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Impact of invasive grasses on Cerrado under natural regeneration

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Abstract Cerrado is the Brazilian neotropical savanna threatened by invasive African grasses. We aimed to quantify the impact of invasive *Melinis minutiflora* and *Urochloa brizantha* on the cover of different functional groups (native graminoids, forbs, shrubs) and the structure (bare soil and the cover of natives' and invasives' dead biomass) of regenerating plant communities. We hypothesized that the impact of invasives would be negative and more pronounced in the rainy period, given the great influence of seasonality in savannas. In three community types (non-invaded, invaded by *M. minutiflora* and invaded by *U. brizantha)* we evaluated the cover of functional groups and structural components by sampling 120 1 m × 1 m plots, four times a year. Using the Cohen's D impact index, we showed that both invasive species reduced the cover of all native functional groups, decreased bare soil and increased total dead cover. Greatest effects occurred when *M. minutiflora* was present. *M. minutiflora*'s impact on total graminoids varied from positive in the Early-Dry season to negative in the Mid-Dry season, while the negative impact of *U. brizantha* on bare soil became more pronounced from the dry to the rainy season. Differences in the impacts caused by the invasive species are probably due to the large biomass produced by *M. minutiflora* versus the fast colonization and soil occupancy by *U. brizantha*. Overall, invaded versus non-invaded communities differed in structure, as well as both invaded communities differed from each other. Our results demonstrate the need to control these species for conservation and restoration of Cerrado ecosystems.

Keywords Biodiversity conservation · Community restoration · *Melinis minutiflora* · Neotropical savanna · *Urochloa brizantha*

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Introduction

Introduced grasses can negatively affect grassland biodiversity and function (Flory and Clay 2010). Worldwide, this type of biological invasion is often caused by African grass species (Reed et al. 2005; Baruch et al. 1989; Rossiter et al. 2004; Pivello et al. 1999a). In temperate grassland prairies, invasive *Andropogon bladhii,* dominates the system by outcompeting the former commonly occurring native species, *Andropogon gerardii*, consequently altering the fire cycle (Reed et al. 2005). In the Venezuelan savannas, invasive *M. minutiflora* displaces native species due to its quick growth dynamics, phenology and biomass allocation (Baruch et al. 1989). In Australian savannas, invasive *Andropogon gayanus* alters fire regime, nutrient cycling and the use of water, thus affecting the richness and abundance of the understory functional groups and pushing the savanna to alternative stable states (Rossiter et al. 2004; Brooks et al. 2010). Furthermore, in the Cerrado (Neotropical savanna), invasive C_4 African species like *M. minutiflora* P. Beauv. (molasses grass) and *Urochloa* spp. are responsible for both the decline and loss of biodiversity (Pivello et al. 1999a, b; Durigan et al. 2007). The release of allelopathic compounds by *Urochloa* species (Barbosa et al. 2008; Oliveira et al. 2016) and the increased fuel load (mostly composed of dead biomass; Gorgone-Barbosa et al. 2015) also contribute to the alteration of fire behavior, as well as the dynamics of the native community, thus increasing the risk of wildfires (Hoffmann et al. 2004).

Also, in areas undergoing a regeneration process, invasive grasses can hinder the vegetation recovery (Durigan et al. 1999; Hoffmann and Haridasan 2008) despite the Cerrado's high resilience (Hoffmann 1998; Barreira et al. 2000; de Abreu et al. 2011; Pilon et al. 2018). Therefore, the invasive African grasses not only impact and decrease diversity in the Cerrado, but can be considered one of the most important biotic filters for the regeneration and restoration of those native systems (da Silveira et al. 2013). The Cerrado, like other tropical savannas, is characterized by strong seasonality, which has selected for particular physiological characteristics and therefore tailored community structure (Eiten 1972; Coutinho 1990; Franco 2002). As a result, the majority of the herbaceous layer dries out in the dry season, and resumes growing as environmental conditions become favorable during the wet season (Munhoz and Felfili 2005). Consequently, plant communities in the Cerrado are very dynamic, with vegetation structure (proportion of live to dead biomass) shifting over the year (Batmanian and Haridasan 1985), what could also cause seasonal variations in the impact of invasive grasses on native plant communities composition, structure and dynamics intra-annually.

In this study we aimed to (1) quantify the ecological impact of *M. minutiflora* and *Urochloa brizantha* on the native community structure of an open Cerrado under natural regeneration post *Pinus caribeaea* removal; and (2) quantify the effect of intra-annual seasonality on the ecological impact of both *M. minutiflora* and *U. brizantha*. We hypothesized that the invasive grasses would differently reduce the cover of functional groups of native plants, but the magnitude of such negative impacts would be greater for native graminoids due to greater overlap in resources and conditions relative to the invasive graminoids. Additionally, we hypothesized that the ecological impact of both invasive species would be greater in the rainy period, when vegetation growth is at its peak (Gorgone-Barbosa 2016; Damasceno et al. unpublished data). As a consequence of invasive species impacts, the functional groups and structure of native communities would be altered, thus leading to dissimilarity in the invaded versus non-invaded communities. Furthermore, invasive grass identity would lead to functional and structural dissimilarity between the two invaded communities.

Materials and methods

Study area

The study was conducted at the Itirapina Ecological Station (EEI, 22°11′–22°15′S and 47°45′–48°00W; 710–830 m a.s.l.) in São Paulo State, Brazil (Zanchetta et al. 2006). Most of the area is composed of grasslands and open physiognomies of the Cerrado: dominant herbaceous layer with forbs and C_4 grasses, scattered shrubs and dwarf trees. The climate is mesothermic with a marked dry season from April to September; mean annual temperature is 21.9 °C and mean annual precipitation is 1459 mm. The dominant soil type is Arenosol (Zanchetta et al. 2006).

The study site is 33 ha, and until the year 2000 it was planted with the exotic *Pinus caribaea* var. *hondurensis*. After that, pine trees were removed, grazing was excluded, fire was suppressed, and the area has been left to natural regeneration. However, at the beginning of this study there wasn't a remaining layer of pine needles on the ground anymore. *Melinis minutiflora* and *Urochloa brizantha* have invaded the area, and patches of these species can be found incorporated into the native vegetation matrix, varying in size (250 m^2–2 ha) and proximity (5–100 m apart).

Data acquisition

Vegetation sampling was carried out in three communities, dominated by (1) *M. minutiflora* P. Beauv., (2) *U. brizantha* (Hochst. ex A. Rich.) R.D. Webster and (3) native species. We selected four large patches with the minimum size of 20 × 20 m dominated by each of the two invasive species (at least 70% of cover) and four of these patches with only native species (in total, 12 large patches). In each large patch we randomly established 10 plots of 1 × 1 m (40 plots/community, total of 120 plots, with a minimum distance of 2 m between plots) avoiding termites, ant nests, armadillo holes and large areas of bare soil. Using a modified Braun-Blanquet method of quadrat frames (Wikum and Shanholtzer 1978) we evaluated in each plot the percentage cover (intervals of 5%) of community structural parameters: bare soil, dead plant cover (native and invasive dead) and live plant cover according to functional groups—native graminoids, *M. minutiflora*, *U. brizantha*, forbs and shrubs. We sampled each 1 m^2 plot four times within a year: at Early-Dry (May 2014), Mid-Dry (August 2014), Late-Dry (September 2014) and Mid-Rainy seasons (February 2015), in order to capture all changes in plant communities due to seasonality.

Data analyses

We used the Cohen's D index to quantify the magnitude of invasive species impact on the community by the pooled ratio of response variables in the invaded plots relative to non-invaded ones (Deeks et al. 2001). The equation for Cohen's D index of a functional component (native graminoids, bare soil, etc.) is given by the formula:

$$d = \frac{m_i - m_{ni}}{\sqrt{\frac{s_i^2 + s_{ni}^2}{2}}},$$

where m$_i$ and m$_{ni}$ are the mean values of a given component in the invaded and non-invaded plots respectively, and s$_i$ and s$_{ni}$ are the standard deviations of the same functional component in the respective invaded and non-invaded plots. Consequently, a positive value of d for a given functional component (native graminoids, bare soil, etc.) means that the presence of invasive grasses increased the cover of this functional component in relation to non-invaded plots. On the other hand, a negative value of d means that the invasive species decreased the cover of this component in the invaded communities in relation to the non-invaded ones. Finally, values of Cohen's D index near to zero mean that the invasive grasses had little impact on the given functional component.

As this metric is calculated from the difference of the same component in invaded and non-invaded communities, it is not possible to consider individually the invasive grasses as they are absent in non-invaded communities. Therefore, to include the invasives in the community analysis we created the categories total graminoids (native + invasive graminoid species) and total dead (native + invasive dead cover).

We first calculated the Cohen's D indices for each large patch (using the measurements of its 10 plots) and then compared communities invaded by *M. minutiflora* and by *U. brizantha* using linear mixed-effect models (lme). In this comparison we also considered interaction with seasonality (two-way analysis). Finally, we investigated the effect of seasonality on the Cohen's D index for each species individually. Further, we assessed statistical differences using pairwise post hoc general linear hypothesis tests of Tukey HSD type.

As we were dealing with non-normal multivariate and temporally correlated data, we compared invaded and non-invaded communities with the multivariate non-parametric analysis of variance—PERMANOVA (Anderson 2001)—and Principal Coordinates Analysis (PCoA). We used data from the 120 plots on community structural components (bare soil and dead plants cover), live plant cover according to functional groups (native graminoids, forbs and shrubs), and the two created categories (total graminoids and total dead). As data was expressed as abundance (%) and is

therefore upper limited, we used the chord distance to generate the dissimilarity matrix for both analyses (Orlóci 1967). Statistical analyses were performed in the R program (R Development Core Team 2016) with the packages nlme (Pinheiro et al. 2016), vegan (Oksanen et al. 2016) and multcomp (Hothorn et al. 2008).

Results

Overall, Cohen's D impact indices of both invasive species were negative on the community structural components and functional groups. On regenerating communities, both invasive species had a similar effect ($p = 0.32$, $- 1.12 \pm 2.30$ and $- 0.86 \pm 1.77$ for *M. minutiflora* and *U. brizantha* respectively; mean $\pm$ SD for all results). The impact of *M. minutiflora* and *U. brizantha* differed for bare soil ($p = 0.03$; $- 1.94 \pm 0.66$ and $- 1.33 \pm 0.77$, respectively) and total dead cover ($p = 0.009$; 2.93 ± 1.27 and 1.90 ± 0.86). In both cases, *M. minutiflora* has a stronger impact than *U. brizantha*: higher increase in the percentage of total dead cover and higher decrease in the percentage of bare soil.

Both invasive species reduced the cover of every native functional group (graminoids, forbs and shrubs) and native dead cover (Fig. 1). The most negatively impacted groups both by *M. minutiflora* or *U. brizantha* were the native graminoids (Cohen's D index of $- 4.24 \pm 1.45$ and $- 3.29 \pm 1.34$, respectively), and the native dead cover, with values of $- 3.28 \pm 1.276$ and $- 2.70 \pm 0.98$. When considering the categories that include the invasive species (total dead cover and total graminoids) the impact of invasion was positive due to their contribution to both dead and live biomass (Fig. 1).

The negative impact of invasive grasses was not influenced by seasonality when considering structural components and functional groups altogether across time ($p = 0.90$; Table 1). Considering each functional group separately, only the total graminoids varied seasonally in the communities invaded by *M. minutiflora*, from a positive effect (1.209 ± 0.606) in the Early-Dry period to a negative one ($- 2.178 \pm 1.608$) in the Mid-Dry season ($p = 0.02$; Fig. 1a). For *U. brizantha* plots, a significant difference was detected in the bare soil, which changed from $- 0.697 \pm 0.481$

in the Mid-Dry to $- 1.998 \pm 0.659$ in the Mid-Rainy season ($p = 0.03$; Fig. 1b).

Thus, the presence of both invasive species led to dissimilarity in structure and functional composition of invaded versus non-invaded communities (PERMANOVA, $p = 0.01$); and communities invaded by *M. minutiflora* and *U. brizantha* were dissimilar between each other (PERMANOVA, $p = 0.04$). The PCoA illustrates these patterns by the shift in location of invaded and non-invaded communities in two dimensions (axes), which together explained 71.2% of the total variation in functional composition (Fig. 2).

Discussion

Impact of invasive species on functional components

Urochloa brizantha and *Melinis minutiflora* reduced the cover of bare soil, native functional groups and native dead biomass. Additionally, these impacts were mostly constant over the year, leading to different communities where the invasive species were present. *Urochloa* spp. and *M. minutiflora* have been described as very aggressive, and the most common invasive species in Cerrado (Pivello et al. 1999b; Zenni and Ziller 2011; Ziller and Dechoum 2013; Sampaio and Schmidt 2014). Some authors had already shown negative impacts of these species on the invaded systems (Klink 1994; Pivello et al. 1999a; Almeida-Neto et al. 2010; Martins et al. 2011; Rossi et al. 2014). The presence of *M. minutiflora,* for example, inhibited the establishment of native tree species (Hoffmann and Haridasan 2008), hindering the recovery of degraded areas by increasing its abundance and excluding native species (Martins et al. 2004). It has been shown that these African grasses negatively affect native grasses (Pivello et al. 1999a) and Asteraceae shrubs (Almeida-Neto et al. 2010). Moreover, *Urochloa* species may reduce the germination of native species due to the production of allelopathic compounds (Almeida et al. 1997; Barbosa et al. 2008). However, despite describing the effects of African grasses, the above-mentioned studies did not quantify the impact caused by these invasive species nor evaluated their effect on functional groups or according to seasonality.

In this study we verified that the strongest cover reduction caused by *M. minutiflora* and *U. brizantha*
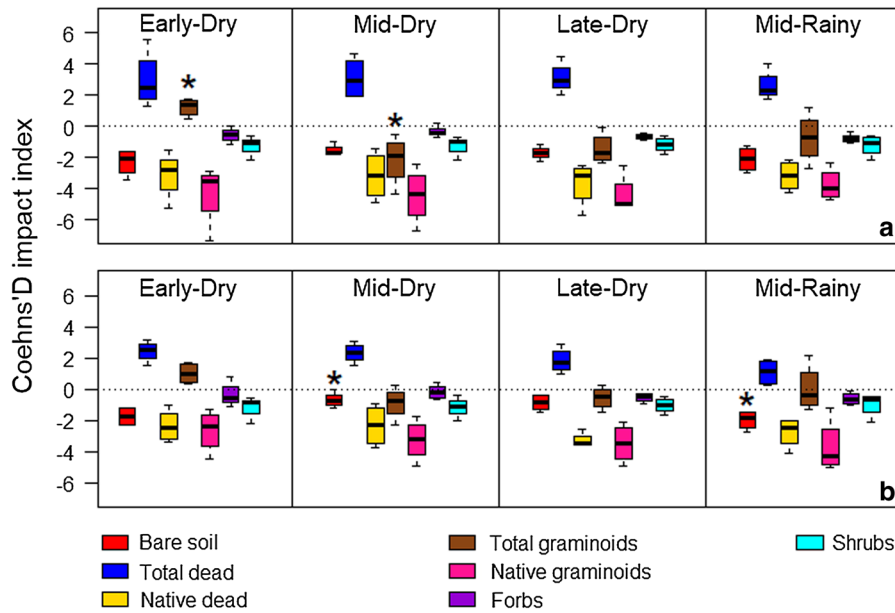
Fig. 1 Cohen's D impact index for *Melinis minutiflora* (**a**) and *Urochloa brizantha* (**b**) on the community structural components (bare soil, total dead plant cover, native dead plant cover), live plants cover according to functional groups (total graminoids, native graminoids, forbs, and shrubs). Boxplots represent the median (black line), and the first and third quartiles (lower and upper lines, respectively). Statistical differences in Cohen's D impact index among the four seasons (Early-Dry, Mid-Dry, Late-Dry, Mid-Rainy) are marked with asterisk (*)

Table 1 Cohen's D impact index (mean ± SD) of *Melinis minutiflora* and *Urochloa brizantha* over a year on regenerating communities considering structural components (bare soil and plant dead cover) and functional groups (native graminoids, forbs and shrubs) altogether

Invasive	All-time	Seasons			
		ED	MD	LD	MR
Melinis minutiflora	− 1.12 ± 2.30	− 0.90 ± 2.49	− 1.21 ± 2.40	− 1.23 ± 2.32	− 1.13 ± 2.08
Urochloa brizantha	− 0.86 ± 1.77	− 0.59 ± 1.81	− 0.75 ± 1.78	− 0.98 ± 1.77	− 1.14 ± 1.76

No statistical differences were found either between the two species or across seasons for each species ($p > 0.05$ in all cases). *ED* Early-Dry, *MD* Mid-Dry, *LD* Late-Dry, *MR* Mid-Rainy seasons

was on native graminoids. However, contrary to our hypothesis, seasonality did not enhance or decrease their impact on the vegetation. Both invasive species are perennial and produce high amounts of biomass during the rainy season. Most of that biomass dries out in the dry season but remains attached to the plant (Gorgone-Barbosa 2016; Damasceno and Fidelis unpublished data). In the next rainy season, when water is available, the invasive grasses quickly resprout (Fisher and Kerridge 1996; Zanchi et al. 2009) and bring negative and persistent impacts to the community. The reduction of native graminoids

caused by both African grasses that was observed in this study contrasts with others in which functional similarity limited the community invasion by plants from the same functional group (Fargione et al. 2003; Pokorny et al. 2005; Emery 2007; Emery and Gross 2007). However, explanations can be related to factors other than functional redundancy, such as the community richness, or the tridimensional structure given by plant height, above-ground architecture and/or rooting depth, which establish a spatial niche partitioning (Anten and Hirose 1999; Fargione and Tilman 2005; Mozdzer et al. 2016).
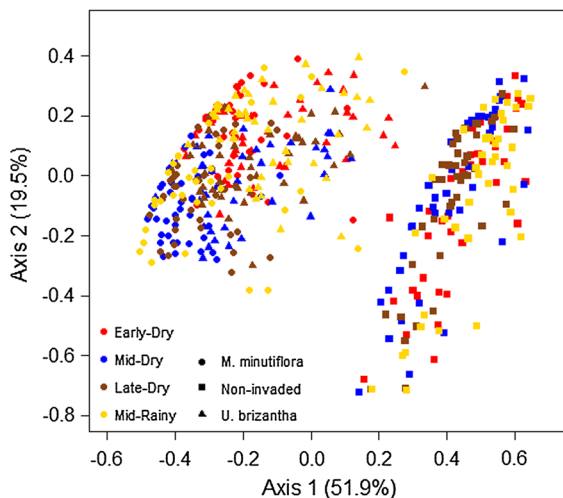
Fig. 2 Principal Coordinates Analysis (PCoA) for the non-invaded communities and communities invaded by *Melinis minutiflora* or *Urochloa brizantha* during four periods. Every point represents the position of a plot (1 m²) regarding functional groups composition (total graminoids, native graminoids, forbs and shrubs) and community structure (bare soil, total and native dead cover). Different symbols refer to distinct communities (non-invaded and dominated by each invasive grass) and different colors refer to distinct sampling periods

Moreover, according to phenotypic characteristics that favor the dominance of invasives over native species (Daehler 2003), both *M. minutiflora* and *U. brizantha* are usually taller than Cerrado grasses, shading the heliophile native graminoids (G. Damasceno, personal observation). Additionally, their architecture may also contribute to this spatial niche partitioning: *M. minutiflora* is a stonoliferous species, a characteristic that could facilitate its soil colonization, while the huge production of biomass by *U. brizantha* would be facilitated by its cespitose architecture.

Furthermore, a temporal niche partitioning can be achieved through different phenological strategies (Engelhardt and Anderson 2011). In our system, invasive species usually flourish and disperse in the dry season (Gorgone-Barbosa et al. unpublished data) while the most dominant native grasses in the area, e.g. *Axonopus pressus* and *Gymnopogon foliosus,* reproduce in the rainy season. However, it is common to see *Urochloa* spp. individuals producing flowers and seeds throughout the year. Both *M. minutiflora* and *U. brizantha* have evolved under grazing pressure in the African savannas and thus have become good

competitors in assimilating nutrients and producing biomass (Baruch et al. 1985; McNaughton 1985; Lannes et al. 2012), and are probably more efficient in resource and water acquisition than the native Cerrado grasses (Rossiter et al. 2004; Mozdzer et al. 2016). They rapidly cover the soil by producing and accumulating biomass, thus hampering conditions for the establishment and development of native plant seedlings (Williams and Baruch 2000; Silva and Haridasan 2007; Hoffmann and Haridasan 2008; Assis 2017).

As a consequence of the decrease in the cover of native grasses cover, the native dead biomass cover was also reduced by both invasive species, which may lead to changes in decomposition rates and nutrient cycling (Vitousek 1992; Vila et al. 2011). Additionally, the amount and quality of dead biomass in a system can alter species dominance in an herbaceous community undergoing succession (Facelli and Facelli 1993). In our study site, the huge production of dead biomass by the invasive species, and their efficiency in colonizing bare soil, hinders the establishment and recovery of native species, especially those from the same functional group, by modifying the micro-habitat and the conditions for native species development (Williams and Baruch 2000; Silva and Haridasan 2007; Hoffmann and Haridasan 2008) and by creating a physical barrier that might affect seedling establishment (Flory and Clay 2010). Finally, the greater amount of dead biomass could lead to more intense fires, thus affecting the fire behavior in the invaded communities (Gorgone-Barbosa et al. 2015). These changes could lead to a positive feedback-cycle between invasive grasses and fire, which could be another factor contributing to the success of invasive species over natives (D'Antonio and Vitousek 1992).

Impact on plant communities: implications for restoration and conservation

The production of vast quantities of persistent biomass produced by *M. minutiflora* and *U. brizantha* will probably lead to dissimilar communities at the detriment mainly of native grasses. Our results could be interpreted as an early stage of the differentiation between invaded and non-invaded communities, which may drive modifications in the community composition (species richness, evenness, diversity) or in the relationships among native species (Kuebbing

et al. 2014), and consequently, in diversity, productivity and seedling establishment (Drake et al. 2008; Kuebbing et al. 2015). In the long-term, the ecosystem processes of the altered communities may be modified, such as changes related to decomposition and nutrient cycling, water conservation, and fire regime (Vitousek 1992; D'Antonio and Vitousek 1992; Hoffmann and Haridasan 2008; Gorgone-Barbosa et al. 2015), which may ultimately lead the system to alternative stable states (Westoby et al. 1989; Brooks et al. 2010). Particularly in ecosystems under a multiple-pathway succession, invasive species can alter the trajectory through the loss of species and changed ecosystem properties (Suding et al. 2004; Suding and Gross 2006; Brooks et al. 2010). Moreover, exotic invasive grasses can persist in ecological systems over long periods of time, thus creating the need for management actions to exclude them from the system (D'Antonio and Meyerson 2002). Similar to temperate grasslands, plant invasions by *M. minutiflora* and *Urochloa* spp. in the Cerrado can promote the transition from preserved open formations into degraded states (Pivello and Coutinho 1996), ultimately altering the community diversity-stability mechanisms (Wilsey et al. 2014) to a point where a "degraded land" (sensu Pivello and Coutinho 1996) persists. The control or eradication of *M. minutiflora* and *U. brizantha* is thus needed to redefine the trajectory towards restoration of a diverse community where mechanisms of diversity-stability are maintained.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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