturbance, and environmental factors (see the conceptual diagram in Figure 1).

## 1.1 | Landscape mosaic

Island theory predicts that small and isolated forest islands have smaller and less viable species populations because of higher extinction risks and lower immigration rates (MacArthur & Wilson, 2015). At the edge of a forest patch there is a different microclimate and a higher disturbance frequency compared to the forest center; light availability and wind intensity are higher and trees are more exposed to inundation, fire, and cattle grazing (Camargo & Kapos, 1995; Cochrane & Laurance, 2002; Williams-Linera, 1990).

## 1.2 | Disturbance

Palm regeneration is affected by cattle ranching, and naturally occurring and human-induced fires (Yamashita & de Barros, 1997). Cattle ranching leads to browsing and trampling of juveniles, and increased soil compaction reduces soil aeration and root penetration (Langstroth, 1996; Yamashita & de Barros, 1997). Adult *Attalea* palms are fire resistant, because the apical meristem is well above the ground fire, and insulated by leaf bases that protect the palm against high temperatures (McPherson & Williams, 1998; Souza, Martins, &

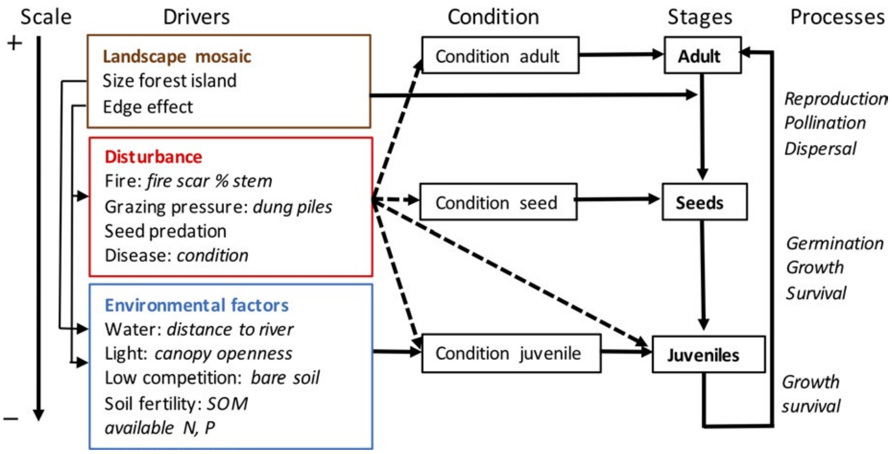

**FIGURE 1** Conceptual model showing the hypothesized effects of landscape mosaic, disturbance, and environmental factors (boxes, left side) on the condition and life cycle of *Attalea* (boxes, right side). These factors operate at broad to small spatial scales, as indicated by the vertical arrow. Each of the factors affects a different phase and process in the life cycle. Arrows indicate the expected positive (solid line) and negative (broken line) effects on the condition and density of individuals at the different life cycle stages, and the effects on the regeneration processes (italics)

Matos, 2000). In contrast, juveniles are fire intolerant because of their superficial meristem position (McPherson & Williams, 1998; Souza & Martins, 2004) and intense fires can strongly reduce germination by damaging the fruits (Anderson, May, & Balick, 1991). Additionally, large-seeded palms such as *Attalea* suffer from density-dependent seed predation by bruchid beetles (*Pachymerus cardo*) (Salm, 2006), and parasites and diseases may also increase *Attalea* mortality (Gilbert & Webb, 2007).

### 1.3 | Environmental factors

Environmental factors such as soil characteristics, inundation, and light availability have a direct influence on the survival and regeneration of *Attalea*. The *Attalea* genus is known to be present at a nutrient, alkalinity, soil texture, and inundation gradient (Grégoire, 2010; Salm, Prates, Simoes, & Feder, 2015). *Attalea* occurs on dry to seasonally flooded soils; therefore, this species can be expected close to seasonally inundated areas (Moraes & Zenteno-Ruiz, 2017). As most palm species, *Attalea* is a light-demanding pioneer species associated with medium shade tolerance (Fredericksen, 1999), although shaded, moist environments stimulate seed germination (Anderson et al., 1991).

### 1.4 | Aims and hypotheses

Currently, the population density of *Attalea* on the forest islands is decreasing and the population structure is changing due to a low regeneration rate (T. Boorsma, *pers.obs.*). If in the next 100 years the regeneration rate does not recover, the majority of the palms may disappear with large consequences for the landscape mosaic as whole, and for the numerous plant and animal species that depend on this palm species. This study aims to describe the current population structure of *Attalea* and analyze how the landscape mosaic, disturbance, and environmental factors affect its population structure and abundance (cf. Figure 1).

We hypothesize a positive relationship between palm population density and forest island size, soil nutrient concentration of the soil and proximity to the river, because we expect that larger islands have a lower extinction rate (MacArthur & Wilson, 2015), soil nutrient concentration positively affects this species (Grégoire, 2010), and this palm is adapted to a seasonally flooded environment (Moraes & Zenteno-Ruiz, 2017). We hypothesize a negative relationship between population density and edge effect, seed predation rate, diseases, grazing pressure, and fire intensity, as we expect that disturbances are more severe at the edge (Camargo & Kapos, 1995; Cochrane & Laurance, 2002; Williams-Linera, 1990), seed predation lowers viable seed availability (Salm, 2006), and disturbances affect the viability and density of the individuals (Gilbert & Webb, 2007; Yamashita & de Barros, 1997). Light-demanding adult palms are expected to be more abundant with increased light availability (Fredericksen, 1999), and juvenile density is expected to be higher in a more shaded environment, as shade stimulates seed germination (Anderson et al., 1991).

## 2 | METHODS

### 2.1 | Study area

The Beni savanna is located in the Amazon Basin of northern Bolivia and covers an area of 16 million ha (Mayle et al., 2007). The study was executed in the Barba Azul Nature Reserve (11,000 ha), situated in the center of the Beni savanna (coordinates field station: 13°45′45″S 66°5′54″W). Mean annual temperature is 26°C, mean annual precipitation is 1,800 mm/year (Herrera-MacBryde, Dallmeier, MacBryde, Comiskey, & Miranda, 2000), and the wet season lasts from October to May (Haase & Beck, 1989). The forest islands and center of the gallery forests are not flooded during the wet season, as they are elevated (Mayle et al., 2007). The Beni savanna is classified as a hydromorphic climatic savanna, meaning that the savanna is mainly flooded by rainwater and receives limited sediment from the catchment, resulting in a nutrient-poor soil (Junk et al., 2011).

### 2.2 | Study species

Recently, a species revision was performed on *Attalea phalerata* in the Beni savanna, resulting in correcting the species to *Attalea princeps* throughout most of the ecosystem (Moraes & Zenteno-Ruiz, 2017; Pintaud, del Castillo, Ferreira, Moraes, & Mejía, 2016). The habitat of *Attalea princeps* spreads from 150 up to 1,000 meter in the Amazon and Subandean forest in Bolivia, Peru, and West-Brazil (Pintaud et al., 2016). It occurs in high flood-free forests, seasonally flooded forests, and river edges with fluctuating water levels (Moraes & Zenteno-Ruiz, 2017). *Attalea princeps* is a single stemmed palm, has a maximum stem height of 15 m, and the crown is formed of 15–20 arching leaves (Pintaud et al., 2016). The staminate flowers are spirally inserted on rachillae, and both staminate and pistillate inflorescences are placed in between the leaves, unisexual, and occur on the same plant. The palm may flower throughout the year, and the most important pollinators are nitidulid beetles of the genus *Mystrops*. The infructescences are pendulous along the stem with 350–500 fruits, each containing 2–5 seeds (Pintaud et al., 2016). The removal of the mesocarp, shaded and moist environment stimulates germination, which generally takes 3 months (Anderson et al., 1991).

### 2.3 | Research design

At the Barba Azul Nature Reserve, *Attalea* occurs on 25 forest islands ranging from 0.02 to 0.8 ha in size (5.7 ha in total) and 8 patches of riverine gallery forest ranging from 8 to 60 ha in size (245 ha in total). To study the different habitat types of *Attalea*, 91 plots of 10 × 20 m were established at least 60 m apart in the center and edge of forest islands and gallery forest: 16 random plots in the forest island center, 25 plots in the forest island edge, 25 plots in the gallery forest center, and 25 plots in the gallery forest edge. From the forest edge to 10 m into the forest islands or gallery forest was considered edge habitat, as *Attalea* is one of the dominant canopy species and it has an average adult height of 10 m. The edge plots in the forest island and gallery forest were randomly placed at the North or South edge to avoid an illumination bias. In case the diameter of the forest island was <40 m, only an edge plot was established. To quantify the landscape characteristics of forest islands, the diameter of the forest islands was measured with a Nikon Forestry 550 clinometer.

## 2.4 | Plot measurements

Grazing pressure was inferred by counting the number of dung piles in each plot. To have a measure for competition, the number of all trees (including palms) with a stem diameter (dbh) >5 cm was recorded. Also, the overall ground cover was scored in percentages measuring bare soil, grass, and shrubs. To have a measure for water availability, the distance from every plot to the river was measured in Google Earth (Google Inc. 2016). To evaluate soil fertility, a soil sample at 30 cm depth in the center of the plot was taken with a closed hand auger. The soil samples were analyzed for organic matter, available phosphate, available nitrogen, and pH at the laboratory of the Plant ecology and nature conservation group, Wageningen University. Percentage organic matter was examined by heating the soil samples for 2 hr at 105°C, followed by heating for 12 hr at 550°C. The samples were measured before and after placement in the oven to determine soil organic matter. The available phosphate and nitrogen were analyzed with a 0.01 M $CaCl_2$ extraction method. The pH was measured with a WTW inoLab pH/cond level 1 measurement device.

## 2.5 | Palm measurements

*Attalea* with stem were defined as adults. The following measurements were taken from the 498 adult palms; height (measured with a Nikon Forestry 550 clinometer), dbh, number of leaves, number of inflorescences, and number of infructescences. Fire intensity was estimated by measuring fire scar height and width on adult palms, from which the percentage of scarred stem was calculated. Light availability for each adult was estimated with the Dawkins crown illumination classes: (a) no direct light, (b) lateral light, (c) some overhead light, (d) full overhead light, and (e) crown fully exposed (Jennings, Brown, & Sheil, 1999). The health condition of adults was scored as good, medium, or bad based on the condition of the stem and the color and degree of damage (intactness) of the leaves. Under each adult palm, a 1-$m^2$ subplot was randomly established to examine the total amount of fallen fruits and the amount of fruits infected by bruchid beetles.

*Attalea* without stem were defined as juveniles. Four juvenile subplots of 5 by 5 m were established in the forest island plots, and two subplots were established in the gallery forest plots. Two subplots were representative for juvenile density in the gallery forest, but due to larger variation in juvenile abundance in forest islands, four subplots were established. For each of the 3,699 juveniles, the length of the longest leaf and the form of the leaves were noted as closed, open, or both (Supporting Information Figure S1). The health condition of the juveniles was scored as good, medium, or bad based on the color and degree of damage (intactness) of the leaves. As a measure for light availability, we used canopy openness which was examined with a spherical densiometer, Forestry Suppliers, Inc. model A.

## 2.6 | Data analysis

To analyze how habitats differ in population density and (a)biotic variables, a two-way ANOVA with interaction term was performed with forest type (*i.e.*, forest island or gallery forest) and position (*i.e.*, forest center or forest edge) as independent variables, using a Tukey HSD as post hoc test (R package stats). The residuals were tested for normality with a Shapiro–Wilk test, and the homogeneity of variances was evaluated with a Levene's test. To normalize the data, the variables juvenile density, adult density, amount of fruits, dung piles, and percentage organic matter were log10-transformed. The amount of fruits produced by each palm was calculated by extrapolating the fallen fruits on 1–6.6 $m^2$. Fruits disperse on average up to 1.5 m from the stem, and the surface of the dispersal area minus the average DBH results in a surface of 6.6 $m^2$ around the stem covered with fruits.

To explore how population characteristics, (a)biotic variables of forest islands and gallery forest were associated, a Principal Component Analysis was performed (Oksanen et al., 2016). The twelve variables with the highest components loadings on the first two axes are visualized in the *PCA graph* (Figure 3). These variables are habitat, juvenile density, condition juvenile, adult density, condition adult, amount of fruits, infected fruits, fire damage, dung piles, available phosphate, percentage organic matter, and bare soil cover.

Based on the conceptual model (Figure 1) and field observations, a path model was developed to analyze the mechanism behind the differences in population density between the forest islands and gallery forest. Three different models were developed, (a) a model at the plot level, (b) a model at the individual level of the adult, and (c) a model at the individual level of the juvenile. Models on individual adult and juvenile level were developed as it became clear from the path models that the condition of the individual and results of measurements on individual level were important to explain the juvenile density. In the models on individual level, the plot number is used as a nesting factor. The variables were analyzed with a generalized linear model from the Gaussian family. The regression coefficient was used to quantify the direction of the relationship in the model (lm.beta function from the R package QuantPsyc; Fletcher, 2012).

To test the overall correctness of the resulting path models, structural equation models were developed. With structural equation modeling, it is not only possible to test the hierarchical relations between variables, but also test the correctness of the whole model (SEM, as implemented in the R package Lavaan; Rosseel, 2012). A SEM on plot level and a SEM on the individual level of the adults were developed. It was not possible to develop a correct SEM on individual level of the juveniles with the restricted number of variables on individual juvenile level present. As the final path models on plot and individual adult level consisted of many variables, the SEM's were constructed starting with the significant relationships to juvenile density. Juvenile density is the most important dependent

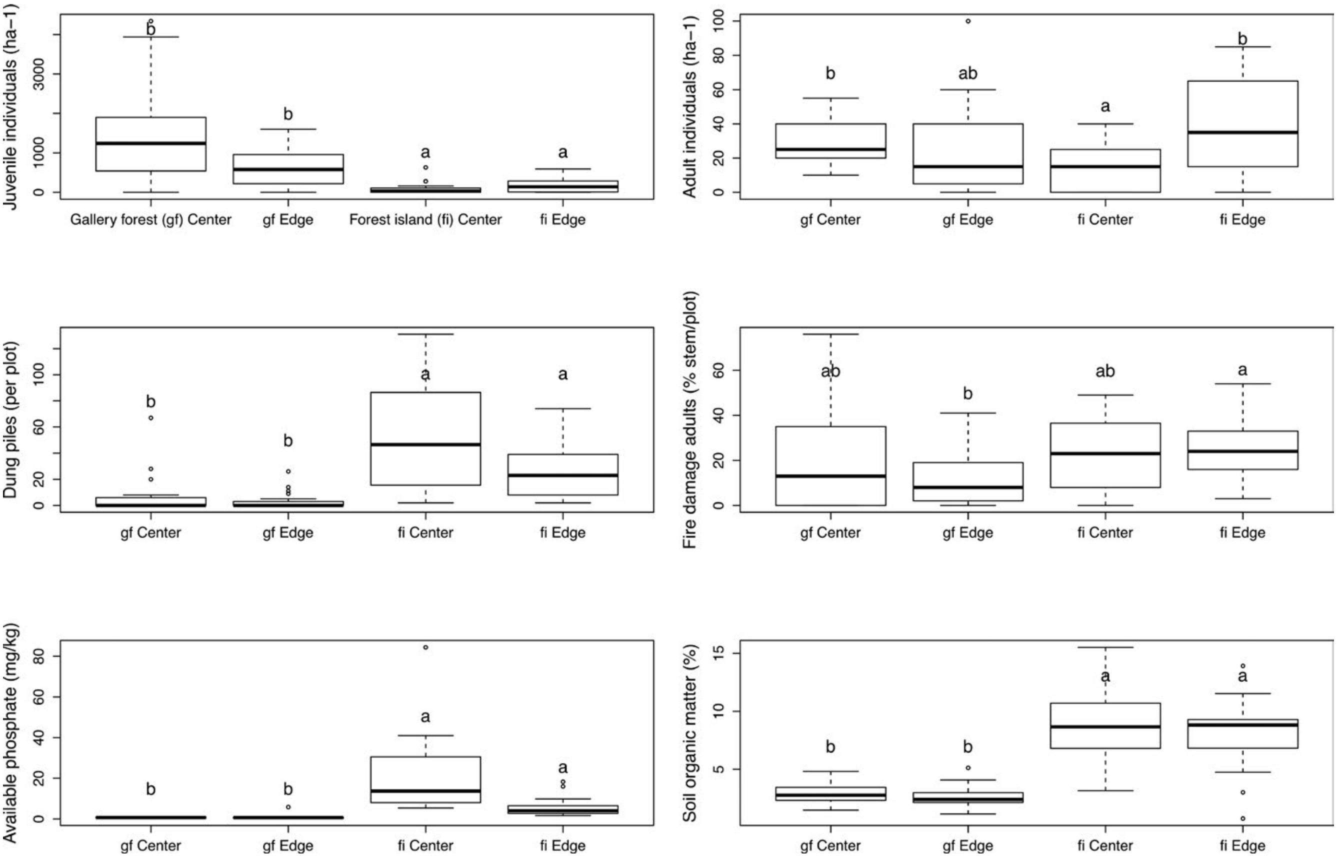

**FIGURE 2** The effect of four habitat types (forest island [fi] vs. gallery forest [gf], and forest edge vs. forest center) on *Attalea princeps* population density, disturbances, and environmental factors. The boxes indicate the data range of the second and third quartile, with the horizontal line as median, and the whiskers indicate the entire data range. Boxes accompanied by a different letter are significantly different (Tukey post hoc test, $p < 0.05$). The data are analyzed on plot level ($N = 91$)

variable in this study explaining the difference in regeneration rate. The resulting SEM's were selected on a chi-square *p*-value >0.05, lowest Akaike's Information Criterion (AIC), Tucker–Lewis index (TLI) >0.95, and Root Mean Square Error of Approximation (RMSEA) <0.01 indicating an excellent model fit. See for an overview of the correlation values between the variables Supporting Information Table S2. All statistical analyses were carried out using R Studio v. 3.3.2 (Development Core Team 2011).

## 3 | RESULTS

### 3.1 | Habitats differ in population density and (a)biotic factors

Significantly more juveniles (ANOVA, $p < 0.0001$) and fruits (ANOVA, $p = 0.0002$) are present in gallery forest compared to forest islands (Figure 2). Also, juvenile condition is better in gallery forest (ANOVA, $p < 0.0001$), compared to forest islands (ANOVA, $p = 0.001$). In the forest island edge and gallery forest center, the adult density is higher compared to the forest island center (Tukey, $p = 0.018$). Fire damage of adults is higher in the forest island edge compared to the gallery forest edge (Tukey, $p = 0.0468$), and adults have a better condition in the gallery forest center compared to the forest island edge (Tukey = 0.0078). Crown illumination is higher in the forest islands compared to the gallery forest (ANOVA, $p < 0.001$). Cattle pressure (ANOVA, $p < 0.0001$), bare soil surface (ANOVA, $p = 0.0287$), phosphate availability (ANOVA, $p < 0.0001$), nitrogen availability (ANOVA, $p = 0.0021$), and percentage organic matter (ANOVA, $p < 0.0001$) are significantly higher in the forest islands. The pH value of the soil does not show a significant difference between the habitats.

The diameter of the forest island did not have a significant effect on juvenile, adult, or fruit abundance (Pearson correlation coefficient, $p > 0.05$). The distance of the gallery forest plots to the river is on average almost 250 m larger than the forest island plots (ANOVA, $p < 0.001$), as also gallery forests are found in old, dried up river arms, indicating that they currently occur in a drier environment.

### 3.2 | (a)Biotic factors influencing the *Attalea* population

It became clear that the four habitat types show significant differences in population density and (a)biotic factors, the underlying mechanisms influencing the *Attalea* population are tested with a continuous data approach, because within each habitat a large variation as found. Associations between palm characteristics and environmental variables were analyzed with a Principal Component Analysis (PCA) (Figure 3). The first two axes explain together 44 percent of the variation. The first axis is mostly associated with habitat, health condition of the juvenile, organic matter, and available phosphate. The second axis is explained by adult density, fire damage, amount of infected fruits, and bare soil cover. The first axis separates the gallery forest to the left side and forest islands to right side, while center and edge plots are not clearly separated.

The relationship between (a)biotic factors and the population structure of *Attalea* was analyzed using a structural equation model (Figure 4). The health condition of the adults had a positive influence on the fruit production (Figure 5a) and therefore a positive effect on juvenile density (Figure 5b). The model shows that more fruit production resulted in more fruits being infected by bruchid beetles. The juvenile density was positively affected by the health condition of the juvenile (Figure 5c), but negatively affected by the organic matter content and phosphate availability of the soil. Cattle pressure had a negative effect on health condition of the juveniles (Figure 5d) and therefore indirectly on the juvenile density. The density of the adults had a positive effect on juvenile density, but this relationship was not significant, resulted in a 10% higher AIC value, and this relationship is therefore not included in the final model. In the best fitting model on plot level, without a nested design, this relationship was significant (Supporting Information Figure S3).

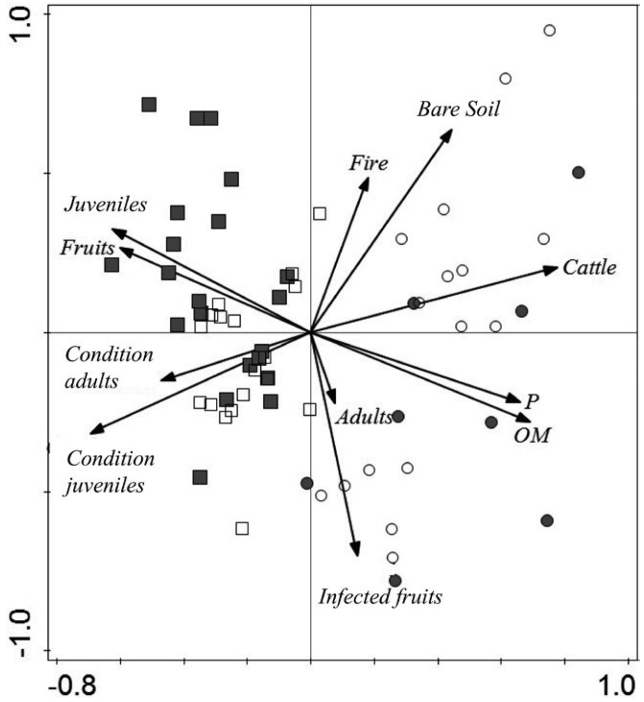

**FIGURE 3** Principal component analysis (PCA) of eleven variables related to *Attalea princeps* density and condition, disturbance (fire, cattle), and soil conditions (P and Soil Organic Matter-SOM). The first axis explains 29% of the variation, the second axis 15% of the variation between the plots ($N = 91$). Symbols indicate the four habitat types: forest island plots (circles), gallery forest plots (squares), center plots (filled symbols), and edge plots (open symbols)

## 4 | DISCUSSION

The aim of this study was to describe the current population structure of *Attalea* and analyze how the landscape mosaic, disturbances, and environmental factors affect its population structure and abundance. First, we will discuss the lifecycle of *Attalea*, followed by a discussion of all components presented in the conceptual model (Figure 1), explaining the effect of (a)biotic factors on the population abundance.

### 4.1 | Life cycle of *Attalea*

We hypothesized that high adult density increases fruit production, which positively affects juvenile density and therefore adult density. Adult density has indeed a positive, but non-significant, effect on the fruit production (Supporting Information Figure S3), but fruit production is most strongly influenced by the health condition of the adults (Figure 3). As expected, the amount of fruits has a positive effect on juvenile density, but contrary to the hypothesis, juvenile density does not influence adult density (Figure 3).

### 4.2 | Landscape mosaic

In line with the island theory, we hypothesized that smaller islands and forest fragments have a lower adult palm density, due to stronger edge effects and a higher probability of palm extinction due to a smaller population size (Souza & Martins, 2004; Williams-Linera, 1990). However, we found that the size of the forest island was not related to the number of fruits, juveniles, or adults present on the forest island. The variation in the landscape mosaic is expected to be large enough to detect differences, as the diameter of forest islands varied fivefold (from 20 to 100 m). One reason for the lack of landscape effects could be explained by edge effect and/or environmental disturbances like grazing to be more important than the size or position of the habitat fragment (Laurance, 2008).

We hypothesized that forest edges contain lower densities of juveniles and adults compared to the center, due to an increased disturbance intensity. However, we found no difference in juvenile density between the center and edge (Figure 2), which is probably caused by a stronger competition at the edge due to a higher grass, shrub and tree cover, resulting in a stronger competition for nutrient and water resources at the edge (Svenning, 2001; Williams-Linera, 1990), which compensates for the decrease in juvenile density in the center due to grazing pressure. Also, as the edge of the raised forest descends toward the savanna, the seeds or juveniles could become inundated for a long period during the wet season resulting in mortal anaerobic conditions (Gurnell, Goodson, Thompson, Mountford, & Clifford, 2007; Veneklaas, Fajardo, & Lozano, 2005).

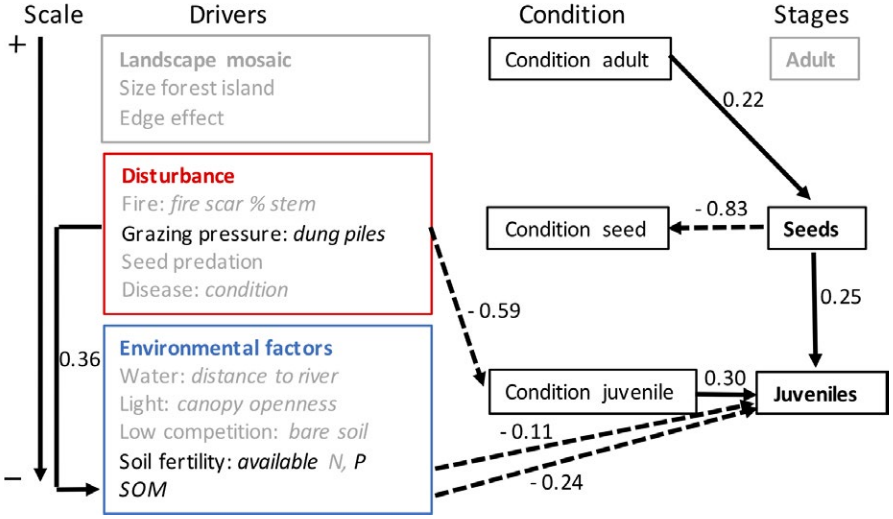

**FIGURE 4** Structural equation model at the individual adult level, with adults ($N$ = 498) nested within plots ($N$ = 91). Results of the best fitting structural equation model ($N$ = 91) indicate the (a)biotic factors affecting the abundance of juvenile *Attalea*. The arrows indicate significant positive (solid line) and negative (broken line) relationships ($p < 0.05$) on the condition, density of individuals at the different stages or regeneration processes (italics), the numbers next to the arrows indicate the standardized path coefficients. This model explains 29% of the variation in the amount of juveniles present

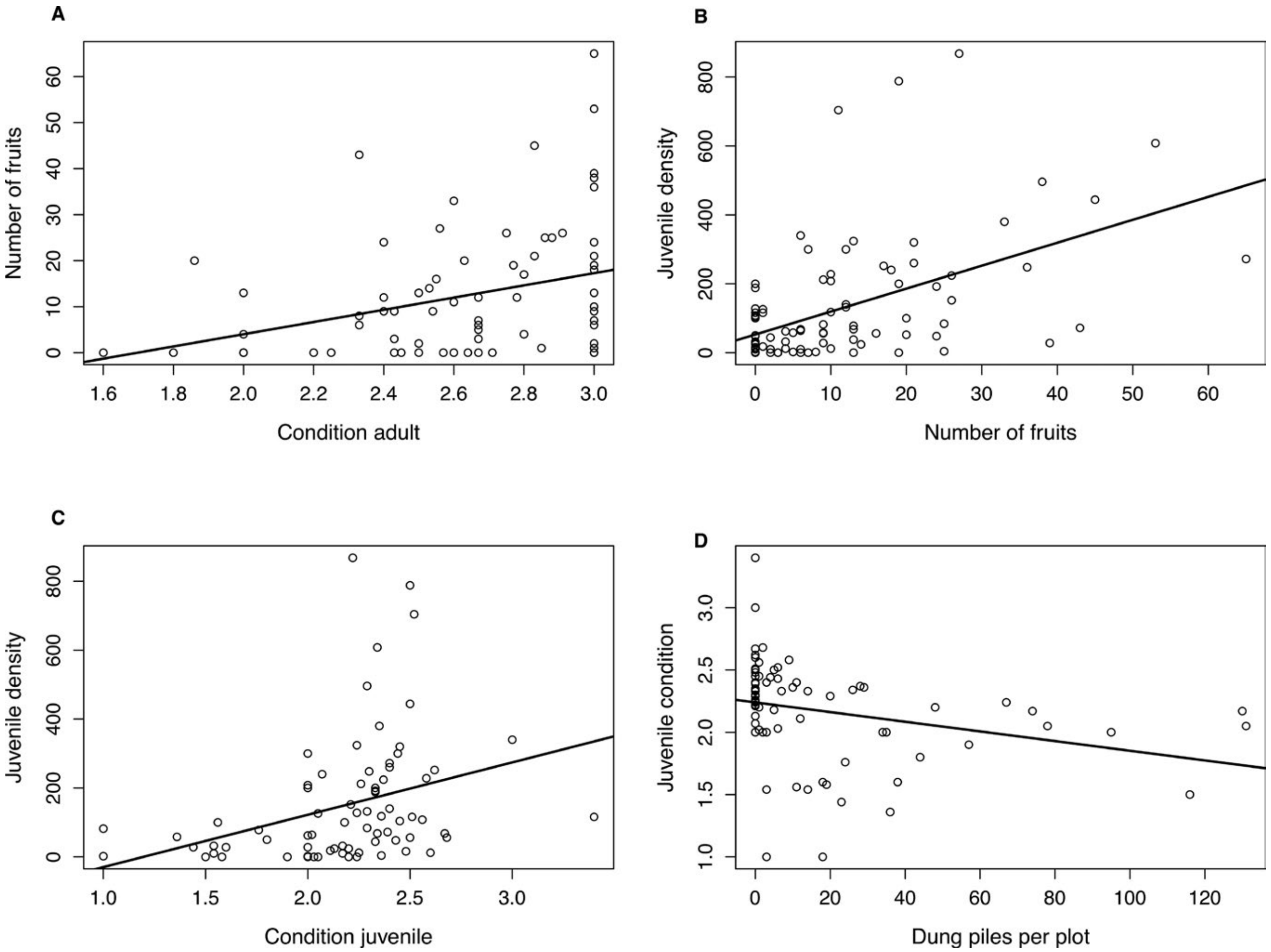

**FIGURE 5** Scatterplots with a fitted linear regression line of relationships between variables influencing juvenile density according to the structural equation model on individual adult palm level. (a) shows the effect of adult condition on fruit production. The health condition is scaled from 1 (bad) to 3 (good). (b and c) visualize the influence of fruit abundance and health condition on juvenile *density* per plot. (d) shows the effect of grazing pressure on the juvenile health condition

We found that within the forest islands, adult density is higher in the edge than the center, whereas in the gallery forest, adult density does not differ between the edge and the center (Figure 2). A higher adult density in the edge of the forest island can be explained by higher cattle pressure in the center. Cattle use mainly the center of the forest island to find shelter and rest, where they browse and trample *Attalea* regeneration (Yamashita & de Barros, 1997) resulting in less juveniles and therefore adult individuals over time. The lower vigor of adults in the forest island edge can be explained by the fact that the lower situated edge is inundated for a longer period, resulting in anaerobic conditions that may increase palm mortality (Junk et al., 2011).

To summarize, the size of the forest fragment does not affect the population density. However, the landscape context is important, as in the gallery forest edge the juvenile density is slightly lower than in the center, because of higher competition and flooding at the edge. In contrast, adult density is higher in the forest island edge compared to the center, probably because of lower cattle pressure in the edge.

## 4.3 | Disturbance

We hypothesized that grazing pressure would have a negative effect on the regeneration of *Attalea* through trampling, grazing, and soil compaction by cattle (Yamashita & de Barros, 1997) (Figure 1). Grazing has indeed a negative influence on juvenile density by diminishing their health condition (Figure 4c) (Eaton, Keuroghlian, Maria do Carmo, Desbiez, & Sada, 2017; Endress, Gorchov, & Noble, 2004; Langstroth, 1996; Mandle & Ticktin, 2012; Shepherd & Ditgen, 2005). Although grazing pressure is higher in forest island compared to gallery forest, it does not have a significant effect on adult density (Figure 2), probably because adult leaves are out of reach for cattle, or because adults are more robust and resilient, which allows them to recover quickly from browsing.

We hypothesized that fire intensity would have a negative effect on juvenile density and adult health condition. Instead, we found that fire does not affect adult health condition nor juvenile density. There is a weak negative correlation (Pearson correlation coefficient −0.21, $p = 0.08$) between fire and juvenile health condition (see Supporting Information Table S2), which indicates a possible indirect effect of fire on juvenile density. However, this fire effect was not included in the final structural equation model as it resulted in a lower model fit. *Attalea* is a fire-adapted species, because the apical meristem is covered and well insulated by leaf bases that protect the palm against high temperatures (Feil, 1996; McPherson & Williams, 1998; Souza et al., 2000).

We hypothesized that seed predation rate and diseases have a negative effect on the viability of seeds, juvenile, and adult density of *Attalea* (Figure 1). Seed viability is indeed negatively affected by density-dependent predation, as we found that the number of fruits increased the number of fruits infected by bruchid beetles, resulting in a lower juvenile density (Figure 3) (Jansen, Visser, Joseph Wright, Rutten, & Muller-Landau, 2014; Salm, 2006).

We hypothesized that high juvenile density would lead to an increase in diseases and decreased health, but found instead that juvenile density led to an increase in juvenile health (Figure 4d). A possible explanation for this positive relationship is that healthy juveniles may lead to a better survival and higher juvenile abundance, or, that both vitality and density are positively affected by the same beneficial environmental conditions (Alvarez-Clare & Kitajima, 2009). In contrast, adult health condition is not related to adult density, probably due to an observed high resilience of the adult individuals. The health condition of the adult has a positive effect on fruit production, therefore indirectly increasing the juvenile density (Figure 4b), and the health condition of the adult is only better in the gallery forest center compared to the forest island edge.

To summarize, grazing pressure negatively affects the juvenile density through biomass removal, while fire disturbance does not have a significant effect on population density or the condition of individuals. Bruchid beetles do affect seed viability, but overall, we assume that diseases do not influence the population density.

## 4.4 | Environmental factors

We hypothesized that reduced stress (less competition) and a high resource availability (nutrients, water, light) would increase the density of juveniles and adults, as the *Attalea* genus is thought to have high nutrient requirements (Grégoire, 2010). The amount of bare soil surface had, contrary to the expectations, a negative effect on juvenile density, probably because the seeds germinate in a shaded environment (circumstances which are more likely with vegetation cover) (Anderson et al., 1991), and growing in bare soil could increase the chance at desiccation (Padilla & Pugnaire, 2007). Alternatively, bare soil surface is an indicator of cattle pressure, as grazing and trampling by cattle lead to a reduced vegetation cover (see Supporting Information Table S2, Figure S3). In contrast to the expectation, an increase in soil organic matter and soil phosphate content resulted in a decreased juvenile density, while nitrogen did not have a significant effect. This result is probably an indirect effect of cattle pressure, as defecation by cattle pressure increases soil organic matter, and nitrogen and phosphate availability in the forest islands (Haynes & Naidu, 1998; Parham, Deng, Raun, & Johnson, 2002; Whalen, Chang, & Olson, 2001). No differences in soil pH were found between the four habitat types, indicating that cattle pressure is not influencing the alkalinity of the soil, although a higher soil organic matter would be expected to result in a higher pH (Walker, Clemente, & Bernal, 2004). Neither competition nor resource availability had an effect on adult density.

We hypothesized that the proximity to the nearest river has a positive effect on palm abundance, as the adult is adapted to a seasonally flooded environment and requires sufficient water. We found, however, that distance to river is not related to the density or health condition of juveniles or adults. Distance to river alone is probably not a good proxy for water availability, due to the height differences caused by the landscape relief in the Beni savanna (Erickson, 2000; Mayle et al., 2007) and inundated of the savanna is caused by rainfall and not solely river overflooding (Junk et al., 2011).

We hypothesized that sufficient light enhances adult density (Fredericksen, 1999), while a more shaded environment enhances juvenile density, as the seeds germinate in a shaded environment (Anderson et al., 1991). We found that light availability is not related to adult health condition or adult density. Light is probably not a limiting factor for adults in this ecosystem, as the adult crowns form the forest canopy. Canopy openness did not affect the density or health condition of juveniles according to the results of the SEM (Figure 4), but a significant negative correlation was detected between the condition of the juvenile and canopy openness, probably because a higher canopy openness increases the risk of desiccation (Supporting Information Table S2). Mean canopy openness above the juveniles is 30 percent (standard deviation = 20%) indicating that the majority of the seedlings occurred in fairly light conditions.

To summarize, only juvenile *Attalea* density is negatively affected by soil fertility, which is probably not a direct causal effect, but reflects increased cattle pressure and defecation. Neither juvenile density nor adult density is affected by light availability, insufficient water availability, or inundation by flooding rivers.

### 4.5 | Management implications

Our results suggest that a decreased grazing pressure will improve the condition of the juveniles which will lead to an increased juvenile density. Fencing of individual islands with a low juvenile density would be desirable to protect the most vulnerable islands and give the time to the population to recover. Reducing cattle density or rotation of cattle to diminish the overall *grazing* pressure in the long term is recommended as well (Giroldo & Scariot, 2015), where the rotation regime will depend on the observed recovery time of the population and the goals of the farmers.

## 5 | CONCLUSIONS

This study shows that *Attalea princeps*, a robust species adapted to a dynamic ecosystem of fire and flooding, is negatively affected by human-induced disturbances like cattle ranching. Currently, palm density is almost 8 times higher in the gallery forest in comparison with forest islands, caused by a higher juvenile density. Juvenile density is positively related to health condition of the juveniles and the amount of fruits. In contrast, juvenile density is negatively influenced by grazing, affecting the health condition of the juvenile, as well as organic matter and phosphate availability in the soil. Management practices that decrease the grazing pressure on forest islands, such as fencing off vulnerable forest islands and the implementation of a cattle rotation system, could result in *Attalea* population recovery, and the long-term maintenance of the landscape mosaic of the Beni savanna.

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## DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8824sd0 (Hordijk, Meijer, Nissen, Boorsma, & Poorter, 2018).

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## REFERENCES

Alvarez-Clare, S., & Kitajima, K. (2009). Susceptibility of tree seedlings to biotic and abiotic hazards in the understory of a moist tropical forest in Panama. *Biotropica*, *41*, 47–56. https://doi.org/10.1111/j.1744-7429.2008.00442.x

Alvez-Valles, C. M., Balslev, H., Carvalho, F. A., Garcia-Villacorta, R., Grandez, C., & Menini Neto, L. (2018). Endemism and conservation of Amazon palms. *Biodiversity and Conservation*, *27*, 765–784. https://doi.org/10.1007/s10531-017-1463-0

Anderson, A. B., May, P. H., & Balick, M. J. (1991). *The subsidy from nature: Palm forests, peasantry, and development on an Amazon frontier*. Columbia University Press.

Berkunsky, I., Cepeda, R. E., Marinelli, C., Simoy, M. V., Daniele, G., Kacoliris, F. P., … Gilardi, J. D. (2016). Occupancy and abundance of large macaws in the Beni savannahs, Bolivia. *Oryx*, *50*, 113–120. https://doi.org/10.1017/S0030605314000258

BirdLife International (2015). *Ara glaucogularis*. The IUCN Red List of Threatened Species 2015.

Brook, B. W., Bradshaw, C. J. A., Koh, L. P., & Sodhi, N. S. (2006). Momentum drives the crash: Mass extinction in the tropics. *Biotropica*, *38*, 302–305. https://doi.org/10.1111/j.1744-7429.2006.00141.x

Camargo, J. L. C., & Kapos, V. (1995). Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology*, *11*, 205–221. https://doi.org/10.1017/S026646740000866X

Cochrane, M. A., & Laurance, W. F. (2002). Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology*, *18*, 311–325. https://doi.org/10.1017/S0266467402002237

Corrêa, C. E., Fischer, E., & dos Santos, F. A. M. (2012). Seed banks on *Attalea phalerata* (Arecaceae) stems in the Pantanal wetland, Brazil. *Annals of Botany*, *109*, 729–734. https://doi.org/10.1093/aob/mcr317

de Carvalho, W. D., & Mustin, K. (2017). The highly threatened and little known Amazonian savannahs. *Nature Ecology & Evolution*, *1*, 100. https://doi.org/10.1038/s41559-017-0100

Denevan, W. M. (1966). *The aboriginal cultural geography of the Llanos de mojos of Bolivia*. National Academy of Sciences - National Research Council Washington DC Foreign Field Research Program.

Development Core Team R (2011). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Eaton, D. P., Keuroghlian, A., Maria do Carmo, A. S., Desbiez, A. L. J., & Sada, D. W. (2017). Citizen scientists help unravel the nature of cattle impacts on native mammals and birds visiting fruiting trees in Brazil's southern Pantanal. *Biological Conservation*, *208*, 29–39. https://doi.org/10.1016/j.biocon.2016.09.010

Endress, B. A., Gorchov, D. L., & Noble, R. B. (2004). Non-timber forest product extraction: Effects of harvest and browsing on an understory palm. *Ecological Applications*, *14*, 1139–1153. https://doi.org/10.1890/02-5365

Erickson, C. L. (1995). *Archaeological methods for the study of ancient landscapes of the Llanos de Mojos in the Bolivian Amazon*. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511521188

Erickson, C. L. (2000). An artificial landscape-scale fishery in the Bolivian Amazon. *Nature*, *408*, 190–193. https://doi.org/10.1038/35041555

Feil, J. P. (1996). Fruit production of *Attalea colenda* (Arecaceae) in coastal ecuador—an alternative oil resource? *Economic Botany*, *50*, 300–309. https://doi.org/10.1007/BF02907337

Fletcher, T. D. (2012). *QuantPsyc: Quantitative psychology tools. R package version 1.5*.

Fredericksen, T. S. (1999). Regeneration status of important tropical forest tree species in Bolivia: Assessment and recommendations. *Forest Ecology and Management*, *124*, 263–273.

Gilbert, G. S., & Webb, C. O. (2007). Phylogenetic signal in plant pathogen–host range. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 4979–4983. https://doi.org/10.1073/pnas.0607968104

Giroldo, A. B., Nascimento, A. R. T., Silva, P. P. F., & Pinho, G. V. (2012). Population structure and density of *Attalea phalerata* Mart. Ex (Arecaceae) in a semideciduous forest. *Revista Árvore*, *36*, 637–645.

Giroldo, A. B., & Scariot, A. (2015). Land use and management affects the demography and conservation of an intensively harvested cerrado fruit tree species. *Biological Conservation*, *191*, 150–158. https://doi.org/10.1016/j.biocon.2015.06.020

Google I. (2016). Google earth (version 7.1.7.2606).

Grégoire, B. (2010). *Le rôle des propriétés du sol dans la distribution des palmiers du genre Attalea (Palmae) et des cations échangeables de la région du Bas Tapajos (Amazonie brésilienne)*.

Gurnell, A., Goodson, J., Thompson, K., Mountford, O., & Clifford, N. (2007). Three seedling emergence methods in soil seed bank studies: Implications for interpretation of propagule deposition in riparian zones. *Seed Science Research*, *17*, 183–199. https://doi.org/10.1017/S0960258507774718

Haase, R., & Beck, G. (1989). Structure and composition of savanna vegetation in northern Bolivia: A preliminary report. *Brittonia*, *41*, 80–100. https://doi.org/10.2307/2807594

Hansen, J., Nazarenko, L., Ruedy, R., Sato, M., Willis, J., Del Genio, A., … Menon, S. (2005). Earth's energy imbalance: Confirmation and implications. *Science*, *308*, 1431–1435. https://doi.org/10.1126/science.1110252

Haynes, R. J., & Naidu, R. (1998). Influence of lime, fertilizer and manure applications on soil organic matter content and soil physical conditions: A review. *Nutrient Cycling in Agroecosystems*, *51*, 123–137. https://doi.org/10.1023/A:1009738307837

Herrera-MacBryde, O., Dallmeier, F., MacBryde, B., Comiskey, J. L., & Miranda, C. (2000). La Reserva de la Biosfera Estación Biológica del Beni, Bolivia. Biodiversidad, Conserv. y Manejo la Región la Reserv. la Biosf. Estac. Biológica del Beni. Boliv. SI/MAB, *4*, 21–25.

Hesse, A. J., & Duffield, G. E. (2000). The status and conservation of the blue-throated macaw *Ara glaucogularis*. *Bird Conservation International*, *10*, 255–275. https://doi.org/10.1017/S0959270900000216

Hordijk, I., Meijer, F., Nissen, E., Boorsma, T., & Poorter, L. (2018). Data from: Cattle affect regeneration of the palm species *Attalea princeps* in a Bolivian forest-savanna mosaic. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.8824sd0

Ibisch, P. L., Beck, S. G., Gerkmann, B., & Carretero, A. (2003). *Ecoregiones y ecosistemas*. P. L. Ibisch and G. Mérida (Eds.). Ministerio de Desarrollo Sostenible y Planificación, Editorial FAN, Santa Cruz de la Sierra, Bolivia.

Jansen, P. A., Visser, M. D., Joseph Wright, S., Rutten, G., & Muller-Landau, H. C. (2014). Negative density dependence of seed dispersal and seedling recruitment in a *Neotropical palm*. *Ecology Letters*, *17*, 1111–1120. https://doi.org/10.1111/ele.12317

Jennings, S. B., Brown, N. D., & Sheil, D. (1999). Assessing forest canopies and understorey illumination: Canopy closure, canopy cover and other measures. *Forestry*, *72*, 59–74. https://doi.org/10.1093/forestry/72.1.59

Junk, W. J., Piedade, M. T. F., Schöngart, J., Cohn-Haft, M., Adeney, J. M., & Wittmann, F. (2011). A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands*, *31*, 623–640. https://doi.org/10.1007/s13157-011-0190-7

Killeen, T. J. (1991). The effect of grazing on native Gramineae in Concepción, Santa Cruz, Bolivia. *Tropical Grasslands*, *25*, 12–19.

Killeen, T. J., Siles, T. M., Grimwood, T., Tieszen, L. L., Steininger, M. K., Tucker, C. J., & Panfil, S. (2003). Habitat heterogeneity on a forest-savanna ecotone in Noel Kempff Mercado National Park (Santa Cruz, Bolivia): Implications for the long-term conservation of biodiversity in a changing climate. In *How Landscapes Change* (pp. 285–312). Springer, Berlin: Heidelberg. https://doi.org/10.1007/978-3-662-05238-9

Langstroth, R. P. (1996). *Forest islands in an Amazonian savanna of northeastern Bolivia*. Madison: University of Wisconsin.

Laurance, W. F. (2008). Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation*, *141*, 1731–1744. https://doi.org/10.1016/j.biocon.2008.05.011

Lombardo, U. (2014). Neotectonics, flooding patterns and landscape evolution in southern Amazonia. *Earth Surface Dynamics*, *2*, 493–511. https://doi.org/10.5194/esurf-2-493-2014

Lombardo, U., Szabo, K., Capriles, J. M., May, J.-H., Amelung, W., Hutterer, R., … Veit, H. (2013). Early and middle Holocene hunter-gatherer occupations in Western Amazonia: The hidden shell middens. *PLoS ONE*, *8*, e72746. https://doi.org/10.1371/journal.pone.0072746

Loreau, M. (2010). *From populations to ecosystems: Theoretical foundations for a new ecological synthesis (MPB-46)*. Princeton, NJ: Princeton University Press. https://doi.org/10.1515/9781400834167

MacArthur, R. H., & Wilson, E. O. (2015). *Theory of Island biogeography (MPB-1)*. Princeton, NJ: Princeton University Press.

Mandle, L., & Ticktin, T. (2012). Interactions among fire, grazing, harvest and abiotic conditions shape palm demographic responses to disturbance. *Journal of Ecology*, *100*, 997–1008. https://doi.org/10.1111/j.1365-2745.2012.01982.x

Mayle, F. E., Langstroth, R. P., Fisher, R. A., & Meir, P. (2007). Long-term forest–savannah dynamics in the Bolivian Amazon: Implications for conservation. *Philosophical Transactions of the Royal Society B Biological Science*, *362*, 291–307. https://doi.org/10.1098/rstb.2006.1987

McPherson, K., & Williams, K. (1998). Fire resistance of cabbage palms (*Sabal palmetto*) in the southeastern USA. *Forest Ecology and Management*, *109*, 197–207. https://doi.org/10.1016/S0378-1127(98)00243-6

Moraes, M., & Zenteno-Ruiz, F. S. (2017). El género *Attalea* (Arecaceae) de Bolivia: Afinidades con sistemas ecológicos regionales. *Revista Peruana de Biología*, *24*, 273–282. https://doi.org/10.15381/rpb.v24i3.13913

Naeem, S., Duffy, J. E., & Zavaleta, E. (2012). The functions of biological diversity in an age of extinction. *Science*, *336*, 1401–1406. https://doi.org/10.1126/science.1215855

Navarro, G., & Maldonado, M. (2002). *Geografía ecológica de Bolivia: vegatación y ambientes acuáticos*. Centro de Ecología Simón I. Patiño.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2016). *vegan: Community ecology package. R package version 2.4-0*.

Padilla, F. M., & Pugnaire, F. I. (2007). Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Functional Ecology*, *21*, 489–495. https://doi.org/10.1111/j.1365-2435.2007.01267.x

Parham, J. A., Deng, S. P., Raun, W. R., & Johnson, G. V. (2002). Long-term cattle manure application in soil. I. Effect on soil phosphorus levels, microbial biomass C, and dehydrogenase and phosphatase activities. *Biology and Fertility of Soils*, *35*, 328–337.

Pintaud, J. C., del Castillo, A. R., Ferreira, E. J. L., Moraes, M., & Mejía, K. (2016). Towards a revision of Attalea in Amazonia. *Palms*, *60*, 57–77.

Rios, R. S., & Pacheco, L. F. (2006). The effect of dung and dispersal on postdispersal seed predation of *Attalea phalerata* (Arecaceae) by bruchid beetles. *Biotropica*, *38*, 778–781. https://doi.org/10.1111/j.1744-7429.2006.00209.x

Rosseel, Y. (2012). Lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, *48*, 1–36.

Salm, R. (2006). Invertebrate and vertebrate seed predation in the Amazonian Palm *Attalea maripa1*. *Biotropica*, *38*, 558–560. https://doi.org/10.1111/j.1744-7429.2006.00163.x

Salm, R., Prates, A., Simoes, N. R., & Feder, L. (2015). Palm community transitions along a topographic gradient from floodplain to terra firme in the eastern Amazon. *Acta Amazonica*, *45*, 65–74. https://doi.org/10.1590/1809-4392201401533

Shepherd, J. D., & Ditgen, R. S. (2005). Human use and small mammal communities of Araucaria forests in Neuquén, Argentina.=. *Mastozoología Neotropical*, *12*, 217–226.

Souza, A. F., & Martins, F. R. (2004). Population structure and dynamics of a neotropical palm in fire-impacted fragments of the Brazilian Atlantic Forest. *Biodiversity and Conservation*, *13*, 1611–1632. https://doi.org/10.1023/B:BIOC.0000029326.44647.7f

Souza, A. F., Martins, F. R., & Matos, D. M. S. (2000). Detecting ontogenetic stages of the palm *Attalea humilis* in fragments of the Brazilian Atlantic forest. *Canadian Journal of Botany*, *78*, 1227–1237.

Svenning, J.-C. (2001). On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). *Botanical Review*, *67*, 1–53. https://doi.org/10.1007/BF02857848

Veneklaas, E. J., Fajardo, A., & Lozano, J. (2005). Gallery forest types and their environmental correlates in a Colombian savanna landscape. *Ecography*, *28*, 236–252. https://doi.org/10.1111/j.0906-7590.2005.03934.x

Walker, D. J., Clemente, R., & Bernal, M. P. (2004). Contrasting effects of manure and compost on soil pH, heavy metal availability and growth of *Chenopodium album* L. in a soil contaminated by pyritic mine waste. *Chemosphere*, *57*, 215–224. https://doi.org/10.1016/j.chemosphere.2004.05.020

Watt, A. S. (1947). Pattern and process in the plant community. *Journal of Ecology*, *35*, 1–22. https://doi.org/10.2307/2256497

Whalen, J. K., Chang, C., & Olson, B. M. (2001). Nitrogen and phosphorus mineralization potentials of soils receiving repeated annual cattle manure applications. *Biology and Fertility of Soils*, *34*, 334–341. https://doi.org/10.1007/s003740100416

Williams-Linera, G. (1990). Vegetation structure and environmental conditions of forest edges in Panama. *The Journal of Ecology*, 356–373. https://doi.org/10.2307/2261117

Yamashita, C., & de Barros, Y. M. (1997). The blue-throated macaw *Ara glaucogularis*: Characterization of its distinctive habitats en savannahs of the Beni, Bolivia. *Revista Brasileira de Ornitologia*, *5*, 10.

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