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Abiotic drivers shape seed inputs and outputs in a tropical wetland on *Croton trinitatis* population

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Abstract

Background: Predicting how natural and anthropogenic drivers shape different ecological indicators, such as plant populations along environmental gradients, can be a relevant tool for establishing management and conservation criteria of tropical wetlands. We aimed to assess the effects of seasonal flood disturbance, type of grasslands and topographical conditions on *Croton trinitatis* population distribution in a tropical wetland.

Methods: The study was carried out in a seasonally flooded grassland (Central-West Brazil). We conducted samplings of soil on the dry and flood hydrophases of the Pantanal. We took the samples in eight seasonal ponds, with 1 km interval between them. Transects were marked during the flood period, observing the water level, one in the lowest zone, in the middle of the pond = low (ca. 60 cm deep), one at the pond edge = mid (ca. 30 cm deep) and one in the higher zone, on the external part = high (ca. 1 cm deep).

Results: The results showed that the topography, seasonality, and types of grassland determine differences in the abundance patterns of adult plants and seedlings, and seed bank and seed predation. The abiotic factors can shape plant population-related ecological processes and patterns, with outputs (germination and predation) and inputs (local dispersion and from neighbouring areas) of proportional seeds for the population maintenance in this environment.

Conclusion: We emphasize the importance of these findings, to show that abiotic factors are not the only ones to be considered in ecological studies of distribution and structuring of populations in habitats with extreme seasonal events.

Keywords: Environmental filter, Flood disturbance, Pantanal, Population ecology, Seasonal change, Seed predation, Seedling, Soil seed bank

Introduction

Tropical wetlands are among the most biodiverse wetlands and productive ecosystems on earth, harboring unique aquatic and terrestrial plant communities (Junk et al. 2006; Kolka et al. 2016). Wetlands are disturbance-dependent ecosystems, where seasonal flood is

considered the primary environmental filter that determines the dynamics of plant communities and populations (Bao et al. 2018a, 2019). Furthermore, presently tropical wetlands are being heavily threatened by land-use change, such as pasture expansion (i.e., cultivated grassland by *Urochloa humidicola*) (Pott and Silva 2015), which can induce changes in the dynamics of plant communities and populations along environmental gradients (Brock 2011; Rissi et al. 2017). In the Brazilian Pantanal, topographical gradient differences that vary between 1 and 1.50 cm (Pott and Silva 2015) are fundamental

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in determining species diversity in plant communities (Souza et al. 2021). At low topographical positions, temporary ponds are established during the flood season through river overflow (Pott and Silva 2015). During the dry season, the water recedes and the temporary ponds dry, allowing different topographical levels of seed capture (Bao et al. 2014), which leads to an explosion of herbaceous seeds germination (Bao et al. 2018b).

The soil seed bank is the soil compartment, where persistent seeds are stored and remain dormant for a long time, and where transient seeds remain without dormancy for a short time (Boedeltje et al. 2002). This storage allows the seeds to remain dormant without losing their viability; when these seeds (persistent and transient) have favorable environmental conditions they can germinate, or they either lose their viability or are attacked by herbivores (Huang et al. 2020). Thus, to select a reference/key indicator species that allows monitoring and predicting ecosystem dynamics and stability (e.g., Stapanian et al. 2013; White et al. 2020), it is necessary to further evaluate anthropogenic and environmental filters (such as seasonality, type of grasslands and topography), and measure biotic factors on population-related ecological processes (e.g., predation on seed bank) (Maron and Crone 2006). However, predation assessment within seed banks is scarce in wetlands, mainly because it is technically and ecologically hard to evaluate (Bao et al. 2021a, b). After knowing the effect of predation on some key species, this may be a relevant premise to avoid underestimating or overestimating the effect size of environmental filters (and wetland dynamics and stability) on those species whose predation is not possible to measure in the seed bank.

Seedling recruitment is especially dependent on the seed bank in the soil (Bao et al. 2014, 2018a, b). The seed input reflects the seed rain, which is the plants' function to release seeds in the place (Kettenring and Galatowitsch 2011) and from neighbouring areas. The output is represented by germination (Brock 2011), parasitism losses (Stucchi et al. 2019), predation (Hembrough and Borowicz 2017), and other hazards. Thus, seed predation can change the distribution, abundance or characteristics of species or populations from patterns correlated to environmental changes (Maron et al. 2002; Solbreck and Knape 2017). For example, seed herbivory causes significant losses, and thus influences plant fitness across ecological and evolutionary scales (Braker and Chazdon 1993). Seed predation as a mortality factor can lead to a consistent loss in the next life stages (Crawley 2000), influencing the ecology and evolution of different populations (Maron et al. 2002; Schädler et al. 2004). Predation has a potential impact on species abundance and distribution (Stevens 2010),

competitive state (Chase et al. 2002), life cycle traits (Costanzo et al. 2011) or any other plant adaptations to the environment (Kolb et al. 2007).

Differences in predation damage within the seed bank, regarding seedlings and stand plants, can be significant even when the loss magnitude is small (Wenny 2000; Maron et al. 2002). Comparative experimental data are needed to determine the relative effects of seed predation to the seed germination dynamics and survival rate of seed that do not germinate (Harper 1977). The direct count seeds assessment method is an alternative to estimate the effect of seed predation on the abundance and distribution in the soil (e.g., Thompson et al. 1997), which can assist in population studies (Bao et al. 2021a, b). However, it is difficult to predict whether the circumstances under high seed losses within populations become significant, especially if adding environmental changes (Solbreck and Knape 2017).

In wetland areas, different populations are part of the plant community according to variations in flood and drought periods (Pott and Silva 2015). From that, we asked, what are the specific situations that seed predation changes on plant population-related ecological processes and patterns in wetlands? Based on this question, we propose a specific study on a population of *Croton trinitatis*, which is abundant (2.884 seeds·m²) in the Brazilian Pantanal seed banks (Bao et al. 2014), as well as in the seedling banks (1.430 seedlings·m²) (Bao et al. 2018a, b) and the standing vegetation in native and cultivated grasslands (Bao et al. 2015). In a study of seed bank assessment methods, it was found that *C. trinitatis* presented about 32% of seeds predated (Bao et al. 2021a, b). This species' seeds are often the largest (\pm 4.1 mm length \times 3 mm width) inside the seed banks from grassland areas (Bao et al. 2021a, b), which can lead to increased predator demand (Boutin et al. 2006). *C. trinitatis* is an herbaceous plant dependent on seeds for recolonization and has persistence in disturbed environments (Pott and Pott 1994), such as in seasonally flooded grasslands (Bao et al. 2014, 2015), that make this species ideal for studying.

In this context, we aimed to assess the effects of seasonal flood disturbance (post-flood and post-dry disturbance), type of grasslands (native and cultivated) and topographical conditions on *Croton trinitatis* population distribution in a tropical wetland. For this purpose, we tested the hypothesis that abiotic conditions (seasonality, type of grasslands and topography) affect the growth stages (adults and seedlings) and population-related ecological processes (seed bank and predation) of *C. trinitatis*. Thus, we established as the main prediction that abiotic conditions can interfere on predation effect and

initial establishment stages (seed and seedling banks), and adult plants distribution along time. Finally, we tested the following specific predictions:

- (i) Seasonality predicts predation: we expect that flood periods increase predation. *C. trinitatis* is a terrestrial species that can remain seeds inactive in the seed banks during flood periods (ca. 3–4 months in Brazilian Pantanal), so the probability of predation is high by aquatic invertebrates. However, the dry season can decrease predation, where those seeds germinate quickly after disturbance (Bao et al. 2014, 2015).
- (ii) Type of grasslands is the main predictor to *C. trinitatis* population: adult plants and seedlings are well distributed in cultivated grasslands, as *C. trinitatis* is an indicator of disturbed areas, and we also predict that the cultivated grasslands have less herbivory (predation), due to the use and treatment of the soil for grazing.
- (iii) Finally, we presume that the high seed flow can be seen in the different topographical levels (low, mid and high), which present different seed capture and, consequently, differences in the establishment and distribution of seedlings and adult plants.

Materials and methods

Study area

The study was carried out in the subregion of Abobral, Pantanal, Mato Grosso do Sul (Central-West, Brazil—19° 29' 27,3" S; 57° 01' 55,9" W, Additional file 1: Fig. S1a). The grassland is flooded annually during the summer (between November and April), from local rain and river overflow (Silva and Abdon 1998), with pluvial and fluvial fluctuations, with maximum (7.34 m) and minimum level (2.37 m) of the Miranda River (data collected at *Base de Estudos do Pantanal—BEP*, between 2005 and 2015). The grassland is characterized by native and exotic species (cultivated). In the absence of grazing, tall tussock grasses return and shade out existing short grasses (Pott and Silva 2015) and low herbs (Pott and Pott 2004). The existing grassland species can withstand moderate grazing and trampling (Pott and Pott 2004). Commercial seeds of *Urochloa humidicola* have been sown at Fazenda São Bento, while the native vegetation has been plowed and the shrubs cleared. In the study area, *U. humidicola* was sown 2 years before our first sampling, when the short-lived grass (annual species) had already died.

We conducted samplings on the dry and flood hydro-phases of the Pantanal: two at the end of the dry periods (2013 and 2014/September) and two at the end of the flood periods (2014 and 2015/July) (Additional file 1: Fig. S1b). We took the samples in eight seasonal ponds

(extension $\pm 50 \text{ m} \times 100 \text{ m}$), with 1 km interval between them. The Pantanal floodplain presents differences in relief, that form several seasonal ponds (Pott and Silva 2015), which show variation in the vegetation structure (Bao et al. 2015). To achieve a higher amplitude of seed capture variation, we collected soil samples along three contour lines (i.e., transects), representing relative elevation differences (topographic gradients).

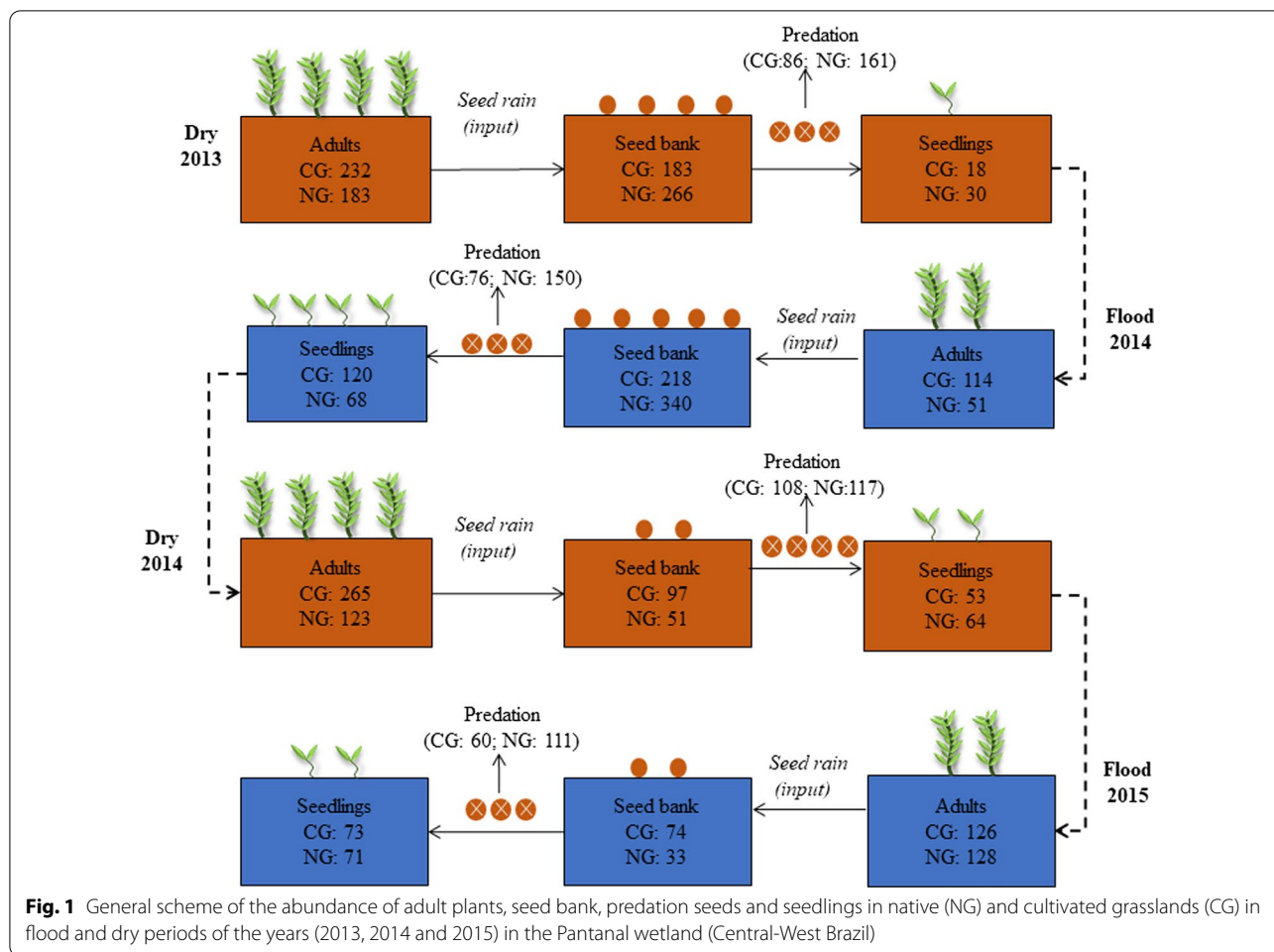
Thus, we classified the topographical gradient into three levels: (1) low—longer duration of flood; (2) mid—intermediate level; and (3) high—short duration of flood (Additional file 1: Fig. S1c). Transects were marked during the flood period (in 2013), observing the water level, one in the lowest zone, in the middle of the pond=low (ca. 60 cm deep), one at the pond edge=mid (ca. 30 cm deep), and one in the higher zone, on the external part=high (ca. 1 cm deep) (e.g., Bao et al. 2014). In each area (seasonal pond), we collected soil samples randomly (using a table of random numbers from 1 to 50 m) (e.g., Bao et al. 2014, 2015, 2018a, b).

Seed bank and seed predation assessments

In each transect, we sampled five random replicates, and we took one soil sample, with 20 \times 20 cm and 3 cm deep each, adding to 120 samples for each seasonal period. We chose this size to increase precision in estimating species abundance in the seed bank (e.g., Bao et al. 2014). The samples were stored in plastic bags and transported to the laboratory of the Federal University of Mato Grosso do Sul. We used the seed screening and counting assessment; this method was applied for determining the number of *Croton trinitatis* seeds in the soil by manual counting. For this, soil samples were washed through a sieve (0.50 mm) to trap seeds (Additional file 1: Fig. S2a, b) (Bonis et al. 1995; Mcfarland and Shafer 2011) and determine the total number of seeds in the sediment (Simpson et al. 1989). The retained seeds were preserved in alcohol 50%. We counted and separated the *C. trinitatis* seeds under a stereoscopic microscope (Additional file 1: Fig. S2c). All predated seeds had the same mark (Additional file 1: Fig. S2d), thus seeds damaged by ground friction or broken were discarded. As they are large seeds, the viability test was based on their opening, all of which presented endosperm were considered viable (e.g., Loubéry et al. 2018).

Adult plants and seedling bank assessment

The numbers of adult plants (Additional file 1: Fig. S2e) and seedlings (Additional file 1: Fig. S2f) of *C. trinitatis* were quantified at each transect, at the end of the dry and flood periods. We sampled five random replicates at the same points where the soil samples were collected (e.g., Goodman et al. 2011). Only seedlings that displayed



cotyledons up to the second pair of leaves (Brasil 2009) were considered for counting; the rest were considered adult plants (see Additional file 1: Fig. S2e).

Data analysis

All analyses were run in R 4.0.5 (R Development Core Team 2021), and to draw the graphs illustration in this study, we used the ‘ggplot2’ package (Hadley 2015). We used the Shapiro–Wilk test and Q–Q plot to evaluate the normal data distribution of all variables (number of seedlings and adults, and number of viable seeds in the soil and predated seeds), and homogeneity of variances by Bartlett’s test using the *graphics* and *dplyr* packages (Crawley 2012). We compared the mean of number of seedlings and adults, and number of seed bank and predated seeds (non-normally distributed data) between seasonal flood disturbance (post-flood and post-dry disturbance) and type of grasslands (native and cultivated) performing Wilcoxon-tests. To compare seedlings and adults, number of seeds in the soil, and number of predated seeds between topographical conditions, we used

Kruskal–Wallis’s test followed by a posterior Dunn’s test performed with the ‘dunn.test’ package (Dinno 2017).

We tested different linear mixed-effects models (LMMs, with random and fixed effects) to explain the main effects of seasonal flood disturbance (first prediction), type of grasslands (second prediction), and topographical conditions (third prediction) on growth stages of the population (adults and seedlings) and population-related ecological processes (seed bank and predation of seeds). These population-related variables, i.e., number of seedlings and adults, and number of seed bank and predated seeds, were the response variables in all models. Despite the previous analysis of data distribution, the most suitable distribution and link function (i.e., Additional file 1: Fig S1) was adjusted a Gaussian distribution (Zuur et al. 2009; Crawley 2012). Explanatory variables with fixed effect were grouped into three predictor categories: (1) topographical conditions (included three levels, low, mid, and high position), seasonal floods (have two levels, post-flood and post-dry) and type of grasslands (have two levels, native and cultivated). According

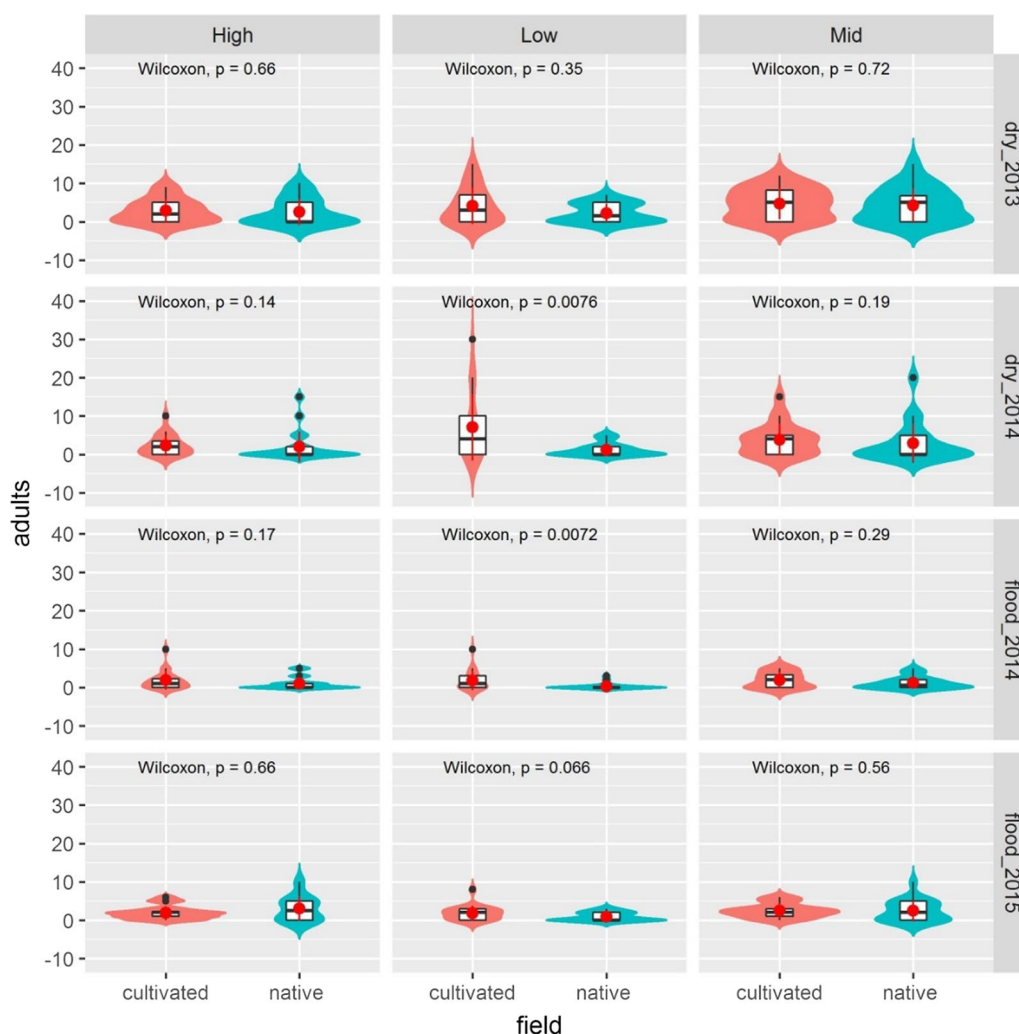


Fig. 2 Differences in number of adult individuals between type of grasslands (native and cultivated), by seasonal flood disturbance (post-flood and post-dry disturbance) and topographical conditions (low, mid, high), Pantanal wetland. We classified the topographical gradient into three levels: (1) low–longer duration of flood; (2) mid–intermediate level; and (3) high–short duration of flood

to each predictor used in each model as fixed factor, the other predictors joint with the plots were considered as a random effect. For example, $\text{model1} = \text{adults} \sim \text{topographical conditions} + (1 \mid \text{seasonal floods/type of grasslands})$, family = Gaussian), where topography is the fixed factor and the seasonal floods and type of grasslands are the random factors. This same linear model structure was tested for all the indicated response variables, and also combinations of predictors as fixed and random factors. All models were calculated using the package “lme4” (Bates et al. 2019) in the platform R (R Development Core Team 2021). Finally, to select the best models (LMMs) tested, we applied a multi-model inference approach with the *Dredge* function of the “MuMIn” package (Barton 2017), using the theoretical approach information based

on the Akaike Information Criterion (AIC), considering all models with $\text{AIC} < 2.0$ as equally plausible (Burnham and Anderson 2002; Burnham et al. 2011). We also used the predictor coefficients’ estimates to interpret parameter estimates on a comparable scale utilizing the “jtools” package (Long 2020).

Results

The topography, seasonality, and types of grassland determine differences in the abundance patterns of adult plants and seedlings, and seed bank and seed predation. Adult plants presented significant differences between types of grassland ($p = 0.0076$), and they were better distributed in cultivated grassland (737 plants) than native (485 plants) (Fig. 1), as well as with seasonality during

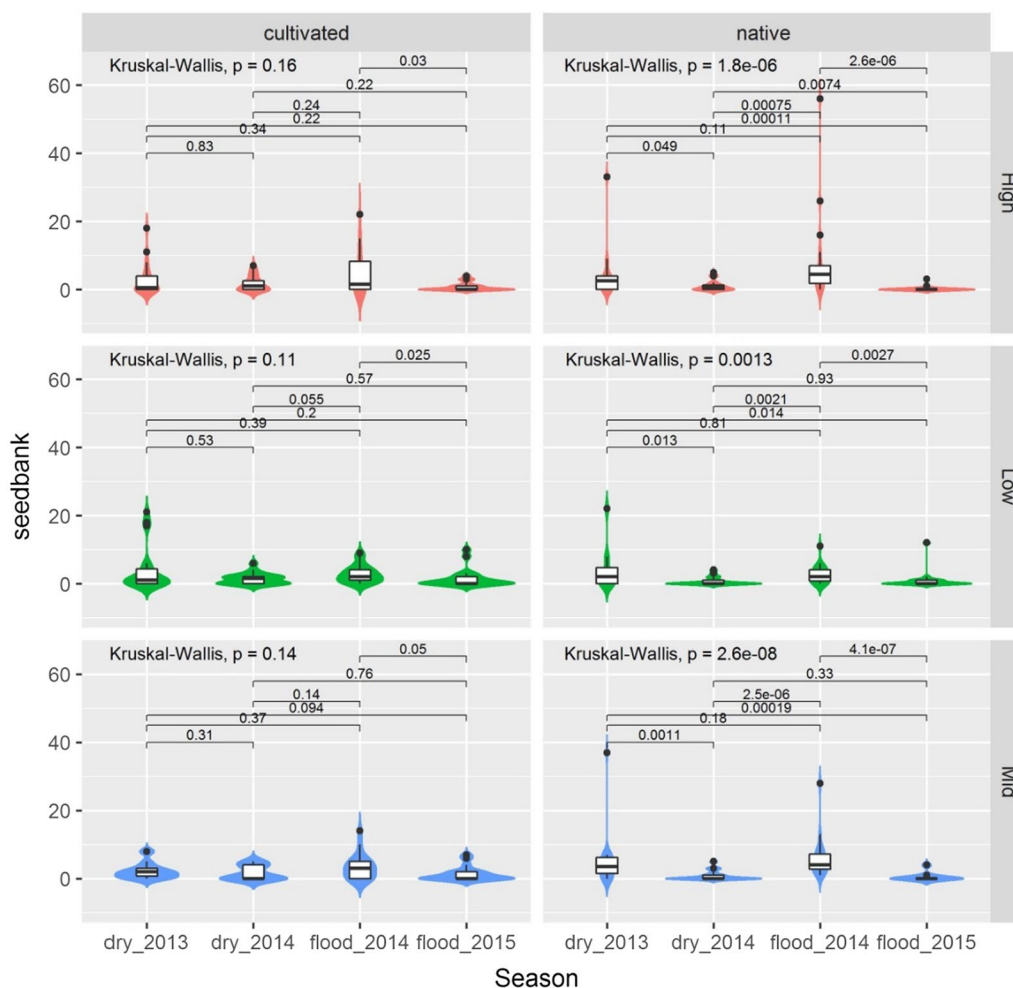


Fig. 3 Differences in number of seed in topsoil bank between seasonal flood disturbance (post-flood and post-dry disturbance) by type of grasslands (native and cultivated) and topographical conditions (low, mid, high), Pantanal wetland. We classified the topographical gradient into three levels: (1) low–longer duration of flood; (2) mid–intermediate level; and (3) high–short duration of flood. Differences at posteriori analyses are indicated (Dunn test, $p < 0.05$)

the flood period-2014 (cultivated: 114, native: 51 plants; Fig. 1) and the lower level of the topographical gradient (Fig. 2), but there were no marked differences with the topography (Additional file 1: Fig. S4).

The seed bank presented significant changes between seasons ($\chi^2 = 84.65$, $df = 3$, $p < 0.001$; Fig. 3). Seedlings also presented significant differences due to seasonal changes ($\chi^2 = 21.85$, $df = 3$, $p < 0.001$), mainly due to flood periods (Fig. 4), and topography ($\chi^2 = 6.48$, $df = 2$, $p = 0.019$), mainly due to lower topographical level (Additional file 1: Fig. S5). However, no significant changes in seed predation were observed due to seasonality and topography (Additional file 1: Figs. S6, S7), though predation was higher in native grassland (539 seeds) than cultivated

(330 seeds) (Fig. 1) and differed significantly between types of grassland (Fig. 5).

The models showed that seasonality and type of grassland are the main predictors that determine changes in the abundance patterns of adult plants and seedlings, and seed bank and seed predation (Fig. 6; Tables 1, 2). Our best-tested models showed that both native grassland (Table 1, Est. = -0.32 , $t = -4.21$, $p < 0.001$) and seasonality by flood/2014 (Table 1, Est. = -0.47 , $t = -4.33$, $p < 0.001$) have significant negative effects on adult plants (Fig. 6a; Table 2). However, seed bank variability was positively influenced by the flood/2014 period (Est. = 0.25 , $t = 2.41$, $p < 0.01$) and explained 92% of their variation, and negatively by the other seasons (Table 1), without significant effect of the topography and type of grassland

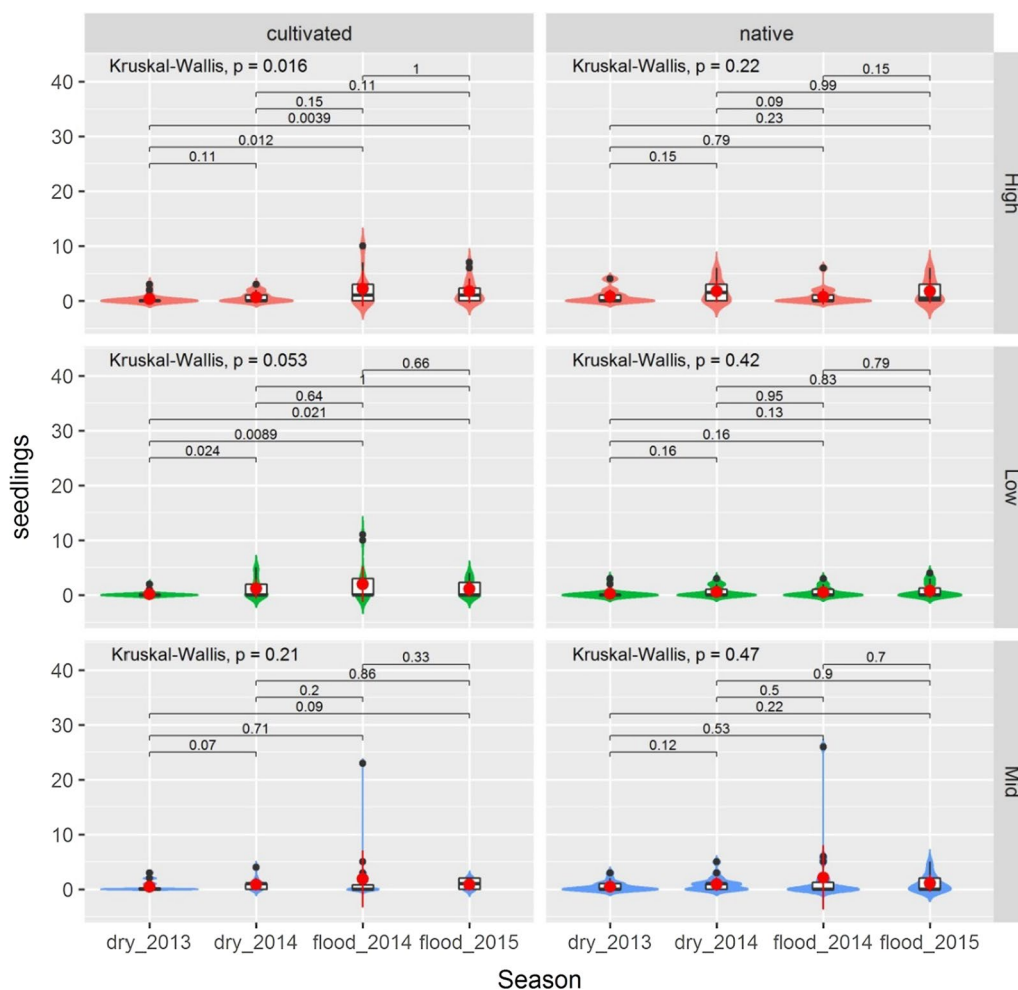


Fig. 4 Differences in number of seedlings between seasonal flood disturbance (post-flood and post-dry disturbance) by type of grasslands (native and cultivated) and topographical gradient (low, mid, high), Pantanal wetland. We classified the topographical conditions into three levels: (1) low–longer duration of flood; (2) mid–intermediate level; and (3) high–short duration of flood. Differences at posteriori analyses are indicated (Dunn test, $p < 0.05$)

(Fig. 6b; Table 2). Conversely, seedlings were positively affected in different seasons, but negatively by topography (Est. = -0.17, $t = -2.52$, $p < 0.01$), both being the best models observed (Fig. 6c; Table 2). The models used for seed predation showed that native grassland is the main driver that explains 99% of the variation (Table 2), with significant positive effects (Fig. 6d, Est. = 0.29, $t = 4.42$, $p < 0.001$), and without effects of topography and seasonality (Table 2).

Discussion

Seed bank and seed predation

In the present study, *C. trinitatis* populations showed consistent responses to predation in native grasslands, with significant losses in the dry and flood periods. In

view of many seed bank studies in wetlands, the greatest difficulty in estimating predation is the seed size (Bonis et al. 1995; Boedeltje et al. 2002; Brock et al. 2003; Brock 2011), but *C. trinitatis* seeds were the largest in this grassland, and it made this evaluation possible. *C. trinitatis* proved to be an ideal indicator species to study predatory effects. Most studies with seed banks show that the effects of seasonality are indicated as the main driver for structuring populations and communities (Bao et al. 2014; Oliveira et al. 2015; Souza et al. 2016; Kohagura et al. 2020). However, our results showed that probably predation is also a biotic filter of populations in this wetland. In addition, isolating the effect of predation enabled us to have the real knowledge of seasonal variability,

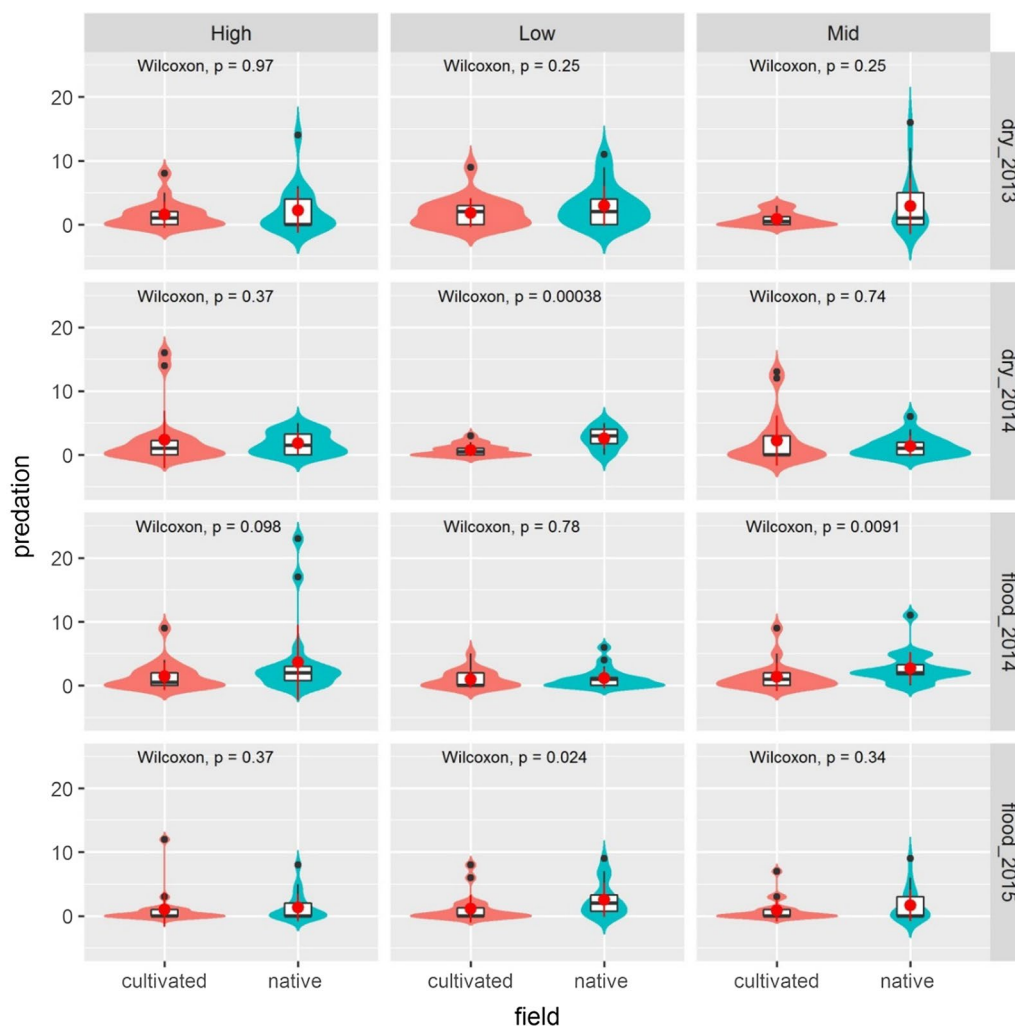


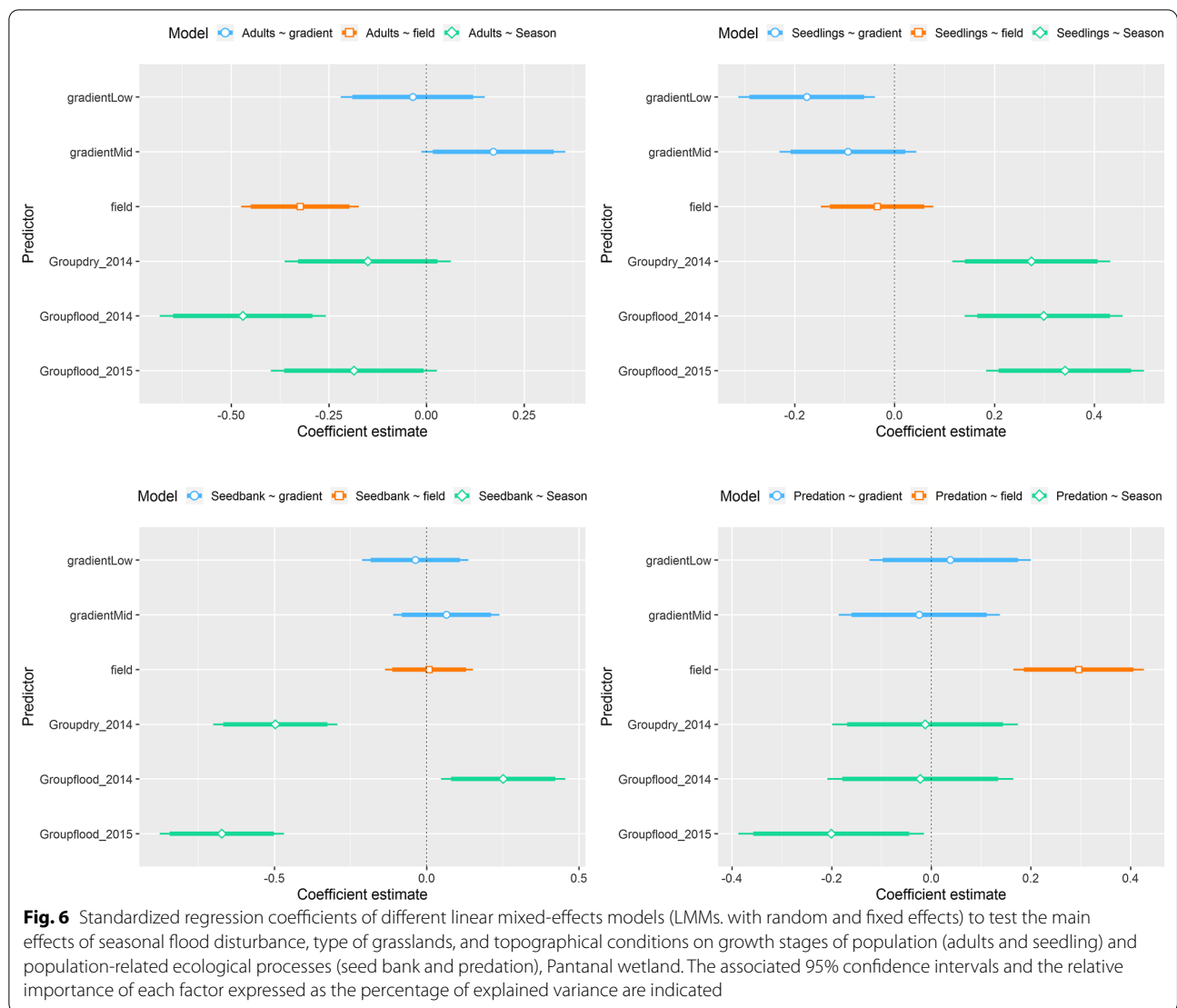
Fig. 5 Differences in number of seed predated between type of grasslands (native and cultivated), by seasonal flood disturbance (post-flood and post-dry disturbance) and topographical gradient (low, mid, high), Pantanal wetland. We classified the topographical conditions into three levels: (1) low–longer duration of flood; (2) mid–intermediate level; and (3) high–short duration of flood

which takes us to another step to monitor the dynamics and stability of wetlands.

Despite the higher abundance of seeds at low topographical levels, there was no effect on the seeds demand. Many studies suggest that the higher availability of resources (seeds) will result in higher predation (Brody 1997). However, it did not happen in this wetland because the lower elevation has a long duration of flooding, which may have decreased the number of predatory invertebrates, compared with other wetlands (e.g., Dube et al. 2017). Although there was a tendency towards greater predation in dry periods, we found no significant effects between predation and seasonality. Thus, environmental disturbances reveal that they may not have been the main driver of *C. trinitatis* when evaluated together

with predation. Seed predators can affect plant population distribution and structure (Notoman and Gorcho 2001; Maron et al. 2002).

Our results showed that the type of grasslands is a significant predictor that explains higher variability of seed predation; for example, predation was higher in native grassland than cultivated. This finding suggests that the native grassland is the primary driver of predation in this wetland. That was already expected due to the land-use change (i.e., agriculture intensification) that can decrease weed seeds predation (Hulme 1996). Many predators, as they seek various food and are not restricted to a single area of foraging, may have some flexibility and preferred places to feed (Schupp 1988; Schädler et al. 2004). Some studies have already shown that seed predators may have



different preferences concerning specific microhabitats formed by pioneer vegetation (Thompson 1982; Schädler et al. 2004). For example, wetlands have high species turnover between flood and dry periods, and topographical differences create different habitats within a short space (Pott and Silva 2015).

The low incidence of predated seeds can be supported by plants, which would not influence the population demographic regulation (Harper 1977). Our study revealed that despite high predation, there was no negative demographic effect on *C. trinitatis* populations, as can be seen in the high abundance of viable soil seeds, especially due to the positive effect of the flood that acts as the main source of seed replenishment (Schneider et al. 2020). The effects of predation when associated with abiotic factors alter the species abundance and diversity of different ecosystems and, affect the likelihood

that seed predators will visit a given location (Casazza et al. 2020). Some insects depend on various habitat types during their lives and the ability to move between them (Samways et al. 2020). Furthermore, they can be highly susceptible to certain disturbances, such as flood events, as observed, which generated higher predation in dry periods (472 seeds) than in flood periods (397 seeds). Thus, by isolating predation, we see that it can also be a biotic filter that shapes the seed bank and growth stages (seedlings and adults), consequently.

Despite the high number of seeds in the soil (in general: 1262 seeds/m²), less than half germinated (467 seedlings/m²). First, we must consider the number of predated seeds (869 predated), which may have affected our results. In addition to seed predation, what the plant perceives belowground is reflected above ground (Pillar et al. 2009). For example, if the plant perceives a lot of danger

Table 1 Coefficients of linear mixed effect models to explain the main effects of topographical conditions (included three levels, low, mid, and high position), seasonal floods (have two levels, post-flood and post-dry) and, type of grasslands (have two levels, native and cultivated) on growth stages of population (adults and seedling) and population-related ecological processes (seed bank and predation), Pantanal wetland

Response variable	Model	Estimate	t	p
Adult plants	Gradient			
	~Low	-0.03	-0.37	0.71
	~Mid	0.17	1.81	0.07
	Type of grasslands			
	~Field	-0.32	-4.21	0.001
	Seasonality			
	Dry_2014	-0.15	-1.38	0.16
Seedling bank	Flood_2014	-0.47	-4.33	0.001
	Flood_2015	-0.18	-1.71	0.08
	Gradient			
Seed bank	~Low	-0.17	-2.52	0.01
	~Mid	-0.09	-1.33	0.18
	Type of grasslands			
	~Field	-0.03	-0.60	0.54
	Seasonality			
	Dry_2014	0.27	3.39	0.001
	Flood_2014	0.29	3.70	0.001
Predation seeds	Flood_2015	0.34	4.22	0.001
	Gradient			
	~Low	-0.03	-0.41	0.67
	~Mid	0.06	0.72	0.46
	Type of grasslands			
	~Field	0.01	0.10	0.91
	Seasonality			
Dry_2014	-0.50	-4.78	0.001	
Predation seeds	Flood_2014	0.25	2.41	0.001
	Flood_2015	-0.67	-6.47	0.001
	Gradient			
	~Low	0.03	0.45	0.001
	~Mid	-0.02	-0.29	0.77
	Type of grasslands			
	~Field	0.29	4.42	0.001
Seasonality				
Dry_2014	-0.01	-0.12	0.28	
Predation seeds	Flood_2014	-0.02	-0.23	0.81
	Flood_2015	-0.20	-2.11	0.001

below ground (e.g., competition, parasitism, predation), it can accelerate or delay germination (Bao et al. 2021a, b). Below ground herbivory can reduce resident plant species' competitive ability and facilitate colonization by late-successional species (Schädler et al. 2004). However, if it has fast germination in inadequate conditions,

it increases the risk of death by predation or competition above ground (Dyer and Rice 1999).

Seedlings

The results highlight that the seasonal flood disturbance is a significant predictor that explains the *C. trinitatis* population pattern in our study area. Thus, we observed that seedlings are positively affected in different seasons in Pantanal grasslands, where there are more seedlings in post-flood (332) than in post-dry periods (165). Accordingly, we presumed that this observed pattern is mainly due to *C. trinitatis* being a pioneer species in Pantanal grasslands, where germination occurs under unflooded conditions (Bao et al. 2014, 2018a, b). In that period, there is a high number of annual and perennial species, terrestrial and amphibious species that germinate simultaneously (Bao et al. 2018a, b). However, *C. trinitatis* is a competitive pioneer species that colonizes immediately after disturbance, which shows high abundance within the seed bank (Bao et al. 2018a, b).

In both ecological processes (seed and seedling banks), the flooding promotes high abundance, mainly at lower topographical level. These results suggest that intense floods are relevant and informative to the maintenance and establishment of *C. trinitatis* and can induce an environmental response alone. Notably, the high potential of annual plants in wetlands (Bao et al. 2018a) has distinct germination strategies, and can remain dormant for months or even years in the seed bank, varying according to the environmental conditions (Wen-zhi et al. 2009).

Indicator plant species not only contribute in different ways to different dimensions of ecosystem stability (Stapanian et al. 2013; White et al. 2020), but also can simultaneously have a stabilizing and destabilizing influence (White et al. 2020). Despite that our study was restricted on the *C. trinitatis* population as a key species, we presumed that this species could shape the plant assembly community in this wetland. Predation can exert strong top-down effects on the vegetation of productive sites by affecting dominant plant species and altering competitive balances (Schädler et al. 2004). Thus, quality wetlands can be predicted by the absence or presence of indicator plant species (Stapanian et al. 2013).

Adult plants

The seasonality and type of grassland are the main predictors that determine changes in the abundance patterns of adult plants, seedlings, and seed bank. Thus, adult plants present differences between types of grassland, are better distributed in cultivated grassland (737 plants) than native (485), as well as with seasonality during the flood period-2014 (cultivated: 114, native: 51) and the lower level of the topographical gradient, but there are no

Table 2 Candidate linear mixed effect models predicting the main effects of seasonal flood disturbance (Seasonality), type of grasslands (Field), and topographical conditions (Gradient) on growth stages of population (adults and seedling) and population-related ecological processes (seed bank and predation) based on most suitable error distribution and link function (linear mixed effects model—lme)

Response variable	Model	df	LL	AICc	ΔAIC	AICcWt
Adult plants	~Field*	4	−607.1	1222.3	0.00	0.74
	~Seasonality*	6	−606.5	1225.2	2.93	0.17
	~Gradient	5	−608.3	1226.7	4.37	0.08
Seedling	~Seasonality*	6	−462.8	937.9	0.00	0.58
	~Gradient*	5	−464.4	938.9	1.00	0.35
	~Field	4	−467.1	942.5	4.57	0.06
Seed bank	~Seasonality*	6	−582.1	1176.4	0.00	0.92
	~Gradient	5	−585.6	1181.5	5.08	0.07
	~Field	4	−593.9	1196.0	19.6	0.001
Seeds predation	~Field*	4	−537.5	1083.2	0.00	0.99
	~Seasonality	6	−543.2	1098.7	15.49	0.00
	~Gradient	5	−544.3	1098.8	15.60	0.00

Result of information-theoretic-based model selection is indicated (Akaike criterion corrected for small samples). Models with significant effects (*)

AICc Akaike information criterion for small samples; ΔAICc Difference between the AICc of a given model and that of the best model (ΔAIC < 2); AICcWt Akaike weights (based on AIC corrected for small sample sizes)

marked differences with the topography. In other studies, it has already been observed that *C. trinitatis* has a wide distribution in the Pantanal grasslands (Bao et al. 2014, 2015; Souza et al. 2016). Adult plants show high vegetation cover in both grasslands and at different topographical levels (Bao et al. 2015). It is possible to collect seeds of this species throughout the year, with a decrease in flood periods, as it is a terrestrial species, whose seeds are the primary means of reproduction. There is no evidence of post-flood regrowth of the species.

We see a connection of seasonality, mainly with the seed bank, due to the flow of seeds that enter in flood periods (Fig. 1), leading to the highest number of seedlings in the post-flood, since the collections were made immediately after the water was drained in the field. The opposite occurs with the number of adults, higher in the post-dry period, when all terrestrial plants are established, but die underwater during the flood period (Fig. 1). Therefore, all growth stages are shaped by the flood and dry periods. However, for predation, the determining factor is the type of grassland, where native grasslands as expected to lose a larger number of seeds to predators (Fig. 1).

The number of predated seeds and viable seeds that enter the seed bank is similar. Therefore, we cannot conclude what is the most important in structuring populations of *C. trinitatis*, predation or abiotic factors (flood and dry periods). Despite the high predation of seeds in native grassland, we also find high input of seeds at the flood periods. Thus, there is a natural balance in the field, with outputs (germination and predation) and inputs

(local dispersion and from neighbouring areas) of proportional seeds for the population maintenance in this environment. We emphasize the importance of these findings, to show that abiotic factors are not the only ones to be considered in ecological studies of distribution and structuring of populations in habitats with extreme seasonal events.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-021-00353-x>.

Additional file 1: Figure S1. Seasonally flooded grassland in the Pantanal wetland (Central-West Brazil). **Figure S2.** Seeds counting method assessment. **Figure S3.** Example to test the most suitable distribution and link function using histogram and Q-Q considering the bests models with AIC < 2.0. **Figure S4.** Differences in the number of adult individuals between topographical conditions (low, mid, high) by seasonal flood disturbance (post-flood and post-dry disturbance) and type of grasslands (native and cultivated), Pantanal wetland. **Figure S5.** Differences in the number of seedlings between topographical conditions (low, mid, high) by seasonal flood disturbance (post-flood and post-dry disturbance) and type of grasslands (native and cultivated), Pantanal wetland. **Figure S6.** Differences in the number of seed predated between seasonal flood disturbance (post-flood and post-dry disturbance) by type of grasslands (native and cultivated) and topographical gradient (low, mid, high), Pantanal wetland. **Figure S7.** Differences in the number of seed predated between topographical conditions (low, mid, high) by seasonal flood disturbance (post-flood and post-dry disturbance) and type of grasslands (native and cultivated), Pantanal wetland.

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Authors' contributions

FB: The first author conducted this research during her PhD; this is a result of the maintenance of wetlands through the rich seed bank. This work is part of the research in fulfilment of one of the objectives. She played a significant role in conceptualization, field, and greenhouse data collection, writing of original drafts. AP: supervision of the first author during her PhD. He helped with the elaboration of concepts and understanding of the study areas. PMV: researcher was invited to collaborate in the study. He helped in the conceptualization and elaboration of the hypotheses. In addition, he contributed to the analysis of the results. All authors read and approved the final manuscript.

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Availability of data and materials

The data sets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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