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ECOSYSTEMS

Palm density and grazing effects on plant communities: implications for livestock management in a *Butia* palm grove

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Abstract: Some grasslands in ecotones with forests tend to be encroached by woody species, because of changes in climate and land use. Such structural changes in vegetation can be facilitated when the grassland community presents an autochthonous arboreal component, like *Butia* palms. We aim to identify the responses of taxonomic and functional diversity on grassland community with the occurrence of arborescent/arboreal species (autochthonous and encroaching) to palm density and grazing intensity. The study was conducted in a *Butia odorata* palm grove under cattle management, in Southern Brazil. To assess the taxonomic and functional composition we performed ordinations analysis with the vegetational data and using path analysis we assessed the causal relationships between variables of interest. Density of *Butia odorata* and woody plants were strongly positive related, suggesting a facilitation process in the establishment of arborescent plants on the grassland matrix. The abundance of less palatable plants and grazing pressure were inversely related, indicating a selection process induced by higher grazing intensity. We suggest that the grazing intensity management must be based on the autochthonous tree density, applying higher grazing intensity in areas with higher density of encroaching plants, in addition to maintaining other regions conducive to *Butia* palm regeneration through fallows.

Key words: Disturbances, grazing, Pampa biome, species composition, subtropical grasslands, sustainable activity.

INTRODUCTION

Grasslands are among the oldest and most biodiverse ecosystems in the world, dominated by a relatively continuous herbaceous layer, representing a stable alternative to forests, and maintained by disturbances such as fire and grazing, besides edaphic and climatic factors (Parr et al. 2014, Veldman et al. 2015, Bond 2022). In tropical and subtropical regions of South America, after the extinction of large native grazers (Megafauna) and the increase in temperature and humidity during the late Holocene, the maintenance of these areas occurred mainly by fire events, and more recently (in the 17th century) by the introduction of domesticated grazers (Pillar & Quadros 1997).

The evolutionary history of grazing disturbance has provided selective pressures on the local species pool that co-evolved with grazers, selecting traits that favor their maintenance under varying grazing intensities (Coughenour 1985). Characteristics such as fast regrowth, fast growing (biomass gain), and clonal growth organs presence make up the traits of species adapted to this disturbance

(Coughenour 1985, Díaz et al. 2007, Buisson et al. 2019).

In addition to the evolutionary aspect, the structure and composition of local grasslands communities are dependent on grazing intensity derived from recent management history. Grazing exclusion can promote clump formation by replacing prostrate species with upright and/or lignified species, which reduces incident radiation and results in structural homogenization of vegetation (Lezama et al. 2014, Ferreira et al. 2020). On the other hand, high-intensity grazing tends to select species that are more resistant and resilient to grazing and ultimately, when overgrazing is reached, leading them to community dominance (Baldissera et al. 2010, Buisson et al. 2019).

The recent changes in land management (e.g.: fire regimes alteration) and climate change (increasing temperature and rainfall alterations) makes certain grassland regions subject to woody species encroachment, generally associated with the advancement of forest ecosystems in grassland-forest ecotones (Guido et al. 2017, Dechoum et al. 2018). This structural change in vegetation, caused by the presence of trees or arborescent species in grasslands, influences the microclimate below their crowns, affecting soil moisture (Pressland 1973), nutrient cycling (Chendev et al. 2019), and the composition of the herb layer, favoring shade-tolerant species (Stuart-Hill & Tainton 1989, Roques et al. 2001, Pinheiro et al. 2016).

However, some open ecosystems can naturally present a high stratum composed by arborescent species (e.g., *Butia* palm groves (Chaneton et al. 2012, Sosinski Jr et al. 2019), “espinal” with *Prosopis caldenia* (Chaneton et al. 2012) and “espinilho” with *Vachellia caven* (Chaneton et al. 2012, Macias et al. 2014)). In these cases, the woody encroachment, when present, can be intensified by the facilitating effect generated by the autochthonous woody element (Chaneton et al. 2012, Overbeck et al. 2018). The presence of arborescent plants in the grassland matrix can act as perches for dispersing avifauna, increasing the seed rain of woody species, besides the microhabitat alteration by increment of shading, that favors the recruitment and development of woody plants (Duarte et al. 2006, Chaneton et al. 2012, Prather et al. 2017), two key aspects in the encroachment process. In ecosystems where this process occurs, the disturbance caused by grazing is an important factor to avoid the woody encroachment (Chaneton et al. 2012, Overbeck et al. 2018).

In the grasslands of *Río de la Plata* region, in South America, the *Butia* palm groves are a physiognomy marked by upper stratum dominated by palm trees of the genus *Butia* and a lower herbaceous layer largely grazed by cattle (Barbieri et al. 2016, Sosinski Jr et al. 2019). In southern Brazil, in the coastal plain of the Rio Grande do Sul, the palm groves with *B. odorata* are found in an ecotone with Restinga forests (Marques et al. 2011). In these ecotones woody forest species currently tend to advance over the grassland (Sosinski Jr et al. 2019), being part of the expansion and contraction cycles of a forest-*Butia* palm grove dynamic, current in the region in the last 11,000 years BP (Salgado et al. 2021). The effects of the tree component (autochthonous such as *Butia* palm or by encroachment of forest species) on the grassland matrix in interaction with livestock management on the plant community structure are still poorly studied in this kind of system (Chaneton et al. 2012, see Wieczorkowski & Lehmann 2022 for encroachment effects).

The higher grazing intensity can be responsible for preventing the recruitment of new palm trees (Sosinski Jr et al. 2019), but also limits the woody encroachment (Macias et al.

2014) and contribute to the maintenance of the heterogeneity of the herbaceous stratum. Thus, improving management to meet these ambiguous demands of conservation of *Butia* palm groves (conservation of the palm trees regeneration and control of woody species encroachment) can be a challenging task.

In this study, we describe the taxonomic and functional composition of the plant communities in a *Butia odorata* palm grove ecosystem in a gradient of palm density and grazing pressure, to test whether the observations conform to the predictions of five competing hypotheses, as follows: (1) adult palms (***P***) affect grazing (***G***) and vegetation composition (***V***); (2) ***P*** and ***G*** affect ***V***; (3) ***P*** and ***V*** affect ***G***; (4) ***G*** mediates the effect of ***P*** in ***V***; and (5) ***V*** mediates the effect of ***P*** in ***G***. The relationship ***P → G*** would arise if dense palm grooves prevents cattle access or if cattle prefers resting and/or feeding in denser palm canopies due milder microclimate conditions; the ***P → V*** relationship would occur if palm density results in competition or microclimatic conditions that changes the performance of other plant species; the ***G →V*** would happen if the grazing pressure could change the composition of plant communities; the ***V → G*** relationship would occur if vegetation composition drives foraging behavior of cattle. Finally, implications of the ecological findings to sustainable livestock management were discussed in order to promote the conservation of the palm grove, by palm regeneration promotion, and avoid the tree species encroachment.

MATERIALS AND METHODS

Study site

The study was carried out on a *Butia odorata* palm grove at São Miguel Farm, in the municipality of Tapes, state of Rio Grande do Sul, Brazil. This area integrates a large palm-grove remnant (*ca.* 9,500 ha) known as *Butiazal de Tapes* (Ramos et al. 2007, Fig. 1a). This vegetation type covers a Pleistocene depositional sedimentary system (Lagoon-Barrier – I, *ca.* 400 kyears BP), mainly on elevated barrier facies (*ca.* 80 m asl), characterized by red quartz-feldspathic sand with fine to medium granulation, embedded in an abundant diagenetic silt-clay matrix (Villwock & Tomazelli 2007). The climate type is humid subtropical (Cfa) according to the Köppen-Geiger classification (Alvares et al. 2014), with temperatures varying from 22-26 °C in the hottest month to 10-15 °C in the coldest month, and the annual rainfall is well-distributed along the year (1000~1500 mm.year^{-1}) (Becker et al. 2007).

The *Butia* palm grove of São Miguel farm has about 650 ha, with *B. odorata* forming an arborescent layer of variable density, ranging from 20 to 300 palm trees ha^{-1} (Sosinski Jr et al. 2015). The herb layer of the *Butia* palm grove is dominated by species of Poaceae, Asteraceae, Fabaceae and Cyperaceae (Marchi et al. 2018). The surrounding landscape is also composed of Restinga forests remnants and wetlands, in addition to anthropic crops and pastures.

The area is subdivided into large paddocks (30 to 260 ha), managed for extensive cattle production, with an animal load of approximately 1 animal.ha^{-1} (mostly adult and less selective animals) during all the year (personal communication from the managers of the São Miguel Farm, Fig. 1b). In areas with a low density of palm trees, mowing is eventually done. To improve the quality of forage for cattle in some areas, the invasive exotic grass *Urochloa decumbens* (Stapf) R.D.Webster was sown in the past and remains until the present by seed-bank persistence. To promote the regeneration of *B. odorata*, a 55-ha paddock was installed in the palm grove and managed, since 2013, with a lower load (0.8 animals.ha^{-1}) of young animals (between 1-1.5 years old) during the

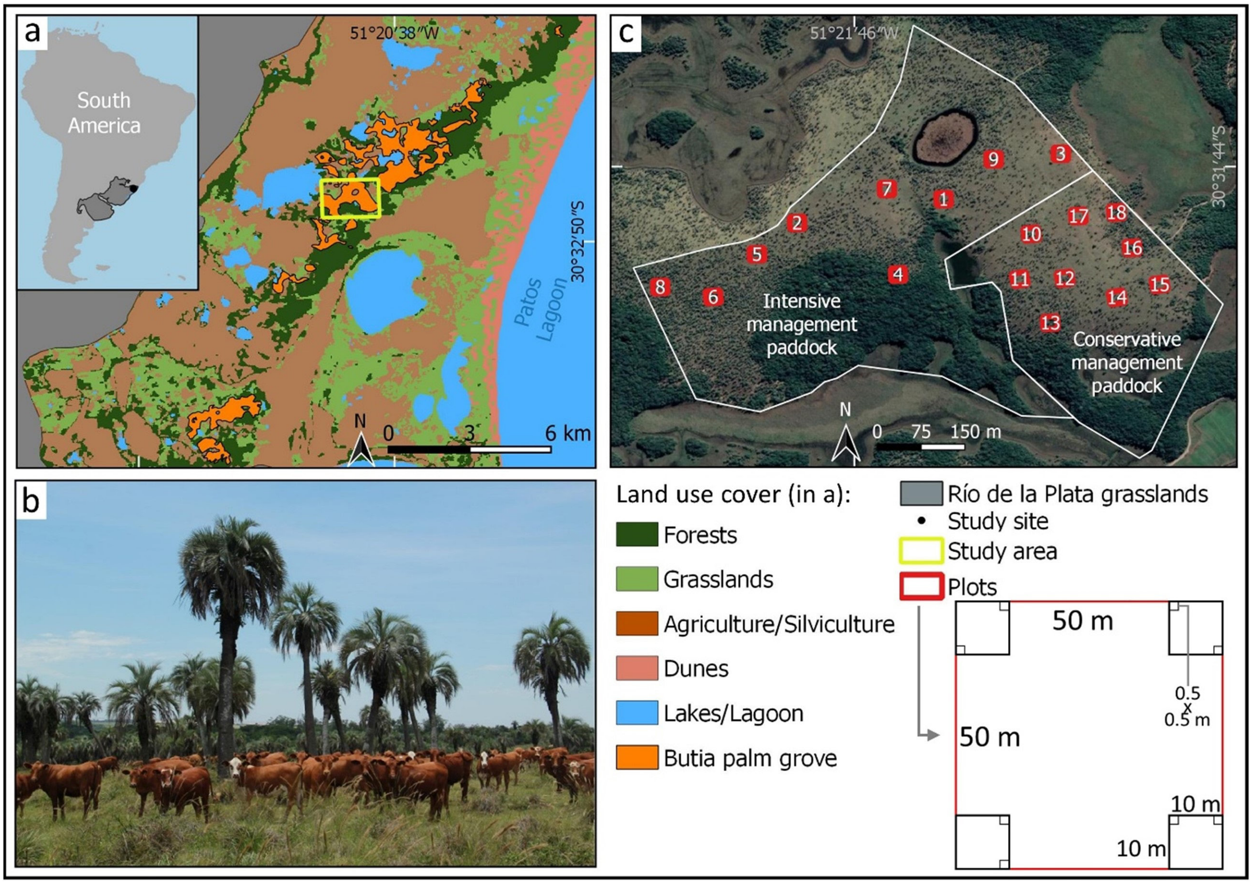

Figure 1. Location of the study area and sample design description. (a) Location of the study area in relation to the Río de la Plata grasslands, the *Butiazal de Tapes* region and associated ecosystems; (b) Vegetation and cattle profile at São Miguel farm; (c) Distribution of the sample sites (illustrated in the lower right corner; areas of 0.25 m² out of scale) in intensive and conservative management paddocks at São Miguel farm. Sources: Soriano et al. (1992); Ramos et al. (2007); Mapbiomas (2021); IBGE (2017); Google Satellites, image from 2021; photograph in C: E.E. Sosinski Jr. Geographic Coordinate System, Datum SIRGAS 2000.

spring and summer, without grazing in fall and winter (Sosinski Jr et al. 2015). The paddocks of intensive management used in this experiment will be referred to from here on as "traditional management paddocks", while the paddock with reduced animal load and fall/winter cattle exclusion will be referred as "conservative management paddocks".

Experimental design

We established 18 plots of 50 x 50 m in the palm grove, nine in the traditional and nine in the conservative management paddocks. Within each paddock the plots were distributed to comprise the density gradient of *Butia* palms according to the mapping carried out by Costa et al. (2017) (Fig. 1c). The minimum distance between plots was 150m, and the same distance was adopted in relation to sources of water and food supplementation to avoid effects of spatial autocorrelation. In the plots, we sampled the woody plants with stem equal to or greater than 5 cm in diameter at breast height (dbh), and taller than 300 cm (high stratum). Within each plot, we sampled, inside four 10 x 10 m subplots at their vertices, woody plants with stem smaller than 10 cm in dbh, and total height between 150 cm and 300 cm (intermediate stratum). For each

10 x 10 m subplot, we sampled, inside two 0.5 x 0.5 m sub-subplots on their vertices (randomly selected), herbs and woody plants smaller than 150 cm in height (low stratum; Fig. 1c).

Species identification and estimative of abundance were carried out monthly, in fieldworks from September 2018 to September 2019. For the upper stratum, we counted individuals per species, while for the lower strata we estimated species cover percentage (according to Causton 1988). Cover estimates were scaled to the 50 x 50 m plots by computing mean cover values among subplots and sub-subplots. For the species sampled in the lower strata, we estimated traits related to grazing and development, detailed in Table I.

To describe the grazing pressure on a continuous scale, we estimated the dry-weight fecal load adapting the comparative fecal loading method (Marques et al. 2001). In the summer of 2019, the cattle feces found inside the 10 x 10 m subplots were collected, dried in an oven at 60 °C until reaching a constant weight and then weighed. The fecal load estimates were scaled to the 50 x 50 m plots by computing the mean dry-weight values among 10 x 10 m subplots. Since the animal load and the rotation practiced on the farm is relatively constant over the last few years, and especially during the months in which this work was carried out, we assume that this measurement of grazing pressure in the summer of 2019 is a good representation of the general grazing pressure that these areas are normally exposed to.

Data analyses

We performed rarefaction analyzes to assess the sampling sufficiency of the species found in the 0.5 x 0.5 m sub-subplots at each plot, in order to observe how well our samples represents the overall richness of the studied area. For this we used the iNEXT package (in R software, version 4.0.3, Chao et al. 2014, Hsieh et al. 2020, R Development Core Team 2021), where the extrapolation of the species incidence frequency was pondered by the sample coverage.

To describe taxonomic and functional trends in vegetation, we performed metric

Table I. Description and ecological function of traits obtained from sampled species in a *Butia* palm grove, municipality of Tapes, southern Brazil (RG: grazing resistance capacity-P: mainly in relation to persistence, R: mainly in relation to regeneration); and trait attributes (binary or categorical).

Trait	Description	Ecological function	Classes in the matrix
Woodiness	Defined by the presence or not of secondary stem growth based on field observations	RG-P	0: absence; 1: presence
Plant height	The stratum in which the species were more frequently observed in the field	RG-P	1: lower stratum 2: intermediate stratum 3: upper stratum
Plant height potential	The height estimated based on literature descriptions and information contained in the Plant Traits Database (TRY; Kattge et al. 2020).	RG-P	1: lower stratum 2: intermediate stratum 3: upper stratum
Palatability	The preferred species of animals (according Rosengurtt 1979)	RG-R	0: unpalatable 1: palatable 2: very palatable
Clonal growth organ (CGO)	Presence or not of any spatial occupation strategies of clonal plants below-ground	RG-R	0: absence 1: presence

ordinations and correlation analyses. Species sampled in more than one stratum, in the 50 x 50 m plots, were considered in the stratum that had the highest frequency. To assess the taxonomic composition, we performed a Principal Coordinate Analysis (PCoA) based on the Hellinger distance between plots (Legendre & Gallagher 2001) and described by the cover of species from intermediate and lower strata. To assess the functional composition and abundance, a community weighted matrix of traits per plot was obtained (Díaz et al. 1992) and subjected to Principal Component Analysis (PCA) based on Pearson correlation between traits. The first two axes of each ordination were retained for interpretation using biplot scatter diagrams. To see whether taxonomic and functional gradients correspond to each other or whether they are independent patterns we performed Pearson correlations between each Taxonomic and Functional ordination axes; null probabilities for the correlation coefficients between axes scores were estimated with permutation tests (Legendre & Legendre 2012).

We assessed the validity of the five competing hypotheses of causal relationships between adult palm abundance (***P***), grazing pressure (***G***) and vegetation composition (***V***), through Path Analysis based on *d*-separation tests (Shipley 2000a, b) and AIC model selection (Shipley 2013), as follows. Each hypothesis was modeled as a Direct Acyclic Graph (Fig. 2), implying a singular basis set, *i.e.*, the set of independence claim(s) between pair(s) of variables without a direct path and any possible causal variable of them. For each model, the null probabilities for the basis set claims were estimated and combined using the Fisher's C statistic, which follows a chi-squared distribution with 2c degrees of freedom. Using the C-statistic as a maximum-likelihood estimate, we calculated the Akaike Information Criteria corrected for small samples (AIC_C) and applied the procedures of multimodel inference, comparing the AIC_c difference between each model and the model of lowest AIC_c (ΔAIC_C). Concerning the best model (with the lowest AIC_C), models with ΔAIC_C values lower than three were considered to have substantial support, values between three and seven were

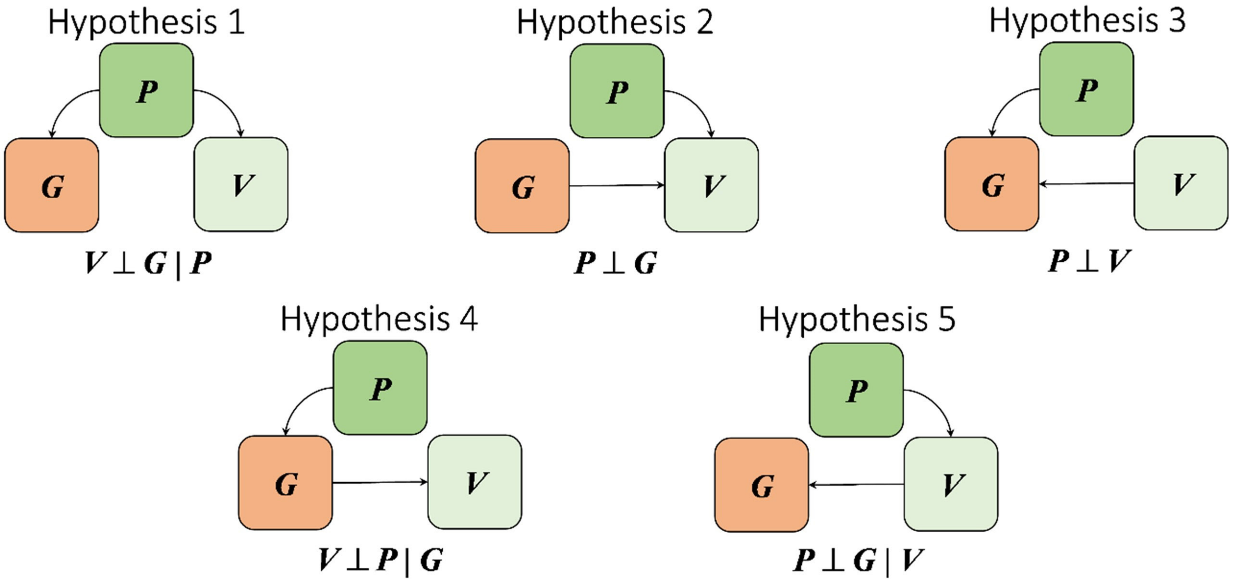

Figure 2. Direct Acyclic Graphs (path models) and respective basis set depicting five competing hypotheses of causal relationships between adult palm abundance (*P*), grazing pressure (*G*) and vegetation composition (*V*) in a *Butia odorata* palm grove.

considered to have considerably less support, and values higher than 10 were considered to have essentially no support (Shipley 2013).

For the Path Analyses, ***P*** was a vector with values of *B. odorata* abundance in the upper strata per plot, ***G*** was a vector with cattle fecal load values per plot, and ***V*** was a matrix with ordination scores of the first two functional composition axes per plot. The null probabilities for the independence claims were obtained through Procrustes partial correlations with permutation tests (Legendre & Legendre 2012). Initially, we performed the analyses with unrestricted permutations within paddocks to consider a wider gradient of grazing pressure (variation in grazing pressure of all plots in the study). Because the wider grazing gradient may be confounded with unknown idiosyncratic factors between paddocks, we also performed the analyses restricting permutations within paddocks, resulting in a narrower grazing amplitude (variation in grazing pressure between plots separately in their paddocks) with a better controlled experimental set. Finally, for models with $\Delta AIC_c < 3$, we estimated standardized path coefficients, and their null probabilities via permutation tests (Legendre & Legendre 2012). These analyses were performed on software Multiv version 3.76b (Pillar 2006). The complete dataset (species occurrence matrix per plot used in ordinations and the variables used in the path analyses) can be found in Supplementary Material - Tables SI and SII.

RESULTS

Vegetation composition

With rarefaction analyzes we observed a sample coverage of species in the lower strata above 90% in most plots, never below 80% and considering all sub-subplot per paddock (conservative and traditional) the sample coverage reached almost 100% in each (Supplementary Material - Figure S1).

We sampled a total of 79 plant species classified into 64 genera and 26 families. The species with higher occurrence and abundance (mean percentage cover or mean stem density) were: the grasses *Urochloa decumbens* (18 plots; 13%) and *Schizachyrium tenerum* (18 plots; 7%), the prostrate forb *Centella asiatica* (18 plots; 6.4%) and the rosette herb *Eryngium horridum* (17 plots; 7.9%) in the lower stratum (among 61 species); the tree *Eugenia hiemalis* (13 plots; 7.2%) and the succulent shrub *Opuntia monacantha* (11 plots; 1.4%) in the intermediate stratum (among 25 species); the palm tree *Butia odorata* (18 plots; 144 stems.ha^{-1}) and the tree *Myrsine guianensis* (2 plots; 4 stems.ha^{-1}) in the upper stratum (among eight species). Besides being the characteristic species in the upper stratum, *B. odorata* was recorded in the lower strata in only one plot. See Table SIII for a list of species frequency and abundance estimates.

The ordination analyses showed taxonomic and functional compositional gradients. The PCoA of the taxonomic matrix (Fig. 3a) showed in axis 1, which accounted for 28% of the total variation, a gradient from communities with the graminoid herbs *U. decumbens* and *Aristida laevis* (species correlation with axis $r \leq -0.74$) to communities with the trees *E. hiemalis* and *Erythroxylum argentinum*, the shrub *Varronia curassavica* and the graminoid herb *Paspalum ionanthum* (species correlation with axis $r \geq 0.64$). Axis 2 of the PCoA, representing 16% of the total variation, showed a gradient from communities with the rosette herb *E. horridum* and the graminoid herb *S. tenerum* (species correlation with axis $r \leq -0.62$) to communities with the graminoid herb *A. laevis* (correlation with axis $r = 0.63$).

The PCA of the functional matrix (Fig. 3b) showed in axis 1 (75% of the total variation), a

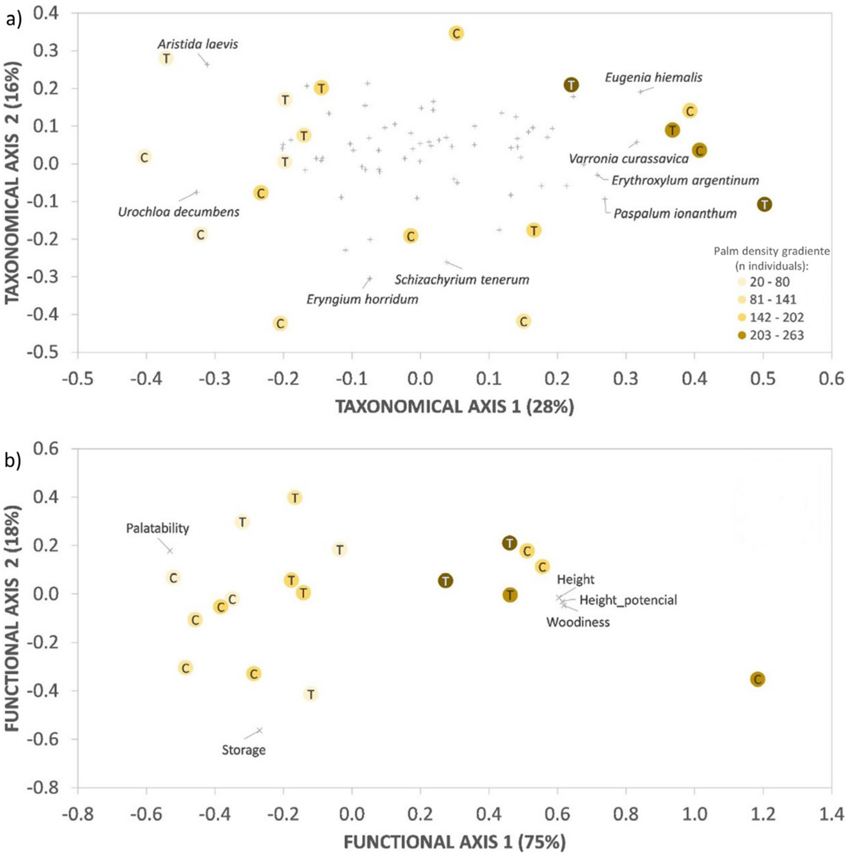

Figure 3. **Ordination biplots showing major trends in vegetation composition of *Butia odorata* palm groves. (a) illustrates a Principal Coordinate Analysis based on Hellinger distance between 18 plots (dots) described by percentage cover of 78 species (+); species names are shown for those with stronger correlation with axis 1 or 2. (b) illustrates a Principal Component Analysis, based on Person correlation between six community weighted plant traits (×) estimated for 18 plots (dots). Color scale denotes the palm tree abundance (number of individuals) per plot (color legend in the figure); T: Traditional management plots; C: Conservative management plots.**

gradient from communities with non-woody, shorter and palatable plants (correlation of palatability with axis r = -0.84) to communities with woody, taller and non-palatable plants (correlation of woodiness, height, and height potential with axis $r \geq 0.96$). The Axis 2 of the PCA (18% of the total variation) depicted a gradient from plant communities with below-ground clonal growth organs (correlation with axis r = -0.89) to plant communities without this specialization.

The correlation analysis showed significant associations between taxonomic and functional axes. Functional axis 1 was strongly associated with taxonomic axis 1 (r = 0.74; p = 0.001) and moderately with taxonomic axis 2 (r = 0.5; p = 0.044), while functional axis 2 was moderately associated with taxonomic axis 2 (r = 0.51; p = 0.041) and not associated with taxonomic axis 1 (r = -0.02; p = 0.926). Thus, the more informative functional axes (in terms of variance retained), besides representing major patterns in the trait space, also represent trends in species composition, being preferred in the further analyses of causal relationships between vegetation composition, grazing pressure, and adult palm abundance (its axes 1 and 2 were represented in the path analysis model as $\boldsymbol{V}_1$ and $\boldsymbol{V}_2$ respectively; Fig. 4).

Causal models

On wider (unrestricted permutations between paddocks) or narrower (restricted permutations between paddocks) gradients of grazing pressure, the model-fitting descriptors (Table II) showed that the model of hypothesis 5 was significant ($p \geq 0.6$) and the best fitted (lowest AIC_c). The model of hypothesis 2 was also significant ($p \geq 0.58$) and as much supported as the best-fitted model ($\Delta AIC_c \leq 0.338$), while models of

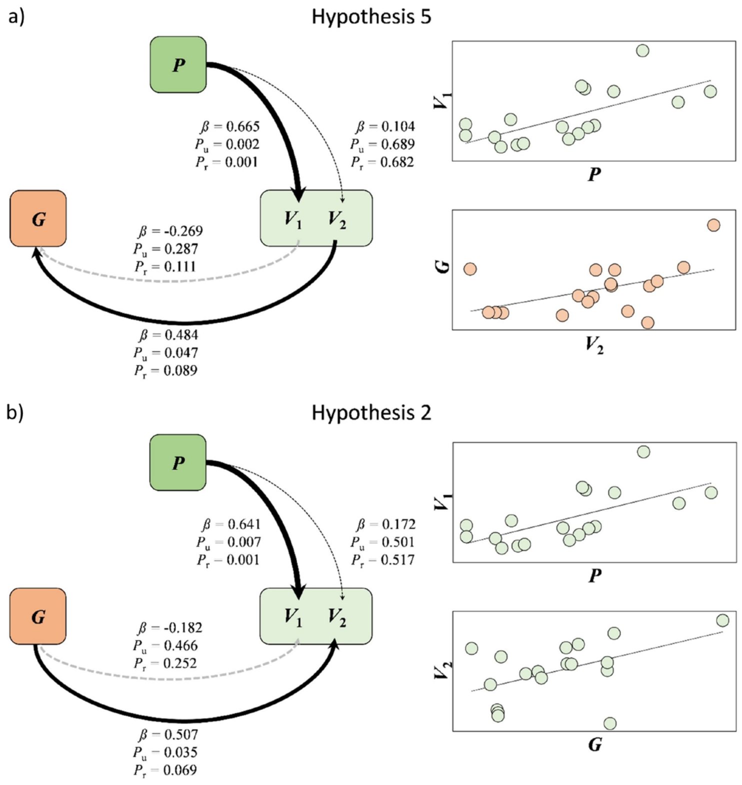

Figure 4. **Path models of hypotheses 5 (a) and 2 (b), depicting causal relationships between adult palm abundance (*P*), grazing pressure (*G*) and vegetation composition (V_1 and V_2), in *Butia odorata* palm groves. *P* was a vector with *B. odorata* abundance values in the upper strata per plot, *G* was a vector with cattle fecal load values per plot, V_1 was a vector with ordination axis 1 scores of the functional composition matrix, which describes the palatability gradient (lower values tend to greater palatability), and V_2 was a vector with ordination axis 2 scores of the same matrix, which describes the presence of below-ground clonal growth organs specialization (lower values tend to greater presence of that specialization). For each path, standardized coefficients (β) and their respective null probabilities, estimated with permutations unrestricted (P_u) and restricted within paddocks (P_r), are shown. Paths considered to be non-significant ($p > 0.089$) are presented as dashed arrows. Scatter diagrams show observed and predicted values of response variables for the significant causal variables.**

hypotheses 1, 3 and 4 were not significant ($p \leq 0.07$) and substantially less supported than the best-fitted model ($\Delta AIC_c \geq 4.524$). Therefore, standardized path coefficients were estimated for the models of hypothesis 5 and hypothesis 2. The significance of the path coefficients was similar on wider and narrower gradients of grazing pressure (Table II).

According to the path model of hypothesis 5 (Fig. 4a), denser adult palm strata strongly increased the abundance of woody, taller and non-palatable plants in the lower strata ($\boldsymbol{P \rightarrow V_1}$), and higher abundance of plants with below-ground clonal growth organs moderately decreased the grazing pressure ($\boldsymbol{V_2 \rightarrow G}$). The path model of hypothesis 2 (Fig. 4b) showed a very similar influence of adult palm density on lower vegetation strata and confirm the reverse causal relationship between vegetation and grazing, i.e., higher grazing pressure moderately decreased the abundance of plants with below-ground clonal growth organs ($\boldsymbol{G \rightarrow V_2}$).

DISCUSSION

We carried out a taxonomic and functional evaluation of grassland plant communities in a *Butia* palm grove ecosystem under cattle grazing and with a variable density of adult palm trees in the grassland matrix. We found a strong relationship between the increase in the density of palm trees and woody plants encroachment in this context, and that the abundance of palatable species increases according to greater grazing intensity.

The observed taxa agree with the sampling previously done by Marchi et al. (2018) for the same location, and shares 11 families, 15 genera and 4 species with Rivas et al. (2014), in a *B. odorata* palm grove in Uruguay. We found a greater richness of species of Poaceae and

Table II. Model fit of five path models depicting competing hypotheses of causal relationships between adult palm abundance, grazing pressure, and vegetation composition in *Butia odorata* palm groves, municipality of Tapes, Southern Brazil. Models were fitted considering wider or narrower grazing gradients, respectively, by computing *C* statistics based on unrestricted permutations or permutations restricted within paddocks of intensive and conservative management. Models are ordered according to AIC$_c$ values. “df”: degrees of freedom.

Model	*C* statistic (df; *p*)	AIC$_c$	ΔAIC$_c$
Wider grazing gradient			
Hypothesis 5	0.731 (2; 0.694)	15.731	0.000
Hypothesis 2	1.069 (2; 0.586)	16.069	0.338
Hypothesis 1	5.594 (2; 0.061)	20.594	4.863
Hypothesis 3	8.846 (2; 0.012)	23.846	8.115
Hypothesis 4	9.657 (2; 0.008)	24.657	8.926
Narrower grazing gradient			
Hypothesis 5	0.852 (2; 0.653)	15.852	0.000
Hypothesis 2	1.065 (2; 0.587)	16.065	0.213
Hypothesis 1	5.377 (2; 0.068)	20.377	4.524
Hypothesis 4	9.657 (2; 0.003)	24.657	8.804
Hypothesis 3	11.043(2; 0.004)	26.043	10.191

Asteraceae, common in the *Río de la Plata* grasslands region (Andrade et al. 2018). Our work brings new information regarding the quantitative and functional description of the plant community in a *Butia* palm grove, allowing us to verify the structure and conservation of the plant community of this ecosystem.

It is relevant to point out the predominance of the invasive alien species *U. decumbens* and the native species *E. horridum*, which were the main influencers of both ordination (PCoA and PCA) axis 1 and 2 respectively (Fig. 3) and consequently exert a greater influence on the relationship of these axes with the models variables. They have high abundance, the first being due to introduction by direct seeding in past decades and its great competitive ability and grazing resistance (Rolim et al. 2015), dominating the conditions of greater palatability associated with lower palm density (Fig. 4). The second species, because of its capacity to persist supported by a well-developed rhizome (PCA axis 2 descriptor trait) and its foliar adaptations that prevent grazing when at an advanced stage of development (Fidelis et al. 2008), being the most associated with the low grazing condition in our models (Fig. 4).

Plant community responses

We can assume that the large number of fruits produced by *B. odorata* in this ecosystem attracts the disperser fauna, generating an increase in seed rain below its crown, characterizing it as a perch species (Chaneton et al. 2012, Prather et al. 2017). The greater coverage of tree and shrub species, such as *E. hiemalis* and *O. monacantha*, for example, observed in plots with higher density of palm trees, may be a consequence of this effect, since both species have zoochoric dispersion syndrome (Bregman 1988, Lorenzi 2002).

Woody species capable of colonizing grassland ecosystems, modify the microhabitat conditions under their crowns (Duarte et al. 2006, Root-Bernstein et al. 2017). In this context, greater shading can act in synergy with greater recruitment of woody species, by providing a more favorable microclimate for their development (Duarte et al. 2006, Chaneton et al. 2012). At the same time, shading affects the plants of the herbaceous extract, decreasing its photosynthetic performance and growth rate (Fernández & Altesor 2019). Considering that most of the grasses present in the study area are C4 and require high light incidence (Fernández & Altesor 2019), the forage species of interest to maintain livestock activity must be in higher abundance, with better growth, in conditions of greater luminosity. This pattern was confirmed by presenting the highest coverage of palatable species in areas with a lower density of palm trees, which consequently are the areas with less shading by palm trees or other woody elements.

A consequence of the palatable species abundance is the greater intensity of grazing in these areas. The greater presence of cattle, attracted by the forage supply, has a driving role in community heterogeneity (Rook et al. 2004). Mechanisms such as selective defoliation by food choices (changes in light intensity by direct removal of phytomass, Bullock & Marriott 2000), trampling (niches opening for colonizing species, Dunne et al. 2011) and nutrient cycling (manure and urine concentration, Rook et al. 2004), allow for an increase in species richness. However, it is important to emphasize that this heterogeneity promoting effect depends on the animal load applied, where overgrazing conditions can lead to the exclusion of palatable species.

Under low grazing intensity, observed in areas with higher density of palm trees and consequent lower abundance of palatable species, the caespitose species defoliation is less expressive, allowing the formation of clumps. This mechanism is probably responsible for the greater abundance of *E. horridum* and *A. laevis* in our study sites. The formation of clumps can facilitate the establishment of woody species, including the *Butia* palm tree itself, by favoring the cycling of nutrients by plant decomposition (Lett & Knapp 2003, Starr et al. 2013, Chendev et al. 2019), modifying temperature and humidity (Pinheiro et al. 2016) and/or serving as mechanical protection. For example, *E. horridum* can generate a positive effect, by increase the *B. odorata* regeneration, but also can be an aggravating factor for the advancement of trees already favored by the density of palm trees.

Implications for management

Considering that the *Butia* palm grove ecosystem is in an ecotone region, and according to the paleoenvironmental record, the current forest advance is part of a dynamic historical process of expansion and retraction in the region (Salgado et al. 2021), it is likely that the increase in woody species will be inevitable in the palm grove if there is no proper disturbance management in order to reduce this encroachment. In the past, disturbance was often caused by fires, but today this disturbance is exerted only by cattle management.

A widely applied practice of forage management in subtropical grasslands is the adoption of fallows and adequacy of animal load to the ecosystem's carrying capacity, allowing the increase of available biomass and meeting the feeding needs of herds (Monroe et al. 2016, Jaurena et al. 2016, 2021). This strategy, depending on the stocking rate used, makes possible to reduce the feed selectivity of animals and evenly distribute their impact in the area, define the conditions of grasslands, increase plant coverage and generate greater richness and diversity of species (McDonald et al. 2019). In the case of *Butia* palm groves in the southern Brazil, Argentina and Uruguay, it also allows the regeneration and development of new individuals of the palm species (Báez & Jaurena 2000, Sosinski Jr et al. 2015, Rivas et al. 2017). This aspect is fundamental, considering the longevity of existing palm trees and the lack of regeneration that is strongly linked to intensive grazing, as cattle feed on seedlings or trample them, preventing their establishment (Sosinski Jr et al. 2015, Rivas et al. 2017). However, the effects of this technique on plant community structure remain unknown until now. This assessment is especially important to verify the effects when considering the areas of grassland-forest ecotone with a tendency to woody encroachment (Myster 2012).

The sustainable management practices evaluated in *B. odorata* palms in Brazil and

Uruguay follow these precepts (Báez & Jaurena 2000, Sosinski Jr et al. 2015, Rivas et al. 2017), and the results of local experiments ensured the possibility of reconciling the survival of *Butia* species together with a lucrative income-generating activity. However, in this area of study, despite the positive effects on the regeneration of palm trees (Sosinski Jr et al. 2015), our results show that the applied animal load in this management (high selective animals, after a seasonal exclusion) can facilitate the clump formation and posteriorly the woody encroachment. With this indicator, it is possible to verify the knowledge gaps for the development of efficient management practices for the conditions of the region.

The recognition of the arboreal component presence in a grassland matrix is necessary to guide the configuration of the paddocks and the grazing intensity. The density of trees per hectare has to be considered to adapt the animal load and thus maintain the composition of the herbaceous layer with good palatability, controlling woody encroachment in more sensitive areas (with higher densities of trees); and in others, allowing the regeneration of key arboreal individuals like the palm trees.

Thus, places with higher density of palm trees would be benefit with high-intensity grazing to prevent the growth of woody species, as indicated for other grassland physiognomies (Altesor et al. 2006, Boavista et al. 2019, Zhang et al. 2019). On the other hand, places with low density are more suitable for the regeneration of populations of key species without harming the maintenance of grasslands. Furthermore, in *Butia* palm groves, such locations are ideal for recruiting new individuals, as the smaller number of palm trees will avoid competition between them (Rivas et al. 2017). In these places, the seasonal fallow during the winter months and the reduction in animal load (grazing intensity) can allow the regeneration of *Butia* palm trees and help maintain the physiognomy, as already observed in other palm groves (Báez & Jaurena 2000, Rivas et al. 2017). Finally, after the period of conservative management to increase new palm trees, this managed area will be able to receive a usual animal load. This procedure will help to control the wood invasion, as expected by the tendency of our models. The animal load needed to control the woody encroachment or the dominance of caespitose clumps will required constantly adjustment according to the environment condition (e.g. palm tree density or wood invasion rate).

The results reported in this work provide subsidies for the improvement of management techniques to optimize the conservation of grassland ecosystems associated with palm trees (or other autochthonous woody elements) through good practices in livestock management. Considering that there are 22 species of palm trees of the genus *Butia*, which occur in Brazil, Argentina, Paraguay and Uruguay (Soares 2015, Noblick 2014, Deble et al. 2017, Sant'Anna-Santos 2021), often associated with grasslands in the *Río de la Plata* region, which have great potential for livestock (Sosinski Jr et al. 2015). Filling this knowledge gap may be important for the sustainable use of these grassland ecosystems with characteristics tree species, a conservation alternative little explored so far.

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SUPPLEMENTARY MATERIAL

Figure S1.
Tables SI, SII, SIII.

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