

Grassland type and seasonal effects have a bigger influence on plant diversity than prairie dog disturbances in semi-arid grasslands

Maria Rodriguez-Barrera¹, Ingolf Kühn², Andrés Estrada Castellón³, and Anna Cord⁴

¹Technische Universität Dresden

²Helmholtz Centre for Environmental Research UFZ Research Unit Ecosystems of the Future

³Universidad Autonoma de Nuevo Leon

⁴TU Dresden

January 29, 2022

Abstract

1. Prairie dogs (*Cynomys sp.*) are considered keystone species and ecosystem engineers for their grazing and burrowing activities (summarized here as disturbances). As climate changes and its variability increases, the mechanisms underlying organisms' interactions with their habitat will likely shift. Understanding the mediating role of prairie dog disturbance on vegetation structure, and its interaction with environmental conditions through time, will increase knowledge on the risks and vulnerability of grasslands. 2. Here, we compared how plant taxonomic and functional diversity metrics, along with community-weighted trait means (CWM), respond to prairie dog disturbance across grassland types and seasons in a conservation priority, semi-arid grassland of Northeast Mexico. 3. Our findings suggest that functional metrics and CWM analyses responded to interactions between prairie dog disturbance, grassland type and season, whilst species diversity and cover measures were less sensitive to the role of prairie dog disturbance. Contrary to previous studies, we found weak evidence that prairie dog disturbance has a negative effect on vegetation structure, except for minimal effects on C4 and graminoid cover, which depend mainly on season. Grassland type and season explained most of the effects on plant functional and taxonomic diversity as well as CWM traits. Furthermore, we found that leaf area as well as forb and annual cover increased during the wet season, independent of prairie dog disturbance. 4. Our results provide evidence that prairie dog disturbance is less important than grassland type and that environmental effects have a stronger role than grazing and animal disturbances on vegetation. We argue that a focus on disturbance and grazing effects is misleading, and instead attention is needed on the relationships between vegetation and environmental conditions which will be critical to understand semi-arid grassland dynamics in the region. In addition, explicit management strategies to mitigate climate change would need to consider these relationships

Introduction

Prairie dogs (*Cynomys sp.*) have evolved together with grasslands (Goodwin, 1995; Castellanos et al. 2016; Seersholm et al. 2020) and provide key ecosystem engineering activities which make them valuable for grassland conservation (Davidson, Ponce, Lightfoot et al. 2010; Davidson et al. 2012; Martinez-Estevéz et al. 2013). Their grazing and burrowing activities (from here on summarized as disturbances) directly and indirectly alter habitat structure crucial for other species' presence (Davidson & Lightfoot, 2007; Duchardt et al. 2019), prevent shrub encroachment (Weltzin et al. 1997; Ceballos et al. 2010; Ponce-Guevara et al. 2016), maintain landscape heterogeneity (Bangert and Slobodchikoff, 2000; Davidson and Lightfoot, 2006; Gervin et al. 2019) and increase fodder quality for cattle by reducing leaf age, which increases the plants nitrogen intake (Sierra-Corona et al. 2015). Nevertheless, their disturbances have also been shown

to have negative effects on vegetation structure and characteristics that are prioritized by ranchers, e.g. by reducing biomass and cover of grasses as well as by increasing forb and annual species cover, which reduces fodder quantity (Connell et al. 2019). All this has led to the belief that prairie dogs are degrading grassland vegetation, altering agricultural fields and competing with livestock, resulting in the species being threatened by recreational shooting and poisoning by ranchers and farmers (Miller et al. 2007). Although some conservation measures have been taken to preserve them (e.g. through agri-environmental schemes and the designation of conservation areas), these have not been able to change the socio-ecological views of local communities (Miller, Ceballos & Reading, 1994; SEMARNAT, 2018).

Many grasslands are disturbance-adapted ecosystems (Gibson, 2009), on which small-scale disturbances by herbivorous burrowing mammals have played a fundamental role for vegetation structure (Davidson et al. 2012). As climate changes and its variability increases, the mechanisms underlying organisms' interactions with their habitat will likely shift. Understanding the mediating role of prairie dog disturbance on vegetation structure, and its interaction with environmental conditions through time, will increase knowledge on the risks and vulnerability of grasslands, allowing for nature-based solutions that can be applied to grassland management (Pörtner, 2021). Despite this, it is only recently that studies have started to include interactions between disturbance and multiple environmental conditions like soil, precipitation and temperature (Buzhdygan et al 2020; Jaschke et al. 2020; Ahlborn et al. 2021), and very few have explored the role burrowing herbivorous mammals have on these changes (Coggan et al. 2018).

Plant functional traits, i.e. physiological, phenological and morphological features, mediate between habitat disturbances and ecosystem functions and hence call for exploring trait variations within communities (Mouillot et al. 2013; Hanisch et al. 2020). For instance, plant responses to grazing have shown to directly alter the distribution and variation of specific leaf area (SLA) as well as leaf nitrogen content (van der Plas et al. 2016). However, impacts on these traits would easily be ignored by looking solely into taxonomic diversity, which in most cases is not comparable between communities that are dissimilar or not complementary to each other, making generalization difficult (Chao et al. 2000). Whereas, functional diversity indices summarize species' traits and their abundances via their distribution within the functional space, allowing to explore complementary characteristics between communities (Mouchet et al. 2010). Furthermore, the distribution of trait variations can be captured through environmental filtering (the act of environmental conditions acting as a filter that allow only certain traits to persist; Zobel et al. 1997) allowing for the identification of niche processes (Mason et al. 2005; Villéger et al. 2008; Mouillot et al. 2013). Paired with community-weighted means (CWM), we can analyse community composition and their trait-environment relationships (Funk et al. 2017; Miller et al. 2019).

Here, we focus on traits that have proven useful to identify vegetation responses to grazing, semi-arid habitats and seasonality effects. Namely, specific leaf area (SLA) and vegetative height are proxies for multiple ecosystem functions like biomass production, erosion control, fodder quality, soil fertility, water regulation and competitive ability, and traits such as photosynthetic pathway, life history and growth form relate to temperature, CO² levels, available nutrients, and water efficiency, as well as timing and duration of survival (Moles et al. 2009; Hanisch et al. 2020). Furthermore, the selected traits are key to relate vegetation structure dynamics with ecosystem conditions within semiarid grasslands which have evolved through droughts and disturbance regimes since the Pleistocene, developing high numbers of C4, perennial and shrub species (Gibson, 2009). To the best of our knowledge, no other study has yet examined the functional relationship between different grassland types and the response of vegetation to disturbance by prairie dogs. Furthermore, no study that we know of has analysed how these relationships change over the seasons.

Our aim here was to identify vegetation responses to disturbance by the prairie dog species *Cynomys mexicanus* (endemic to northeastern Mexico) in different grassland types and seasons using taxonomic and functional diversity as well as CWM traits. We assume that functional diversity metrics will be more sensitive and will help to provide an in-depth understanding of the mechanisms or patterns of community changes. Understanding these complex ecosystem interactions will help inform future management and conservation strategies to protect prairie dogs and to maintain vegetation diversity and the essential functions of semi-arid

grassland under future environmental changes. We therefore used the traits mentioned above and calculated plant functional diversity and CWM traits for the prairie dog-dominated grasslands within GPCA El Tokio, to answer the following questions: 1) Is there an effect of prairie dog disturbance on taxonomical and functional plant diversity, and how are CWM traits being filtered? 2) Is the effect constant across different grassland types? 3) Does season influence these effects?

Methods

Study area and species

This study was conducted in the Grassland Priority Conservation Area (GPCA) of El Tokio (Figure 1a) within the Chihuahuan Desert in northeastern Mexico. El Tokio, designated as a GPCA by the Commission for Environmental Cooperation (CEC) in 2009 due to its ecological importance and threatened nature, covers an area of 2.3 million ha and encompasses the Mexican states of Nuevo Leon, San Luis Potosi, Zacatecas and Coahuila. The area consists mostly of natural halophyte and gypsophilous shrublands, with some remaining grasslands covering approximately 35,000 ha. These grasslands are today highly fragmented due to anthropogenic activities related to livestock and agriculture (Estrada-Castillón et al. 2010), but contain the last remaining colonies of *C. mexicanus*, a prairie dog species endemic to Mexico. The climate of El Tokio is semi-arid with mean annual temperatures between 16 and 18 °C, a mean temperature of the driest quarter (January-March) of 13.9 °C and a mean temperature of the wettest quarter (July to September) of 19.5 °C (Baez-Gonzalez et al. 2018). Precipitation ranges from 300 to 600 mm, with an average monthly precipitation of the driest quarter at 14.0 mm (January-March), here considered as the dry season, and an average monthly precipitation of the wettest quarter being 60 mm (July-September), here considered as wet season, (Baez-Gonzalez et al. 2018). Altitude ranges from 1,550 to 1,800 m asl., and the area has at least 5 different soil types, mostly gypsum and xerosol soils with low calcium carbonate content and a loamy-silt texture, followed by loamy-clayey soils and loamy-sandy soils (Pando-Moreno, 2013). The vegetation is mostly dominated by the families Poaceae, Chenopodiaceae and Frankeniaceae (Rzedowski, 2006). The dominant graminoid species are *Muhlenbergia villiflora* var. *villiflora*, *Scleropogon brevifolius* and *Bouteloua dactyloides*. The region is also rich in endemic species such as *Nerisyrenia mexicana*, *Frankenia margaritae*, *Calylophus hartwegii* ssp. *maccartii* and *Gaillardia comosa* (Estrada-Castillón et al. 2010).

Site selection and experimental design

Data-driven identification of grassland types

First, a total of 49 independent grassland locations with active prairie dog colonies within GPCA El Tokio were identified with the use of previous literature (Ceballos et al. 1993; Trevino-Villarreal et al. 1998; Scott-Morales et al. 2004; Estrada-Castillon et al. 2010), up-to-date Google Earth imagery and historical and present delimitations of colonies (provided by the Mexican organizations PROFAUNA and Organizacion Vida Silvestre A.C.-OVIS). In order to select a representative sample of sites covering the varying environmental conditions from these locations, a data-driven clustering approach was used. We used a self-organizing map (SOM), a type of artificial neural network that is trained using competitive learning and well suited to finding clusters within data, as implemented in the package kohonen (Wehrens and Buydens, 2007; R version 4.0, R Development Core Team 2020). Using geospatial data on mean annual precipitation, elevation, slope, soil type and mean annual temperature (see Appendix S1 for the specific data sets used), this analysis clustered all grassland locations into eight groups, four of which occupy most of GPCA El Tokio and are therefore here considered as distinct grassland types (Fig. 1a): 1) Agricultural (Agri): characterized by agricultural land use, xerosol haplic soils, total annual precipitation between 300 to 400 mm and temperature between 14-16 °C; 2) Arid: characterized by solonchak orthic soils, low elevation and total annual precipitation from 200-400 mm; 3) Calcareous (Calc): characterized by xerosol calcic soils, total annual precipitation between 300 to 400 mm, low elevation and temperatures between 14-16 °C and 4) Mountain (Mount): characterized by litosol, high precipitation ranging from 400 to 500 mm, temperature between 14-16 °C and high elevation.

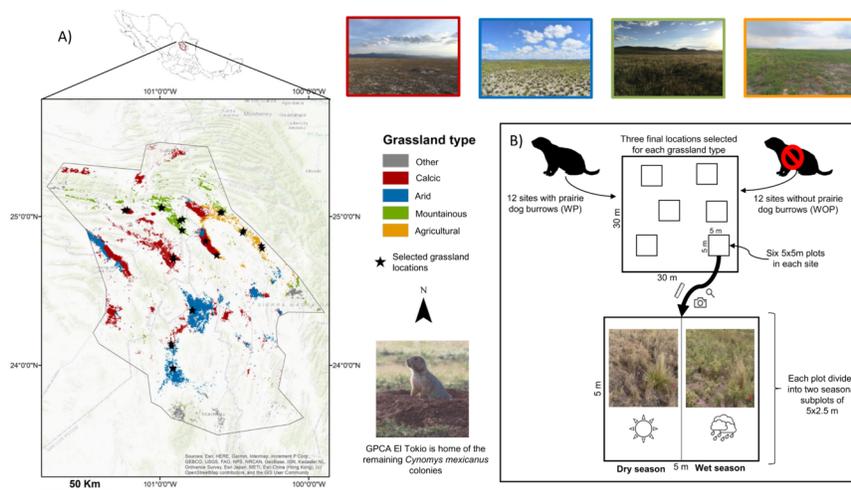


Fig. 1 GPCA El Tokio study site in Mexico (encompasses the states of Nuevo Leon, San Luis Potosi, Zacatecas and Coahuila) and experimental design. (A) Grassland types and selected grassland locations (3 in each grassland type). (B) Experimental design: each grassland location had one site with active prairie dog burrows (WP) and one site without (WOP). A 30x30 m quadrant was delimited in each site with 6 plots each, further divided into two temporal subplots.

Study plots

Out of the 49 independent grassland locations with active prairie dog colonies, three locations were selected for each grassland type, resulting in a total of 12 grassland locations. Locations were selected based on accessibility and spatial distance. We selected locations with at least 5 km separation, due to prairie dogs average dispersal distance (Garret and Franklin, 1988). Preference was also given to locations where community-based conservation projects had already been implemented or are currently implemented by local organizations to ensure feasibility of the study results for future conservation efforts within GPCA El Tokio. Cattle activity was observed at all selected locations and has been documented by Estrada-Castillón et al. (2010), but no detailed information was available on the number of cattle or stocking densities. In each of the 12 grassland locations, we selected two sites differing in prairie dog disturbance (WP = with active prairie dogs burrow section, WOP = without active prairie dog burrows section) and marked a randomly selected 30x30 m quadrat for each condition, considered as site (n=24). All sites were representative of the vegetation and placed congruent to the cardinal directions. WP and WOP sites within the same location had a minimum distance of 1 km, except for sites in one of the mountain locations, where WP and WOP sites were only 300 m apart due to lack of availability of alternative study areas. Within each site, six random 5x5 m plots, aligned along their edges following the cardinal directions, were delimited as well. Randomization was performed by blindly throwing six 60 cm diameter rings to fall at random. The burrow closest to the rings was selected as the center of the WP plots. Whenever the selected site had less than 6 burrows within it, all burrows were selected for plots and the leftover plots were randomly selected and assigned as non-burrow plots. To account for seasonal effects, the 5x5 m plots were further halved to create two 5x2.5 m subplots, which from here on are considered as seasonal subplots. Seasonal subplots were assigned as eastern (rainy season) and western (dry season; Figure 1b) halves. Data collection took place during August-September 2019 (rainy season) and during December 2019-January 2020 (dry season).

Vegetation sampling and trait measurements

We compiled a full list of species, based on the list provided on Estrada-Castillón et al. (2010), for each subplot. Plant cover for each species was estimated using a modified Daubenmire plot and its cover scale method (Daubenmire, 1968) where each species is individually assessed and classified within one of 6 designated cover

classes and assigned a midpoint value: (1) 0-5% = 2.5%; (2) 5-25% = 15%; (3) 25-50% = 37.50; (4) 50-75% = 62.50%; (5) 75-95% = 85%; (6) 95-100% = 97.50%. Daubenmire cover estimates were also compared against species and total cover results of the line-point-intercept method (Herrick et al. 2005) in Agri sites. This method consisted of point readings at every meter of three 30m transects that were 8 meters apart within the site, marked by a measuring tape. Both methods gave very similar results in identifying the site’s cover and species, so the Daubenmire method was selected because it was easier and faster to implement in the field. A total of six traits (Table 1) were selected due to the feasibility to obtain them in the field (Reich, 2014) and their relationship with key grassland functions in vegetation studies (Garnier et al. 2007). Three traits, namely vegetative height, leaf area, and habit, were assessed in the field following the guidelines by Pérez-Harguindeguy et al. (2013), i.e. all measures were taken from at least 5 healthy individuals of each species. Leaf area was measured using the app LeafByte, version 1.3.0. (Getman-Pickering et al. 2020). Due to the COVID-19 virus restrictions in Mexico, the measurement of leaf dry mass was not possible, so leaf area was used instead of SLA. Plant habit was considered as erect or prostrate to further specify the species life form. Traits obtained from the literature were life history, photosynthetic pathway and life form (Table 1). We did not use other traits because it was difficult to find information even for the traits commonly used in plant trait studies (Blumenthal et al. 2020). Many of the plant species in GPCA El Tokio have been poorly studied. We could obtain traits for 63 out of 92 of the species, which together accounted for 96% of the total cover.

Table 1. Selected plant functional traits, and classification levels (if applicable) or values.

| Trait | Measurement units or classes |
|------------------------|-----------------------------------|
| Vegetative height | cm |
| Leaf area | cm ² |
| Life history | annual, perennial |
| Photosynthetic pathway | C3, C4 |
| Life form | forb, graminoid, sub-shrub, shrub |
| Habit | erect, prostrate |

Statistical analyses

Taxonomic diversity metrics

Species richness and cover were averaged across the 6 seasonal subplots in each site. Species evenness was obtained by using the Inverse Simpson index (considered as “simpson”) in the *adiv* package (Pavoine, 2020). The index is as follows: $(1 / \sum j p_{ij}^2) / S_i$, where S_i is the number of species in a community, p_{ij} is the relative abundance of species j in community i . This index was selected due to its high sensitivity to both dominant and rare species with symmetry between them (Smith & Wilson, 1996; Beisel et al. 2003).

Functional diversity metrics

Three functional metrics based on Villéger et al. (2008) and Mouillot et al. (2013) were selected: functional evenness (FEve), functional divergence (FDiv), and functional specialization (FSpe). These metrics were obtained by plotting all traits jointly in functional space and measuring the positions within this space in relation to the species abundances and trait distributions within it. FEve measures the changes in abundance distributions within the functional space based on a Minimum spanning tree (MST). FDiv measures the changes in distance to the mean abundance (center) in relation to species abundances, i.e. if species with high abundance have a greater distance than the overall mean, divergence will be higher. FSpe measures abundance of generalist or specialist species by measuring the mean distance from the rest of the species pool in the functional space (Cornwell et al. 2006; Villéger et al. 2008; Mouillot et al. 2013). Functional richness (FRic) was not selected because it is highly correlated with taxonomic richness (Botta-Dukat & Czúcz, 2016). A fourth metric of functionality, Rao’s quadratic entropy (RaoQ), was obtained with the “FD”

package in R (Laliberté et al. 2015). The index follows the formula:

$$RaoQ = \sum_{I=L}^{S-1} \sum_{J=I+1}^s d_{ij} p_i p_j$$

Where p_i is considered as S -species community characterized by the relative abundance vector $\mathbf{p} = (p_1, p_2, \dots, p_s)$ such that $\sum_{i=1}^S p_i = 1$, and d_{ij} is the difference between the i -th and j -th species ($d_{ij} = d_{ji}$ and $d_{ii} = 0$). RaoQ measures changes in the sum of weighted abundances of pairwise functions between species. It combines the information provided by FRic and FDiv and is suitable for detecting trait convergence and divergence. The higher the measure, the higher the dissimilarity and abundances of traits within the habitat (Botta-Dukat & Czúcz, 2016). To obtain all previously mentioned indices of functional diversity, all numerical variables were standardized to zero mean and unit standard deviation to reduce the relative influence of variables in different orders of magnitude prior to analysis. To examine the overall differences between individual traits, we also obtained CWM using the “FD” package in R (Laliberté et al. 2015).

Data Analysis

To test how grassland types, prairie dog grazing and seasons relate to taxonomic, functional and CWM trait measures, generalized and linear mixed models were fitted. Prairie dog disturbance (WP and WOP), season (wet or dry) and grassland type (Agri, Arid, Mount and Calc) were treated as fixed factors and grassland location as a random factor. We tested for interactions as well, to see if the effects were modified between variables, pointing to relevant ecological processes. Residual graphics were used to examine homoscedasticity. Since FEve, FDiv, Fspe, and evenness range between zero and one, they were analyzed using beta regressions with the glmmTMB package (Brooks et al. 2017). A generalized linear mixed model following a Poisson distribution was fitted for richness using the lme4 package (Bates et al. 2015). All other models were fitted using linear mixed models using the lme4 package. To remove skews, RaoQ, CWMheight, CWMleaf area, C3 cover were log transformed and annual cover, prostrate cover, forb cover, sub-shrub cover were log transformed + 1. F-tests, χ^2 , respectively, and degrees of freedom were obtained using parametric bootstrap with 10,000 iterations for glmm and the Kenward–Roger’s approximation for lmm, respectively, both obtained in the pbkrtest package (Halekoh and Højsgaard, 2014). Beta regression inferences were obtained using Anova tables from the car package (Fox and Weisberg, 2019). We considered all the variables and their interactions to be biologically important and hence included them all in the full model. Best fit models were selected by comparing AICc (Bartoń et al. 2018; Appendix S2, Table S1) and selecting the model with the lowest one. Marginal pseudo- R^2 (R^2_m) values were obtained with the Nakagawa et al. (2017) method available in the performance package (Lüdecke et al. 2020). Once the best fit model was selected, Tukey’s HSD post-hoc test was used to compare levels within variables using the emmeans package (Lenth, 2021). All analyses were conducted using R Version 4.0.3 (R Core Team, 2020). Error probabilities are interpreted as recommended by Muff et al. (2021) with respect to their strength of evidence rather than significance.

Table 2. Results of linear and generalized linear mixed models to test how grassland types, prairie dog grazing and seasons relate to taxonomic, functional and CWM trait measures. Prairie dog disturbance (WP and WOP), season (wet or dry) and grassland type (Agri, Arid, Mount and Calc) were treated as fixed factors and grassland location as a random factor. The table is shown only for final models selected based on Akaike’s Information Criterion (AIC).

Explanatory variables

Diversity measures

Richness

Grassland type

Explanatory variables

Season

Cover

Grassland type

Prairie dog disturbance

Evenness

Grassland type

FSpe

Grassland type

Prairie dog disturbance

Grassland type x Prairie dog disturbance

RaoQ

Prairie dog disturbance

Season

Prairie dog disturbance x Season

Traits

Perennial cover

Grassland type

Erect cover

Grassland type

Prairie dog disturbance

Graminoid cover

Grassland type

Prairie dog disturbance

Season

Prairie dog disturbance x Season

C4 cover

Grassland type

Prairie dog disturbance

Annual cover

Season

Forb cover

Season

CWM Leaf area cover

Prairie dog disturbance

Season

Explanatory variables

The table shows the test type χ^2 and F-test. nDF= numerator degrees of freedom, dDF0= denominator degrees of freedom

Results

Effects on diversity measures

Overall, measures related to species diversity, i.e. richness, evenness and cover were all influenced by grassland type and showed no evidence of interactions. There was strong evidence of season having an effect on species richness. There was only weak evidence of prairie dog disturbance having an effect on cover, but on the other hand there was moderate evidence of prairie dog disturbance having interactive effects on functional diversity measures, specifically on FSpe and RaoQ (Table 2).

There was strong evidence of mountain grasslands having a positive effect on richness and cover, and these were higher than in all other grassland types (Fig. 2a & b). The wet season positively affected richness compared to the dry season (Fig 2d). There was weak evidence of prairie dog disturbance having a negative effect on cover (Fig. 2e). On the other hand, contrary to richness, there was strong evidence of evenness being higher in both agricultural and arid grasslands, compared to mountain grasslands which showed a negative effect (Fig. 2c).

There was no evidence that FEve was influenced by any of the variables nor their treatments or interactions, similar to FDiv which showed no evidence after pairwise post-hoc analysis (Appendix S3, Table S2). The FSpe model revealed strong evidence of grassland type moderating the effect of prairie dog disturbance on FSpe. This effect was particularly important for agricultural grasslands where sites with prairie dogs had a lower FSpe than sites without prairie dog disturbance (Fig 2f). RaoQ showed strong evidence of being influenced by the interaction of prairie dog disturbance and season. Grasslands without prairie dog disturbance (WOP) had higher RaoQ during the dry season compared to the wet season. There was no evidence of differences in RaoQ between seasons for grasslands disturbed by prairie dogs (WP). In the wet season, no evidence was shown regarding differences between conditions of prairie dog disturbance, in contrast to the dry season where RaoQ values varied greatly between conditions (Fig 2g).

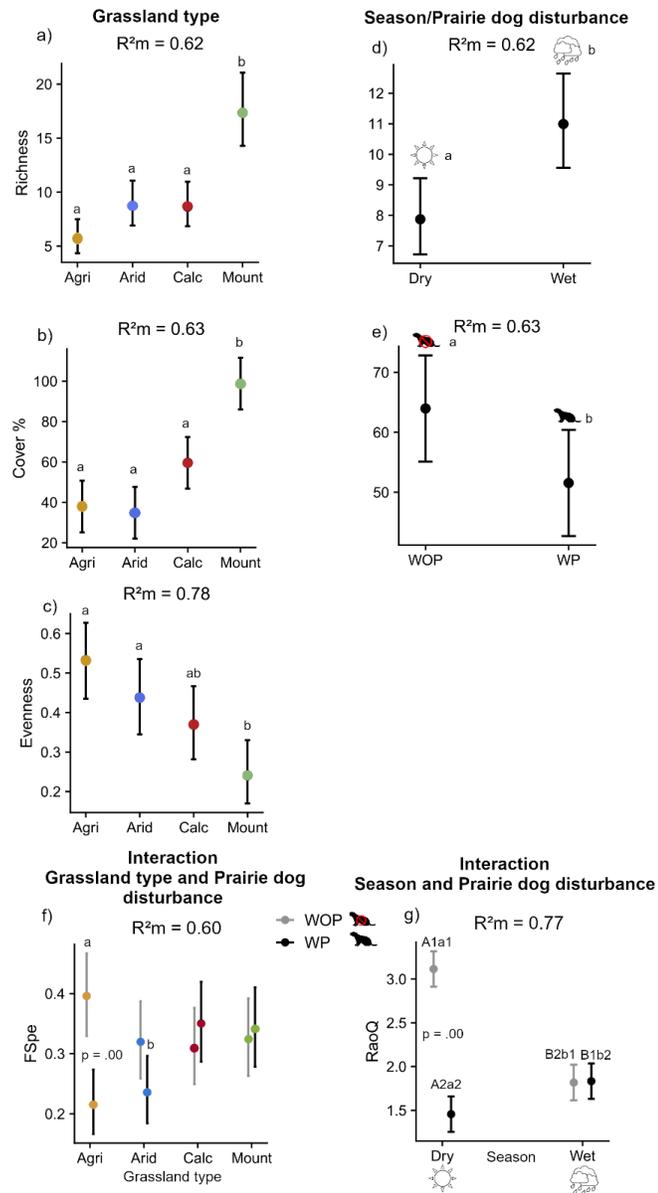


Fig. 2 Comparison of marginal effects on different diversity indices (both taxonomic and functional). The graphs are shown only for models revealing very strong, strong and moderate evidence of effects. For models with no interactions (a-e): Results with $P < 0.05$ are represented by lowercase letters, levels sharing a letter have no evidence of being affected. For models with interactions (f-g): (f) FSpE: Results comparing prairie dog disturbance in the same grassland type are shown with $p < 0.05$, evidence of effects between grassland types are indicated by lowercase letters. (g) RaoQ: Differences between prairie dog disturbance in the same season are shown with $p < 0.05$, evidence of effects between WOP and WP in different seasons is shown with different capital letters that have the same number, evidence of effects between WOP in different seasons is shown with different lower case letters that have the number one, and evidence of effects between WP in different seasons is shown with different lower case letters that have the number two.

Trait filtering effects

Effects of prairie dog disturbance were captured only by C4 cover and graminoid cover, whereby graminoid cover was mediated by an interaction with season and C4 differences were explained by grassland type and prairie dog disturbance but not by an interactive effect. Grassland type had an effect on almost all traits except for annual cover, forb cover and leaf area which were influenced mostly by season (Table 2).

There was strong evidence of higher perennial cover in mountain grasslands compared to arid and agricultural grassland types (Fig 3a). Erect and graminoid cover was higher in mountain grassland compared to all other grassland types (Fig 3b-c). There was weak evidence of prostrate cover being higher in calcic grasslands compared to agricultural sites (Appendix S3, Table S2). Annual cover, forb cover and CWM leaf area revealed strong evidence of increasing during the wet season (Fig 3e-g). There was only weak evidence of C3 species cover having a higher response to the wet season (Appendix S3, Table S2). There was moderate evidence of C4 cover being higher in mountain grassland and compared to agricultural and arid grassland types which had a lower C4 cover (Fig 3d). There was also strong evidence of C4 cover being higher in WOP sites (Fig 3h). There was no evidence of graminoid cover having differences between seasons for WP sites. On the contrary, WOP sites showed contrasting effects between seasons, having almost double graminoid cover during the dry season, revealing moderate evidence of a positive effect compared to the WP sites (Fig 3i). There was no evidence of CWM vegetation height having an effect on any of the grassland types, sites or seasons conditions (Appendix S3, Table S2).

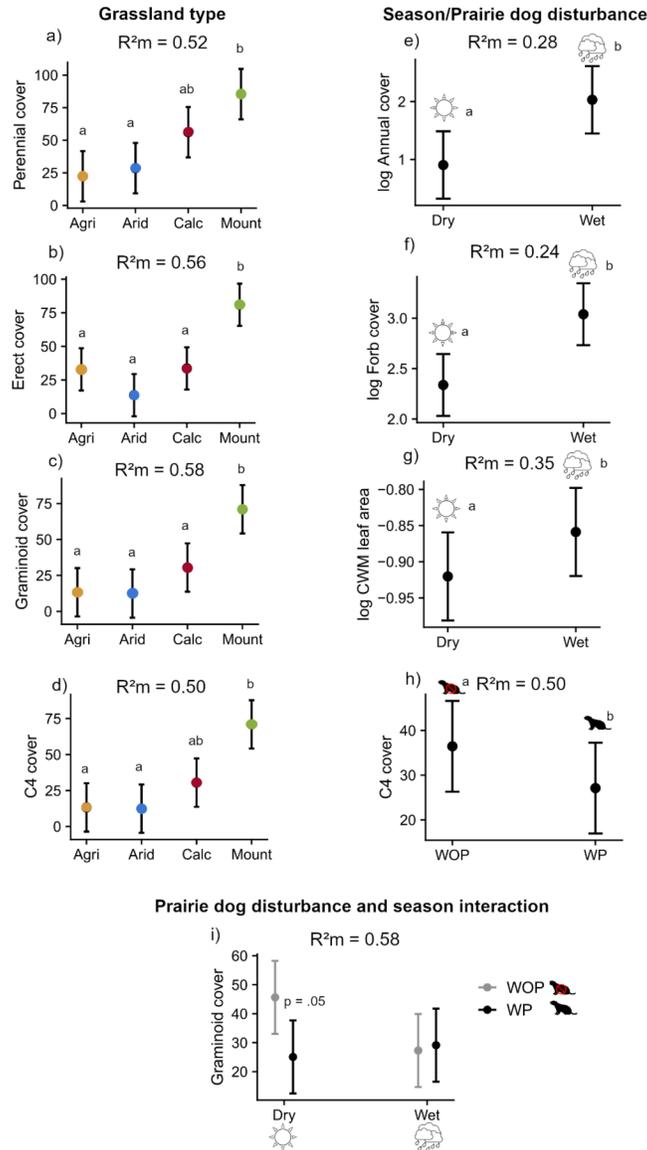


Fig. 3 Comparison of marginal effects on trait filtering model effects. The graphs are shown only for models revealing very strong, strong and moderate evidence of effects. For models with no interactions (a-h): Results with $P < 0.05$ are represented by lowercase letters, levels sharing a letter had weak to no evidence of effects. For models with interactions: (i) Graminoid cover: Results comparing prairie dog disturbance in the same season are shown with $p < 0.05$.

Discussion

Effects of prairie dog disturbance on diversity and CWM means Disturbance by prairie dogs has been shown to affect multiple vegetation parameters (Connell et al. 2019; Duchardt et al. 2021). The main objective of this study was to understand the effects prairie dogs have on the GPCA El Tokio grasslands, using functional and taxonomic diversity measures. Contrary to our expectations, prairie dog disturbance

showed an effect mostly when it was moderated by grassland type or season. In fact, only cover had an independent effect that was slightly higher without prairie dog disturbance. These findings are in contrast to studies stating that prairie dogs have negative effects on cattle due to their disturbance activities, e.g. forage consumption (Vermiere et al. 2004; Derner et al. 2006). Our findings in fact add to the literature of how environmental variables play a stronger role than grazing and animal disturbances on vegetation (Török et al. 2018; Grinath et al. 2019; Jäschke et al. 2020). It is also important to note that there were no independent effects with at least moderate evidence of prairie dog disturbance on the CWM height and leaf area, traits that are usually associated with grazing pressure (Diaz et al. 2007). In fact, CWM leaf area was only dependent on season and there was no evidence that CWM height was affected. We found moderate to weak evidence that prairie dog disturbance did filter C4 cover, which was higher in sites without prairie dog disturbances. This can be explained by the fact that prairie dogs prefer to feed on grasses (Mellado et al. 2005). Most grasses present in the study area are C4, specifically the grasses with highest cover such as *Muhlenbergia villiflora* in almost all grassland types, *Sporobolus cryptandrus* in agricultural grasslands, *Aristida pansa* in calcareous grasslands and *Bouteloua dactyloides* in mountain grasslands, and so a lower cover would be expected. However, it is important to mention that a recent study, covering a period of 72 years (Augustine et al. 2017), showed that some of these C4 species are being outcompeted by C3 species in the long term, and have a larger decline without grazing effects.

In addition, we found that functional diversity, but not species diversity, responded to the joint effects of grassland type and seasonality with prairie dog disturbance, confirming not only the need of including multiple environmental variables and their interactions to identify ecosystem complexity (Dainese et al. 2015), but also the importance of considering functional diversity to further understand the instances of these patterns (Cadotte et al. 2011). Prairie dog disturbance moderated FSpe in agricultural grasslands, possibly explained by the suppression of rapid growing species with extreme traits (eg. *Salsola kali*, *Machaeranthera tanacetifolia*, *Kochia scoparia*) that have higher LA and height and are able to grow and dominate in agricultural grasslands without prairie dog disturbance. These species grow despite the lack of ideal water availability and soil conditions, because they benefit from the gain of resources due to nutrients from fertilization that remain after abandonment (Laliberte et al. 2012). Prairie dogs need short vegetation for predator avoidance (Hoogland, 1995), and their suppressing effect has been shown in previous literature (Ponce-Guevara et al. 2016; Hale et al. 2020). However, since the mechanism behind this suppression is unclear, further studies are needed to determine whether prairie dogs colonize agricultural grasslands before or after rapid-growing species have a chance to grow, or whether other mechanisms are at work (e.g. drought avoidance; Blumenthal et al. 2020). We further found no evidence of positive or negative effects on FEve and FDiv between grassland types, nor between any other of the measured conditions. This indicates that traits were mostly unchanged in their distribution and abundance between communities in the functional space volume. We can assume that the redundancy of traits is most likely increasing due to the restrictive environmental conditions that only well-adapted species can withstand (Villéger et al. 2008, Mouillot et al. 2013). **2) Grassland types as major effect drivers**

We found that grassland types explained most of the effects on plant functional and taxonomic diversity as well as CWM of traits. There was very strong evidence that mountain grasslands were positively affected in almost all measures, usually followed by arid, calcareous and agricultural grasslands, respectively. This can be explained by the tendency of mountain grasslands to have leptosol soils, highly variable slopes as well as higher elevation and lower atmospheric pressure, leading to higher precipitation and lower temperatures (Gommes, 2002; Anjos et al. 2015). These conditions are known to often cause an increase in plant species richness and cover (Speed et al. 2013; Buzhdygan et al. 2020). In addition, Pando-Moreno et al. (2013) found that many of the sites in mountain grasslands within GPCA El Tokio had a lower level of electrical conductivity and absence of gypsum, while sites that fall within calcareous, arid and agricultural grassland types had at least some percentage of gypsum in them. The presence of gypsum most likely acts as a habitat filter for CWM traits, as gypsum soils are known to limit plant life due to their chemical and physical properties which restrict plant growth (Escudero et al. 2015). Calcareous and mountain grasslands have similar filtering effects on perennial and C4 cover; the effect is most likely due to calcareous soils having

lower gypsum levels. Although gypsum soils have been classified as calcareous soils and vice versa in many soil classification systems (Herrero, 2004), they have distinct effects on biodiversity, and it is even possible that a mix of both soil types could lead to higher biodiversity (Meyer et al. 1992; Luzuriaga et al. 2015). Arid grasslands in this study are also dominated by gypsum soils and have higher temperatures which, together with low precipitation, result in higher level of aridity which can act as a strong filter for most CWM traits (Vicente-Serrano et al. 2012; Munson et al. 2013). Similarly, the strong filtering effect of agricultural grasslands is most likely due to the lack of evolutionary history of vegetation, where surrounding landscape factors might play a greater role in species establishment due to continuous land use changes over many years (Gustavsson et al. 2007), paired with the restrictive conditions faced by vegetation on gypsum and calcareous soils (Meyer et al. 1992). Future studies, disentangling the climatic and edaphic effects of these grasslands types are needed to properly understand these patterns (Le Bagousse-Pinguet et al. 2017). On the other hand, the Inverse Simpson evenness showed an opposite result. It was higher for agricultural grasslands, which may be explained by the fact that the index assigns a higher evenness value to communities with an almost equal amount of rare and dominant species (Smith and Wilson, 1996). Hence, the higher the amount of rare species is, the lower is the Inverse Simpson evenness (Magurran, 2004).

3) Seasonal effects

Season independently affected species richness, annual and forb cover, as well as CWM leaf area. Leaf area and other leaf traits are considered to be directly related to the amount of water plants receive, especially in dry habitats (Sack and Holbrook, 2006; Wellstein et al. 2017). Most plants thus have higher leaf area during the wet season. Additionally, multiple studies have shown that annual and forb species strongly respond to increased precipitation levels (Yan et al. 2015; Spence et al. 2016). This is most likely due to their high germination rates and seed innate and water-controlled dormancy, as well as specific dispersal adaptations (Freas & Kemp, 1983; Miranda et al. 2009) which together allow them to grow when the best conditions occur. Our study supports this body of literature and shows that, in fact, prairie dog disturbance has no effect on annual plant species and forb cover (Baker et al. 2012; Perez-Camacho et al. 2012).

Moreover, season modulated the effect of prairie dog disturbance on RaoQ. We found strong evidence that this index was different between prairie dog disturbance conditions during the dry season, where disturbed sites had a lower RaoQ. No difference, however, was found between disturbance conditions during the wet season. This result is consistent with a recent three-year study conducted in northeastern Wyoming (Connell et al. 2019) which showed that overall comparisons of aboveground biomass were not different between sites with and without prairie dogs, but that there was strong evidence of lower aboveground biomass on sites with prairie dogs during years with dry springs, and a reverse effect during wet springs. Furthermore, we found no differences in graminoid cover for sites with prairie dog disturbance between the dry and the wet season. Additionally, there was strong evidence that sites without prairie dog disturbances increased graminoid cover during the dry season. This is most likely due to prairie dogs feeding on graminoids after the wet season, which reduces the grass cover that could remain in the dry season but allows to maintain an overall stable graminoid cover throughout the year (Mellado et al. 2005). However, due to the nature of drylands to have variable precipitation (D'Odorico & Battachan, 2012), further long-term studies are needed to monitor these interactions, especially in light of future climate change projections for the area, which predict an increase in rainfall variability (Baez-Gonzalez et al. 2018). Likewise, although our results show interactions between seasonality and disturbance, these effects only show short-term trends. Sampling multiple years and seasons is necessary to obtain an overall pattern and identify the mechanisms behind it, as so many variables are interdependent and most likely have non-linear effects (Paruolo et al. 2008).

Conclusion To the best of our knowledge, this is the first study to examine the effects of prairie dog disturbance on vegetation using functional diversity indices. Like other research, we support the idea that community trait-based measures are more closely associated with competitive interactions and environmental filtering, compared to taxonomy-based approaches. Additionally, we found that prairie dogs had only a minor negative effect on vegetation cover, even though our study design focused on burrows and surrounding disturbance, favoring stronger differences between conditions with and without active prairie dog colonies.

The effects of prairie dogs on C4 and graminoid cover were particularly demonstrated in the dry season, with the latter negatively affecting functional diversity only in the dry season, while offsetting it in the wet season. Together with these previous results, this study provides further evidence of the large impact environmental conditions have on these grasslands. Tailored management strategies focusing on climate change mitigation would be key to conserving and restoring this threatened, semi-arid ecosystem. As climate change scenarios predict more consecutive dry days and irregular, more intense rainfall (Baez-Gonzalez et al. 2018), this could further aggravate plant cover and functional diversity responses and thus reduce resilience. Hence, longer-term interannual variation studies combining both types of diversity measures should be undertaken. Future studies in GPCA El Tokio can take advantage of the fixed location of prairie dog disturbance, as well as varying environmental conditions within the relatively small area, to assess responses of different grasslands to disturbance and environmental change.

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