

Can an invasive African grass affect carbon and nitrogen stocks in open habitats of the Brazilian Cerrado?

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Abstract

Considering the emergence of ecosystems dominated by invasive species, there is growing interest in estimating the effect of biological invasions in ecosystem processes and provision of services. African grasses are the most invasive plants in the *Cerrado* (Brazilian savanna), but their impact on C and N stocks is poorly known. We compared patterns of C and N stocks in the aboveground biomass, root biomass and soil in open *Cerrado* (*campo sujo*) sites, both uninvaded and invaded by the African grass *Urochloa decumbens*. In both sites we estimated the aboveground biomass of *U. decumbens* and native grasses, as well as the root biomass up to 50 cm. We obtained C and N contents in the soil, as well as C and N stocks, up to 1 m depth, and variation in soil $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Although invasion did not affect the aboveground biomass, it did affect belowground biomass, leading to higher C stock in fine roots and soil N content close to soil surface, as well as higher C content along the soil profile. C and N soil stocks, soil $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values did not significantly differ between invaded and uninvaded site. Even a relatively low level of invasion by *U. decumbens* changed the root distribution pattern and increased C and N contents in the upper soil, which may promote ecosystem changes by altering nutrient dynamics. Although still preliminary, our study shows that dominance by *U. decumbens* can have severe effects in the *Cerrado* belowground environment.

1. Introduction

Invasive exotic species may cause a wide variety of impacts on invaded environments, which often lead to biodiversity loss and changes in ecosystem processes (Simberloff et al. 2013; Downey and Richardson 2016). While some biological invasions produce easily detectable patterns, others become noticeable only after causing severe negative effects, such as the loss of regulating ecosystem services (Castro-Diez et al. 2021). Invasive plant species often show high photosynthetic and growth rates, and many of them make associations with N-fixing organisms (Ehrenfeld 2003, 2004; Simberloff et al. 2013; Vitousek and Walker 2014). As a result, they may change both above and belowground nutrient stocks – especially carbon and nitrogen – and affect biogeochemical cycles and balances, as well as other ecosystem processes and services (Ehrenfeld 2003; Vilà et al. 2011). By stocking, producing or emitting C and N through their metabolic pathways, invasive plant species can synergistically affect the balance of atmospheric gases, thus increasing local C and N pools (Litton et al. 2008; Rossiter-Rachor et al. 2009; Macdougall and Wilson 2011) and changing patterns of primary productivity and nutrient cycling (Ehrenfeld 2003, 2010; Standish 2004; Liao et al. 2007; Greaver et al. 2016).

Savannas and grasslands are very important C sinks all over the world (Scurlock and Hall 1998; Grace et al. 2006), as they store carbon mainly in the root system and soil (Grace et al. 2006). The *Cerrado* is the richest savanna in the world (Silva and Bates 2002), with more than 13,100 vascular species, about 80% of which belong to the herbaceous-shrub layer (Mendonça et al. 2008; Overbeck et al. 2015). However, intensive cattle foraging based on exotic species as fodder (Ratter et al. 1997; Klink and Machado 2005; Silva et al. 2006) has promoted the invasion of many African C4 grasses in the *Cerrado*, which pose a great threat to this biodiversity hotspot (Pivello et al. 1999a, b; Klink and Machado 2005; Damasceno et al. 2018). Grasses of the genus *Urochloa* (brachiarias) have shown great capacity to invade and rapidly dominate the herbaceous layer of open Neotropical savannas (Damasceno et al. 2018) thanks to their high efficiency in producing biomass (Williams and Baruch 2000), favoured by effective N acquisition associated with symbiotic organisms (Boddey and Victoria 1986; Okumura et al. 2013), as well as an effective seed regeneration strategy (Xavier et al. 2021) and the release of allelopathic substances to inhibit other species germination (Gorgone-Barbosa et al. 2008).

In a scenario of climate change, warmer climates with altered precipitation patterns are expected to intensify (Hoegh-Guldberg et al. 2018), probably facilitating the establishment and spread of invasive species (Barnosky et al. 2012; Chown et al. 2015), and specially C4 grasses which are well adapted to such conditions (Edwards and Still 2008). Therefore, it is essential to predict the impacts of grass invasions on ecosystem processes and services in the *Cerrado*, and hence support effective management. However, to date no study has investigated the effect of invasive species on C and N stocks and fluxes in the *Cerrado*.

In this study we compared patterns of C and N stocks in the aboveground biomass, root biomass, and soil in open *Cerrado* sites, both in uninvaded and invaded by *Urochloa decumbens* Stapf. We specifically aimed to answer: i) Does invasion by *U. decumbens* increase C stocks in the aboveground biomass? (Hypothesis: Invasive species are highly productive, leading to high C assimilation and high production of aboveground biomass.); ii) Are there differences in C stocks in the root biomass between uninvaded and invaded sites along the 0–50 cm soil profile? (Hypothesis: Highly productive invasive species demand higher nutrient uptake from the upper soil layers and a greater production of roots than native species); iii) Are the soil contents and stocks of C and N different between uninvaded and invaded sites throughout the soil profile? (Hypothesis: Different patterns of root production and decomposition between native and invasive species, as well as the association of *U. decumbens* with N-fixing microorganisms modify distribution patterns of elements throughout the soil profile.); iv) Does the soil $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differ between invaded and uninvaded sites? (Hypothesis: Invaded sites with a more homogenous grassy layer and N-fixing species show higher $\delta^{13}\text{C}$ and lower $\delta^{15}\text{N}$ soil values).

2. Materials And Methods

2.1. Study Area

The study was conducted at Itirapina Ecological Station (IES, 22°11'–15' S; 47°51'–55' W), a 2,300 ha *Cerrado* protected area in Southeast Brazil (IF 2006). Regional climate is subtropical with hot summers and mild winters (Köppen's Cwa), and average temperatures range from 17.8° C in June to 24.9° C in January. Average annual rainfall is 331 mm in the dry season (April to September), and 1128 mm in the rainy season (October to March) (IF 2006). In the IES, soils are Entisol, Gleysol and Histosol (IUSS Working Group WRB 2015), which correspond to Neossolo Quartzarênico, Gleissolo and Organossolo in the Brazilian classification (Santos et al. 2018), and the vegetation is dominated by open *Cerrado* physiognomies (see Coutinho 1978; Ribeiro and Walter 1998).

Crop plantations (mostly sugarcane), forestry (*Eucalyptus* spp. and *Pinus* spp.) and brachiaria (*Urochloa* spp.) pastures surround the IES. The brachiaria was introduced to the reserve by the 1980's and has spread and become dominant in parts of the IES, but open physiognomies still show high plant diversity (Tannus and Assis 2004; Xavier et al. 2019). This study was conducted in a well-drained open savanna (*campo sujo*) where trees or shrubs have remained sparse for at least 40 years (Leite et al. 2018). We delimited an uninvaded (visually free of *U. decumbens*, ca. 4000 m²) and an invaded (where *U. decumbens* was one the most abundant species, ca. 2500 m²) area, where we collected soil and vegetation samples (respectively six and eight samples in each area) during the rainy season. The soil in this site is an Entisol with 96% sand and 4% clay; pH is 4.2 and the amount of organic matter is around 11 g dm⁻³ (Xavier et al. 2019, Suppl. Material); the minimum annual water table depth is 2.7 m and there is less than a month of less than-optimal soil water availability close to the soil surface (20 to 30 cm) (Xavier et al. 2017). Previous studies found little spatial variation in the hydrological regime and soil properties within this area (Leite et al. 2018, Xavier et al, 2017, Xavier et al. 2019) suggesting that soil moisture and fertility conditions are similar in the uninvaded and invaded site.

2.2. Carbon stocks in the biomass

We visually estimated the percent cover of *U. decumbens* and native herbaceous vegetation in both uninvaded and invaded sites in ten 1 x 1 m plots at least 15 m apart using a wooden frame divided by a 10 x 10 cm string grid. In the same plots we collected aboveground live and dead biomass, separated live biomass into *U. decumbens* and native species, and oven-dried the material at 60° C until constant weight. We thus estimated the total aboveground biomass (live + dead, dry weight), and the aboveground biomass of native species and *U. decumbens* for both sites.

At eight sampling points in both uninvaded and invaded sites, at least 15 m apart from each other and 1 m apart from the aboveground biomass sampling plots, we sampled the roots contained in 20 x 20 x 10 soil blocks collected at 0–10, 10–20, 20–30, and 40–50 cm soil depth. Samples were air dried and treated with pyrophosphate decahydrate sodium solution (0.27%) to release the roots (Böhm, 1979), which were then washed in water and separated into fine roots (diameter ≤ 2 mm) i.e., those responsible for most of the water and nutrient uptake (Jackson et al. 1996), and coarse roots (diameter > 2 mm). Roots were oven-dried at 60° C for 48h and weighed. Both the aboveground and belowground biomass were sampled in the wet season (November-January).

We determined carbon stocks in the aboveground biomass and roots assuming 45% of their dry weight was carbon (Paruelo et al. 2010), for both dead and live biomass (Schlesinger 1977).

2.3 Carbon and nitrogen contents and stocks in the soil

To estimate soil C and N stocks we collected soil samples at six random locations at least 15 m apart in both the uninvaded and invaded sites. As the amounts of C and N in the soil are expected to decrease and show less variation as the depth increases (Jobbágy and Jackson 2000; Donovan 2012), soil samples were taken at eight layers with smaller intervals close to the surface: 0–5, 5–10, 10–20, 20–30, 30–40, 40–50, 70–80 and 90–100 cm. The soil samples were dried at 40°C for 48h, homogenized and sieved through a 0.2 mm mesh. Fractions of 15–30 mg of pounded soil from each sample were sealed in tin capsules and loaded into a ThermoQuest-Finnigan Delta Plus isotope ratio mass spectrometer (Finnigan-MAT; CA, USA) interfaced with an Elemental Analyzer (Carlo Erba model 1110; Milan, Italy) at the Laboratory of Isotope Ecology (CENA-USP, Brazil). The gas from the combustion was purified by gas chromatography column and introduced directly into the mass spectrometer for analysis of total C and N contents. Stable isotope ratios were measured according to internationally recognized standards (Atropine, Yeast and LECO) which were included in every run. Stable isotope values are reported in “delta” notation as δ values in parts per thousand (‰), so that δ ‰ = (R sample / R standard – 1) × 1000, where R is the molar ratio of the rare to abundant isotope (δ¹⁵N/ δ¹⁴N or δ¹³C/ δ¹²C) in the sample and the standard. Atmospheric air was used as nitrogen standard. The precision of isotope ratio measurements was ± 0.3‰ for δ¹⁵N and precisions of N and C concentrations were 0.15 % and 0.01%, respectively.

In four of the eight soil sampling locations of both the uninvaded and invaded sites we collected undeformed soil samples with a bucket-auger from six soil depth layers (0–5, 5–10, 10–20, 30–40, 40–50, 70–80 cm); the soil bulk density of each sample was obtained by dividing the soil dry weight by the sample volume. Soil C and N stocks (Mg ha⁻¹) were then calculated based on the concentration of total carbon and nitrogen in the soil, soil bulk density and the thickness of the sampled layer (Fernandes and Fernandes 2008):

$$stock(Mg. ha^{-1}) = \frac{variable\ concentration[g. kg^{-1}] \times soil\ bulk\ density[g. cm^{-3}] \times soil\ layer\ thickness[cm]}{10}$$

2.4 Data analysis

The effect of invasion by *U. decumbens* on the total aboveground C stock was estimated using generalized least square models with Restricted Maximum Likelihood estimation, considering invasion as a categorical fixed effect. We used linear mixed models including each sampling location as random effect to assess the influence of invasion, soil depth, and their interaction on: (1) the C stock in the root biomass (four soil layers), (2) soil C content, soil N content, C:N content ratio, ¹³C content and soil ¹⁵N content (eight soil layers), (3) C and N stocks in the soil (six soil layers). Models for the root biomass were implemented separately for fine (<2mm) and coarse (>2mm) roots, and all root classes pooled together.

We plotted model residuals for checking violations of distribution assumptions and removed outliers associated with very high C stock on the root biomass, as well as very high C and N stocks in the soil, to improve model estimation. Residual variation in models for root and soil stocks was often greater in the invaded than in the uninvaded site, and hence we implemented models allowing for different variances for each site. Likewise, residual variation in models for the C:N content ratio was much lower in the 0–50 cm soil layer than in the 50–100 cm layer, and in this case we allowed a distinct variance for each of these layers. Experimental variograms showed no association between distance of sampling locations and residual variance. We used maximum likelihood ratio tests to compare models that included or not these variance structures and interaction terms. All analyses were implemented in the R package nlme (Pinheiro

et al. 2018). When the best models included a significant effect of soil depth or interactions we performed all combinations of *a posteriori* comparison between factor levels in the R package "emmeans" (Lenth et al. 2018). All analyses were implemented in the R statistical environment (R Core Team 2021).

3. Results

3.1. Carbon stocks in the aboveground biomass

Estimated average aboveground C stocks in the uninvaded and invaded site were respectively 3.26 Mg.ha⁻¹ (± 0.66) and 3.29 Mg.ha⁻¹ (± 0.98). Although the invasive grass *U. decumbens* accounted for approximately 24% of the ground plant cover and 25% of the aboveground C stock in the invaded site, the total C stock in the aboveground biomass (native + *U. decumbens* + dead) did not differ between the invaded and the uninvaded site (t = 0.36, p = 0.727; Fig. 1a); as expected, the C stock of native species was higher in the uninvaded site (t = 2.39, p = 0.033, Fig. 1b).

3.2. C stocks in the root biomass

The C stock in the root biomass at a depth up to 50 cm was generally higher in the invaded than in the uninvaded area but this effect was variable depending on root diameter and soil depth (Table 1, Table 1S). The C stock in all roots (F = 2.89, p = 0.111) and in coarse roots (F = 32.03, p = 0.176) did not differ between the uninvaded and invaded sites (Table 1) but it varied according to soil layers (Table 1S); post-hoc comparisons showed that at the 0 to 50 soil profile the C stock in coarse roots and in all roots was high at 10 to 20 cm depth (Fig. 2). By contrast, the best model for the C stock in fine roots included significant effects of invasion, depth, and a marginally significant (F = 2.36, p = 0.086) interaction between invasion and soil layer (Table 1). Post-hoc comparisons showed that in the invaded site the biomass of fine roots was much higher at 0 to 10 cm than in deeper soil layers (p < 0.001), whereas in the uninvaded site the C stock at 0 to 10 cm was only marginally higher than at 10 to 20 cm (t = 2.643, p = 0.054) (Fig. 2); in addition, the C stock in fine roots in the upper soil layer (0–10 cm) was 30% higher in the invaded than in the uninvaded site (Fig. 2).

Table 1
Effect of *U. decumbens* invasion and soil depth on the C stock at different aspects of the root biomass in open *Cerrado* sites in the Southeast Brazil. Overall main effects and significance were based on the best mixed linear models with REML estimation. (numDF = numerator degrees of freedom; denDF = denominator degrees of freedom).

	numDF	denDF	F-value	p-value
fine roots				
invasion	1	14	4.65	0.049
depth	3	41	16.98	< 0.001
invasion×depth	3	41	2.36	0.086
COARSE roots				
invasion	1	14	2.03	0.176
depth	3	44	3.72	0.018
all roots				
invasion	1	14	2.89	0.111
depth	3	43	2.99	0.041

3.3. δ¹³C, δ¹⁵N, C and N concentration of soil samples

Consistent with C stock patterns in the fine root biomass, the soil C content was higher in the invaded than in the uninvaded site in all soil layers (F = 10.02, p = 0.010, Table 2, Fig. 3a). In both sites the soil C content decreased approximately 50% from the soil surface to the 20–30 cm soil layer, but showed smaller variation in deeper soil layers (Fig. 3a, Table 2S). The best model for the variation in N soil content and C:N ratio along the soil profile included, respectively, a marginally significant (F = 1.93, p = 0.077) and a significant interaction (F = 2.40, p = 0.290) between invasion and soil depth layer (Table 2). Post-hoc comparisons showed that the soil N content was over 20% higher in the invaded than in the uninvaded site in the top 5 cm layer (t = 3.54, p = 0.005); in both sites the soil N content decreased from the soil surface to the 20 to 30 cm soil layer (p < 0.05) and exhibited less variation in deeper layers, although that decrease was greater in the invaded than in the uninvaded site (Fig. 3b). In contrast, the C:N ratio was higher in the invaded site at the 20 to 30 cm soil layer (t = 3.81, p = 0.003); in both sites values increased along the soil profile from 10 to 40 cm (p < 0.05), but there were no consistent differences in deeper layers (Fig. 3c).

Table 2

Results of Generalized Linear Mixed Models assessing the effect of soil depth and invasion by *Urochloa decumbens* on the contents of C, N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the soil, as well as C:N ratio in both uninvaded and invaded open *Cerrado* sites in southeast Brazil. (numDF = numerator degrees of freedom; denDF = denominator degrees of freedom).

	numDF	denDF	F-value	p-value
Soil C content				
invasion	1	10	10.02	0.010
depth	7	77	130.86	<0.001
Soil N content				
invasion	1	10	1.23	0.294
depth	7	70	164.87	<0.001
invasion×depth	7	70	1.93	0.077
Soil C:N content ratio				
invasion	1	10	3.73	0.082
depth	7	70	57.71	<0.001
invasion×depth	7	70	2.40	0.029
Soil $\delta^{13}\text{C}$				
invasion	1	10	1.93	0.194
depth	7	77	3.04	0.007
Soil $\delta^{15}\text{N}$				
invasion	1	10	1.88	0.200
depth	7	77	191.15	<0.001

There were no significant differences in $\delta^{13}\text{C}$ values between the uninvaded (-17.9 to -18.1‰) and invaded (-17.4 to -18.0‰) sites ($F = 1.93$, $p = 0.194$, Table 2). The $\delta^{15}\text{N}$ values also did not differ between sites ($F = 1.88$, $p = 0.200$) and varied from 2.4 to 9.3‰ and from 1.8 to 8.1‰ at the first 100 cm of soil depth in uninvaded and invaded areas, respectively. In both sites $\delta^{15}\text{N}$ values increased (~ 7‰) along the soil profile (Fig. 4).

3.4. Soil bulk density, C and N stocks

The invasion by *U. decumbens* did not significantly affect soil bulk density ($F = 2.69$, $p = 0.152$, Table 3); as expected, in both sites values of soil bulk density were lower very close to the soil surface (0 to 10 cm) than in soil layers deeper than 30 cm (Fig. 1S).

Table 3
Effect of invasion and soil depth on the soil bulk density and on the soil stocks of C and N, in open *Cerrado* areas in southeast Brazil. Overall main effects and significance were based on the best mixed linear models with REML estimation using the Satterthwaite method for degrees of freedom approximation. (numDF = numerator degrees of freedom; denDF = denominator degrees of freedom)

	numDF	denDF	F-value	p-value
Soil density				
invasion	1	6	2.69	0.152
depth	6	42	9.22	< 0.001
C soil stock				
invasion	1	6	1.07	0.340
depth	6	42	32.64	< 0.001
N soil stock				
invasion	1	6	1.03	0.3495
depth	6	35	71.82	< 0.001
Invasion×depth	6	35	2.70	0.029

Although C soil stock values were slightly higher in the invaded than in the uninvaded site, differences were not significant ($F = 1.07$, $p = 0.340$; Fig. 5a, Table 3). In both sites C soil stock values were initially lower, peaking at a depth of 10 to 20 cm, and then remaining at intermediate levels (Fig. 5a). Also, N soil stocks were higher in the invaded than in the uninvaded site in the first soil layers and tended to be lower below 20 to 30 cm, but differences were not significant ($F = 1.03$, $p = 0.349$; Fig. 5b, Table 3).

4. Discussion

Estimates of C stocks in the *Cerrado*, especially belowground, are scarce and highly variable, across different *Cerrado* physiognomies and soil depths (Paiva and Faria 2007; Maquère et al. 2008; Neto et al. 2010; Fidelis et al. 2013; Oliveras et al. 2013; Brito et al. 2019). Similarly, there are few estimates of N stocks in *Cerrado* ecosystems, which point to a much higher concentration in the first 50 cm soil layer (Bustamante et al. 2006; López-Poma et al. 2020). However, the effects caused by biological invasions in the *Cerrado* C and N stocks have not been reported to this moment, and this is a vital issue especially in times of global warming and changes in the natural ecological cycles. We compared C stocks aboveground, and C and N stocks belowground along the soil profile between an uninvaded open *cerrado* and a site invaded by the African grass *U. decumbens*. Invasion did not affect the overall aboveground C stock, soil C and N stocks and the distribution of C and N along the soil profile, but the C stock in fine roots and the C and N contents in the upper soil layers were higher in the invaded site.

4.1. Aboveground C stock

The overall aboveground C stock in the invaded site ($3.29 \text{ Mg}\cdot\text{ha}^{-1} \pm 0.978$) was very similar to that of the uninvaded open *cerrado* ($3.26 \pm 0.658 \text{ Mg}\cdot\text{ha}^{-1}$). This finding was unexpected since *U. decumbens* often maintains high productivity even in the typically infertile soils of Neotropical savannas (Braz et al. 2013; Gómez et al. 2013), which is pointed as one of the main reasons of its success as invasive in the *Cerrado* (Pivello et al. 1999a; Klink and Machado 2005; Forzza et al. 2012). In fact, in a review study Liao et al. (2008) found that 83% of the invaded communities significantly increased productivity. As in our study *U. decumbens* accounted for only 24% of the ground cover in the invaded site it is possible that at such level of invasion the biomass produced by *U. decumbens* possibly was just compensating the biomass of displaced native species. Alternatively, low soil fertility in our study site may be limiting the dominance and primary productivity of *U. decumbens*, thus contributing to the lack of difference in aboveground biomass between the invaded and uninvaded sites even after about three decades of invasion.

4.2. Root biomass C stock

We observed larger C stock due to fine roots in the upper layer (0–10 cm) in the invaded site. This indicates that *U. decumbens* produces more fine roots than *Cerrado* native grasses in the first 10 cm of soil, increasing by 30% the C stock in that layer; this difference tended to be lower at greater soil depths. There was also a tendency of more coarse roots at lower soil layers in the uninvaded site. Higher biomass of coarse roots at greater depths (also found by Castro and Kauffman 1998, and Abdala et al. 1998) may relate to the presence of sparse shrubs in the *campo sujo* physiognomy, which produce thicker and deeper roots. This may also have contributed to the high variation in the C stock values of coarse roots in both the uninvaded and invaded site. The general pattern of root distribution along the soil profile observed in both uninvaded and invaded sites – where fine roots are more plentiful in upper soil layers to uptake resources, and the coarse roots concentrate in layers just below – was expected and found in other *Cerrado* areas (Abdala et al. 1998; Castro and Kauffman 1998; Oliveira et al. 2005; Paiva and Faria 2007; Oliveras et al. 2013; Morais et al. 2017). This high investment on the production of fine roots – is consistent with the idea that plants need to expand their absorption area in infertile soils to meet their nutritional demands (Bustamante et al. 2012). African grasses are highly effective on soil nutrient uptake (Williams and Baruch 2000; Guenni et al. 2002), which is a major reason for their high productivity and dominance over native

grasses in invaded Neotropical savannas (Williams and Baruch 2000). A high production of roots in the first 50 cm of soil by *U. decumbens* was reported by Guenni et al. (2002).

4.3. Soil C stock

Even though the soil C content was significantly higher in the invaded than in the uninvaded site along the soil profile, there were no statistical differences in the soil C stocks between sites. Other authors reported higher soil carbon contents and stocks in grassy ecosystems invaded by exotic species, especially in the upper layers, (Liao et al. 2007; Zhang et al. 2018, Haubensak and Parker 2004). In contrast, Litton et al. (2008) and MacDougall & Wilson (2011) found no difference in the soil organic carbon stocks at different depths between native areas in North America and ecosystems invaded by African grasses. Interestingly, MacDougall & Wilson (2011) found that although the invaded sites had twice as many roots than uninvaded areas there were no differences in the amounts of soil carbon; the authors attributed this fact to high decomposition rates in the invaded area that resulted in no C accumulation in the soil. We found higher fine root C stock at the upper soil layer and higher soil C content along the soil profile in the site invaded by *U. decumbens* than in the uninvaded site, but differences in C stock along the soil profile were small and statistically non-significant. Since we obtained C stock values for each soil layer by multiplying soil C content and soil bulk density, this discrepancy is likely related to the fact that soil bulk density tended to be lower in the invaded sites, especially in soil layers up to 50 cm (Fig. 1S). Such lower values of soil bulk density could be associated with the high production of fine roots by *U. decumbens*, which thus may increase soil aeration and promote a better environment for soil decomposing organisms (Swift 1979). Also, the increase of soil organic matter is directly related to soil water retention, which is an important soil hydraulic property (Yang et al. 2014), and thus is a major driver of ecological functions. Further studies are needed to compare soil microbial activity and water retention in both uninvaded *Cerrado* sites and invaded by exotic grasses.

Some studies have shown that especially shrubs from open *Cerrado* physiognomies have very deep roots, ranging from 2 to 18 m (Rawistcher 1948, Castro and Kauffman 1998; Franco 2005). Therefore, the C stock in the total underground biomass of a native *campo sujo* must be much greater than that obtained in this study, where our estimates refer to the top 80 cm of soil and mainly based on fine roots. Also, the low cover and density of woody individuals in our study site (Leite et al. 2018) possibly contributed to low underground C stocks. In a *campo sujo* converted to *Urochloa brizantha* pasture, Rodin (2004) estimated a reduction in the fine-roots C stock of about 15% up to 3m soil depth, and around 70% due to coarse-roots at a depth of 4 m. Thus, considering higher soil depths we expect the dominance by *U. decumbens* and consequent elimination of native species will decrease the soil C stock.

4.4. Soil N stock and C:N ratio

Several authors have reported greater concentration of N in the soil due to biological invasions, as well as increased nitrification and N-mineralization processes, usually associated to N-fixing organisms (Ehrenfeld et al. 2001; Haubensak and Parker 2004; Liao et al. 2007, 2008; Parker and Schimel 2010). We also found higher N levels in the first 5 cm of soil in the invaded than in the uninvaded site, which we attribute mainly to the association of *Urochloa* species with N-fixing microorganisms (Boddey and Victoria 1986). Several authors have found a diversity of symbiotic N-fixing bacteria colonizing the roots of *Urochloa* species or in the rhizosphere (Reis et al. 2001; Okumura et al. 2013; Silva et al. 2013). The association of plants with N-fixing microorganisms often increases the amount of N in the leaves and, consequently, in the soil after their decomposition (Vitousek and Walker 2014). Still, the quality of N-rich organic material is generally better, thus stimulating microbial activity and decomposition (Liao et al. 2008). The *Cerrado* soils are typically N-limited (Bustamante et al. 2006; Haridasan 2008), so that the presence of exotic species that increase N amounts in the soil may lead to imbalance in the system. Native *Cerrado* species are adapted to low soil fertility (Furley and Ratter 1988) and the input of N caused by the African grasses – which are more N-demanding – may create a positive feedback mechanism that favors their dominance over native species. The existence of this feedback in sites invaded by *U. decumbens* is consistent with the high production of fine roots in the top 5 cm soil layer, as this could allow the species to efficiently uptake the available soil N. In addition, the soil biota may be significantly modified under this fertilization condition, and the new microflora can also benefit the exotic species to the detriment of the natives (Ehrenfeld et al. 2001; Parker and Schimel 2010). These feedbacks as a result of changes in N dynamics have been demonstrated in other ecosystems subjected to grass invasions (Rossiter-Rachor et al. 2009; Lee et al. 2012).

In our study, the high N content in the most superficial soil layer of the invaded site contrasted with a rapid decline in soil N content along the soil profile compared to the uninvaded site. Below that thin layer the C:N ratio increased steadily along the soil depth up to a 20–30 cm soil depth, where the addition of C was much higher than that of N, and the C:N ratio was higher in the invaded site. Therefore, it seems that better conditions of soil for microbial activity and decomposition in the site invaded by *U. decumbens* were restricted to the top 5 cm soil layer. Previous studies also found higher C:N ratio in ecosystems invaded by exotic grasses (Drenovsky and Batten 2007; Yang et al. 2013), whereas others reported a small decrease (Haubensak and Parker 2004).

4.5. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of soil sample

We found little variation in soil $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between the invaded and uninvaded sites along the soil profile. The soil $\delta^{13}\text{C}$ concentration in savannas tends to decrease as the woody cover increase (Boutton et al. 1998), so that invasion by C_4 African grasses would lead to enrichment on $\delta^{13}\text{C}$ if these invaders replaced either herbaceous or woody species with C_3 metabolism. Lack of $\delta^{13}\text{C}$ variation in our study is possibly associated with the prevalence of C_4 photosynthesis among *Cerrado* grasses (Klink and Joly 1989) and the low woody cover in our study site (Leite et al. 2018). Likewise, variation in leaf and soil $\delta^{15}\text{N}$ in savannas is often associated with distinct N acquisition strategies (Schmidt and Stewart 2003; Bustamante et al. 2004), and hence soil $\delta^{15}\text{N}$ values would be expected, for example, as a result of dominance by invasive N-fixing species and deposition of ^{15}N depleted leaf material (Haubensak and Parker 2004). Although *U. decumbens* has a high N-fixing potential and this may be reflected in $\delta^{15}\text{N}$ signatures (Boddey and Victoria 1986), leaf $\delta^{15}\text{N}$ values are often similar among grass species (Wang et al. 2013). Therefore, even though N acquisition strategies among native *Cerrado* species are largely unknown, it is possible that N fixing ability is also common among abundant native *Cerrado* grasses.

5. Conclusion

Even a relatively low level of invasion by the African grass *Urochloa decumbens* in an open *Cerrado* caused significant changes in the belowground environment, as the most superficial soil layer in the invaded site showed higher fine root stock and soil C and N contents compared to the uninvaded site. Such inputs may modify the soil microbiota and decomposition dynamics, thus affecting C and N cycles. Besides, the increase of N in the *Cerrado* soils would create a positive feedback mechanism favoring invasive grasses, promoting further invasions and hindering the reestablishment of native vegetation. Further studies based on replicated plots along a gradient of invasion would detect dominance thresholds after which *U. decumbens* may shift underground stocks and nutrient cycling in the *Cerrado*. Although still limited to a single site, this study already shows serious effects of the *Cerrado* invasion by *U. decumbens* in the soil compartment, which is much less visible to managers.

Declarations

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Conflicts of interest/ Competing interests

The authors declare that they have no conflicts of interest.

Availability of data and material

All data associated with this manuscript are available in a open repository (https://figshare.com/articles/dataset/Can_an_invasive_African_grass_affect_carbon_and_nitrogen_stocks_in_open_habitats_of_the_Brazilian_Cerrado_/12550)

Authors' contributions:

DBG, ROX and VRP contributed to the interpretation of data and manuscript writing. Material preparation, data collection and analysis were performed by DBG, ROX, PBC and VRP. The first draft of the manuscript was written by DBG and ROX. Revised versions were produced by ROX, VRP and SAV. All authors read and approved the final manuscript.

References

- Abdala GC, Caldas LS, Haridasan M, Eiten G (1998) Above and belowground organic matter and root: shoot ratio in a cerrado in Central Brazil. *Brazilian Journal of Ecology* 2:11–23
- Barnosky AD, Hadly EA, Bascompte J, et al (2012) Approaching a state shift in Earth's biosphere. *Nature* 486:52–58
- Boddey RM, Victoria RL (1986) Estimation of biological nitrogen fixation associated with *Brachiaria* and *Paspalum* grasses using ¹⁵N labelled organic matter and fertilizer. In: *Nitrogen Fixation with Non-Legumes*. Springer, pp 265–292
- Böhm W. (1979) *Methods of Studying Root Systems*. Ecological Studies (Analysis and Synthesis), Ecological Studies vol 33. Springer, Berlin, Heidelberg.
- Boutton TW, Archer SR, Midwood AJ, et al (1998) $\delta^{13}C$ values of soil organic carbon and their use in documenting vegetation change in a subtropical savanna ecosystem. *Geoderma* 82:5–41.
- Braz SP, Urquiaga S, Alves BJR, et al (2013) Soil Carbon Stocks under Productive and Degraded *Brachiaria* Pastures in the Brazilian Cerrado. *Soil Science Society of America Journal* 77:914–928.
- Brito GS, Bautista S, López-Poma R, Pivello VR (2019) Labile soil organic carbon loss in response to land conversion in the Brazilian woodland savanna (cerradão). *Biogeochemistry* 144:31–46
- Bustamante MMC, Martinelli LA, Silva DA, et al (2004) ¹⁵N Natural Abundance in Woody Plants and Soils of Central Brazilian Savannas (cerrado). *Ecological Applications* 14:200–213.
- Bustamante MMC, Medina E, Asner GP, et al (2006) Nitrogen Cycling in Tropical and Temperate Savannas. *Biogeochemistry* 79:209–237.
- Bustamante MMC, Brito DQ, Kozovits AR, Luedemann G, Mello TRB, Pinto AS, Munhoz CBR, Takahashi FC (2012) Effects of nutrient additions on plant biomass and diversity of the herbaceous-subshrub layer of a Brazilian savanna (Cerrado). *Plant Ecology* 213: 795-808.
- Castro EA, Kauffman JB (1998) Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. *Journal of Tropical Ecology* 14:263–283.

- Castro-Díez P, Alonso A, Saldaña-López A, Granda E (2021) Effects of widespread non-native trees on regulating ecosystem services, *Science of The Total Environment* 778: 146141.
- Chown SL, Hodgins KA, Griffin PC, et al (2015) Biological invasions, climate change and genomics. *Evolutionary applications* 8:23–46
- Coutinho LM (1978) O conceito do cerrado. *Revista Brasileira de Botânica* 1:17–23
- Damasceno G, Souza L, Pivello VR, et al (2018) Impact of invasive grasses on Cerrado under natural regeneration. *Biol Invasions* 20:3621–3629.
- Donovan P (2012) Measuring soil carbon change. A flexible, practical, local method. Available in: <https://soilcarboncoalition.org/files/MeasuringSoilCarbonChange.pdf>
- Downey PO, Richardson DM (2016) Alien plant invasions and native plant extinctions: a six-threshold framework. *AoB plants* 8:plw047.
- Drenovsky RE, Batten KM (2007) Invasion by *Aegilops triuncialis* (barb goatgrass) slows carbon and nutrient cycling in a serpentine grassland. *Biological invasions* 9:107–116
- Edwards EJ, Still CJ (2008) Climate, phylogeny and the ecological distribution of C4 grasses. *Ecology Letters* 11: 266-276.
- Ehrenfeld JG (2003) Effects of Exotic Plant Invasions on Soil Nutrient Cycling Processes. *Ecosystems* 6:503–523.
- Ehrenfeld JG (2004) Implications of Invasive Species for Belowground Community and Nutrient Processes1. *Weed Technology* 18:1232–1235
- Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Annual review of ecology, evolution, and systematics* 41:59–80
- Ehrenfeld JG, Kourtev P, Huang W (2001) Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological applications* 11:1287–1300
- Fernandes FA, Fernandes A (2008) Cálculo dos estoques de carbono do solo sob diferentes condições de manejo. Embrapa Pantanal-Comunicado Técnico (INFOTECA-E)
- Fidelis A, Lyra MF di S, Pivello VR (2013) Above-and below-ground biomass and carbon dynamics in Brazilian Cerrado wet grasslands. *Journal of Vegetation Science* 24:356–364
- Forzza RC, Baumgratz JFA, Bicudo CEM, et al (2012) New Brazilian floristic list highlights conservation challenges. *BioScience* 62:39–45
- Franco AC (2005) Biodiversidade de forma e função: implicações ecofisiológicas das estratégias de utilização de água e luz em plantas lenhosas do Cerrado. *Cerrado ecologia, biodiversidade e conservação* (Eds A Scariot, JC Souza-Silva, JM Felfili) pp 179–196
- Furley PA, Ratter JA (1988) Soil resources and plant communities of the central Brazilian cerrado and their development. *Journal of Biogeography* 97–108
- Gómez S, Guenni O, Guenni LB de (2013) Growth, leaf photosynthesis and canopy light use efficiency under differing irradiance and soil N supplies in the forage grass *Brachiaria decumbens* Stapf. *Grass and Forage Science* 68:395–407.
- Gorgone-Barbosa E, Pivello VR, Meirelles ST (2008) Allelopathic evidence in *Brachiaria decumbens* and its potential to invade the Brazilian cerrados. *Brazilian archives of biology and technology* 51:625–631
- Grace J, José JS, Meir P, et al (2006) Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography* 33:387–400.
- Greaver TL, Clark CM, Compton JE, et al (2016) Key ecological responses to nitrogen are altered by climate change. *Nature Climate Change* 6:836–843
- Guenni O, Marín D, Baruch Z (2002) Responses to drought of five *Brachiaria* species. I. Biomass production, leaf growth, root distribution, water use and forage quality. *Plant and Soil* 243:229–241.
- Haridasan M (2008) Nutritional adaptations of native plants of the cerrado biome in acid soils. *Brazilian Journal of Plant Physiology* 20:183–195.
- Haubensak KA, Parker IM (2004) Soil changes accompanying invasion of the exotic shrub *Cytisus scoparius* in glacial outwash prairies of western Washington [USA]. *Plant Ecology* 175:71–79.
- Hoegh-Guldberg O, Jacob D, Taylor M, et al (2018) Impacts of 1.5 C global warming on natural and human systems. In: *Global warming of 1.5° C.: An IPCC Special Report*. IPCC Secretariat, pp 175–311
- IF (2006) Plano de manejo integrado das unidades de Itirapina. Estação Ecológica e Experimental de Itirapina/SP
- IUSS Working Group WRB (2015) World reference base for soil resources 2014, update 2015: International soil classification system for naming soils and creating legends for soil maps. *Fao Rome*
- Jackson RB, Canadell J, Ehleringer JR, et al (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia* 108:389–411

- Jobbágy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological applications* 10:423–436
- Klink CA, Joly CA (1989) Identification and distribution of C3 and C4 grasses in open and shaded habitats in Sao Paulo state, Brazil. *Biotropica* 21:30–34.
- Klink CA, Machado RB (2005) Conservation of the Brazilian cerrado. *Conservation Biology* 19:707–713
- Lee MR, Flory SL, Phillips RP (2012) Positive feedbacks to growth of an invasive grass through alteration of nitrogen cycling. *Oecologia* 170:457–465. <https://doi.org/10.1007/s00442-012-2309-9>
- Leite MB, Xavier RO, Oliveira PTS, et al (2018) Groundwater depth as a constraint on the woody cover in a Neotropical Savanna. *Plant and Soil* 1–15
- Lenth R, Singmann H, Love J, Buerkner P, Herve M (2018). *Emmeans: Estimated marginal means, aka least-squares means*. R package version, 1(1), 3. Liao C, Luo Y, Jiang L, et al (2007) Invasion of *Spartina alterniflora* enhanced ecosystem carbon and nitrogen stocks in the Yangtze Estuary, China. *Ecosystems* 10:1351–1361
- Liao C, Peng R, Luo Y, et al (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New phytologist* 177:706–714
- Litton CM, Sandquist DR, Cordell S (2008) A non-native invasive grass increases soil carbon flux in a Hawaiian tropical dry forest. *Global Change Biology* 14:726–739
- López-Poma R, Pivello VR, de Brito GS, Bautista S (2020) Impact of the conversion of Brazilian woodland savanna (cerradão) to pasture and Eucalyptus plantations on soil nitrogen mineralization. *Science of The Total Environment* 704:135397
- MacDougall AS, Wilson SD (2011) The invasive grass *Agropyron cristatum* doubles belowground productivity but not soil carbon. *Ecology* 92:657–664
- Maquère V, Laclau J-P, Bernoux M, et al (2008) Influence of land use (savanna, pasture, Eucalyptus plantations) on soil carbon and nitrogen stocks in Brazil. *European journal of soil science* 59: 863–877
- Mendonça RC, Falfile JM, Walter BMT, et al (2008) Flora Vascular do bioma Cerrado: checklist com 12.356 espécies. In: *Cerrado: ecologia e flora*. Embrapa Cerrados, Planaltina, pp 421–1279
- Morais VA, Santos CA, Mello JM, et al (2017) Spatial and vertical distribution of litter and belowground carbon in a Brazilian Cerrado vegetation. *Cerne* 23:43–52
- Neto MS, Scopel E, Corbeels M, et al (2010) Soil carbon stocks under no-tillage mulch-based cropping systems in the Brazilian Cerrado: an on-farm synchronic assessment. *Soil and Tillage Research* 110:187–195
- Okumura RS, Mariano D de C, Dallacort R, et al (2013) *Azospirillum*: a new and efficient alternative to biological nitrogen fixation in grasses. *J Food Agric Environ* 2:1142–1146
- Oliveira RS, Bezerra L, Davidson EA, et al (2005) Deep root function in soil water dynamics in cerrado savannas of central Brazil. *Functional Ecology* 19:574–581.
- Oliveras I, Meirelles ST, Hirakuri VL, et al (2013) Effects of fire regimes on herbaceous biomass and nutrient dynamics in the Brazilian savanna. *International Journal of Wildland Fire* 22:368–380
- Overbeck GE, Vélez-Martin E, Scarano FR, et al (2015) Conservation in Brazil needs to include non-forest ecosystems. *Diversity and Distributions* 21:1455–1460.
- Paiva AO, Faria G de (2007) Estoque de carbono do solo sob cerrado sensu stricto no Distrito Federal, Brasil. *Revista Trópica–Ciências Agrárias e Biológicas* 1:59
- Parker SS, Schimel JP (2010) Invasive grasses increase nitrogen availability in California grassland soils. *Invasive Plant Science and Management* 3:40–47
- Paruelo JM, Piñeiro G, Baldi G, Baeza S, Lezama F, Altesor A, Oesterheld M (2010) Carbon stocks and fluxes in rangelands of the Río de la Plata Basin. *Rangeland Ecology & Management* 63:94–108.
- Pinheiro J, Bates D, DebRoy S, et al (2018) nlme: linear and nonlinear mixed effects models. R package version 3.1-137. Vienna, Austria: R Foundation
- Pivello VG, Shida CN, Meirelles ST (1999a) Alien grasses in Brazilian savannas: a threat to the biodiversity. *Biodiversity and Conservation* 8:1281–1294.
- Pivello VR, Carvalho VMC, Lopes PF, et al (1999b) Abundance and distribution of native and alien grasses in a “Cerrado” (Brazilian savanna) Biological Reserve. *Biotropica* 31:71–82. R Core Team RC (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing; URL <https://www.R-project.org/>.
- Ratter JA, Ribeiro JF, Bridgewater S (1997) The Brazilian Cerrado Vegetation and Threats to its Biodiversity. *Annals of Botany* 80:223–230. Rawitscher F (1948) The Water Economy of the Vegetation of the ‘Campos Cerrados’ in Southern Brazil. *Journal of Ecology* 36:237–268.

- Reis VM, dos Reis Jr FB, Quesada DM, et al (2001) Biological nitrogen fixation associated with tropical pasture grasses. *Functional Plant Biology* 28:837–844
- Ribeiro JF, Walter B (1998) Fitofisionomias do bioma cerrado. In: Cerrado: ambiente e flora. Embrapa Cerrados, Planaltina. Embrapa Cerrado, Planaltina, pp 89–152
- Rodin P (2004) Distribuição da biomassa subterrânea e dinâmica de raízes finas em ecossistemas nativos e em uma pastagem plantada no Cerrado do Brasil Central. MSc Thesis. Universidade de Brasília, Instituto de Ciências Biológicas, Brazil
- Rossiter-Rachor NA, Setterfield SA, Douglas MM, et al (2009) Invasive *Andropogon gayanus* (gamba grass) is an ecosystem transformer of nitrogen relations in Australian savanna. *Ecological Applications* 19:1546–1560.
- Santos HG, Jacomine PKT, Dos Anjos LHC, et al (2018) Sistema brasileiro de classificação de solos. Brasília, DF: Embrapa, 2018.
- Schlesinger WH (1977) Carbon balance in terrestrial detritus. *Annual review of ecology and systematics* 8:51–81
- Schmidt S, Stewart GR (2003) $\delta^{15}\text{N}$ values of tropical savanna and monsoon forest species reflect root specialisations and soil nitrogen status. *Oecologia* 134:569–577.
- Scurlock JMO, Hall DO (1998) The global carbon sink: a grassland perspective. *Global Change Biology* 4:229–233
- Silva JF, Fariñas MR, Felfili JM, Klink CA (2006) Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. *Journal of Biogeography* 33:536–548. Silva MCP, Figueiredo AF, Andreote FD, Cardoso EJBN (2013) Plant growth promoting bacteria in *Brachiaria brizantha*. *World Journal of Microbiology and Biotechnology* 29:163–171
- Simberloff D, Martin JL, Genovesi P, et al (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution* 28:58–66
- Standish RJ (2004) Impact of an invasive clonal herb on epigeaic invertebrates in forest remnants in New Zealand. *Biological Conservation* 116:49–58
- Swift MJ (1979) The influence of the physico-chemical environment on decomposition process. In: *Decomposition in terrestrial ecosystems*. University of California Press, Berkeley, pp 220–266
- Tannus JLS, Assis MA (2004) Composição de espécies vasculares de campo sujo e campo úmido em área de cerrado, Itirapina - SP, Brasil. *Brazilian Journal of Botany* 27:489–506
- Vilà M, Espinar JL, Hejda M, et al (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14:702–708.
- Vitousek PM, Walker LR (2014) Biological Invasion by *Myrica Faya* in Hawai'i: Plant Demography, Nitrogen Fixation, Ecosystem Effects. *Ecological Monographs* 59:247–265.
- Wang L, Okin GS, D'Odorico P, et al (2013) Ecosystem-scale spatial heterogeneity of stable isotopes of soil nitrogen in African savannas. *Landscape Ecol* 28:685–698. <https://doi.org/10.1007/s10980-012-9776-6>
- Williams D, Baruch Z (2000) African Grass Invasion in the Americas: Ecosystem Consequences and the Role of Ecophysiology. *Biological Invasions* 2:123–140.
- Xavier R de O, Leite MB, Silva-Matos DM (2017) Stress responses of native and exotic grasses in Neotropical savanna predict impacts of global change on invasion spread. *Austral Ecology* 42:562–576
- Xavier RO, Leite MB, Dexter K, da Silva Matos DM (2019) Differential effects of soil waterlogging on herbaceous and woody plant communities in a Neotropical savanna. *Oecologia* 190:471–483.
- Xavier, R.O., Christianini, A.V., Pegler, G. et al. Distinctive seed dispersal and seed bank patterns of invasive African grasses favour their invasion in a neotropical savanna. *Oecologia* (2021). Online: <https://doi.org/10.1007/s00442-021-04904-z>
- Yang W, Zhao H, Chen X, et al (2013) Consequences of short-term C4 plant *Spartina alterniflora* invasions for soil organic carbon dynamics in a coastal wetland of Eastern China. *Ecological engineering* 61:50–57
- Yang F, Zhang, G, Yang J, Li D, Zhao Y, Liu F, Yang F, Yang F. (2014) Organic matter controls of soil water retention in an alpine grassland and its significance for hydrological processes. *Journal of Hydrology* 519 (D): 3086–3093.
- Zhang P, Neher DA, Li B, Wu J (2018) The impacts of above-and belowground plant input on soil microbiota: invasive *Spartina alterniflora* versus native *Phragmites australis*. *Ecosystems* 21:469–481

Figures

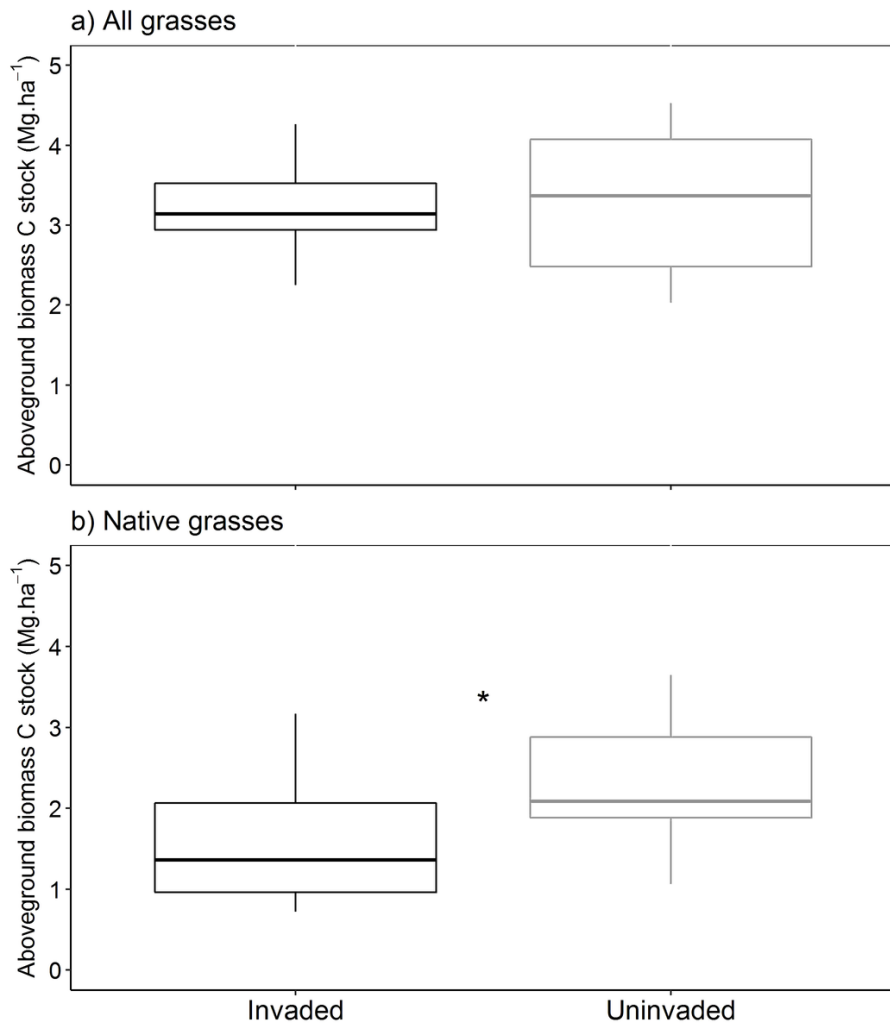


Figure 1
 a) C stock values in the total aboveground biomass (live + dead of natives and invasive), and b) C stock values in the aboveground biomass (live + dead) of native species in open Cerrado sites (campo sujo physiognomy, Itirapina, SP, Brazil) both uninvaded and invaded by *Urochloa decumbens*. Asterisks indicate significant differences between the invaded and uninvaded area (* <0.05 , ** $p<0.01$, *** $p<0.001$) based on post-hoc pairwise comparisons following the results of least square models.

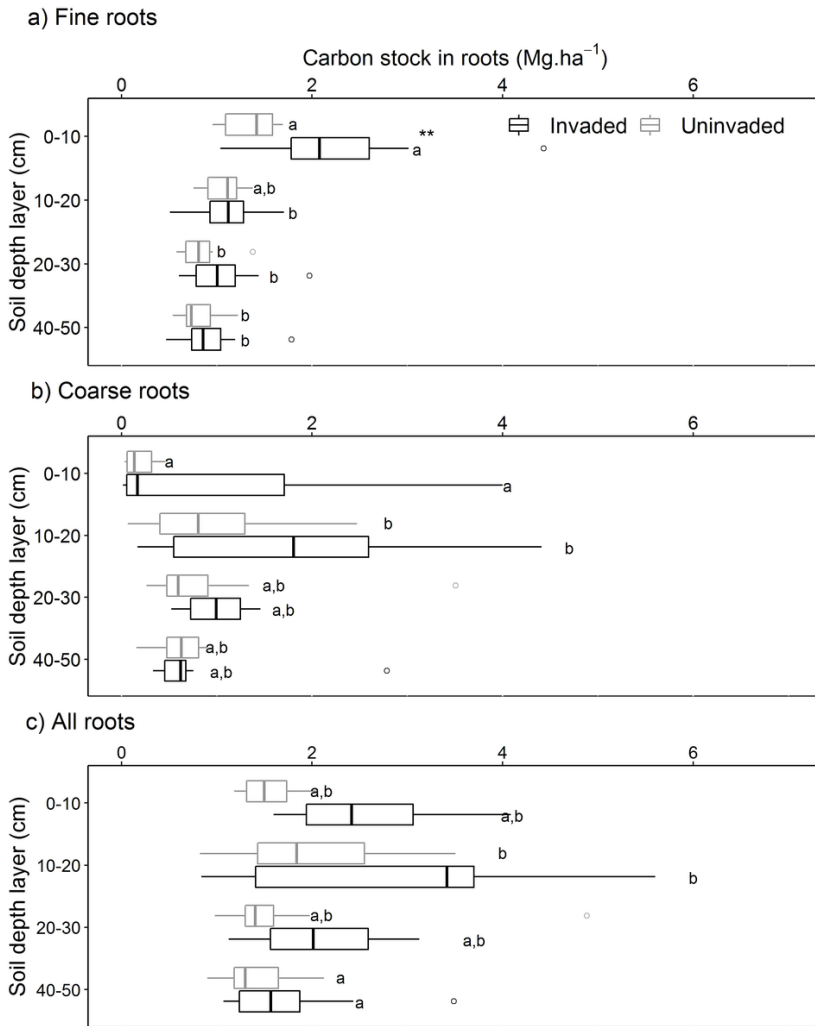


Figure 2

Variation in C stock in: a) fine roots (<2mm), b) coarse roots (>2mm) and c) all roots along the soil profile in open Cerrado sites uninvaded and invaded by the African grass *Urochloa decumbens*. Asterisks indicate significant differences between the uninvaded and invaded areas in each soil depth layer (*- $p < 0.05$, **- $p < 0.01$, ***- $p < 0.001$), and the absence of equal letters indicate differences between soil depth layers within each area, both based on post-hoc pairwise analyses following the results of mixed linear models.

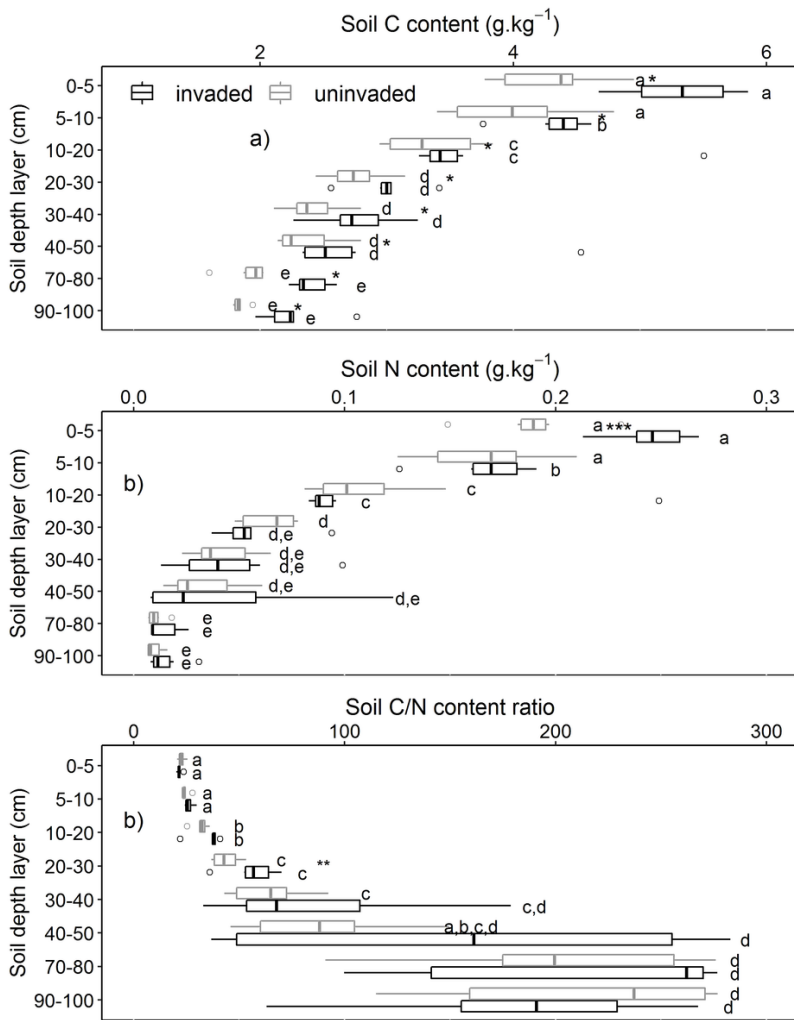


Figure 3

Variation in soil C content (a), soil N content (%) and soil C:N content ratio along the soil profile in open Cerrado sites both uninvaded and invaded by the African grass *Urochloa decumbens*. Different letters indicate significant difference among soil layers within each site and asterisks indicate significant difference between uninvaded and invaded sites, both based on post-hoc pairwise comparisons

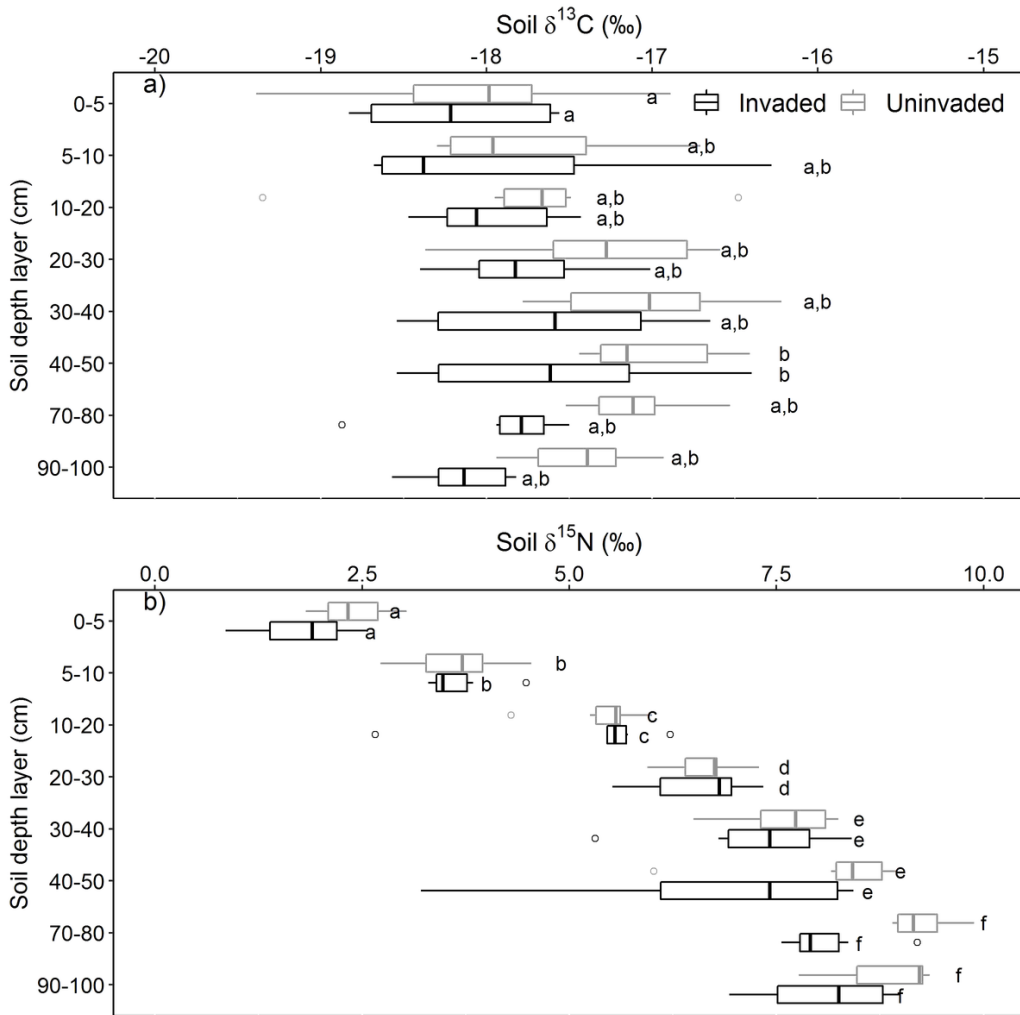


Figure 4
 Variation in carbon and nitrogen isotopes ratios - $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) - along the soil profile in open Cerrado sites both uninvaded and invaded by *Urochloa decumbens*. Different letters indicate significant difference among soil layers based on a posteriori pairwise comparisons. No significant difference was found between uninvaded and invaded sites.

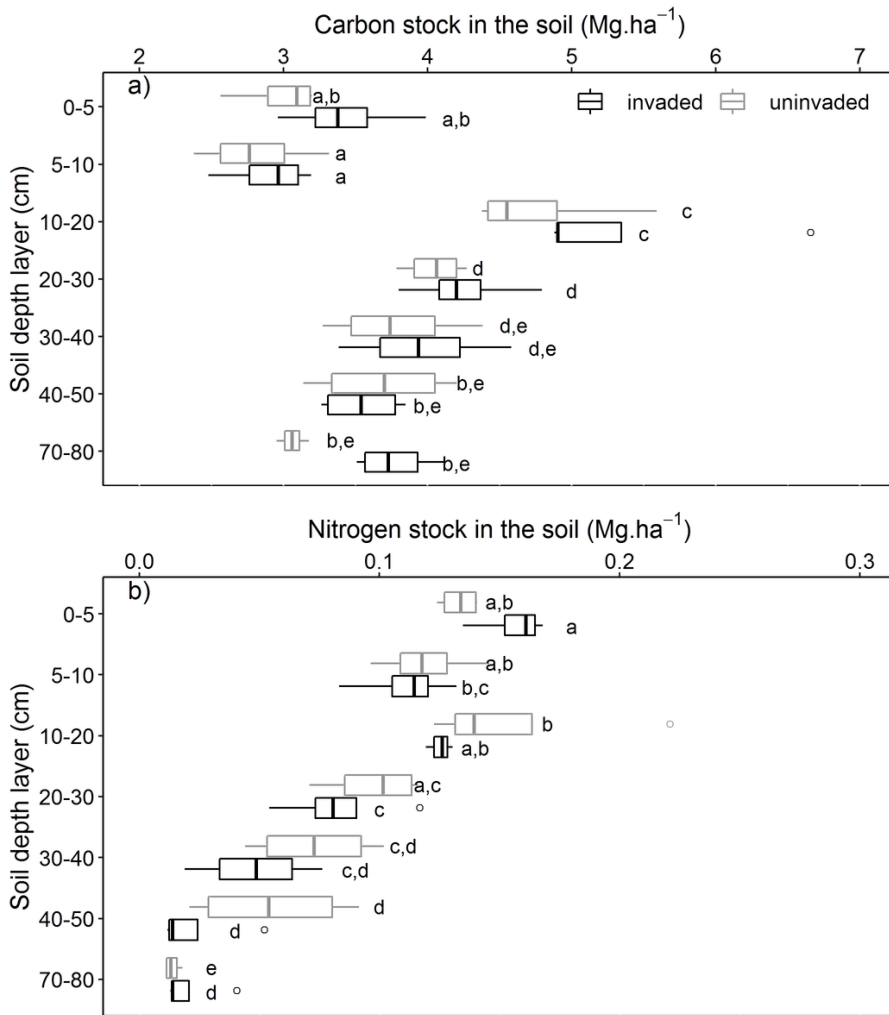


Figure 5
 Variation in C (a) and N (b) stocks along the soil profile in open Cerrado sites both uninvaded and invaded by *Urochloa decumbens*. Different letters indicate significant difference among soil layers based on a posteriori pairwise comparisons. No significant difference was found between uninvaded and invaded sites.

Supplementary Files

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