

# Evidence of plant-soil feedback in South Texas grasslands associated with invasive Guinea grass

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## Abstract

Plant-soil feedback (PSF) processes play an integral role in structuring plant communities. In native grasslands, PSF has a largely negative or stabilizing effect on plant growth contributing to species coexistence and succession, but perturbations to a system can alter PSF, leading to long-term changes. Through changes to soil abiotic and biotic properties, invasion by non-native plants has a strong impact on belowground processes with broad shifts in historical PSFs. Guinea grass, *Megathyrsus maximus*, an emerging invasive in South Texas, can efficiently exclude native plants in part due to its fast growth rate and high biomass accumulation, but its impacts on belowground processes are unknown. Here, we provide a first look at PSF processes in South Texas savannas currently undergoing invasion by Guinea grass. In this pilot study, we addressed the question of how the presence of the invasive *M. maximus* may alter PSF compared to uninvaded grasslands. Under greenhouse conditions, we assessed germination and growth of Guinea grass and the seed bank in soil collected from grasslands invaded and uninvaded by Guinea grass. We found that Guinea grass grown in soil from invaded grasslands grew taller and accumulated higher biomass than in soil from uninvaded grasslands. Plants grown from the seed bank were more species rich and abundant in soil from uninvaded grasslands but had higher biomass in soil from invaded grasslands. In South Texas savannas, we found evidence to support shifts in the direction of PSF processes in the presence of Guinea grass with positive feedback processes appearing to reinforce invasion and negative feedback processes possibly contributing to species coexistence in uninvaded grasslands. Future work is needed to determine the mechanisms behind the observed shifts in PSF and further explore the role PSF has in Guinea grass invasion.

## Keywords

bulk soil, grassland, Guinea grass, invasive species, *Megathyrsus maximus*, *Panicum maximum*, plant-soil feedback, South Texas

## Introduction

Invasive species are an increasingly widespread concern due to their negative impacts on ecosystems and difficulty in controlling their spread (Assessment 2005; Pyšek and Richardson 2010). Invasion by non-natives reduces plant diversity and extreme cases can result in monodominant plant stands and subsequent declines of wider biodiversity (Assessment 2005; Dogra et al. 2010). At the ecosystem level, invasion disrupts nutrient cycling, disturbance regimes, and microbial communities above- and below-ground with some changes persisting for decades (Hawkes et al. 2005; D’Antonio and Flory 2017). A difficulty we face in predicting and preventing invasions is that the outcome of an introduction is largely context dependent, varying with initial plant density, life history, and dispersal traits of the invasive plant (Suding et al. 2013). To address this variability, more examples of invasion need to be studied to discern overarching patterns and to inform management opportunities for distinct invasive species and geographical locations.

By modifying the abiotic and biotic qualities of their soil environment, plants can influence the establishment and growth of subsequent generations of plants within that same soil environment in a process termed plant-soil feedback (PSF) (Bever 1994; Bennett and Klironomos 2019). PSF effects both conspecific and heterospecific plants with three possible outcomes: a) positive feedback through increasing establishment, growth, and/or fitness; b) negative feedback by inhibiting establishment, growth, and/or fitness; or c) neutral in which plant function is not impacted by modifications to the soil environment (Bennett and Klironomos 2019). Additionally, the response of individual species within the plant community is species-specific with both positive and negative PSFs present simultaneously. In native grasslands, PSF has a largely negative or stabilizing effect on plant growth which contributes to species coexistence and succession through negative-density dependent processes (e.g. competition, pathogens, herbivory) (Kulmatiski et al. 2008; Hawkes et al. 2013; Lekberg et al. 2018). Changes to plant community composition as those seen during invasion (Reinhart and Callaway 2006; Hawkes et al. 2013; Zhang et al. 2019; Fehmi et al. 2021) can impact subsequent plant growth, reducing native plant establishment and disrupting historical PSF processes in native communities (see Belnap et al. 2005; Hawkes et al. 2005; Wolfe and Klironomos 2005; Batten et al. 2006; Levine et al. 2006). PSF studies are increasing in frequency, but only about 46% (32 of 69) of studies have looked at non-native species; of these, 65% (21 of 32) focused on grasses with only 23 genera and 34 species within *Poaceae* represented (Crawford et al. 2019). Although some species of *Poaceae* become effective and widespread invaders, others fail to establish or only establish locally, but are unsuccessful at expanding their range. Non-native grasses weaken the negative PSF processes that dominate native grasslands, indicating that this could be a contributing factor in invasion success (Crawford et al. 2019), but studies on a wider range of non-native grasses, including both noxious invaders and naturalized species, need to be conducted to understand this pattern and what drives this shift.

In South Texas, Guinea grass, *Megathyrsus maximus* (Jacq.) B.L. Simon and Jacobs, is emerging as a problematic invasive (CABI 2021). A perennial bunchgrass native to Africa, Guinea grass has been introduced in tropical areas globally as a pasture grass due to its fast growth, high biomass accumulation, and stress tolerance, but these same traits also make it a successful invader (Rhodes et al. 2021a). For instance, the fast growth rates and high biomass accumulation of Guinea grass results in displacement of many native species through direct competition for space and resources (Ho et al. 2016). After senescence, native seedling germination is restricted directly by a thick layer of Guinea grass litter (Rhodes et al. 2021a), but native plant regeneration is also reduced in areas without a litter layer or where Guinea grass has been removed previously (pers. obs). This could indicate factors other than direct shading are inhibiting native plant germination and growth. A study conducted in Hawaii comparing establishment of natives from seeds versus transplants after removal of Guinea grass found that transplants had higher rates of establishment than seeds (Ammond et al. 2013). When compared to rates of germination under greenhouse conditions, rates in the field were approximately 30 times lower (Ammond et al. 2013). Research into methods to control Guinea grass invasion have focused on removal of Guinea grass with herbicides, burn treatments, and grazing followed by reintroduction of natives from seeds or out-plantings, but results have been mixed (Ramirez-Yanez et al. 2007; Ammond and Litton 2012; Ammond et al. 2013; Ellsworth et al. 2015). If Guinea grass does alter PSF processes toward a positive feedback for conspecifics, the reestablishment of native plants could be hindered even when Guinea grass is removed prior to plantings (Reinhart and Callaway 2006). Although soil microbes are known to impact seed germination and survival which could slow the recovery of native communities (Zalamea et al. 2015; Sarmiento et al. 2017), the effect of PSF on germination from the seed bank has received little attention.

Our goal was to assess the study system in South Texas for evidence of PSF in grasslands invaded and uninvaded by Guinea grass specifically addressing the question: how does the presence of invasive Guinea grass alter PSF compared to uninvaded grasslands? Overall, aboveground contributions to the high competitive ability of Guinea grass are well documented (Ammond and Litton 2012; Ho et al. 2016; D'Antonio and Flory 2017; Rhodes et al. 2021a, b), but little is known about how Guinea grass impacts belowground processes (but see Chou and Young 1975) and what role this may have in facilitating invasion. Conducting a greenhouse study using whole soil from invaded and uninvaded grasslands, we hypothesized that germination and growth of Guinea grass would be higher in soil from invaded grasslands than soil from uninvaded grasslands. In contrast, plants from the seedbank would not experience a similar increase in germination and growth in soil from invaded grasslands possibly due to inhibition by Guinea grass (Chou and Young 1975). In uninvaded grassland soils, growth and germination of the seedbank and Guinea grass will be lower than in soils from invaded areas, but species richness of plants from the seedbank would be higher than in soils from invaded sites possibly indicating the presence of negative PSF processes in uninvaded grasslands (Kulmatiski et al. 2008; Hawkes et al. 2013; Lekberg et al. 2018). This is

the first study to assess PSF processes in South Texas savannas and to address whether PSF may be playing a role in Guinea grass invasion. Our research provides a baseline for understanding the role of PSF in Guinea grass invasion into native ecosystems.

## Methods

To test our hypotheses, we conducted a greenhouse experiment that used soil collected in August 2020 from grasslands invaded by Guinea grass, *Megathyrsus maximus*, and uninvaded grasslands in Kleberg County, Texas (27.433, -97.67). Here in its unmanipulated state, grasses form the matrix of a savanna punctuated by clumps or mottes of diverse shrubs and low trees dominated by mesquite (*Prosopis glandulosa*). The area receives on average 73.6 cm of rain per year (Weather Service). Sampled grasslands were located between 4 to 8 km apart, spanning an area of approximately 5.5 km<sup>2</sup>. Soil from the three sites sampled in this study was composed predominantly of sand (mean 92%  $\pm$  1.8%) with minor amounts of silt and clay (mean 5.7%  $\pm$  0.8% and 2.3%  $\pm$  1.5%, respectively). Two of the sample sites were in grasslands that had remained intact at least since the 1980's, while the third site had been mechanically treated in 2000 to partially remove encroaching mesquite (Suppl. material 1). These grasslands are grazed annually with occasional prescribed burns.

## Sampling and experimental design

Within each of three sites, we sampled soil from plots invaded by Guinea grass and uninvaded plots (i.e., predominantly native with no Guinea grass present) ( $n = 6$ ) that were located within 10 m of each other to minimize the confounding effects of distance on soil microbial communities or soil traits (Suppl. material 1). We collected two sets of soil from invaded and uninvaded sites: a) bulk live soil for use as the growth medium from each site and b) soil for use as a supplemental inoculum. For both sets of soil, we removed the litter layer and excavated the soil using a hand trowel to a depth of 15 cm. Bulk soil was collected from two locations in each plot and pooled. For the inoculum, we collected five soil cores from each plot with individual cores located approximately 1 m apart. The inoculum soil was collected individually in plastic bags and stored in a 4 °C fridge. Bulk soil was stored at room temperature in a climate-controlled building (~20–22 °C). Within one week of collection, we sieved all the soil (i.e., bulk soil and inoculum) using a 2 mm soil sieve to remove leaf litter and plant roots. Between each use, the sieve was sterilized with 0.5% NaOCl for five minutes, washed with tap water, and allowed to air dry.

For our experiment, we chose to use bulk soil due to concerns that autoclaving impacts soil nutrient availability and composition/abundance of microbial communities. To confirm the effect autoclaving has on soil nutrient availability, we conducted a small assessment on soil nutrients in the bulk soil pre-autoclaving and after two autoclave times (30 minutes and 60 minutes). We found that autoclaving increased levels of phosphorus, sulfur, sodium, and electrical conductivity with autoclave time (ANOVA results in Suppl.

material 4, also see Skipper and Westermann 1973; Tuominen et al. 1994). Studies on the effect of autoclaving on microbial communities demonstrate that sterilization is incomplete with a subset of the fungal and bacterial communities persisting (Skipper and Westermann 1973; Tuominen et al. 1994; Bárcenas-Moreno et al. 2011). Therefore, we did not autoclave the soil to limit the influence of these confounding factors (see Discussion).

Since we were unable to refrigerate the bulk soil due to its large quantity, we added inoculum that was kept at 4 °C to counter any changes in the microbial community in the bulk soil. For this, we created two sets of inoculums: a pooled inoculum referred to hereafter as a mixed soil sample (MSS) and an unpooled inoculum referred to as an individual soil sample (ISS). To create the MSS inoculum, we pooled inoculum at a 1:1 ratio based on soil origin (invaded or uninvaded grasslands) for each of the three sites to create a common inoculum that was applied to replicates ( $n = 6$  inoculum pools used for MSS treatments). For ISS inoculum, we used distinct (i.e., unpooled) soil cores for each replicate.

For the experiment, treatments included soil origin (invaded grassland, uninvaded grassland) and soil handling method (ISS, MSS). Each cross was replicated five times with soil from three separate sites (20 samples per site, 60 samples total). We filled black plastic pots (2.4 L) with the same amount of unautoclaved bulk soil (2640 g) and then added the additional soil inoculum (3% mass: mass; 79.2 g) to each pot (Van Der Putten et al. 2007b). Pots were randomized in the greenhouse to account for potential variation in temperature and lighting. We matched the bulk soil and the inoculum by soil origin (site and invasion status), i.e. MSS and ISS inoculum treatments from invaded sites were added to bulk soil also from the same invaded site. A soil sample from each of the treatments were submitted for nutrient analysis at the Texas A&M AgriLife Extension Service Soil, Water, and Forage Testing Laboratory. Soils were analyzed for pH, nitrate, phosphorus, potassium, electrical conductivity, calcium, magnesium, sodium, and sulfur (Schofield and Taylor 1955; Mehlich 1984; Rhoades 1984).

In each pot, we sowed approximately 0.015 g of Guinea grass seed collected from the same area and time in South Texas. Although we were unable to quantify the seed bank, we used the same amount of soil in each pot to normalize the seed bank. During the sieving process, we homogenized the bulk soil based on site and soil origin as described above, then placed the same amount of bulk soil and inoculum as stated above into each pot. We visually assessed the sieved litter for seeds to ascertain whether larger seeds were removed during soil sieving (i.e. size sorting of seeds), but noted only plant leaves and roots in the material were removed during sieving.

## Germination and growth of Guinea grass

After three weeks, we counted the total number of Guinea grass seedlings and thinned them to a single seedling per pot. At this stage the seedlings were approximately 5 cm tall and could be identified as Guinea grass. After this point, any new Guinea grass that emerged was counted and then removed from the pot. We monitored growth of these seedlings over the course of the experiment (14 weeks), after which plants were carefully removed from pots to keep as much of the root intact as possible. We measured the

plant height at the end of the experiment, then separated the aboveground tissue from roots at the root collar and placed both in a drying oven at 65 °C for 3–5 days in labeled paper bags. We measured the dry weight of both above- and below-ground tissue.

## Germination and growth of seed bank

We monitored the total number of plant seedlings sprouting from the seed bank weekly. At the end of the experiment, we counted the number of plants present within each pot noting how many were monocots and dicots. We were unable to identify seedlings to species as the plants were juveniles and did not have flowering structures. Therefore, to quantify species richness, we used phenotypic differences to distinguish morphospecies within each pot (hereafter, referred to as species richness) (Benítez-Malvido and Martínez-Ramos 2003; Martini et al. 2021). We acknowledge that using phenotype to delimit species has limitations due to underestimating (Derraik et al. 2002, 2010) or overestimating (Arnold et al. 2007) species richness. To control for this, a single person familiar with plant identification assessed all pots. To measure dry weight (total biomass) of the seedbank community, we placed above- and belowground tissue in drying ovens at 65 °C for five days before weighing. Plants germinating from the seed bank were monitored in the same pots as Guinea grass. We chose this experimental design (germination in same pot as planted Guinea grass) as this more closely mimics field conditions by hopefully overcoming some of the limitations seen in greenhouse studies of PSF (see Heinze et al. 2016; Forero et al. 2019), although a side-by-side comparison of same pot and separate pot studies would be informative.

## Statistical analyses

All statistical analyses were conducted in R and code is available for reproducibility. All data and scripts used for analyses are available on GitHub (eabowman/Bowmanetal-STexasGuineaGrass-PlantSoilFeedback) or at <https://doi.org/10.5281/zenodo.7487382>. To assess the effect of soil origin (invaded or uninvaded grasslands) and soil handling method on Guinea grass growth and germination, we used a mixed effect model to analyze germination, height, root length, and dry biomass. We treated soil origin and soil handling method as fixed variables and site as a random variable. We considered Guinea grass germination rate as the total number of seedlings and did not normalize this number as we used the same mass of seeds (0.015 g) per pot. We evaluated all data for normality and homogeneity of variance prior to analysis. Germination, height, and biomass data were log-transformed prior to analysis. Three pots had no Guinea grass growth and were removed from analyses.

The effect of soil origin and soil handling method on germination and growth of the seedbank plant community was also assessed using mixed-effects models as above. Here we also treated germination as the total number of seedlings that germinated as the amount of bulk soil and inoculum used was the same across all treatments and replicates. As above, all data were assessed to see if they met the assumptions for parametric analysis. Germination counts and plant abundance were log-transformed prior to analysis, whereas species richness and biomass were transformed using the formula  $\log(x + 1)$ .

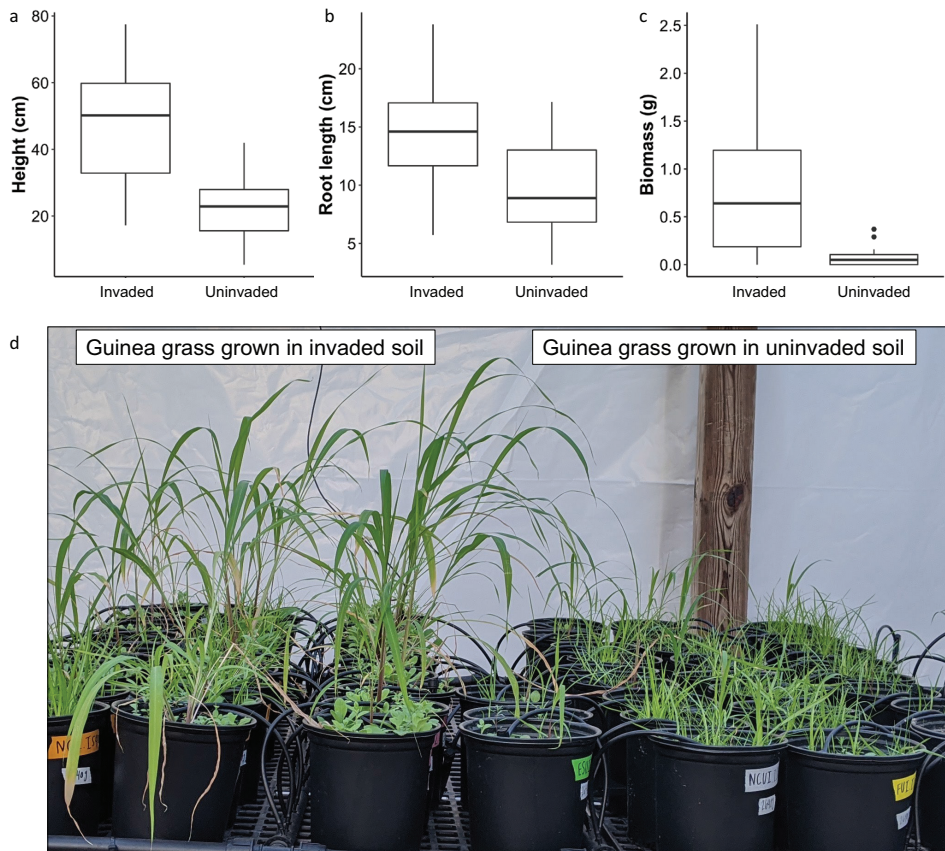


To assess for differences in soil characteristics as a function of invasion, we used a t-test and included only data from unautoclaved soil ( $n = 6$  samples; 3 from invaded sites and 3 uninvaded sites). Electrical conductivity, phosphorus, and sulfur were log transformed prior to analysis.

## Results

### Effect of soil origin (invaded and uninvaded grasslands)

We found a significant difference in Guinea grass growth between invaded and uninvaded sites (Fig. 1; Table 1). Height, root length, and biomass of Guinea grass were higher when grown in soil from invaded sites (height:  $46.6 \text{ cm} \pm 17.4$ ; root length:  $14.1 \text{ cm} \pm 4.2$ ; biomass:  $0.8 \text{ g} \pm 0.7$ ) versus uninvaded sites (height:  $22.1 \text{ cm} \pm 8.3$ ;



**Figure 1.** Guinea grass height (a), root length (b), and biomass (c) when grown in soil collected from i) grassland invaded by conspecifics and ii) uninvaded grasslands dominated by native species. Experimental pots (d) after 14 weeks with larger Guinea grass in soil from invaded grasslands (left). All data shown are non-transformed.

root length:  $9.8\text{ cm} \pm 4.2$ ; biomass:  $0.01\text{ g} \pm 0.1$ ). Germination of Guinea grass did not differ in invaded or uninvaded soil (Table 1), but germination within the first week was higher in soil from invaded sites ( $F_{1,54} = 6.86, p = 0.0114$ ; Suppl. material 2: fig. S2a). Within the first week, average germination of Guinea grass in invaded soil was  $4.1 \pm 4.4$  seedlings compared to  $1.9 \pm 2.3$  in soil from uninvaded sites.

Plant abundance and species richness of plants from the seed bank were significantly higher in soil from uninvaded sites than invaded sites (Fig. 2; Table 2). Average plant abundance was  $54 \pm 21$  in uninvaded soil and  $41 \pm 17$  in invaded soil, and average species richness was  $8 \pm 2$  species versus  $6 \pm 2$ , respectively. Seedling germination overall was higher in uninvaded sites (Fig. 2; Table 2), but when we looked at seedling germination within the first week, we found that seedling germination was initially higher in soil from invaded sites ( $F_{1,54} = 32.74, p < 0.0001$ ; Suppl. material 2: fig. S2b). The seedbank community had higher total biomass (mean  $1.3\text{ g} \pm 0.4$ ) in soil from invaded sites than uninvaded sites (mean  $0.6\text{ g} \pm 0.3$ ) (Fig. 2; Table 2). When we broadly separated plants from the seedbank into dicots and monocots, we found that monocots had significantly higher species richness and abundance in soil from uninvaded sites than invaded sites (species richness: Kruskal-Wallis  $X^2_1 = 13.4, p = 0.0002$ ; plant abundance: Kruskal-Wallis  $X^2_1 = 18.1, p < 0.0001$ ; Fig. 3). Dicots showed no difference.

Effect of soil handling method

Guinea grass germination, seedbank plant abundance, and total biomass of the seedbank plant community showed significant differences between the two soil handling methods we tested. Soil handling method significantly influenced Guinea grass

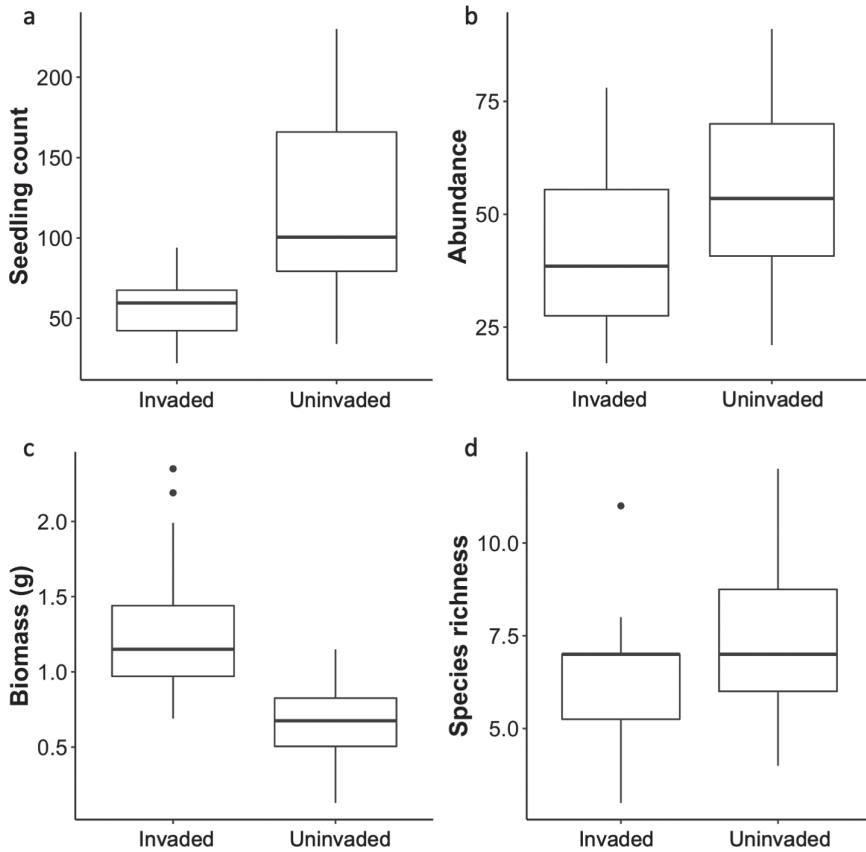
**Table 1.** Results of ANOVA mixed effect model to assess the effect of soil origin (invasion status) and soil handling method on Guinea grass germination and growth. Seedling count is the total seedling number of seedlings in the first three weeks.

	Soil origin		Soil handling method		Interaction	
	$F_{1,51}$	$p$	$F_{1,51}$	$p$	$F_{1,51}$	$p$
Seedling count	0.71	0.4057	7.20	0.0098	2.44	0.1245
Height	38.60	< 0.0001	0.98	0.3278	0.00	0.9789
Root length	14.55	0.0004	0.20	0.6601	0.39	0.5350
Biomass	31.22	< 0.0001	0.08	0.7852	0.03	0.8740

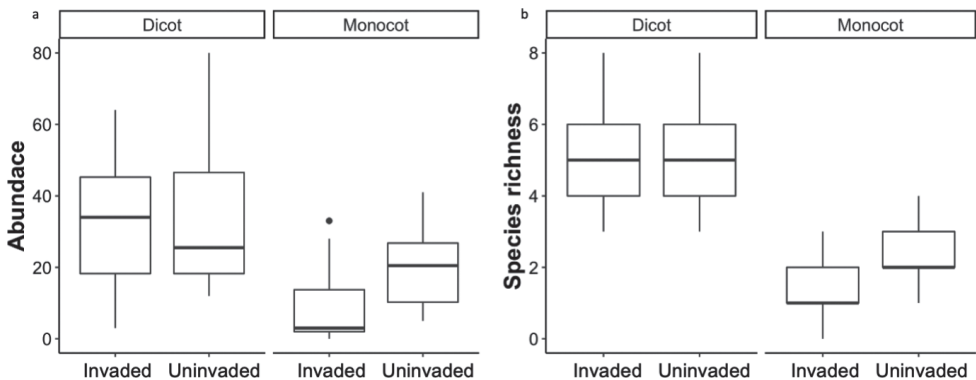
**Table 2.** Results of ANOVA mixed effect model to assess the effect of soil origin (invasion status) and soil handling method on germination and growth of plants from the seedbank. Seedling count here is the total seedling number of seedlings in the first three weeks.

	Soil origin		Soil handling method		Interaction	
	$F_{1,51}$	$p$	$F_{1,51}$	$p$	$F_{1,51}$	$p$
Seedling count	49.31	< 0.0001	0.14	0.7116	4.52	0.0382
Plant abundance	9.05	0.004	5.57	0.0219	3.09	0.0843
Total biomass	51.65	< 0.0001	4.26	0.0439	0.10	0.7539
Species richness	4.52	0.0382	0.02	0.8877	0.08	0.7850





**Figure 2.** Seedling count (a), abundance (b), biomass (c), and species richness (d) of plants which emerged from the seedbank in soil from Guinea grass invaded and uninvaded grasslands. All data shown are non-transformed.



**Figure 3.** Plant abundance (a) and species richness (b) as a function of invasion and plant group. Monocot species richness and plant abundance were significantly higher in soil from uninvaded sites than invaded sites (species richness: Kruskal-Wallis  $X_1^2 = 13.4$ ,  $p = 0.0002$ ; plant abundance: Kruskal-Wallis  $X_1^2 = 18.1$ ,  $p < 0.0001$ ), whereas species richness and abundance of dicots showed no difference. All data shown here are non-transformed.

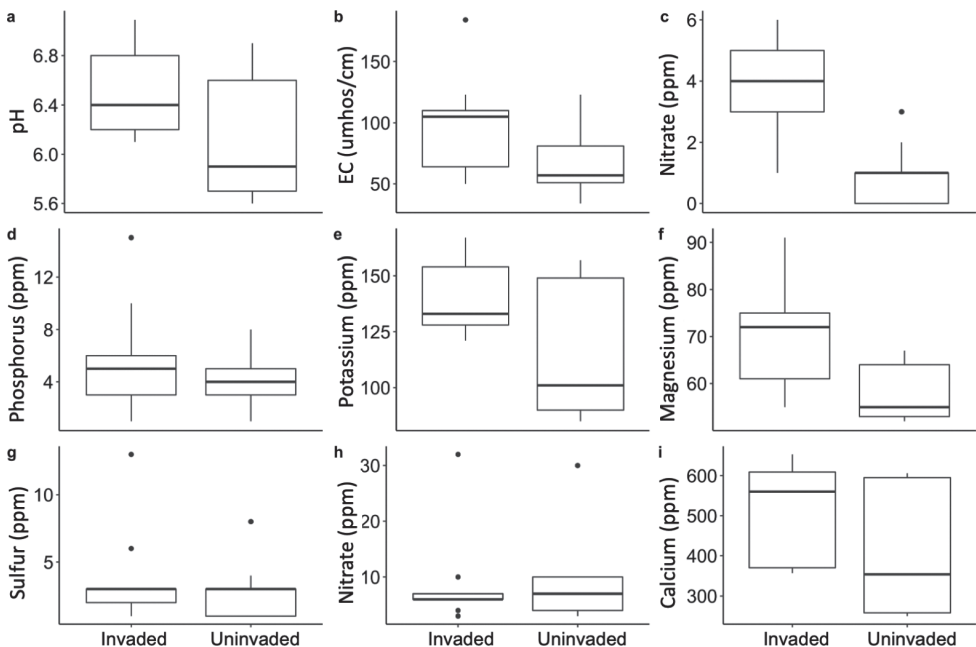
germination with MSS treatments having higher germination (mean  $21 \pm 15$ ) than ISS treatments (mean  $12 \pm 11$ ) (Suppl. material 3; Table 1). Within the seedbank plant community, plant abundance and total biomass were higher in ISS treatments (plant abundance: mean  $53 \pm 21$ ; total biomass: mean  $1.04 \pm 0.5$ ) than MSS (plant abundance: mean  $43 \pm 17$ ; total biomass  $0.85 \pm 0.5$ ) (Fig. 2; Table 2).

## Soil nutrients

We found no significant difference between soil nutrients in invaded and uninvaded sites, although some nutrients trended higher in invaded sites (Fig. 4; Suppl. material 5).

## Discussion

Our experiment presents initial and novel data on PSF processes in the mesquite savannas in South Texas, the impact of Guinea grass invasion on PSF in uninvaded grasslands, and the response of seedbanks to shifts in PSF. In line with our hypothesis, Guinea grass grew taller and accumulated more biomass when grown in soil from invaded grasslands than soil from uninvaded grasslands consistent with a positive PSF on conspecific plants post-invasion (Fig. 1, Table 1). In contrast, plants germinating from the seed bank had



**Figure 4.** Soil characteristics as a function of invasion. None of the soil characteristics were significantly different based on soil origin although in general soil nutrients and characteristics were higher in soil from invaded sites. All data shown here are non-transformed. EC is electrical conductivity.

higher species richness (delimited based on plant morphology) and abundance in soil from uninvaded grasslands consistent with negative feedback processes (Kulmatiski et al. 2008; Hawkes et al. 2013; Lekberg et al. 2018). If negative PSF is present in uninvaded grasslands then the observed decrease in species richness and increase in biomass accumulation of plants from the seedbank in invaded grasslands indicates a possible release from negative feedback processes (Fig. 2, Table 2). Interestingly, we found evidence of a broad phylogenetic signal in the response of monocots and dicots to invaded and uninvaded soil (Fig. 3) indicating that Guinea grass may have a stronger inhibitory effect on more closely related plant species. These results suggest the presence of distinct patterns of PSF in invaded and uninvaded grasslands in South Texas with evidence of positive PSF on Guinea grass in invaded grasslands that reinforces invasion and an overall negative PSF in uninvaded grasslands that could slow invasion.

For a non-native to be a successful invader, it needs to be able to colonize, establish, and disseminate to new environments (Theoharides and Dukes 2007). During colonization, seed germination requires both an appropriate climate and soil conditions, such as texture, nutrients, and microbial community (Theoharides and Dukes 2007; Sarmiento et al. 2017). Despite no difference in climate or soil texture and no statistical difference in soil nutrients, we observed faster initial germination of Guinea grass and the seed bank (Suppl. material 2) in invaded soil, possibly indicating an effect of the soil microbial community on germination. For instance, a low abundance of seed pathogens in the invaded soil can release seeds from negative density dependence processes found in native grasslands (Gilbert and Parker 2006; Halbritter et al. 2012). Ultimately, germination of Guinea grass was not different between the two soil types but was higher overall than we would have expected as, in our observations, Guinea grass has a low germination rate in grasslands (Rhodes et al. 2022). In contrast, germination from the seedbank was higher in uninvaded grasslands which could indicate a low abundance of seed pathogens or conversely higher propagule pressure in these sites. It would be expected that with increasing invasion time, there would be a decrease in native seeds in the seedbank (Robertson and Hickman 2012), but we expect this difference to be small as our invaded and uninvaded plots bordered each other (within 10 m) indicating a relatively short time since invasion and allowing for the introduction of seeds from nearby uninvaded areas.

After germination, the successful establishment of non-native plants is reliant on their fast growth rate, competitive ability with native plants, and efficient resource usage (Theoharides and Dukes 2007). The fast growth rate of Guinea grass has been noted (Rhodes et al. 2021a), but here we show that the presence of Guinea grass in invaded areas further increased its growth and biomass accumulation. This result, in combination with the observed higher biomass of all plants from the seedbank in soil from invaded grasslands, suggests that either the microbial community or soil nutrients play a role in re-enforcing invasion. Although soil nutrients were marginally higher in invaded soil than in uninvaded soil (Fig. 4, Suppl. material 5), these differences were not statistically significant. Invasion is generally found to be associated with shifts in nutrient availability and cycling (reviewed in Ehrenfeld 2003; Sardans et al. 2017). Since our samples number was quite small ( $n = 6$ , 1 sample per treatment

combination), we think a deeper exploration of soil is warranted to fully rule out soil nutrients as a contributing factor.

Invasion has been shown to impact multiple functional guilds within soil microbial communities through several pathways (e.g. phytochemicals, litter inputs) thus altering community processes (reviewed in Wolfe and Klironomos 2005; Reinhart and Callaway 2006; Van Der Putten et al. 2007a). Shifts in soil communities by invasive species can indirectly cause alterations in nutrient cycling by supporting decomposers and rhizosphere mutualists (Zhang et al. 2019). Plant-associated microbes can directly influence the ability of non-natives to invade native ecosystems (Rudgers et al. 2005). Additionally, the enemy release hypothesis posits that movement of plants to novel environments causes a decrease in negative pressures from pathogens, herbivores, and parasites found in their home range (Keane and Crawley 2002). Although we did not sterilize our bulk soil and added only 3% of the supplemental inoculum, we were able to see differences based on our handling of the supplemental inoculum. The observed effect of our soil handling methods supports a possible difference in the microbial communities in invaded and uninvaded grasslands. Guinea grass germination was higher in treatments where soils were pooled and homogenized (MSS) than treatments that were kept distinct (ISS), but abundance and biomass of plants from the seedbank was higher in ISS than MSS (Suppl. material 3). These results could indicate that the plant community is influenced strongly by localized soil microbial communities that are overwhelmed by the wider community upon pooling (e.g. due to rareness or competitive ability) (Batten et al. 2006; Mummey and Rillig 2006; Rúa et al. 2016). Although we did not assess microbial community composition in this study, differences between the soil handling methods could be influenced by shifts in the relative abundance of particular community members after pooling inocula or specificity of PSF effects on native versus non-native plant species (Brinkman et al. 2010; van de Voorde et al. 2012). As part of ongoing research, we are evaluating soil microbial communities, litter decomposition rates, and levels of soil nutrients across invasion and disturbance types to assess changes in the soil environment more fully.

Another possible contributing factor, not considered in this study, is allelopathy. Invasion of non-native plants may cause cascading effects on conspecific native species through allelopathy as examples of the novel weapons hypothesis (Callaway and Ride-nour 2004). Allelochemicals can directly impact fitness of native species or indirectly through conditioning of the soil microbial community, such as has been shown with *Centaurea diffusa* (Callaway et al. 2004; Wolfe and Klironomos 2005). Allelopathic effects have been found to decrease with increasing phylogenetic distance (Zhang et al. 2021), such that species of monocots should be more negatively impacted than dicots in grasslands invaded by Guinea grass. When we assessed differences in the effect of PSF on monocots and dicots, monocot species richness and plant abundance were higher in soil from uninvaded sites than invaded sites, whereas dicots showed no difference (Fig. 3). These results indicate that in invaded grasslands monocot species that are more closely related to Guinea grass phylogenetically do experience a negative feedback. These results raise interesting questions such as whether negative PSF is driving species coexistence in uninvaded communities, whether the switch to an overall positive feedback mechanism in invaded grasslands is due to nutrient availability, and whether allelopathy or patho-

gen accumulation is suppressing other monocot species post-invasion. In our ongoing research, we aim to parse out the effect of Guinea grass invasion on soil nutrients, allelopathy, and soil microbial communities to better understand how Guinea grass impacts PSF processes and how this varies across the heterogeneous landscapes of South Texas.

## Conclusions and future directions

In this initial study, we found evidence that the presence of Guinea grass alters PSF for con- and heterospecific plant species indicating that Guinea grass could reinforce through positive feedback processes. Negative PSFs in uninvaded grasslands were associated with higher species richness and abundance of the plants in the seedbank possibly contributing to species coexistence in native grasslands. We found evidence to suggest that positive PSFs observed in invaded grasslands could be reinforcing establishment of Guinea grass, although the mechanism needs to be explored further. Our results represent the first time PSF processes have been studied in South Texas savannas and show how Guinea grass, an emerging invasive within the southern United States, influences these processes reinforcing its own invasion.

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## Supplementary material 1

**Soil sampling sites showing extent of Guinea grass patch (white boundary, I) and adjacent uninvaded grassland (N) with nearby mesquite tree mottes. Google Earth Imagery date 1/13/2014. Scale bar 70m.**

Authors: Elizabeth A. Bowman, Robert M. Plowes, Lawrence E. Gilbert

Data type: figure

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## Supplementary material 2

**Initial germination of Guinea grass seed (a) and the seedbank (b) during week 1 was higher in soil from invaded sites than uninvaded sites. All data shown here are non-transformed.**

Authors: Elizabeth A. Bowman, Robert M. Plowes, Lawrence E. Gilbert

Data type: figure

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## Supplementary material 3

**Effect of soil handling method on Guinea grass seedling count (a), native community plant abundance (b), and native community biomass (c). MSS: mixed soil sampling; ISS: individual soil sampling. All data shown are non-transformed.**

Authors: Elizabeth A. Bowman, Robert M. Plowes, Lawrence E. Gilbert

Data type: figure

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## Supplementary material 4

**Results of one-way ANOVA examining the effect of autoclave time on soil characteristics. Electrical conductivity, phosphorus, and sulfur were log-transformed prior to analysis.**

Authors: Elizabeth A. Bowman, Robert M. Plowes, Lawrence E. Gilbert

Data type: table

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## Supplementary material 5

**Results of t-test examining differences in soil characteristics between invaded and uninvaded sites. Electrical conductivity, phosphorus, and sulfur were log-transformed prior to analysis.**

Authors: Elizabeth A. Bowman, Robert M. Plowes, Lawrence E. Gilbert

Data type: table

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