

Buffelgrass (*Pennisetum ciliare*) invasion is associated with reduced plant diversity and changes in carbon storage in the Sonoran Desert

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ABSTRACT

Buffelgrass (*Pennisetum ciliare*) is a perennial bunchgrass, invasive in arid ecosystems of the United States, Australia, and Mexico. Buffelgrass invasion detrimentally affects ecosystems, but it is unclear how the amount of invasion affects ecological impact. Here, we investigated how buffelgrass abundance affects: plant diversity, aboveground biomass carbon, and surface soil (0–10 cm) carbon. We established 13 plots in unburned areas, across a range of buffelgrass cover (0–68%) in the Sonoran Desert of Arizona, USA. Shannon diversity decreased significantly with buffelgrass cover. Herbaceous carbon storage significantly increased with buffelgrass cover. There was a significant non-linear relationship between woody carbon storage and buffelgrass cover and positive associations in occurrence between buffelgrass and many woody plant species. This may indicate facilitation of buffelgrass establishment by woody plants, or that buffelgrass does not competitively exclude shrubs and cacti until high cover is reached, or following fire. Total soil carbon in surface soils was significantly lower under buffelgrass and bare ground compared to native vegetation, though did not vary significantly across the buffelgrass gradient, in the absence of fire. Because diversity metrics had linear negative associations with buffelgrass cover, management strategies that reduce buffelgrass cover may still have positive ecological outcomes even without eradication.

1. Introduction

Invasive plants have wide-ranging effects on ecosystems (Pyšek et al., 2012), making them a major concern for global change and biodiversity conservation (Díaz et al., 2019). Buffelgrass (*Pennisetum ciliare*) is an invasive perennial bunchgrass that displaces native flora and fauna and alters wildfire regimes (Marshall et al., 2012) in dryland ecosystems. It is typically 20–150 cm tall, has a rooting depth of up to 2.4 m, and spreads either by seeds carried by wind, water, humans, and animals, or possibly rhizomes (Marshall et al., 2012; National Park

Service, 2019). Buffelgrass characteristics including deep roots which increase access to water resources, drought-tolerance, high seed longevity, opportunistic germination, and rapid growth make it adaptable to a range of conditions including harsh arid and rocky environments and able to outcompete native species (Marshall et al., 2012; Farrell and Gornish, 2019). Although the invasive tendencies of buffelgrass are well known, few studies have evaluated its impacts on carbon storage and biodiversity (Marshall et al., 2012; Scasta et al., 2015), two ecosystem services of global importance. In addition, despite being critical for management, the relationship between buffelgrass

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abundance and its impact on biodiversity and ecosystem carbon is not well understood anywhere in its invaded range. Therefore, additional information about buffelgrass impacts across a gradient of its abundance would help management efforts that seek to reach biodiversity and carbon storage restoration goals in dryland ecosystems.

Buffelgrass is native to Africa and has been introduced to the U.S. multiple times over the last 100 years, largely for forage and erosion control purposes, with the first recorded introductions to the state of Arizona in the 1940s (Marshall et al., 2012). Buffelgrass has a similar introduction history in arid lands of Australia and Mexico, where it is also now considered invasive (Marshall et al., 2012). Because buffelgrass was introduced and managed as a forage crop, early research about the species was focused on forage yields and buffelgrass cultivars (e.g. (Hanselka, 1988, Martin-R et al., 1995), rather than the potential consequences for ecosystems (Marshall et al., 2012). More recently however, several studies have explored how buffelgrass invasion affects ecosystem processes, including competition with native species (Farrell et al., 2022), native diversity (Tinoco-Ojanguren et al., 2013), carbon storage (Vega-Puga et al., 2023), and carbon fluxes (Hinojo-Hinojo et al., 2019; Castellanos et al., 2022).

Conversion to buffelgrass pasture has resulted in a marked decrease in native plant diversity in Mexico (Lyons et al., 2013; Tinoco-Ojanguren et al., 2013), though impacts across native species functional groups vary, likely due to conversion practices (Franklin and Molina-Freaner, 2010). In addition to initial disturbance and ongoing management that may reduce native plant diversity, barriers to seedling establishment of native species may also contribute to reduced native diversity in buffelgrass pastures (Tinoco-Ojanguren et al., 2013). In landscapes where buffelgrass has invaded natural ecosystems, most work related to buffelgrass invasion has focused on comparing highly invaded areas to nearby uninvaded areas without considering how impacts might vary over a gradient of buffelgrass abundance. However, understanding how invasive species abundance affects impact is important for setting management targets, particularly if the impacts of invasion are non-linear (Sofaer et al., 2018; Bradley et al., 2019).

In Arizona in the U.S., some evidence suggests both native plant species richness and cover decrease with buffelgrass abundance (McDonald and McPherson, 2011), a pattern that is supported across native plant functional groups (Olsson et al., 2012). This is consistent with work on buffelgrass in other geographic regions (e.g., Franks, 2002; Jackson, 2005; Sands et al., 2009). Also in Arizona, Abella et al. (2012) found that native plant cover was 43% lower in invaded areas in the Sonoran Desert of Arizona, but that species richness in buffelgrass invaded areas was similar to natural areas. Declines in native species richness and/or cover are particularly important because the Sonoran Desert has high native plant biodiversity compared to other desert ecosystems, with many endemic species, including the iconic saguaro cactus (*Carnegiea gigantea*; Dimmitt, 2015).

In addition to biodiversity, invasive plants can affect ecosystem biomass and carbon storage in dryland systems (e.g., Nagy et al. (2021); Mahood et al. (2022)). Despite having much lower aboveground carbon (compared to forested systems), drylands are still important in carbon storage and cycling (Lal, 2004; Hanan et al., 2021). In these systems, carbon fluxes and storage (Poulter et al., 2014; Ahlström et al., 2015) are tied to seasonal water availability and water use by dominant plant species (Hinojo-Hinojo et al., 2016, 2019; Castellanos et al., 2022).

The effects of buffelgrass invasion on ecosystem carbon dynamics are likely dependent on the level of invasion, the ecosystem invaded, and the carbon pool or flux in question. For example, herbaceous biomass increased linearly with buffelgrass cover in Australia (Miller et al., 2010). However, total aboveground biomass was 70% lower in buffelgrass compared to native desert scrub ecosystems in Sonora Mexico (Vega-Puga et al., 2023) and a reduction in aboveground net primary production (ANPP) (as measured by proxy with the Normalized Difference Vegetation Index; NDVI) was documented in buffelgrass compared to native desert scrub (Franklin and Molina-Freaner, 2010). Castellanos

et al. (2022) found that net ecosystem production (NEP) was always positive in buffelgrass pastures in Sonora Mexico, while more diverse native shrubland NEP could be either a source (in dry years) or a sink. Buffelgrass has also been linked to changes in soil carbon. For example, in the Sonoran Desert of Arizona, soil carbon tended to be higher under buffelgrass patches compared to non-buffelgrass patches (Abella et al., 2012). Despite evidence that buffelgrass does influence carbon, little work exists that examines ecosystem level effects on carbon storage across pools at varying levels of invasion.

Here, we provide the most comprehensive analysis to date of the impacts of buffelgrass invasion in the Sonoran Desert of Arizona ecosystem. We analyze impacts to native plant communities by evaluating changes in species richness, evenness, and diversity across a gradient of buffelgrass cover and provide an assessment of native plant species associations with buffelgrass. We also examined effects on soil, herbaceous, and woody carbon pools to calculate estimates of total ecosystem carbon across a gradient of invasion.

2. Methods

2.1. Study sites

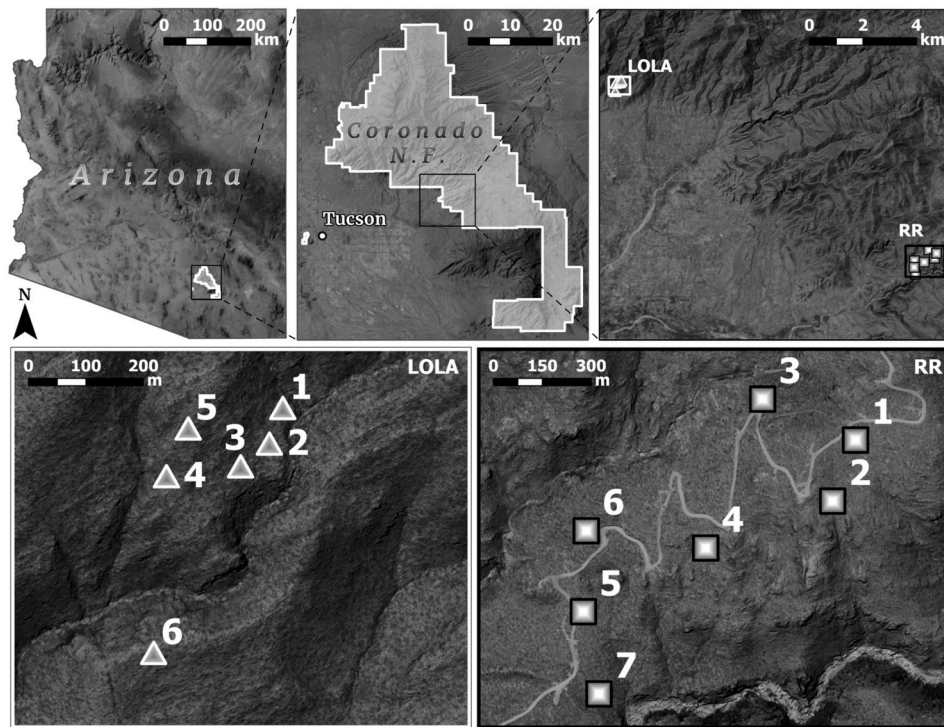
We established 13 (20 × 20 m) plots across a gradient of buffelgrass cover in the Santa Catalina Ranger District of the Coronado National Forest in Arizona, USA. Six plots were located northeast of the city of Tucson (LOLA site), and seven were located directly east of Tucson (RR site) (Fig. 1a). Plots had a nested design where each 20 × 20 m plot was further divided into smaller subplots designed for measuring different ecological characteristics (e.g., plant diversity, aboveground biomass (Figure A1);) following the National Ecological Observatory Network (NEON) protocols for plot establishment (Azuaje, 2019; Barnett et al., 2019). Field sampling was conducted during October and November 2019 across a gradient of buffelgrass invasion to determine the associations of invasion with plant diversity and carbon storage. An example of two of our study plots can be found in Fig. 1b (minimally-invaded by buffelgrass) and Fig. 1c (moderately-invaded by buffelgrass).

Mean annual precipitation across plots ranged from 353 to 385 mm year⁻¹ (confirmed with data from PRISM, 1991-2020 normals (PRISM Group, 2026)). We confirmed that plots had similar topographical characteristics by calculating elevation, aspect, and slope post hoc using U.S. Geological Survey 1 m resolution digital elevation models (U.S. Geological Survey, 2017). Plot elevation ranged from 998 m to 1170 m (mean = 1066.2 m, sd = 54.6 m). Plots tended to be steep and ranged from 2.2 to 22.2° (mean = 16°, sd = 4.3°) and south-facing (aspect mean = 189°, sd = 46.9°) with aspect ranging from southeast to southwest (range = 131-286.4°; Table A1). In addition, we visually assessed scatterplots showing elevation, aspect, and slope across the buffelgrass cover gradient to ensure no underlying topographical biases were present across plots with different buffelgrass cover. Given the potential compounding influence of fire on biomass and soil carbon and plant diversity, all plots were established in areas that have not burned since the year 1984 (confirmed with Moderate Resolution Imaging Spectroradiometer (MODIS) and National Interagency Fire Center (NIFC) data).

2.2. Field measurements

2.2.1. Plot-level cover

We measured cover of buffelgrass, bare ground and all other vegetation at each plot using the line intercept method (Canfield, 1941) along a 20 m transect through the center of plot and two additional randomly placed 20 m transects on either side (3 transects total per plot). Buffelgrass cover was calculated as the average of the three transects.



a)



b)



c)

Fig. 1. Study sites within the Coronado National Forest in Arizona, USA. a) Two site locations (LOLA and RR) with six and seven plots at each, respectively. b) Example of a plot minimally-invaded by buffelgrass. c) Example of a plot moderately-invaded by buffelgrass. Photo credit: Dylan Murphy.

2.2.2. Plant diversity

For all plots, plants in each of the eight 1 m² subplots were identified to the species level and ocular estimates of percent cover were recorded (Figure A1; Barnett et al., 2019). Additional species were recorded as present if found anywhere in the remainder of the 20 × 20 m plot.

2.2.3. Aboveground biomass carbon

We followed the NEON herbaceous biomass sampling protocols (Meier, 2019), where all herbaceous biomass above the mineral soil was clipped in eight 2 m × 0.1 m subplots per plot (separate from the plant diversity subplots) and collected in paper bags. Samples were dried in a drying oven at 60°C for a minimum of 72 h until the mass stabilized and then weighed. Total dry biomass (g) was recorded for each sample. A subsample was ground in a Thomas-Wiley Intermediate Mill to pass a 20 mesh screen for chemical analyses. Samples were analyzed by the University of Georgia Agricultural and Environmental Services Laboratory for % carbon (C) and % nitrogen (N) using the Dumas method (Kirsten, 1979) where they were combusted at 1200°C in a vario MAX total combustion analyzer (Elementar, Ronkonkoma, NY, USA). Herbaceous biomass C (g C m⁻²) for each plot was calculated using the percent carbon for each sample and the following equation:

$$HBC = \frac{DW \times C}{A}$$

where HBC = herbaceous biomass C (g C m⁻²), DW = dry weight (g), C = carbon concentration (%), and A = area of plot (m²). Values were then averaged across subplots to get the plot total.

Because a destructive harvest was not possible for woody plants and cacti, to estimate aboveground biomass, we used allometric equations developed by Búrquez et al. (2010) for Sonoran Desert ecosystems. The sampling scheme varied based on growth form and size, as outlined below.

To sample aboveground biomass of large woody plants and cacti, all large trees, shrubs, and arborescent cacti with a diameter at breast height (dbh) ≥ 10 cm were measured in each plot (Meier, 2017; Hiebert, 2018). Qualifying medium shrubs (1 cm ≤ dbh < 10 cm) and cacti (height ≥ 10 cm) were measured and recorded using nested subplots of one of three sizes: 1 m², 10 m², or 25 m². Subplot size was selected such that at least 20 medium-size individuals per class were measured per plot. Non-arborescent cacti were measured if their height was > 10 cm. In cases where the nested plot sizes were not sufficient for reaching the 20 individual requirement, all individuals in the plot were measured and recorded. A full description of using nested plots for vegetation sampling can be found in the NEON protocols (Meier, 2017; Hiebert, 2018). Additionally, some plots also had a substantial number of shrubs that did not meet the qualifying 1 cm dbh size requirement to be counted with the medium-size individuals (hereafter, small shrubs). For small shrubs, the total number of individuals within the plot was counted.

For each qualifying tree, shrub, shrub-like cactus, and columnar cactus, we measured height, maximum crown diameter, and crown diameter perpendicular to the maximum measurement.

To estimate the canopy volume of small shrubs (< 1 cm dbh), the same measurements were made (i.e., height, maximum crown diameter, and perpendicular maximum diameter) for only three representative individuals in each plot. Canopy volume was then calculated for all small shrubs as the average across the three individuals, multiplied by the number of small individuals in each plot.

For all trees, shrubs, and shrub-like cacti, and qualifying columnar cacti, canopy volume (V, cm³) was estimated as an elliptical cylinder using the equation from Búrquez et al. (2010):

$$V = \pi \times r_1 \times r_2 \times h$$

where r₁ = ½ maximum diameter (cm), r₂ = ½ perpendicular maximum diameter (cm), and h = height (cm).

For arborescent saguaro cacti (*Carnegiea gigantea* (Engelm.)), we

measured total height, diameter, and length as well as diameter and length of each arm and volume was calculated for both the main stem and each arm as a cylinder:

$$V = \pi \times r^2 \times h$$

where V = volume (cm³), r = radius (cm), and h = height (cm).

For pad cacti (*Opuntia engelmannii*) we counted the total number of cactus pads per qualifying plant. We then sampled 55 pads at LOLA (median = 456 cm³) and 60 pads at RR (median = 532 cm³; Figure A2), to estimate median pad volume using the equation:

$$V = L \times W \times H$$

where V = pad volume (cm³), L = maximum length (cm), W = maximum width (cm), and H = height (cm). We then multiplied the pad count by the median pad volume associated with each site.

Canopy volumes per plant (m³ plant⁻¹) were added together within each subplot (m³ subplot⁻¹) and were multiplied based on the subplot size, to calculate total canopy volume per plot (m³ plot⁻¹). This value was then divided by plot area (400 m²) to determine canopy volume (m³ m⁻²).

To convert canopy volume (m³ m⁻²) to biomass (g m⁻²), we used an allometric equation from Búrquez et al. (2010). Búrquez et al. (2010) provides allometric equations based on three Sonoran ecosystem types. Our sites were most similar in species composition to the arroyos sites, therefore, we calculated the plot biomass subtotals (for everything except pad cacti) using the arroyos power equation:

$$AGB = (356.983 \times V)^{1.416}$$

where AGB = aboveground dry biomass (g m⁻²) and V = canopy volume (m³ m⁻²).

Biomass for pad cacti was calculated using an allometric equation from Sáiz and Fernández (1990):

$$DW = 0.0345 \times L \times W \times D$$

where DW = dry weight (g), L = maximum length (cm), W = maximum width (cm), and D = neck thickness (cm). Pad cacti subtotals (g m⁻²) were then added to the plot biomass subtotals (for all plants except pad cacti) to get the plot biomass totals (g m⁻²).

Finally, following Búrquez et al. (2010), biomass carbon was estimated at 50% of total biomass. This provided an estimate for aboveground woody biomass carbon (g C m⁻²) in each plot.

2.2.4. Soil carbon

We used an AMS 5.7 cm diameter regular soil auger to collect nine soil samples in each plot (under three vegetation cover types: buffelgrass, bare ground, and 'other vegetation' that included shrubs, grasses, and cacti) to 10 cm depth to determine texture, total soil C and N, and soil organic C of surface soils. Roots were removed from the sample and the soil was mixed until homogenous and then air-dried. All soil samples were analyzed for % C and % N at the University of Georgia Agricultural and Environmental Services lab using the Dumas method (Kirsten, 1979) where they were combusted at 1200°C in a vario MAX total combustion analyzer (Elementar, Ronkonkoma, NY, USA). Bulk density was sampled by excavating one 1000 cm³ soil pit for each vegetation cover type at each plot. Bulk density samples were oven dried at 105°C for at least 72 h (Blake and Hartge, 1986) and then weighed. We calculated the mean soil bulk density for each vegetation cover type (bare ground, buffelgrass, other vegetation; Table A2) at each of the two sites and used this number to calculate total soil carbon and soil organic carbon content from concentration (%). We collected one soil sample per vegetation cover type per plot to analyze for soil texture. These samples were analyzed by the Oklahoma State University Soil, Water and Forage Analytical Laboratory that calculated the % sand, silt, and clay using a hydrometer (Gee and Bauder, 1986; Gavlak, 2003).

2.2.5. Ecosystem carbon

To get an estimate of total ecosystem carbon storage, we first added the woody and herbaceous biomass carbon per plot to estimate the total vegetation carbon (g C m^{-2}). Then, we calculated a weighted total soil carbon value (g C m^{-2}) per plot based on the percent cover of buffelgrass, other vegetation, and bare ground within each plot. Finally, we added the weighted total soil carbon to the total vegetation carbon to get an estimate of total ecosystem carbon (g C m^{-2}).

2.3. Statistical analysis

2.3.1. Linear models

In order to assess buffelgrass impacts on plant communities, we calculated the species richness, evenness, and Shannon diversity index for each plot (Oksanen et al., 2012). We used general least squares models (Pinheiro et al., 2021) to predict diversity as a function of buffelgrass cover, using site as an interaction term because we expected that diversity at the two distinct locations could vary. To fit our models, we Z-standardized our buffelgrass cover predictor variable, and incorporated an exponential variance structure using buffelgrass cover and site as variance covariates to account for violations of homogeneity of variance (Zuur et al., 2009). When modeling species richness and evenness, we used a combined exponential variance function for buffelgrass cover while grouping by site.

Herbaceous biomass carbon was modeled using a linear model. The response variable (total herbaceous carbon (g C m^{-2})) was log transformed and modeled as a function of buffelgrass cover and site.

To predict total aboveground biomass carbon (g C m^{-2}) as a function of buffelgrass cover, we used general least squares models (Pinheiro et al., 2021), using site as an interaction term. To account for heterogeneity of variance, we incorporated a fixed variance structure that included buffelgrass cover (Zuur et al., 2009). The best model was chosen using Akaike Information Criterion (AIC) and we checked model assumptions by plotting model residuals and examining model co-plots.

We used linear models to analyze total soil carbon and soil organic carbon as a function of cover type. Significance was assessed with type II ANOVAs (Fox and Weisberg, 2019). Response variables for both analyses were log transformed and modeled as a function of cover type and site, and diagnostic assumptions were assessed (Lüdtke et al., 2021). We determined whether differences in carbon storage (g C m^{-2}) were different under cover type post hoc, using estimated marginal means and pairwise comparisons with a Sidak adjustment (Lenth et al., 2021).

2.3.2. Joint species distribution model (JSDM)

In order to look in greater detail at how buffelgrass was associated with the occurrence of other species and functional groups, we created a joint species distribution model using a bayesian framework (Tikhonov et al., 2020). Markov Chain Monte Carlo (MCMC) is a method used to approximate the posterior distribution for each model parameter (Brooks, 1998; van Ravenzwaaij et al., 2018). We created four MCMC chains, each consisting of 150,000 iterations. We discarded the first 50,000 iterations for each chain and then recorded every 100th for a total of 1000 posterior samples per chain, and 4000 total. We assessed model convergence using the effective sample size and the potential scale reduction factor (Gelman and Rubin, 1992). We considered a modal effective sample size that is close to the total number of posterior draws (here, 4000), and a median potential scale reduction factor of less than 1.001 as evidence of good model convergence. We used the model to predict the probability of occurrence in a 1 m^2 subplot, with the 400 m^2 plot in which a subplot occurred included as a random effect. Predictor variables were slope, folded aspect and woody biomass. Folded aspect was calculated as:

$$FA = |180 - |A - 225||$$

where FA = folded aspect (degrees) and A = aspect (degrees) (McCune

and Keon, 2002).

The response variable was an occurrence matrix, where species with low prevalence (<10 occurrences) were grouped together by functional group, if possible (Table A3). The residual correlation is the correlation between response variables (i.e., species or groups of species) that is not explained by predictor variables in the model (Warton et al., 2015). We considered high residual correlations to be evidence of interspecific interactions. In order to assess how buffelgrass influenced the occurrence of each common species or group, we calculated the mean of the absolute value of the residual correlation for each species.

2.3.3. Path model

Because we were examining associations among a wide range of variables, we felt it was important to be able to disentangle potentially confounding relationships by including an analysis that allows for the consideration of all of those variables and the hypothesized relationships between them in a single analysis. Therefore, we built path models using the R package 'lavaan' (Rosseel et al., 2025). Path models are a subset of structural equation models to assess the relative effect size of direct and indirect relationships among variables and examine hypothesized causal processes (Lleras, 2005). We used exogenous and endogenous variables in the path models. Exogenous variables can predict both the endogenous and response variables, but are not predicted by other variables in the model. The exogenous variables here (i.e., woody carbon and folded aspect) accounted for site-level characteristics that are relatively static from year to year, and would not be expected to be affected by changes in buffelgrass cover. Endogenous variables predict the response and are predicted by the exogenous variables. These accounted for site-level characteristics that vary from year to year, e.g., as a result of climatic variability. These were the cover of buffelgrass, the cover of all other plants, herbaceous carbon, the Shannon-Wiener diversity index and species richness.

We built our path model bottom-up, beginning with simple, exploratory path models, and then increased complexity. We used a modification index function from the 'lavaan' package to check for paths that could be added to the model and improve fit. We removed statistically insignificant variables unless their removal resulted in residual correlations rising above 0.1. The model was considered well-fitting if it maximized (>0.9) two measures of good fit, the Comparative Fit Index and Tucker-Lewis Index, and if it minimized (<0.1) two measures of error, the Root Mean Square Error of Approximation and Standardized Root Mean Square Residual.

In path models, there are often associations from different predictor variables on the same response variable, but those two predictors also have causal associations that may dampen or amplify their effects on the eventual response variable. We examined the path model for instances where buffelgrass cover appeared to have such effects, and made additional calculations to determine the indirect and total effects of buffelgrass cover on our response variables.

2.3.4. Software used

All statistical analysis was completed in R version 4.1.0 and all graphical visualizations were created in R using the ggplot2 package (Wickham et al., 2023). Additional R packages used in this study include: tidyverse (Wickham et al., 2019), tidygraph (Pederson, 2024), ggResidpanel (Goode and Rey, 2022), cowplot (Wilke, 2025), ggraph (Pederson, 2025), ggpubr (Kassambara, 2026), classInt (Bivand et al., 2025), car (Fox and Weisberg, 2019), ggtext (Wilke and Wiernik, 2022), HDInterval (Juat et al., 2022), coda (Plummer et al., 2024), snow (Tierney et al., 2021), sf (Pebsma, 2026), FSA (Ogle et al., 2026), and lme4 (Bates et al., 2026).

3. Results

3.1. Buffelgrass cover

Buffelgrass cover across plots ranged from 0% to 67.82% (mean = 24, sd = 23.8; Table A1).

3.2. Species diversity

Species richness ranged from 21 to 46 species per 400 m² plot, and a total of 103 unique species were identified across all plots and sites. Species richness significantly decreased with buffelgrass cover ($p = 0.002$; Fig. 2; Table 1). Buffelgrass cover was also significantly negatively correlated with species evenness ($p < 0.001$) and Shannon diversity ($p < 0.001$; Fig. 2; Table 1).

3.3. Joint species distribution model

Groupings for species (in 1 m² subplots) used for the joint species distribution model are shown in Table A3. The joint species distribution model was well-fit, with a modal effective sample size of approximately 4000 and a median potential scale reduction factor <1.001 (Figure A3). Slope, aspect, and elevation were important environmental filters for many species, with hotter aspects (i.e., southwestern-facing), and especially steeper slopes consistently having negative effects on the occurrence of many species and species groups (Figure A3). Hotter aspects and steeper slopes, in contrast, positively affected the occurrence of buffelgrass. Buffelgrass had the strongest negative interaction with *Lepidium densiflorum* and additional strong negative interactions with *Encelia farinosa*, *Opuntia engelmannii*, *Janusia gracilis*, and perennial graminoid species (Fig. 3). Buffelgrass had strong positive interactions with *Lycium* spp., leguminous shrubs, and other shrub species, in addition to perennial forbs. Buffelgrass had the second highest mean effect on other species (Table A4), these effects were more consistently negative than other species (Fig. 3), and its occurrence was the least affected by environmental filters (Figure A3).

3.4. Aboveground biomass carbon

3.4.1. Herbaceous

Herbaceous biomass carbon ranged from 14 g C m⁻² at 0% buffelgrass cover to 374 g C m⁻² at 64% buffelgrass cover. The mean across all plots was 139 ± 31 g C m⁻². Buffelgrass cover had a significant positive relationship with herbaceous biomass carbon content ($p < 0.001$, adj. $R^2 = 0.861$; Fig. 4, Table 1).

3.4.2. Woody plants and cacti

Woody plant and cactus biomass was the smallest carbon pool,

ranging from 5 g C m⁻² at 64% buffelgrass cover to 214 g C m⁻² at 20% buffelgrass cover. The mean across all plots was 68 ± 16 g C m⁻² and reflects the patchy nature of woody and cacti vegetation in this landscape. The woody plant and cactus biomass C model was most appropriately fit by a quadratic polynomial, where C significantly increased at intermediate levels of buffelgrass cover, and then decreased at high levels ($p = 0.001$, Fig. 4, Table 1).

3.5. Soil

Surface soil (0–10 cm) bulk density ranged from 0.84 g cm⁻³ for buffelgrass at RR to 1.81 g cm⁻³ for bare ground at LOLA (Table A2). This range of measurements was consistent with those taken in similar ecosystems (Throop et al., 2012). Soil texture of surface soils (0–10 cm) was most often classified as sandy loam (Table A2), and often contained small rocks. Total soil carbon (TSC) of surface soils (0–10 cm) at the plot level (weighted by percent cover) ranged from 871 to 2237 g C m⁻² across all plots, with a mean of 1396 ± 92 g C m⁻², and did not significantly vary with buffelgrass cover (Fig. 4, Table 1).

The interaction of cover type with site was not significant for either the TSC model ($p = 0.485$; Table 1) or the soil organic carbon (SOC) model ($p = 0.387$), therefore we reported the estimated marginal means across sites (Table 2). Mean TSC under other native vegetation types was significantly higher compared to buffelgrass ($p = 0.0054$) and compared to bare ground ($p = 0.0455$), but bare ground and buffelgrass were not significantly different from each other ($p = 0.6766$; Table 3, Fig. 5). The same pattern was observed for SOC where mean SOC under other native vegetation types was significantly higher compared to buffelgrass ($p = 0.0222$) and compared to bare ground ($p = 0.0374$), but bare ground and buffelgrass were not significantly different from each other ($p = 0.9724$, Fig. 5).

3.6. Ecosystem carbon

Total ecosystem carbon ranged from 1007 to 2435 g C m⁻² across plots (mean = 1602 ± 100 g C m⁻²) and tended to be higher at the LOLA site than the RR site. Overall, total ecosystem carbon increased slightly, but significantly, with increasing buffelgrass cover (Fig. 4, Table 1).

3.7. Path model

The path model was well fit, with measures of fit close to 1, measures of error near zero (Table A5) and low residual covariance (Table A6). Buffelgrass cover had negative direct effects on total soil carbon, species richness, and diversity (Fig. 6). The indirect effect of buffelgrass on species richness through herbaceous carbon was positive (Fig. 6), but the total effect buffelgrass cover on species richness, after accounting for herbaceous carbon, was negative (Fig. 6).

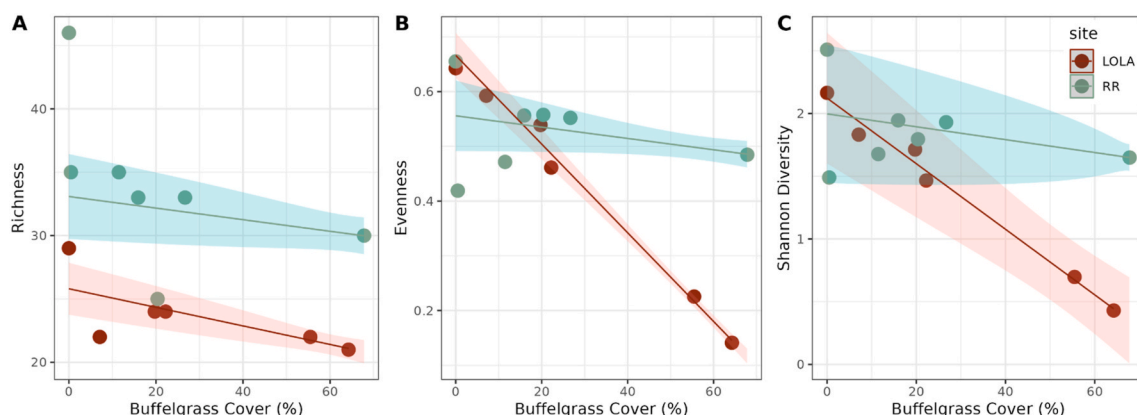


Fig. 2. Buffelgrass cover was negatively correlated with (a) plant species richness, (b) evenness, and (c) Shannon Diversity at both sites.

Table 1

Results from linear models of diversity metrics and carbon storage as a function of buffelgrass cover, site, and their interaction.

Predictor Variable	Estimate	Standard Error	T Value	P-Value	Response Variable
(Intercept)	0.472	0.013	36.782	<0.001	Pielou's Evenness
Buffelgrass Cover	−0.193	0.009	−22.269	<0.001	
Site	0.059	0.025	2.38	0.041	
Buffelgrass Cover x Site	0.168	0.015	10.876	<0.001	
(Intercept)	24.048	0.642	37.47	<0.001	Species Richness
Buffelgrass Cover	−1.741	0.412	−4.226	0.002	
Site	7.94	1.919	4.137	0.003	
Buffelgrass Cover x Site	0.654	1.093	0.598	0.565	
(Intercept)	1.496	0.041	36.269	<0.001	Shannon-Weiner Diversity
Buffelgrass Cover	−0.622	0.029	−21.374	<0.001	
Site	0.378	0.064	5.879	<0.001	
Buffelgrass Cover x Site	0.499	0.039	12.645	<0.001	
(Intercept)	3.289	0.206	15.941	<0.001	Herbaceous C
Buffelgrass Cover	0.045	0.006	7.959	<0.001	
Site	0.978	0.268	3.653	0.005	
Buffelgrass Cover x Site	−0.023	0.008	−2.915	0.017	
(Intercept)	1696.646	37.134	45.689	<0.001	Ecosystem C
Buffelgrass Cover	152.756	45.386	3.366	0.008	
Site	−53.3	322.025	−0.166	0.872	
Buffelgrass Cover x Site	91.717	412.513	0.222	0.829	
(Intercept)	1475.123	61.094	24.145	<0.001	Total Soil C
Buffelgrass Cover	27.709	72.902	0.38	0.713	
Site	−46.486	303.655	−0.153	0.882	
Buffelgrass Cover x Site	99.109	386.37	0.257	0.803	
(Intercept)	84.5	16.914	4.996	0.002	Woody C
Buffelgrass Cover (1st order polynomial)	−114.578	49.945	−2.294	0.055	
Buffelgrass Cover (2nd order polynomial)	−204.705	65.279	−3.136	0.016	
Site	−29.385	22.525	−1.305	0.233	
Buffelgrass Cover (1st order polynomial) x site	80.016	69.953	1.144	0.29	
Buffelgrass Cover (2nd order polynomial) x site	123.625	82.615	1.496	0.178	

4. Discussion

Our analysis shows that buffelgrass invasion is associated with lower native plant species diversity in the Sonoran Desert of Arizona. This is consistent with most previous work in this region (e.g., McDonald and McPherson, 2011; Olsson et al., 2012) and in other buffelgrass-invaded arid ecosystems (e.g., Franks, 2002; Lyons et al., 2013; Tinoco-Ojanguren et al., 2013). In addition to biodiversity

impacts, our results provide the most comprehensive analysis to date of buffelgrass effects on ecosystem carbon storage and suggest that invasion alters carbon storage across different pools. These demonstrated associations underscore the importance of managing buffelgrass invasion to maintain healthy ecosystems and ecosystem services.

4.1. Diversity

Among North American Deserts, the Sonoran Desert is an area of high plant biodiversity, with many endemic species (e.g., saguaro cactus; Dimmitt, 2015). Previous work has demonstrated that buffelgrass may have both positive and negative associations with native species (Smyth et al., 2009). Our results show that buffelgrass had the strongest positive associations with shrubs (Fig. 3, Table A4), which suggests that buffelgrass does not have immediate negative effects on some native shrub species upon invasion, except in cases of active conversion to buffelgrass pasture where native shrub species may be eliminated (Franklin and Molina-Freaner, 2010). Positive associations could also be from shrubs could also be serving as “nurse plants” to buffelgrass, facilitating their initial establishment and growth in a favorable microclimate, an understudied yet likely common process in the harsh environment of the Sonoran Desert (Franklin et al., 2016). However, our study cannot determine the mechanisms or causation behind the positive associations of buffelgrass with native shrub species.

Despite a positive association with some shrubs, buffelgrass had negative associations with the occurrence of many other native plant species. Furthermore, after accounting for all of the direct and indirect effects, the negative effects outweighed the positive effects for a combined effect of buffelgrass cover on species richness that was negative (Fig. 6). Specifically, our results suggest buffelgrass had negative associations with herbaceous annual and perennial natives (Fig. 3, Table A4). The strongest negative association was with common pepperweed (*Lepidium densiflorum*), a forb/herb with an uncertain native/non-native status (Kearney and Peebles, 1960). Other strong negative associations spanned plant functional groups and included the native shrub *Encelia farinosa*, cactus *Opuntia engelmannii*, forb/herb/vine *Janusia gracilis*, and various perennial graminoid species. These negative associations could be from direct competition from buffelgrass, which is able to adjust its growth strategy depending on the water availability and the relative competition with neighboring plants, leading to invasion success (Farrell et al., 2022). Its high water use efficiency may allow buffelgrass to outcompete native species, particularly those that are less drought tolerant (Castellanos et al., 2022; Farrell et al., 2022). Although causation for these associations cannot be established from our gradient-based observational study, previous studies suggest that buffelgrass tends to invade suitable areas, subsequently decreasing native species richness, rather than invading already species-poor communities (McDonald and McPherson, 2011; Olsson et al., 2012).

Furthermore, buffelgrass can reduce the regeneration success of native species by limiting seedling establishment (Tinoco-Ojanguren et al., 2013; Sommers et al., 2022) and additional diversity impacts may become apparent later in some long-lived species (Morales-Romero and Molina-Freaner, 2008). Olsson et al. (2012) found that the age structure of saguaro populations was altered by buffelgrass invasion, with the loss of the younger saguaro cohorts with increasing buffelgrass cover, most likely due to reduced recruitment. While we did not find a significant relationship between buffelgrass cover and saguaro cacti (Fig. 3, Table A4), our study was not designed to detect interactions between long-lived overstory species and understory composition. In order to determine if saguaro regeneration is being hampered by buffelgrass invasion, future studies could include a comparison of the size/age structure of saguaro or other long-lived native species, with the abundance of buffelgrass and the duration of the invasion.

In addition to direct mechanisms related to buffelgrass invasion like competing for water resources and reducing seedling establishment of native competitors, it is also possible that native species are being

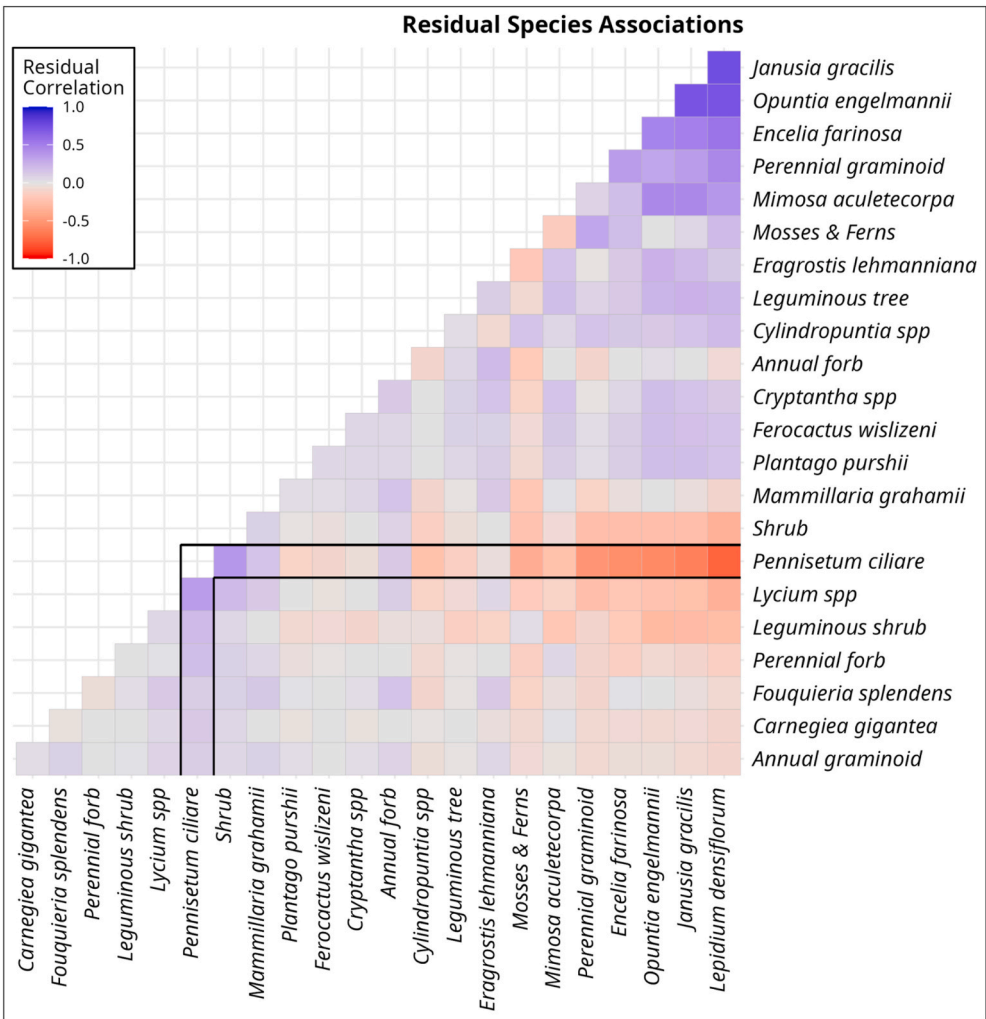


Fig. 3. Residual correlations between species after accounting for environmental filters, as estimated by the joint species distribution model. Visualized with *ggHMSC* (Mahood 2024).

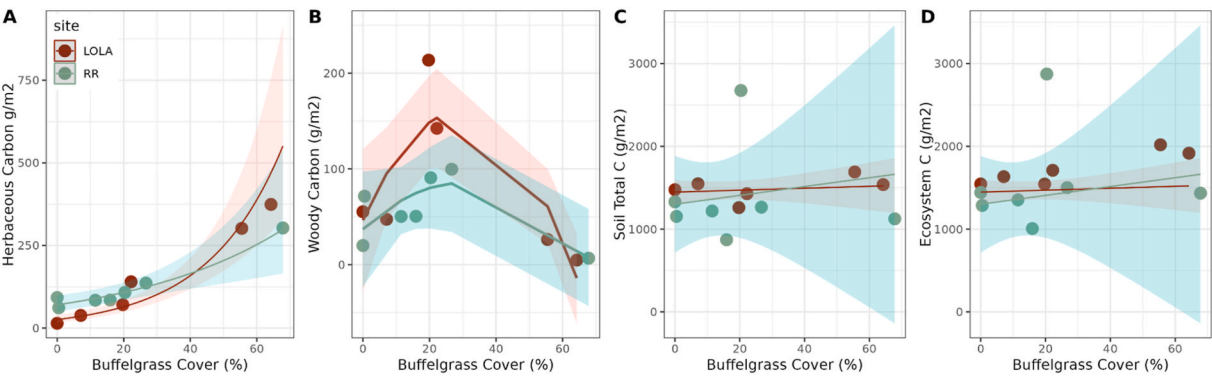


Fig. 4. (A) Total herbaceous biomass carbon significantly increased with buffelgrass cover. (B) Aboveground woody carbon was a small component of the overall carbon pool and buffelgrass cover was a significant predictor in a quadratic polynomial model. (C) There was no significant relationship between total soil carbon and buffelgrass cover. (D) Total ecosystem carbon had a significant positive relationship with buffelgrass cover.

affected by other factors like climate change. Buffelgrass is likely better able to adapt to these changing conditions (i.e., higher tolerance for drought and high temperatures, adaptable growth strategy) than native species (Kornei, 2022), thus buffelgrass may have indirect effects on native diversity. These combined direct and indirect effects are of major concern for conserving native plant species in the face of buffelgrass

invasion, with the suitable climate for buffelgrass expected to expand under climate change (de Albuquerque et al., 2019; Siller-Clavel et al., 2022).

Furthermore, the negative impacts of buffelgrass invasion may take years or even decades to fully manifest. For example, Abella et al., (2012) found that buffelgrass decreased native cover, but not species

Table 2

Estimated marginal means from linear mixed models with site as a random effect. Here SE = Standard Error, df = degrees of freedom, lower.CL = lower confidence limit, upper.CL = upper confidence limit, and var = variable or carbon pool.

Cover Type	Carbon Storage (gC m ⁻²)	SE	df	lower. CL	upper. CL	var
bare	1244.9	102.1	32	1012.5	1530.7	Total soil carbon
buffel	1098.9	102.7	32	868.4	1390.5	Total soil carbon
native	1699.3	139.4	32	1382	2089.3	Total soil carbon
bare	927.6	89.8	32	726.8	1183.9	Soil organic carbon
buffel	879.7	97	32	666.3	1161.4	Soil organic carbon
native	1352.6	131	32	1059.8	1726.2	Soil organic carbon

Table 3

Pairwise comparisons of vegetation cover types' effect on soil organic carbon (SOC) and total soil carbon (TSC). Bold values indicate significant relationships. SE = standard error, df = degrees of freedom, var = variable or carbon pool.

Contrast	Ratio	SE	df	T Ratio	P Value	var
bare/buffel	1.055	0.155	32	0.362	0.931	SOC
bare/native	0.686	0.094	32	-2.757	0.025	SOC
buffel/native	0.65	0.095	32	-2.931	0.017	SOC
bare/buffel	1.133	0.141	32	1.004	0.58	TSC
bare/native	0.733	0.085	32	-2.685	0.03	TSC
buffel/native	0.647	0.08	32	-3.506	0.004	TSC

richness in sites invaded for <10 years. Importantly, buffelgrass has been linked to increased fire occurrence in the Sonoran Desert (Fusco et al., 2019) where fires are historically uncommon. Here, a buffelgrass-fueled fire event could lead to large declines in the abundance of typically slow growing, perennial and woody native plants that are not fire adapted. Although our results suggest a slight positive

association of buffelgrass with saguaro cacti, recent fire events fueled by buffelgrass cover led to mass saguaro mortality (Franklin et al., 2016). Therefore, the benefits of buffelgrass invasion related to species richness might be diminished as the buffelgrass population becomes more dominant over time, particularly if the transition to a buffelgrass-dominated ecosystem is associated with a fire event.

As our results show a negative, linear association between plant diversity metrics and increased buffelgrass cover (Fig. 2), management efforts to reduce buffelgrass cover may benefit native plant biodiversity even when total eradication is not possible. Indeed, efforts to remove buffelgrass have led to increases in native species regeneration and recovery (Lyons et al., 2013; Sommers et al., 2022). Our results show some evidence of biotic resistance to invasion (Enders et al., 2020), where native cover and species richness had a negative effect on buffelgrass cover (Fig. 6). Implementing practices that reduce the impact of invasive species (e.g., treatment and restoration) is critical because on-the-ground efforts are often limited by personnel and funding (Beaury et al., 2020).

4.2. Carbon

4.2.1. Soil carbon

We found the highest surface soil carbon storage (0–10 cm depth) below native plant species, compared to buffelgrass and bare ground, which had similarly low soil carbon storage (Fig. 5). Therefore, losses in surface soil carbon could be expected in locations where buffelgrass replaces native vegetation rather than where it infills on bare ground. However, previous work suggests buffelgrass is particularly adept at colonizing bare ground, or under tree canopies, but not effective at establishing where dense vegetation occurs (McIvor, 2003), which further explains its successful establishment post-fire (Bracamonte et al., 2017). Although herbaceous carbon increased across a gradient of buffelgrass invasion, soil carbon did not; this could simply be due to the time lag that would occur for increased herbaceous biomass (and subsequently litter) to be converted to a measurable increase in the larger soil carbon pool.

Because belowground biomass in dryland systems can extend fairly

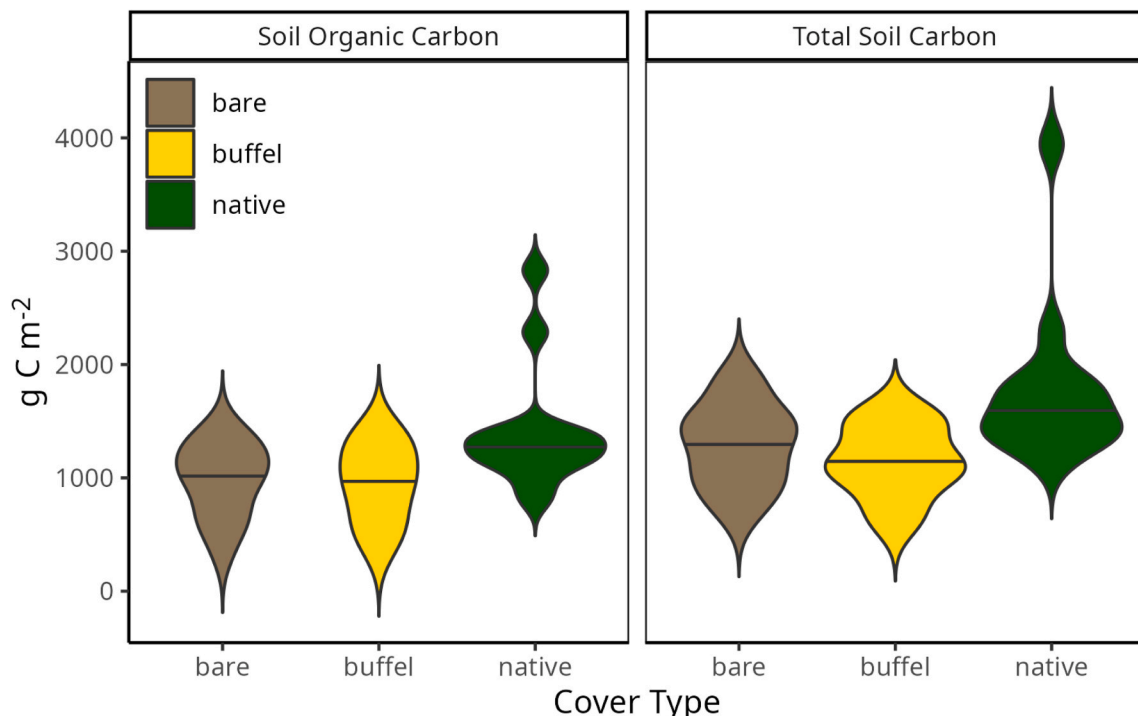


Fig. 5. Soil organic carbon and total soil carbon were both higher under native vegetation than under buffelgrass or bare ground ($p < 0.05$, statistics in Table 3).

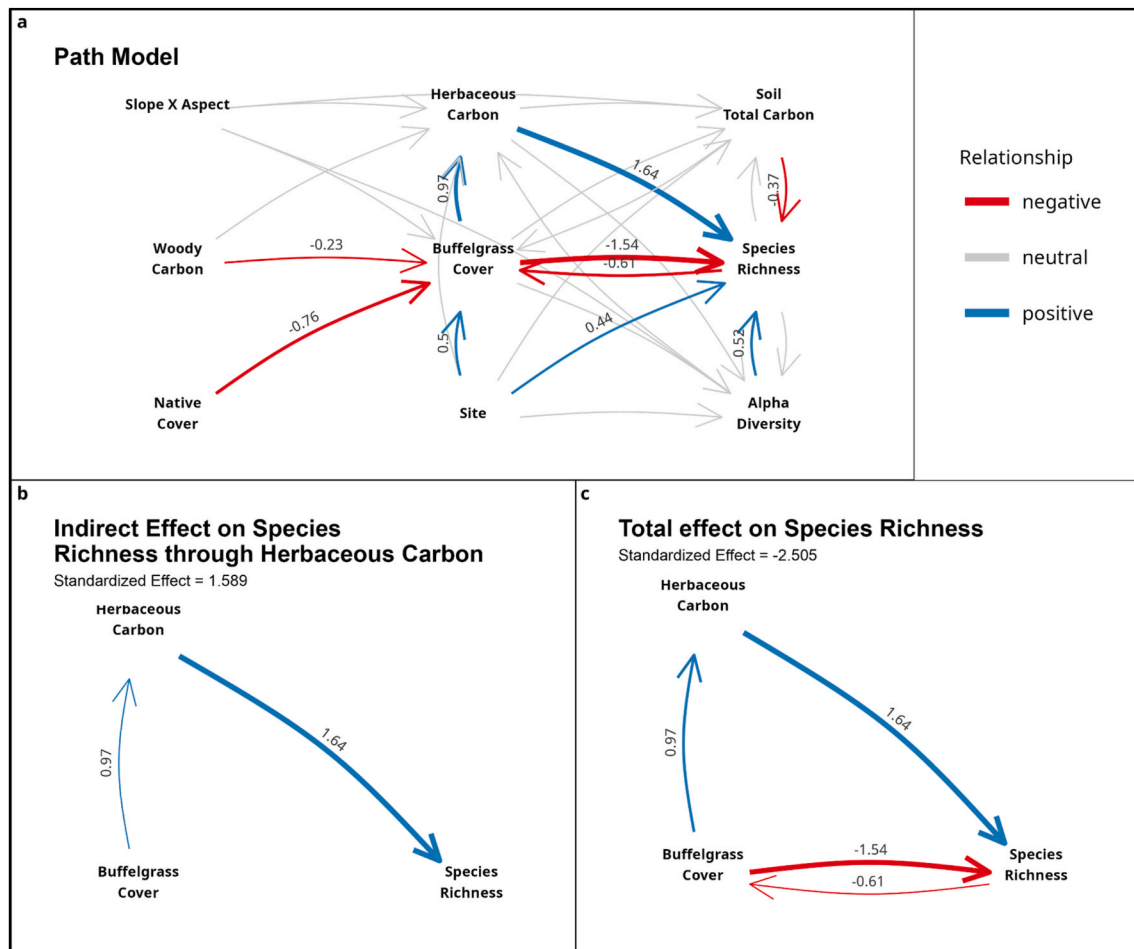


Fig. 6. Path model showing the interconnected relationships between buffelgrass and the rest of the system. Red and blue paths represent relationships that were negative and positive, respectively, and where $p < 0.05$. Width of the arrows corresponds to the effect size as represented by the standardized coefficients. Grey lines were paths that were included in the model but without significantly positive or negative relationships. Buffelgrass had a positive indirect effect on species richness through its influence on herbaceous carbon (left panel), but a negative direct effect. After accounting for all of the direct and indirect effects, the negative effects outweighed the positive effects for a total effect on species richness that was negative. Visualized with *ggsem* (Mahood 2024). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

deep in the soil profile, it is possible that losses in soil carbon could occur if deeply rooted woody vegetation is replaced by buffelgrass. This phenomenon has been observed in other western U.S. ecosystems with cheatgrass invasion (Rau et al., 2011; Nagy et al., 2021; Mahood et al., 2022). However, buffelgrass is also a fairly deep-rooted species, with depths recorded to 2.4 m (Marshall et al., 2012) and thus the organic inputs to the soil carbon pool at greater depths may be similar to those of native species. We suggest that additional work is needed to sample deeper in the soil profile (beyond the top 10 cm sampled here), to include the rooting zone of dominant native species and buffelgrass. However, this is logistically difficult in these arid ecosystems due to the rocky nature of the soils and was not possible for our study.

4.2.2. Aboveground biomass carbon

Our results suggest that woody biomass carbon increases with intermediate levels of buffelgrass cover and decreases at high levels of buffelgrass cover. Buffelgrass may not have an immediate negative relationship with aboveground woody biomass because of its tendency to invade on bare ground (McIvor, 2003; Bracamonte et al., 2017), potentially affecting native woody species through suppressed regeneration (Morales-Romero and Molina-Freaner, 2008), rather than direct competition. However, a mechanism for increased woody biomass carbon at levels of intermediate buffelgrass cover is unclear, and may be a reflection of site history (e.g., time since invasion) or local site

conditions that were not captured in our study design. Our results suggest that at high levels of buffelgrass cover, there is a marked decrease in aboveground woody biomass. Because buffelgrass is also linked with increased fire (Fusco et al., 2019) and native woody species in this ecosystem are not well-adapted to fire, we expect that these declines would be persistent at high levels of invasion, when fire does occur.

Herbaceous biomass carbon increased significantly with increased buffelgrass cover, potentially counteracting losses in woody biomass carbon at high levels of invasion. This is consistent with previous work that documented increased fine fuel loads with buffelgrass invasion (Miller et al., 2010; McDonald and McPherson, 2013). However, due to increased fire risk in buffelgrass invaded ecosystems (Fusco et al., 2019), increases in the herbaceous carbon pool may be short-lived.

It is important to note that unlike herbaceous biomass carbon (where we performed a destructive harvest), our aboveground woody biomass calculations are estimates from field measurements and allometric equations and thus may be less precise. However, it is likely that the relative carbon estimates across sites (i.e., which sites have more or less woody biomass compared to each other) are reliable. Further refinements in allometric equations to quantify aboveground carbon in dryland ecosystems would be beneficial to understand invasion impacts and improve management decisions related to carbon sequestration but may not be possible due to the sensitive nature of these ecosystems. Studies that used integrated satellite-derived measures of aboveground

vegetation (Vega-Puga et al., 2023: total aboveground biomass and Franklin and Molina-Freaner, 2010: NDVI as a proxy for ANPP) found reductions in these aboveground carbon pools and fluxes in buffelgrass-dominated systems compared to native systems.

4.2.3. Ecosystem carbon

The relationship between carbon storage and buffelgrass invasion varied across individual carbon pools, with positive, negative, or no significant correlation across a gradient of buffelgrass cover. However, once these pools were added together, total ecosystem carbon storage showed a slight, but significant increase across an increasing gradient of buffelgrass cover (Table 1). Thus, while surface soil carbon was lower under buffelgrass compared to native vegetation, increases in herbaceous carbon with increasing buffelgrass cover compensated for these differences, in the absence of fire. Eddy-covariance derived estimates of NEP suggested that buffelgrass-dominated systems were usually sinks for C, while native systems could be sinks or sources, depending on the season (Castellanos et al., 2022). To improve carbon accounting in these dryland ecosystems, we need 1) better allometric equations for cacti and woody species coupled with 2) better estimates of soil carbon below 10 cm depth: both of which are logistically difficult to obtain in these ecosystems. Additionally, seasonal sampling of C fluxes, either through field experiments or eddy-covariance techniques, would help refine C dynamics in these dryland systems. Although integration of carbon in management plans is aspirational for many agencies and organizations, it is rarely considered a primary management objective despite being intricately tied to ecosystem health, diversity, and productivity.

4.3. Herbaceous carbon - diversity interactions

The path model suggests that increases in herbaceous carbon may be mitigating losses of plant diversity (Fig. 6). Because higher buffelgrass cover is associated with greater herbaceous carbon (Fig. 4), this appears to contrast the result that buffelgrass cover is negatively associated with plant diversity (Fig. 2). Indeed, herbaceous cover can increase facilitation for native seedlings by providing shade, increased surface soil moisture, protection from herbivory, and greater structural heterogeneity (Niering et al., 1963; Pec and Carlton, 2014). Though our study cannot determine causation, these contrasting results suggest any facilitation process is outweighed by a factor of almost 2-1 (Fig. 2; Table A6), by the direct, negative effects of buffelgrass on species richness (e.g., hindering seedling establishment; Tinoco-Ojanguren et al., 2013; Sommers et al., 2022). In addition, the results from this path model should be interpreted with caution, because the number of variables is high relative to the sample size, which introduces a risk of overfitting. However, given that the main result of the path model—buffelgrass is associated with decreases in native plant diversity—is aligned with both the JSDM and the linear models, we believe it is unlikely to be a spurious result.

5. Conclusion

Perennial and annual plant invasions combined with other global changes (e.g., increasing frequency and intensity of drought and warming), are a major challenge to managing and maintaining healthy dryland ecosystems like the highly diverse and productive Sonoran Desert (Dimmitt, 2015; National Park Service, 2023). Despite the wide ranging benefits of managing invasive species to combat these threats, invasive species managers are often limited by personnel and funding, necessitating that treatment goals and strategies are effectively prioritized. Here we provided information about buffelgrass effects on biodiversity and carbon pools across a gradient of invasion in the Sonoran Desert of Arizona, USA. We observed that high buffelgrass cover was associated with lower alpha diversity and species richness, lower aboveground woody biomass carbon, and higher herbaceous carbon in the absence of fire. Together, this suggests that management

strategies that reduce buffelgrass cover may still have positive ecological impacts even if total eradication cannot be achieved, including increasing biodiversity and carbon storage and reducing the likelihood of high frequency and/or high severity fires. This could also translate to other improvements in ecosystem function not studied here like providing habitat for pollinators and wildlife by protecting or restoring native vegetation. This information can help managers more efficiently prioritize treatments to reach various management objectives. Buffelgrass invasion requires careful management to limit further exclusion of native species and changes to ecosystem carbon storage in dryland ecosystems of the U.S., Mexico, and Australia, where it has become invasive.

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CRediT authorship contribution statement

R. Chelsea Nagy: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Emily J. Fusco:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Adam L. Mahood:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Dylan P. Murphy:** Data curation, Formal analysis, Methodology, Visualization, Writing – review & editing. **Jennifer K. Balch:** Conceptualization, Funding acquisition, Resources, Supervision, Writing – review & editing. **Kimberly Franklin:** Data curation, Methodology, Writing – review & editing. **Bethany A. Bradley:** Conceptualization, Funding acquisition, Investigation, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

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competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendices.

Table A1

Plot characteristics including topography and vegetation cover.

Site	Plot	Mean slope (°)	Mean aspect (°)	Mean elevation (m)	Buffelgrass cover (%)	Other vegetation cover (%)	Bare ground (%)
LOLA	1	18	131	1051	22.22	26.58	51.2
LOLA	2	16	146	1042	7.1	50.2	42.7
LOLA	3	20	146	1040	19.73	25.62	54.65
LOLA	4	22	221	1043	55.47	8.45	36.08
LOLA	5	18	202	1072	64.25	7.71	28.04
LOLA	6	18	215	999	0	45.5	54.5
RR	1	7	158	1170	11.48	39.02	49.5
RR	2	11	143	1150	67.82	14.18	18
RR	3	14	286	1133	0	36.23	63.77
RR	4	20	214	1088	26.68	34.63	38.69
RR	5	15	224	1030	15.93	40.03	44.04
RR	6	11	225	1045	0.47	63.27	36.26
RR	7	17	147	998	20.37	42.38	37.25

Table A2

Soil characteristics under each cover type by site and plot (a) and site means (bulk density only; (b)).

(a)							
Site	Plot	Cover Type	Bulk Density (g cm ⁻³)	% Sand	% Silt	% Clay	Texture Class
RR	1	bare	1.478	77.5	15	7.5	Sandy Loam
RR	1	buffel	0.847	92.5	7.5	0	Sand
RR	1	other	0.895	63.8	23.8	12.5	Sandy Loam
RR	2	bare	0.891	73.8	18.8	7.5	Sandy Loam
RR	2	buffel	0.640	81.3	13.8	5	Loamy Sand
RR	2	other	0.591	76.3	16.3	7.5	Sandy Loam
RR	3	bare	0.498	67.5	22.5	10	Sandy Loam
RR	3	other	0.532	61.3	26.3	12.5	Sandy Loam
RR	4	bare	1.688	67.5	22.5	10	Sandy Loam
RR	4	buffel	0.202	85	7.5	7.5	Loamy Sand
RR	4	other	1.863	68.8	21.3	10	Sandy Loam
RR	5	bare	0.144	66.3	21.3	12.5	Sandy Loam
RR	5	buffel	1.328	68.8	18.8	12.5	Sandy Loam
RR	5	other	1.754	68.8	18.8	12.5	Sandy Loam
RR	6	bare	1.324	72.5	17.5	10	Sandy Loam

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Table A2 (continued)

(a)							
Site	Plot	Cover Type	Bulk Density (g cm ⁻³)	% Sand	% Silt	% Clay	Texture Class
RR	6	other	1.534	68.8	18.8	12.5	Sandy
RR	7	bare	1.601	68.8	21.3	10	Loam
RR	7	buffel	1.207	61.3	23.8	15	Sandy
RR	7	other	1.080	60	25	15	Loam
LOLA	1	bare	n/a	77.5	17.5	5	Sandy
LOLA	1	buffel	0.323	82.5	12.5	5	Loamy Sand
LOLA	1	other	1.632	70	20	10	Loamy Sand
LOLA	2	bare	1.923	75	12.5	12.5	Sandy
LOLA	2	buffel	1.367	75	17.5	7.5	Loam
LOLA	2	other	1.261	77.5	15	7.5	Sandy
LOLA	3	bare	0.270	75	15	10	Loam
LOLA	3	buffel	1.543	72.5	17.5	10	Sandy
LOLA	3	other	1.454	70	17.5	12.5	Loam
LOLA	4	bare	3.448	75	15	10	Sandy
LOLA	4	buffel	1.583	50	37.5	12.5	Loam
LOLA	4	other	1.561	70	20	10	Sandy
LOLA	5	bare	1.653	75	15	10	Loam
LOLA	5	buffel	1.478	72.5	15	12.5	Sandy
LOLA	5	other	1.748	70	17.5	12.5	Loam
LOLA	6	bare	1.775	70	20	10	Sandy
LOLA	6	other	1.431	72.5	12.5	15	Loam
(b)							
Site	Cover		Mean Bulk Density (g/cm ³)				
LOLA	bare		1.814				
LOLA	buffel		1.259				
LOLA	other		1.515				
RR	bare		1.089				
RR	buffel		0.845				
RR	other		1.178				

Table A3Groupings for species (in 1 m² subplots) used for joint species distribution model (Fig. 3).

Species	Group	Prevalence
<i>Centaurea melitensis</i>	annual forb	1
cf <i>Chenopodiaceae</i> sp	annual forb	1
<i>Pectocarya</i> sp	annual forb	1
cf <i>Descurainia sophia</i>	annual forb	2
<i>Cirsium</i> sp	annual forb	2
<i>Erodium cicutarium</i>	annual forb	4
<i>Ipomoea hederacea</i>	annual forb	7
<i>Ambrosia psilostachya</i>	annual forb	8
cf <i>Bromus</i> sp	annual graminoid	1
<i>Vulpia bromoides</i>	annual graminoid	1
<i>Carnegiea gigantea</i>	<i>Carnegiea gigantea</i>	4
<i>Cryptantha</i> sp	<i>Cryptantha</i> spp	1
<i>Cryptantha</i> sp 2	<i>Cryptantha</i> spp	16

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Table A3 (continued)

Species	Group	Prevalence
<i>Cylindropuntia bigelovii</i>	<i>Cylindropuntia</i> spp	2
<i>Cylindropuntia versicolor</i>	<i>Cylindropuntia</i> spp	8
<i>Encelia farinosa</i>	<i>Encelia farinosa</i>	39
<i>Eragrostis lehmanniana</i>	<i>Eragrostis lehmanniana</i>	22
<i>Ferocactus wislizeni</i>	<i>Ferocactus wislizeni</i>	1
<i>Fouquieria splendens</i>	<i>Fouquieria splendens</i>	13
<i>Cottisia gracilis</i>	<i>Janusia gracilis</i>	25
<i>Dalea albiflora</i>	leguminous shrub	2
<i>Calliandra eriophylla</i>	leguminous shrub	7
<i>Acacia</i> sp	leguminous tree	1
<i>Parkinsonia microphylla</i>	leguminous tree	6
<i>Acacia greggii</i>	leguminous tree	7
<i>Prosopis velutina</i>	leguminous tree	10
<i>Lepidium densiflorum</i>	<i>Lepidium densiflorum</i>	33
<i>Lycium</i> sp 2	<i>Lycium</i> spp	2
<i>Lycium</i> sp	<i>Lycium</i> spp	3
<i>Mammillaria grahamii</i>	<i>Mammillaria grahamii</i>	6
<i>Mimosa aculetecorpa</i>	<i>Mimosa aculetecorpa</i>	31
Fern sp	moss fern	1
Moss sp	moss fern	1
Fern sp 2	moss fern	2
<i>Selaginella pilifera</i>	moss fern	13
<i>Opuntia engelmannii</i>	<i>Opuntia engelmannii</i>	14
<i>Pennisetum ciliare</i>	<i>Pennisetum ciliare</i>	50
<i>Artemisia ludoviciana</i>	perennial forb	1
cf <i>Phacelia</i> sp	perennial forb	1
<i>Erigeron</i> sp	perennial forb	1
<i>Phemeranthus aurantiacus</i>	perennial forb	1
<i>Asteraceae</i> sp	perennial forb	2
<i>Eriogonum</i> sp	perennial forb	2
<i>Ipomoea tenuiloba</i>	perennial forb	2
<i>Sida abutilifolia</i>	perennial forb	2
<i>Allionia incarnata</i>	perennial forb	3
<i>Pennellia longifolia</i>	perennial forb	3
<i>Allium</i> sp	perennial forb	4
<i>Jacquemontia pringlei</i>	perennial forb	4
<i>Evolvulus arizonicus</i>	perennial forb	9
<i>Poa</i> sp	perennial graminoid	1
<i>Bouteloua curtipendula</i>	perennial graminoid	3
<i>Bouteloua repens</i>	perennial graminoid	3
<i>Poaceae</i> sp	perennial graminoid	3
<i>Bothriochloa barbinodis</i>	perennial graminoid	4
<i>Hesperostipa neomexicana</i>	perennial graminoid	5
<i>Muhlenbergia porteri</i>	perennial graminoid	9
<i>Plantago purshii</i>	<i>Plantago purshii</i>	10
<i>Abutilon palmeri</i>	shrub	1
<i>Ambrosia deltoidea</i>	shrub	1
<i>Brickellia</i> sp	shrub	1
<i>Gutierrezia sarothrae</i>	shrub	1
<i>Porophyllum gracile</i>	shrub	1
<i>Justicia longii</i>	shrub	3
<i>Trixis californica</i>	shrub	3
<i>Ayenia filiformis</i>	shrub	5
<i>Marina parryi</i>	shrub	5
<i>Jatropha cardiophylla</i>	shrub	6

Table A4

The average strength of the association among each species and all other species (|mean of all residual correlations in Fig. 3|) for the species (and species groups) shown in Fig. 3. Associations of each species with *P. ciliare* are also shown. Prevalence is the number of 1 m² subplots in which each species was encountered.

Species	Prevalence	Average species association strength with all other species	Association with <i>P. ciliare</i>
<i>Lepidium densiflorum</i>	33	0.32	−0.76
<i>Pennisetum ciliare</i>	50	0.31	1
<i>Janusia gracilis</i>	25	0.29	−0.62
<i>Opuntia engelmannii</i>	14	0.28	−0.57
<i>Encelia farinosa</i>	39	0.24	−0.56
Perennial graminoids	25	0.21	−0.51
<i>Mimosa aculetecorpa</i>	31	0.19	−0.24
moss fern	17	0.18	−0.37
Shrubs	24	0.18	0.38
<i>Lycium</i> spp	5	0.17	0.35
<i>Eragrostis lehmanniana</i>	22	0.15	−0.03

(continued on next page)

Table A4 (continued)

Species	Prevalence	Average species association strength with all other species	Association with <i>P. ciliare</i>
Leguminous shrubs	9	0.14	0.21
Leguminous trees	22	0.13	−0.15
<i>Cylindropuntia</i> spp	10	0.13	−0.24
Annual forbs	19	0.12	0.12
<i>Mammillaria grahamii</i>	6	0.12	0.16
<i>Cryptantha</i> spp	17	0.11	−0.05
<i>Plantago purshii</i>	10	0.11	−0.12
<i>Ferocactus wislizeni</i>	1	0.11	−0.09
<i>Fouquieria splendens</i>	13	0.11	0.1
Perennial forbs	24	0.1	0.18
Annual graminoids	2	0.1	0.11
<i>Carnegiea gigantea</i>	4	0.08	0.13

Table A5

Path model measures of fit. Df = degrees of freedom; cfi = comparative fit index; tli = Tucker-Lewis Index; rmsea = Root Mean Square Error of Approximation; srmr = Standardized Root Mean Square Residual.

Measure	Value
df	4
p-value	0.83
Chi-sq	1.46
cfi	1
tli	1.18
rmsea	0
srmr	0.02

Table A6

Residual covariance from the path model. Acceptable measures of fit are indicated when everything is less than 0.1. Variables are defined as follows: herb_C = herbaceous C; soil_TC = total soil C; shannon = Shannon-Wiener diversity index; richness = species richness; PECl_cv = buffelgrass cover; slope_aspect = slope * folded aspect; woody_C = woody biomass C; other_cv = cover of other native species.

Variable	herb C	Soil TC	shannon	richness	PECl cv	Slope * Aspect	Woody C	site	Other cv
herb_C	0	0.002	−0.001	0.003	0	0	−0.03	0	0.016
soil_TC	0.002	0	−0.001	−0.001	0.003	0	−0.069	0	0.018
shannon	−0.001	−0.001	0	−0.002	−0.002	0.001	0.016	−0.001	−0.026
richness	0.003	−0.001	−0.002	0	0.002	0	0.067	0	−0.024
PECl_cv	0	0.003	−0.002	0.002	0	0.001	−0.032	0	0.01
slope_aspect	0	0	0.001	0	0.001	0	0	0	0
woody_C	−0.03	−0.069	0.016	0.067	−0.032	0	0	0	0
site	0	0	−0.001	0	0	0	0	0	0
other_cv	0.016	0.018	−0.026	−0.024	0.01	0	0	0	0

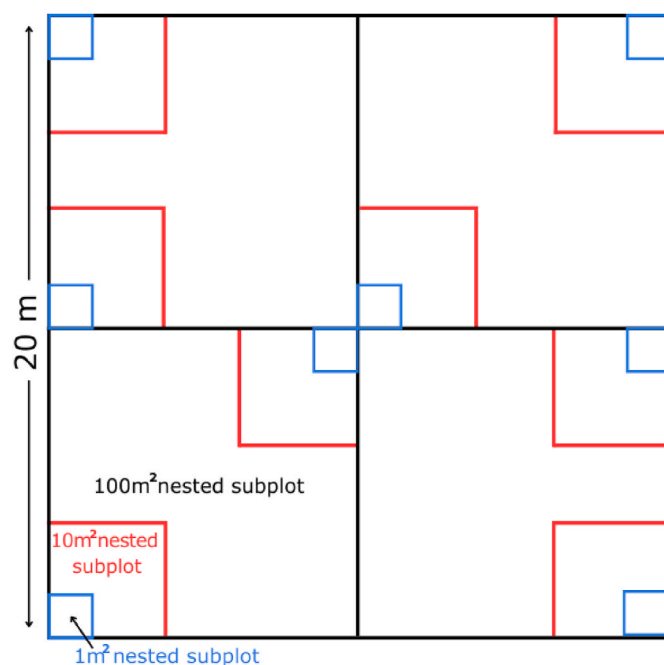


Fig. A1. Nested subplot design for sampling different ecological characteristics (e.g., plant diversity, aboveground biomass).

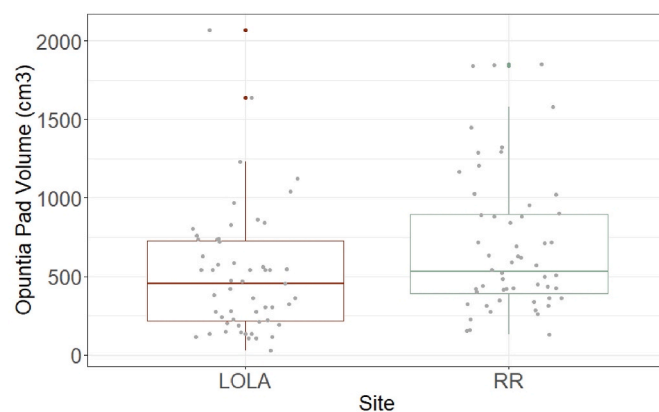


Fig. A2. *Opuntia* pad volume at each of the two sites. These volumes were calculated where pad volume (cm³) = pad length (cm) * pad width (cm) * pad height (cm). The median value was used to calculate total *Opuntia* volume at each plot (i.e., median volume by site multiplied by total pads at each plot).

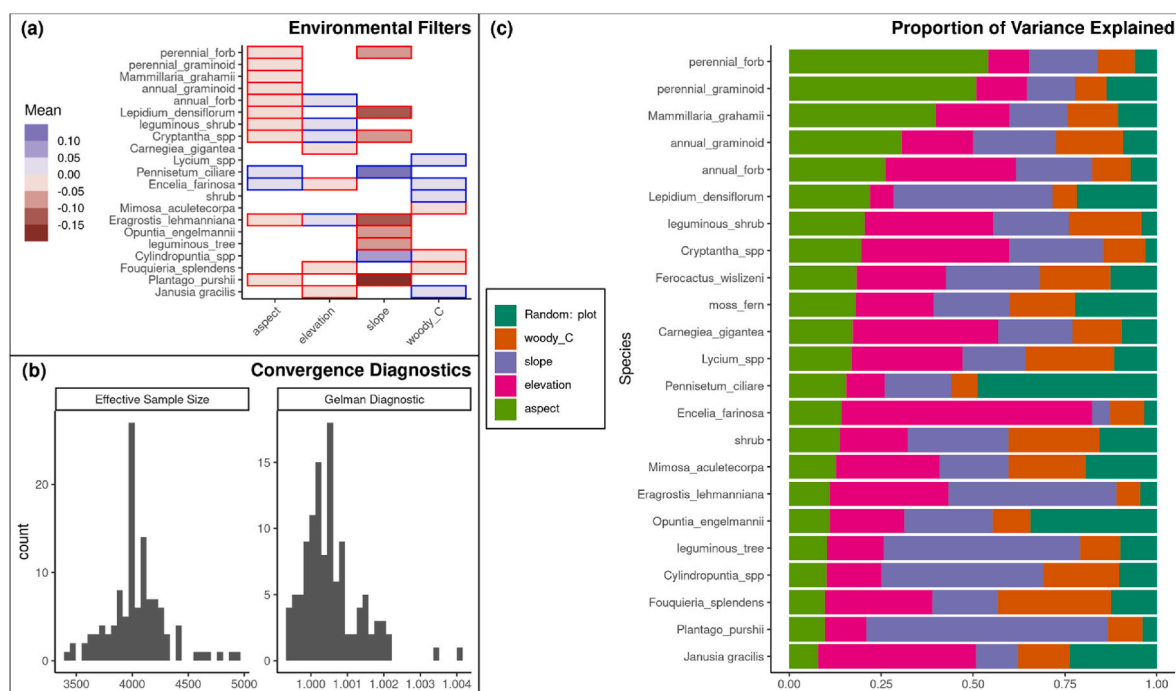


Fig. A3. Joint species distribution model. Panel (a) is the mean effects of the predictor variables on each species. Panel (b) shows good model convergence, with high effective sample sizes and potential scale reduction factors ($\hat{\gamma}$) mostly near 1.0. Panel (c) shows the proportion of variance explained by each predictor variable on each species. Visualized with *gghmsc* (Mahood 2024).

Data availability

All data and code are available at: <https://doi.org/10.5281/zenodo.18487010>.

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