Spatial ecology of the Texas kangaroo rat (*Dipodomys elator*)

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Background Information

The Texas kangaroo rat (TKR; *Dipodomys elator*) is a rare and threatened species (Schmidly and Bradley 2016) that today occurs only in the state of Texas (Braun et al. 2021, Stuhler et al. 2023). Because of its small, endemic geographic distribution (Schmidly and Bradley 2016, Wahle et al. 2018) this species is currently being considered for listing under the Endangered Species Act (ESA). However, a better understanding of the ecology of this species, including distribution, abundance, habitat use, and activity patterns, is necessary before an informed decision can be made regarding whether to list *D. elator* under the ESA.

Distribution and abundance

Dipodomys elator has been documented from 11 counties in north-central Texas (Carter et al. 1985; Martin 2002; Schmidly and Bradley 2016) and two counties in southern Oklahoma (Bailey 1905, Baumgardner 1987). Although *D. elator* is conspicuously absent from the fossil record (Dalquest and Schultz 1992), Dalquest and Horner (1984) speculated that the species may have evolved in mesquite grasslands of northern Texas and southern Oklahoma. It has been hypothesized that the short, sparse, grassland habitat used by TKR was maintained by buffalo (*Bos bison*) and/or prairie dogs (*Cynomys ludovicianus*) as well as naturally-occurring wildfires (i.e., 5-6 year intervals; Stangl et al. 1992). Because neither fire nor the above species have significant impacts in these areas presently, systems of moderate to intense grazing pressure and/or shrub removal may need to be implemented to restore and/or maintain suitable habitat (Stangl et al. 1992, Nelson et al. 2009). In addition to habitat conversion (i.e., rangeland to agricultural and urban areas), the encroachment of grasses, forbs, and shrubs into remaining

habitats likely has a strong impact on TKR persistence (Diamond and Shaw 1990, Nelson et al. 2009).

Today, *D. elator* is present in only five counties in Texas (Ott et al. 2019, Stuhler et al. 2023) and is extirpated from Oklahoma (Braun et al. 2021), suggesting population decline. Numerous lines of evidence indicate that TKR distribution is dynamic across its geographic range, that this species likely forms a metapopulation (Halsey et al. 2022), and that better understanding of habitat use and spatial ecology will greatly inform our understanding of distribution and abundance. First, the last five (Martin and Matocha 1972, Jones et al. 1988, Martin 2002, Nelson et al. 2013, Stuhler et al. 2023) comprehensive surveys of TKR have provided substantively different assessments of distribution and abundance. In particular, different hotspots of abundance were found in different portions of its geographic range. Moreover, across many sites, TKR have been encountered only sporadically through time (i.e., present at one time and not at another; e.g., Nelson et al. 2013), suggesting local colonization-extinction dynamics. Our prior (Halsey et al. 2022) and other population genetic assessments of TKR (Pfau et al.2019) suggest at least two subpopulations.

If TKR exhibit substantive distributional dynamics (i.e., colonization-extinction dynamics) within their geographic range, this may have substantive implications for conservation efforts. For example, this suggests that at any one time, much more suitable habitat exists than is utilized. To this end, conservation strategies will need to include more area than simply that occupied by this species during one snapshot in time. Furthermore, the existence of many unoccupied yet suitable sites can bias estimates of differences between suitable and not suitable habitats and assessments of statistical significance of differences between them. Examining

spatial ecology of TKR, and more specifically drivers of persistence of the species across its range, is necessary to better understand distributional dynamics of this species.

Habitat use and activity

There is general agreement that TKR require a sparse, short grassland habitat and firm clay-loam soils (Dalquest and Collier 1964, Roberts and Packard 1973, Stangl et al. 1992, Martin 2002, Goetze et al. 2007), though this type of habitat is becoming less common throughout the present range of the species (Goetze et al. 2007). An association between honey mesquite (*Prosopis glandulosa*) and TKR has also been well documented (e.g., Dalquest and Collier 1964, Roberts and Packard 1973, Carter et al. 1985). More recent investigations, however, have demonstrated that woody vegetation is not essential for TKR burrows, and rather that burrow site selection by this species appears to be based primarily on a disturbance regime and presence of bare ground (Stangl et al. 1992, Martin 2002, Goetze et al. 2007, Stasey et al. 2010). It appears that TKR prefer areas disturbed by grazing, fire, or drought, although it has been observed that TKR will readily excavate burrows on elevated, open areas (e.g., fence rows, decaying brush piles, road berms; Goetze et al. 2007, Nelson et al. 2009, Stasey et al. 2010, Nelson et al. 2011). As such, associated disturbances such as road construction and discarded equipment that accumulate soil are thought to be beneficial (Roberts and Packard 1973, Stangl and Schafer 1990, Stangl et al. 1992, Martin 2002, Goetze et al. 2007, Stasey et al. 2010).

Existing literature suggests that TKR are most active two to three hours after darkness (Carter et al. 1985), although Goetze et al. (2008) observed activity less than an hour after darkness until early morning hours, with no apparent differences in activity levels or foraging behavior. Similarly, TKR were seen foraging during new, crescent, half, and full moon phases,

despite other studies suggesting that *D. elator* is not active during moonlit periods (Dalquest and

Horner 1984, Jones et al. 1988). There is limited documentation of predation of TKR or

knowledge of how predation risk shapes TKR habitat use and activity. Bailey (1905) described a

specimen taken from the throat of a rattlesnake that had partially swallowed a TKR individual

captured in a snap trap. In a study of regurgitated barn owl (*Tyto alba*) pellets from Wichita

County, Stangl et al. (2005) provided the first documentation of predation on *D. elator*, although

determined that its representation as a prey species was lower than expected. The authors

suggested that this may be due to well-developed predator avoidance mechanisms in *D. elator*.

Similarly, Stuhler et al. (2020) did not detect TKR in 590 samples of *C. latrans* scat collected

from Hardeman County over a 15-year period, and therefore could not determine that *C. latrans*

is an important predator of the species.

Characterizing Texas kangaroo rat spatial ecology and dispersal patterns (Tasks 1-2)

INTRODUCTION

The spatial configuration of a landscape affects animal movement and use, with consequences for the ecology and evolution of mobile species (Wiens et al. 1993). Understanding how organisms respond to landscapes via habitat selection and movement patterns, especially across different habitats, is therefore central to conservation and management efforts aimed at maintaining population persistence and connectivity (Morales et al. 2010). For example, characterizing dispersal patterns provides insight into appropriate scales for management as well as habitat features important for maintaining connectivity among habitat patches (Brown and Crone 2016). Only a few studies have described movement patterns of *D. elator*, such as home range size (Roberts and Packard 1973), time spent in locomotion (Stasey 2005), and foraging distances (Goetze et al. 2008). Yet prior home range estimation was based on a limited number of observations from a trapping grid and the latter two studies were anecdotal accounts based on behavioral observations. While these studies have contributed to our understanding of TKR ecology, the advent of GPS technology for animal tracking has dramatically improved our ability to describe animal movement (Kays et al. 2015). Moreover, to date no work has quantified habitat use and/or avoidance across spatial scales or habitat types.

Identifying such differences is important for a number of reasons. First, processes that govern habitat selection vary across landscapes and scales of analysis (Johnson 1980, Thomas and Taylor 2006), such that ignoring scale risks drawing incorrect conclusions regarding habitat use and importance (Wiens et al. 1987). Thus, examinations of habitat-specific responses of organisms should use a multi-scale approach to inform future management strategies based on habitat needs and how a species is utilizing available habitat (e.g., Wright and Frey 2015).

Second, there is measurable and ecologically important variation in vegetation, soil, and climate across the geographic range of *D. elator*, particularly between eastern and western portions due to a precipitation gradient (PRISM Climate Group, Oregon State University). Thus, Texas kangaroo rat habitat selection involves distinct habitat types on either side of its geographic distribution (i.e., more xeric to the west and more mesic to the east). Changes in plant cover, vegetation structure, and species composition affect habitat quality for small mammals by altering both food availability and susceptibility to predation (Brown 1988), causing shifts in movement patterns and habitat use (Orrock et al. 2003, Delciellos et al. 2019). Identifying such differences could be important for predicting long-term consequences of habitat heterogeneity and/or change on TKR persistence across its range.

We planned to characterize TKR spatial ecology and dispersal patterns by placing GPS units on captured individuals to collect data on: 1) home range size and habitat characteristics, 2) movement, space use, and activity patterns, and 3) habitat selection. Base stations (i.e., handheld devices that download data from GPS units in the field) would be deployed to receive location data from collared individuals at user-defined intervals throughout the night in order to characterize individual activity on a nightly basis. Collecting data via GPS units represents an improvement over radiotelemetry (e.g., Jones 1989, Wright and Frey 2015) because it does not require the investigator to track individuals throughout the night, which may influence the animal's behavior. Moreover, because the location data are automatically sent to the base station, it is not necessary to recapture the animals to collect the data, which should reduce the potential for data loss (Kays et al. 2015) and animal stress. We would then use location data generated from the GPS units to calculate home range sizes, analyze patterns of resource selection, evaluate foraging site selection, and characterize local movement patterns.

METHODS

Between July – October 2020 we surveyed for TKR along unpaved county roads across the historical geographic range of the species (Fig. 1). At each site, we deployed Sherman live traps (Sherman Traps, Inc., Tallahassee, FL, USA) every 10 m along a 400 m transect, for a total of 40 trap nights per site. Sites were selected if they 1) had a documented TKR occurrence within the last few decades (see Task 3) or 2) were in nearby areas with suitable habitat.
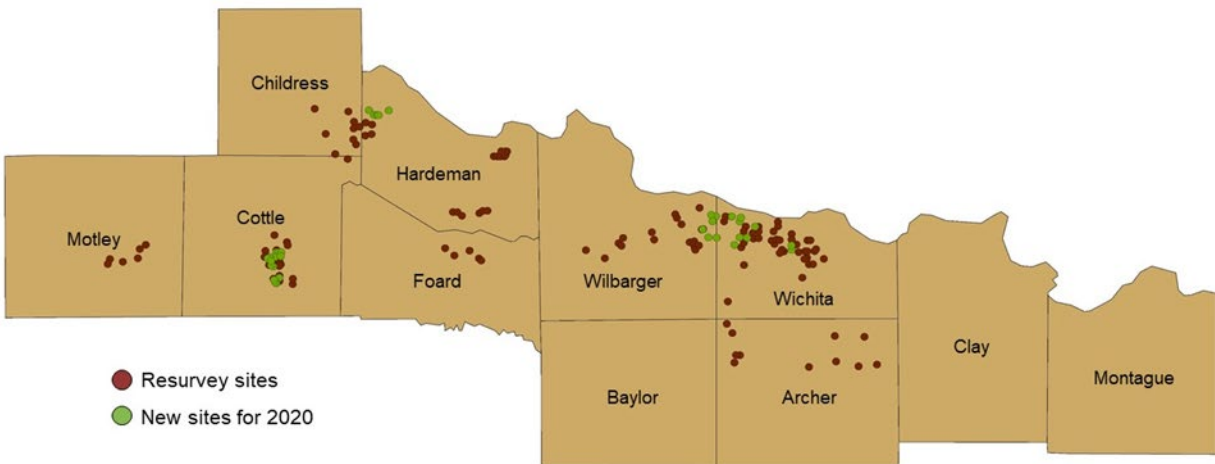

Fig. 1: Locations of trapping sites (i.e., resurveys and new sites) for Summer and Fall 2020. "New sites" refer to sites that had no prior record of TKR but were determined to have suitable habitat at present.

For each captured TKR individual we recorded mass, sex, age, and reproductive condition. We attached a GPS unit (Telemetry Solutions, Concord, CA; mass: ~6 g) to the dorsal surface of individuals greater than 60 g (Sikes et al. 2016) with superglue after trimming a patch of hair. We programmed the GPS units to take readings every 45 minutes between dusk and dawn while utilizing a setting to skip readings when the animal was stationary for a prolonged period (e.g., underground). This setting prolongs the battery life of the unit by skipping attempted location readings when the tagged individual is inactive during the scheduled window. When an individual was successfully fitted with a GPS unit, we returned approximately one week later to deploy a GPS base station (Telemetry Solutions, Concord, CA; Fig. 2) to collect

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data remotely from the GPS unit. We deployed a base station within 50 meters of the capture point, although preliminary testing determined that the base stations could receive location data from units up to 600 m away in this habitat (*Unpublished data*).

Fig. 2: Deployed base station following TKR capture and successful GPS unit attachment.

In addition to live trapping, we performed a nighttime road survey in Cottle County on 18 September 2020 to supplement our trapping efforts and identify areas of TKR presence. The survey began just after sunset and continued for 3 hours throughout the county road network within the proposed US Fish and Wildlife management unit in the county, which is the area southeast of Paducah, TX. No rodents were detected during the survey despite the moon being just 2% illuminated.

RESULTS

Across 6,760 trap nights we captured a total of five TKR individuals at 3 of the 169 (i.e., 2%) survey sites. Three of the five individuals weighed less than 60 g and thus were too small for GPS unit attachment. Of the remaining two individuals, only one had a GPS unit successfully attached to it; however, we were unable to collect location data during subsequent attempts at the capture location. We also captured an additional 387 individuals from 10 species. *Chaetodipus hispidus* (n =137 individuals) and *Peromyscus maniculatus* (n = 101 individuals) were the two most abundant species, together representing over 61% of all captures.

DISCUSSION

Based on these results, the continued difficulty of capturing TKR individuals along roadsides for GPS unit attachment, and the general condition of roadside habitat (i.e., dense grass cover across the region; Fig. 3) during our surveys, we identified a need to adjust our approach to alternative measures of habitat use and spatial ecology (see Task 5).

Fig. 3: Example of roadside conditions during 2020-2021. Near Quanah, TX.

Characterizing metapopulation dynamics of the Texas kangaroo rat (Task 3)

INTRODUCTION

Species often occupy only a portion of potential habitat within their geographic range (MacArthur 1984). Thus, metapopulation dynamics (e.g., patch occupancy, colonization, extinction) arising from habitat heterogeneity and/or dispersal limitation can result in temporally dynamic occurrence of a species across habitats (Hanski and Gilpin 1991). Directly incorporating a metapopulation perspective, in particular colonization-extinction dynamics, when investigating distribution and abundance of threatened and endangered species can improve our understanding of such occurrence patterns (Hanski 1999). More specifically, relating species

persistence to environmental characteristics could help explain past distribution changes and predict future shifts, improve our ability to manage species of conservation interest, and inform the general outlook of its conservation prospects (Beissinger and Westphal 1998, Hanski 1998).

A number of range wide surveys for *D. elator* have been performed over the last four decades (e.g., Martin and Matocha 1972, Jones et al. 1988, Martin 2002, Nelson et al. 2013, Stuhler et al. 2023). Importantly, each survey documented the species within a restricted portion of its distribution, yet these surveys varied with respect to the counties in which *D. elator* was encountered. Similarly, persistence patterns of *D. elator* at the county level have also varied through time (as reviewed in Stuhler et al. 2023). Although these surveys have provided updates as to the distribution of *D. elator*, and despite indications that the distribution is changing (Martin and Matocha 1991, Martin 2002, Nelson et al. 2013), no work has quantitatively evaluated these changes. This is significant because these distribution dynamics suggest that *D. elator* forms a metapopulation (Halsey et al. 2022).

Here, we aimed to relate *D. elator* colonization-extinction dynamics to climate and soil characteristics to better understand metapopulation dynamics of this species. In particular, we compiled a database of historical occurrence records of this species through time and resurveyed these locations to quantify persistence of *D. elator* across its historical geographic range. We then tested whether environmental gradients across these sites could be used to predict persistence patterns of this species across its historical geographic range.

METHODS

We first determined sites by creating a grid of 1-km^2 cells over the 11 counties representing the historical geographic distribution of *D. elator* in Texas. Within this grid we

identified all cells that have been occupied at least once in the past and/or were surveyed for TKR between 2015 – 2018. Selected cells ultimately had records from one or more of the following categories: 1) *Historical* (i.e., historical locations reported in Martin [2002]), 2) *Martin/Nelson* (i.e., surveyed in Martin [2002] and resurveyed by Nelson et al. [2013]), 3) *TTU Presence* (i.e., surveyed between 2015-2018 and TKR encountered), and 4) *TTU Absence* (i.e., surveyed between 2015-2018 and TKR not encountered). Using 1-km^2 cells rather than exact locations mitigates the issue that some exact locations are no longer accessible due to being on private land (e.g., Nelson et al. [2013] resurvey of Martin's [2002] sites).

We resurveyed these sites, as well as additional sites (n = 44) that had not previously been surveyed but were determined to have suitable habitat presently, between July 2020 – August 2021. At each site, we deployed Sherman live traps (Sherman Traps, Inc., Tallahassee, FL, USA) every 10 meters along a 400-meter transect, for a total of 40 trap nights per site. The following morning, we checked all traps and recorded the species of each individual. Voucher specimens were collected and deposited in the Natural Sciences Research Laboratory (NSRL) at the Museum of Texas Tech. Following resurveys, we characterized patterns of site-level extinction, persistence, and colonization.

From this dataset we determined three aspects of colonization-extinction dynamics: 1) colonization events, 2) a measure of persistence and 3) proportional persistence. A colonization event was when *D. elator* was absent from a prior sampling event but present on a subsequent event. Persistence was defined by one of three levels: 1) never at a site, 2) initially present at a site and then absent, and 3) always at the site. Proportional persistence was defined as the proportion of sampling bouts in which *D. elator* was present at a site.
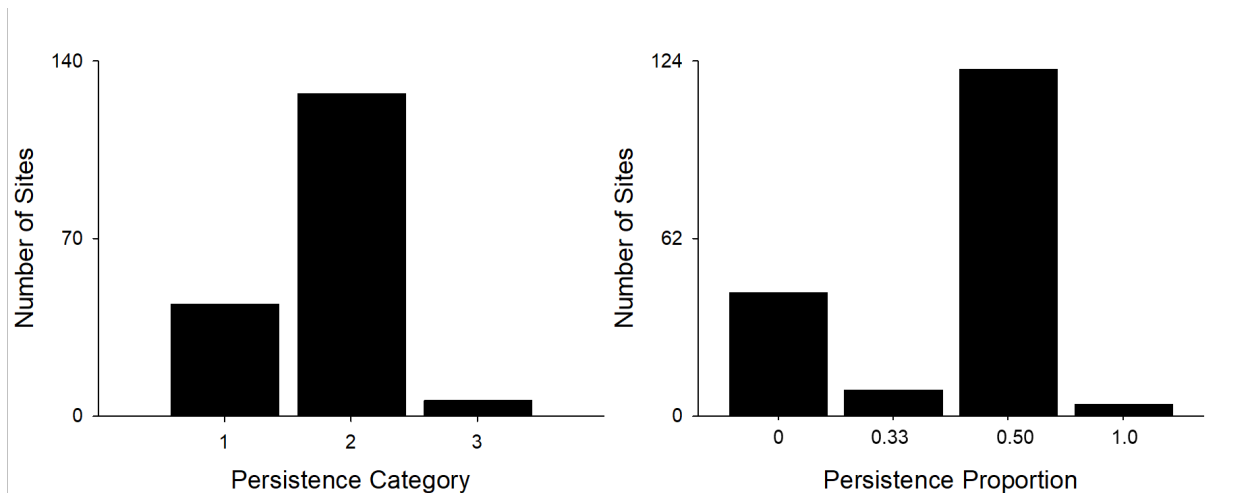
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Figure xx. Frequency of persistence categories (Left) and proportions (right) across 177 sites resampled at least once within the distribution of the Texas kangaroo Rat (D. elator). Categories and proportions are defined in the methods section.

We obtained climate and soil data to characterize the environmental characteristics of each of these sites. We considered 12 climate variables from the WorldClim2 database (Fick and Hijmans 2017). These included annual mean temperature, mean diurnal temperature range, isothermality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual temperature range, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest month, precipitation of the driest month, and precipitation seasonality. Soil data were derived from the NRCS Gridded Soil Survey database (gSSURGO) for Texas (Soil Survey Staff) and included the percent sand, silt, and clay present in the soil. Environmental characteristics were correlated. All variables were log-transformed prior to analyses to normalize the data. We then conducted a principal components analysis (PCA) to create new derived variables that were independent of each other. We used the Kaiser-Gutman stopping rule (Peres-Neto et al. 2005) to determine which PCs to use in inferential analyses.

We used multinomial generalized linear models to determine if colonization-extinction dynamics could be predicted by environmental principal components. Multinomial distributions

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were represented by three categories for persistence and four categories for proportional persistence. Thus, the multinomial generalized linear model determined if different categories were more likely to be found at certain portions of environmental gradients than others. We used a likelihood ratio Chi-square test to determine significance of models containing all significant environmental PCs. If models with all variables were significant, we used Wald Chi-square tests to determine which environmental PCs significantly predicted the position of categories on environmental axes.

RESULTS

During the 2020-2021 resurvey effort and across 233 sites using 9,320 trap nights of effort, we captured a total of 449 individuals from 13 species (Table 1). *Chaetodipus hispidus* was the most abundant species, followed by *Peromyscus maniculatus* and *P. leucopus*, respectively (Table 1). We captured a total of 6 *D. elator* at 4 sites (Table 1). Of these four sites, two sites were new (i.e., surveyed for the first time) whereas two of the sites belonged to the *TTU Presence* category.

We obtained data on 177 sites that were sampled multiple times. Across these 177 sites we never witnessed a colonization event; all dynamics came from local extinctions from one time period to the next. *Dipodomys elator* occurred across all time periods at 6 sites, was never encountered at 44 sites and variably

Species	Individuals	Sites
B. taylori	8	8
C. hispidus	147	76
D. elator	6	4
D. ordii	1	1
N. micropus	1	1
M. musculus	11	9
O. leucogaster	5	4
P. merriami	42	25
P. attwateri	2	1
P. leucopus	69	42
P. maniculatus	113	65
R. fulvescens	2	2
S. hispidus	42	24

Table 1. Summary of capture results from site resurveys between 2020 – 2021.

occupied 127 sites. Overall, proportional persistence across sites where *D. elator* occurred at least once was 0.50.

       Four principal components exhibited eigenvalues that accounted for more variation than the expectation from the Kaiser-Gutman stopping rule. Only PC2 and PC3 were related to characteristics of persistence (see below). PC2 was strongly and positively correlated with mean diurnal range of temperatures (Bio2), maximum temperature in the warmest month (Bio5) and precipitation in the wettest quarter (Bio16) and was strongly negatively correlated with annual range in temperature (Bio7) and mean temperature in the driest quarter (Bio9). This
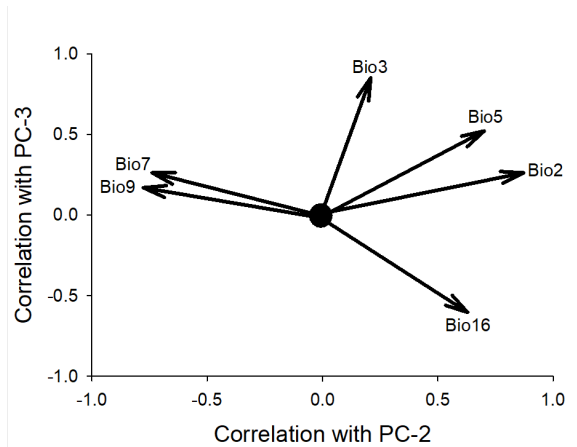
Figure xz. Correlations of the original environmental variables with the second and third principal component. Only those variables with a correlation higher than 0.50 are presented.

environmental gradient is likely one that involves magnitude and variability of temperature, describing sites that are more variable on an annual basis and hotter during the drier portion of the year on the low end and those that are less variable, hotter and wetter on the high end of this axis. PC3 was most highly positively correlated to isothermality (Bio 3) and negatively related to amount of precipitation in the wettest quarter. This axis represents sites that are wetter and less variable in temperature on the low end of the axis and sites that are drier and more variable in temperature on the high end of the axis. Only climatic, and not soil, characteristics were strongly related to environmental PCs.

       Persistence categories could be significantly predicted based on principal components (X^2 = 33.35, df = 4, P < 0.0001). Of the four principal components, PC2 (X^2 = 3.96, df = 1, P = 0.046) and PC3 (X^2 = 21.70, df = 1, P < 0.001) significantly contributed to the overall model.
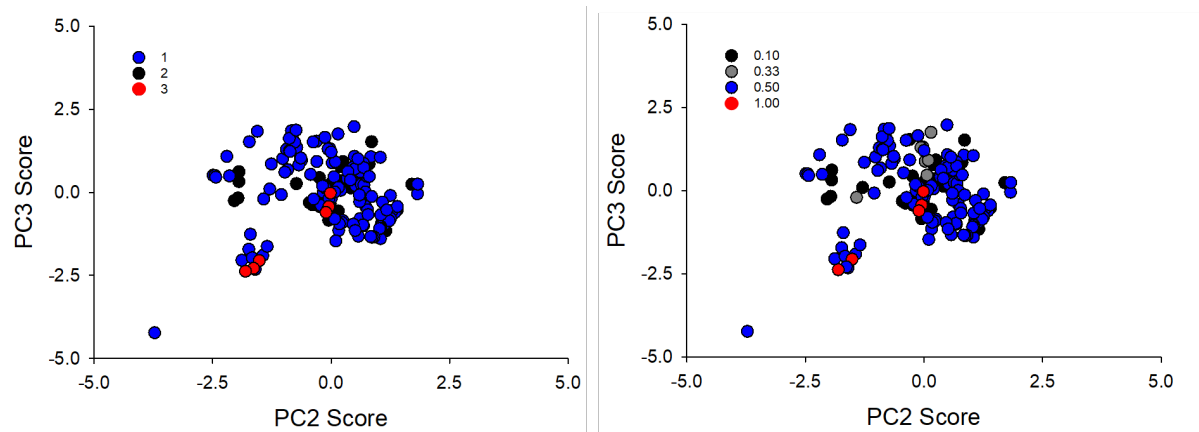
Figure yz. Distribution of persistence categories (Left) and persistence proportions (Right) relative to their positions on the two significant environmental principal components.

There was a similar result for proportional persistence. The overall model was highly significant (X^2 = 38.38, d f= 4, P < 0.001) and PC2 (X^2 = 4.51, d f= 1, P = 0.034) and PC3 (X^2 = 26.21, df = 1, P < 0.0016) were significant contributors,. In general, lower persistence categories and proportions occurred at lower values of PC2 and higher values of PC3 (Figure yz). Lower and intermediate categories were better predicted than the highest category that was always well-nested within the next lower category. Based on comparisons with loadings from the PCA (Fig. xz), the least favorable habitats regarding turnover of Texas kangaroo rats were those with low precipitation and high and variable temperatures. Univariate tests that examined each environmental characteristic separately generally corroborated those based on multivariate PCs.

DISCUSSION

We examined the relationship between *D. elator* colonization-extinction dynamics and environmental characteristics across the historical geographic range of the species to better understand patterns of distribution change over time. We found that 1) the most common resurvey result was that of not encountering TKR at sites where it had previously been

documented (i.e., a site-level extinction event) and 2) TKR persistence was more related to climatic than edaphic characteristics.

Our resurveys of historical TKR sites supported the notion that the species is highly variable in terms of occurrence across its geographic range (Stuhler et al. 2023), given that site-level persistence was low across the region. This agrees with the findings of earlier surveys. For example, Nelson et al. (2013) sought to resurvey TKR occurrence localities documented by Martin (2002) and either did not encounter the species or did not even survey the site if they determined the habitat was no longer suitable. In resurveying all Martin (2002) sites a decade later, we also did not encounter the species. Furthermore, the few sites across the region where *D. elator* did persist were generally characterized as having shorter periods of time between survey efforts (e.g., 4-5 years). Together, this suggests that TKR may persist at sites for short periods of time across its geographic range. An important caveat, however, is that our resurveys and many of those done by Nelson et al. (2013) took place along county roads. Nelson et al. (2013) suggested that, despite not documenting *D. elator* at any of the same sites as Martin (2002), there were large amounts of potential habitat on private land and Goetze et al. (2016) found more frequent use of pastureland by TKR relative to adjacent roadsides in Wichita County. Similar to our findings for Tasks 1-2 (Fig. 3), dense concentrations of introduced grasses along roadsides negatively affect *D. elator* by impeding burrow construction and/or movements. We recommend future research to obtain complimentary estimates of *D. elator* persistence on private land, though we recognize the logistical challenges of such efforts.

Nonetheless, we believe that our findings are relevant for the conservation of this species given that county roads are likely important for dispersal, movement, and foraging of this species (Roberts and Packard 1973) and also remain the best available option for managing this species

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in a range-wide context. Within this context, we suggest that greater attention be given to roadside conditions across the geographic distribution of this species. For example, regular mowing of roadsides in each county could help facilitate movement between interior pastures and unpaved roads, as well as promote greater usage of these areas for burrow construction, dust bathing, and other activities.

In addition to the general finding that *D. elator* does not appear to persist at sites for long periods of time, we also found that persistence was related to climatic characteristics like precipitation and temperature variability. Such findings will likely have implications for the status of the species moving forward. For instance, we found that *D. elator* was more likely to persist at sites with more precipitation and cooler and less variable temperatures. However, future climate projections for the Southern Plains suggest a warming and drying climate with more extreme weather events. Regional temperatures are projected to rise, with up to 30 additional days each year of temperatures above 35˚ C (Kunkel et al. 2013) as well as an overall elevation in minimum temperatures (Shafer et al. 2014). In the Texas High Plains and Rolling Plains, specifically, there are projected increases in both maximum and minimum temperature of 2-3˚ C (Modala et al. 2017). Projected changes in regional precipitation are more complex and less certain, although prolonged periods of high temperatures in the Southern Plains have previously coincided with drought (Hoerling et al. 2014). Thus, a better understanding of the relationship between *D. elator* and environmental change could be an important next step for understanding how to manage the species.

Impacts of a half century of environmental change on taxonomic and functional diversity of rodent communities (Task 3 Addendum)

INTRODUCTION

Biodiversity is declining worldwide at unprecedented rates due to human-induced environmental change (Cardinale et al. 2012, Ceballos et al. 2015). One critical goal for conservation is understanding how organisms are shifting across landscapes. Evidence for species responses to climate change continues to accumulate (Moritz et al. 2008, Tingley et al. 2012, Rowe et al. 2015), as is the understanding that other factors such as availability of suitable land cover could moderate species responses to climate change (Opdam and Wascher 2004, Jarzyna et al. 2016, Northrup et al. 2019). For example, rangeland systems cover approximately 27% of the world's terrestrial surface (Foley et al. 2005, MA 2005) but are experiencing an overall decline in habitat quality and quantity due to changing land management coupled with other global change phenomena (Mitchell 2000, Briggs et al. 2005). As a result, grassland ecosystems are under increasing threat of destruction worldwide (Hoekstra et al. 2005, Tingley et al. 2013) and consequently so are the species relying on those habitats (Jarzyna et al. 2016). Informed and effective conservation of these systems requires an understanding of diversity patterns and how they are changing.

Rodents are dominant mammalian consumers (Kelt et al. 1996) that contribute important community diversity to grassland and shrubland systems globally (Hernández et al. 2005, Yarnell et al. 2007, Cárdenas et al. 2021). Consequently, changes in rodent diversity can affect key ecological processes, plant diversity, and food web structure (Brown and Heske 1990, Meserve et al. 2003, Prugh and Brashares 2012, Maron et al. 2022). Much has been learned from rodents in terms of effects of environmental variation on community organization (Brown 1973,

1975; Kotler and Brown 1988, Ahumada-Hernández et al. 2023). Rodent assemblages can be strong indicators of environmental change because species can track shifts in vegetation, moisture, and temperature (e.g., Lyons 2005, VanBuren and Jarzyna 2022), with responses ultimately manifesting as shifts in occurrence and abundance across the landscape (e.g., Rowe 2007, Rowe and Terry 2014, Cárdenas et al. 2021). Because responses by rodent species to environmental change are likely to be variable, a multifaceted approach may be necessary to identify drivers of community-level responses.

Biodiversity is a multidimensional phenomenon (Magurran and McGill 2011, Stevens and Tello 2014) and there is growing recognition that investigating multiple facets of diversity may improve our ability to infer mechanisms that underlie observed patterns (Violle et al. 2014) while avoiding underestimating community-level responses (Devictor et al. 2010). Spatial variation and temporal changes in biodiversity are traditionally measured with taxonomic diversity (TD) metrics, which are based on the number and abundance of taxa (Dornelas et al. 2014, Newbold et al. 2015). Yet these measures do not consider interspecific variation in ecological functions within a community. A trait-based community-level approach can be powerful for identifying patterns and potential drivers of change (Flynn et al. 2009, Mouillot et al. 2013, Terry and Rowe 2015). Functional traits are measurable properties of organisms, including morphological, physiological, and behavioral features that can be used to quantify the diversity of species niches or functions (McGill et al. 2006, Cadotte et al. 2011). Thus, a functional diversity (FD) perspective describes an assemblage in terms of the evolutionary and ecological characteristics of the species that comprise it. A closer investigation of species traits may improve understanding of changes in community dynamics over space and time (Rowe et al. 2011, Rowe and Terry 2014, Kohli et al. 2021).

Furthermore, an investigation of species traits in a community context could provide important information for the management of rare species. Concomitant responses by species with similar environmental preferences to environmental change would be expected and would indicate a robust signal of faunal response to environmental change as opposed to species-specific idiosyncrasies. This may be especially important for identifying drivers of change in abundance and distribution of rare species, which are likely to have inherently dynamic distributions over time (Hanski 1999; Task 3). In the case of the Texas kangaroo rat, this could provide additional context for its metapopulations dynamics.

Here, we used TD and FD perspectives to characterize trends in rodent diversity in rangeland habitats over the last half century. We combined occurrence records from museum specimens with recent field surveys to create historical and contemporary rodent assemblages. In providing historical accounts of species occurrences, museum specimen records provide insight into previous ecological conditions and how they have changed over time (Grinnell 1910, Shaffer et al. 1998, Malaney and Cook 2018). First, we examined historical and contemporary relationships between species, climate, and land use characteristics. Second, we tested whether different TD or FD metrics have changed over time. We calculated FD metrics by explicitly selecting traits along separate niche axes, including traits mediating responses to climate and habitat change (Supplementary Table 1), to test mechanisms contributing to changes in rodent communities in the region over time.

METHODS

Study area

We studied rodent assemblages within the historical geographic range of the Texas kangaroo rat (*Dipodomys elator*) in Texas (Fig. 1). Like most of Texas, this region experiences two pronounced rainy seasons during the spring and fall (TWDB 2012). At the same time, an important driver of ecological variation across this region is a west-east gradient in average precipitation, in which the westernmost areas receive 51-61 cm/yr and the easternmost areas receive 81-91 cm/yr (PRISM Climate Group 2022). As a result, land in the western portion of this region is primarily shrub/scrub (hereafter "shrubland") habitat, whereas land in the eastern portion is primarily herbaceous grassland (hereafter "grassland") habitat (Figure 1). Cultivated croplands are interspersed throughout the region. As a result of overgrazing and fire suppression, honey mesquite (*Prosopis glandulosa*) and other disturbance-related shrubs, grasses, and forbs have increased in abundance throughout the region (Diamond and Shaw 1990). Average annual temperatures vary less spatially across the region and average around 8-9° C during the winter months and around 23-25° C during the summer months.

Small mammal dataset

We compiled occurrence data for all cricetid and heteromyid rodents that have been documented in the study region. Due in part to the conservation status of *D. elator*, surveys for rodents in this region have been extensive (e.g., Martin and Matocha 1972, Jones et al. 1988, Martin 2002, Nelson et al. 2013, Stuhler et al. 2023). We compiled records between 1960 – 1970 and 2010 – 2020 from VertNet (www.vertnet.org), status reports and published literature (Martin 2002, Nelson et al. 2013, Stuhler et al. 2023), and by visiting the Dalquest Vertebrate

Collections at Midwestern State University. The latter records were then georeferenced using the GEOLocate platform (Rios and Bart 2010) after removing records with imprecise and/or unclear locality descriptions.

Our analyses ultimately considered 18 cricetid and heteromyid rodent species. However, we did not encounter records for *Perognathus flavescens*, *Peromyscus laceianus*, nor *Reithrodontomys megalotis* within our region of interest during the designated time periods. In order to establish ecological communities for each time period, we overlaid a grid of 10 km^2 cells over the region and calculated presence/absence for each rodent based on whether it was documented in a particular grid cell per temporal period. Combining multiple censuses reduces between-sample variability to provide an appropriate representation of the fauna in each time interval (Rowe 2007). Moreover, although potential biases in species-specific capture probabilities may exist (Nichols 1992, Slade and Blair 2000), such biases should likely be constant across space and time, and time-averaging numerous censuses within intervals should also decrease these biases. This ultimately yielded a 151 site × 15 species historical matrix and a 143 site × 14 species contemporary matrix.

Figure 4. Heat map illustrating the spatial distribution of rodent specimen collection efforts during the historical (top) and contemporary (bottom) time periods.
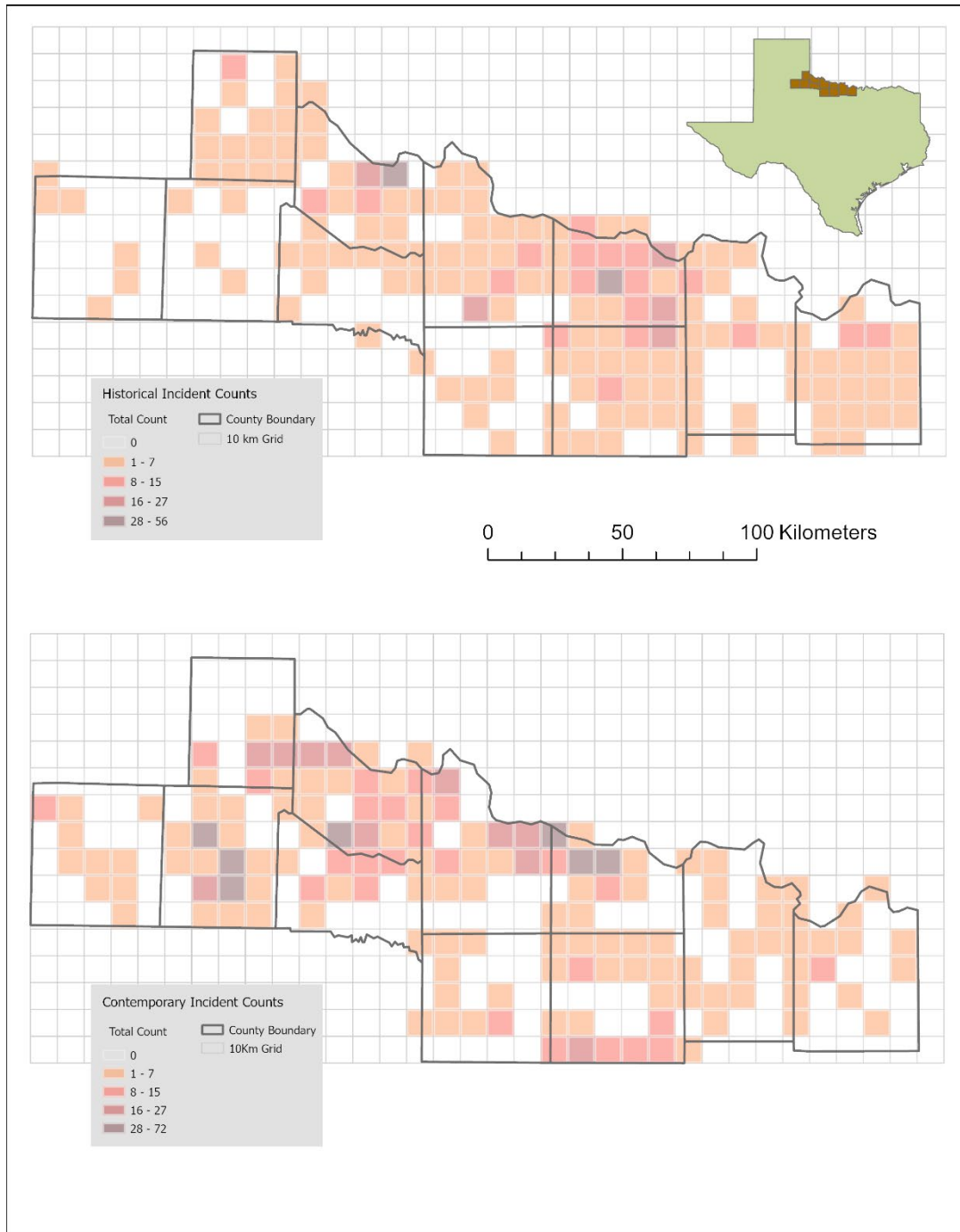
Environmental data

To estimate environmental characteristics of each site we extracted land cover and climate data for each time period. We selected land cover data for 1966 and 2016, respectively. The historical land cover data came from the Modeled Historical Land Use and Land Cover for the Conterminous United States Database (Sohl et al. 2018), which provides estimates of 14 land cover classes at 250 m resolution for each year. The contemporary land cover data came from the National Land Cover Database (Dewitz 2019), which offers estimates of 20 land cover classes at 30 m resolution. To make the land cover datasets comparable, we resampled the contemporary data to the same resolution as the historical data. We also merged the four "Developed" land cover categories from the contemporary data (i.e., "Open Space", "Low Intensity", "Medium Intensity", and "High Intensity") into a single category so that both datasets had 12 matching land cover categories across the sites. For climate data, we obtained average precipitation, average temperature, minimum temperature of the coldest quarter, and maximum temperature of the warmest quarter from the PRISM climate database (PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu). We averaged these data across all years for a given time period (i.e., 1960 – 1970 and 2010 – 2020). Finally, within each 10 km^2 cell we calculated the proportion of land cover categories and the average value of each climate variable.

Trait data

We compiled trait data for 18 traits that we believe broadly encompass how each species interacts with its environment (Supplementary Tables 1-2). Functional trait data were assigned based on available literature (Schmidly and Bradley 2016), existing databases (Jones et al. 2009, Soria et al. 2021), and morphological measurements. Because we were interested in the response

of rodents to environmental change, we organized functional traits under three niche components following the work of Kohli et al. (2021): life history traits, traits mediating response to climate change, and traits mediating response to structural habitat change and associated shifts in the resource base (Supplementary Table 1). Life history traits are related to fitness and can thus influence recovery potential from changes in climate, habitat, and/or the resource base (Lightfoot et al. 2012). We included two life history traits, number of litters per year and average litter size. Climate response traits summarize physiological tolerances of species and have been used previously to relate species distributions to environmental gradients or responses to climate change (Rowe 2007, McCain and King 2014, Kohli and Rowe 2019). We used body size (log_{10}), geographic affinity (north, south, or equivalent), habitat affinity (mesic, xeric, or mixed), daily activity time, and nest location. Geographic affinity corresponds to the location of the majority of the geographic range of a species relative to the median latitude of the study area. Habitat affinity characterized habitat associations of species relative to others based on characteristics such as vegetation cover. Finally, habitat response traits relate to how rodents use and move through a landscape and acquire food resources, and thus reflect responses to habitat or resource base changes (Rosenzweig and Winakur 1969, Kotler and Brown 1988, Kohli and Rowe 2019). We selected locomotor mode (bipedal or quadrupedal), presence of cheek pouches, and eight craniodental measurements (log_{10}) that summarize diet specificity.

The eight linear craniodental measurements are based on previous evidence of their relationship to diet among rodents (Ben-Moshe et al. 2001, Samuels 2009, Martin et al. 2016) and have been used to characterize diet variation among small mammals in the Great Basin (Kohli and Rowe 2019, Kohli et al. 2021). We measured upper incisor width and depth, lower incisor width, upper cheek teeth row length and width, rostrum length and width, and jaw lever

length. Jaw lever length is a measure of mandible robustness and in rodents the point of maximal bite force is the anterior-most point of the second molar (Martin et al. 2016). All measurements were taken at the Natural Science Research Laboratory at the Museum of Texas Tech. We used adult specimens from the 11 counties within the historical range of *D. elator* in Texas, except for *Baiomys taylori* which required specimens to be used from an adjacent county due to limited numbers from the aforementioned study area. We measured five males and five females per species. For all specimens, we measured the right side of the animal unless damage required the left side to be used. All measurements were performed with a digital caliper and repeated three times per individual. The average of these was calculated and used to generate an average value per species for each of the characters.

Diversity metrics

We calculated TD and FD metrics for each site in each time period based on species presence/absence data. For taxonomic diversity, we measured species richness. For functional diversity, we calculated four complimentary metrics: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv; Villéger et al. 2008), and functional dispersion (FDis; Laliberté and Legendre 2010). We calculated functional distance matrices with the R package *FD* (Laliberté et al. 2014) using Gower's dissimilarity to accommodate traits of various types (i.e., binomial, continuous, nominal). We then performed principal coordinates analysis (PCoA) to reduce the dimensionality of the data in traitspace, with the resulting PCoA axes used to calculate functional metrics. Calculating FRic and FDiv relies on finding the minimum convex hull which requires more species than traits (Villéger et al. 2008). Therefore, including sites with very low species richness means only a limited number of PCoA axes can be used in

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computations, resulting in a quantifiable loss of information across the entire dataset. Preliminary analyses found that including sites with three species in the historical dataset (two PCoA axes retained) resulted in FRic and FDiv traitspace qualities around 53%, whereas representation quality improved to roughly 69% when using sites with more than three species (three PCoA axes retained). Thus, we only included sites with four or more species for analyses based on diversity metrics (Historical: n = 45; Contemporary: n = 51). All PCoA axes were always used to estimate FEve and FDis, which are not limited by low species richness.

Statistical analyses

First, we examined relationships between environmental characteristics and individual species for each time period separately. We used canonical correspondence analysis (CCA; Ter Braak 1986), whereby the 16 climate and land use characteristics were independent variables and rodent species incidence across sites were dependent variables. The CCA selects a combination of independent variables that maximally accounts for variation in dependent variables, as well as the amount of variation accounted for by dependent variables and the statistical significance of the result. We conducted CCA in Canoco 5 (Ter Braak and Smilauer 2012) with 999 permutations to determine the significance of relationships. For species-specific analyses, we only included species that occurred at more than 5% of the sites during a given time period, following the recommendation of (McGarigal et al. 2000) for removing rare species. Thus, we excluded *B. taylori*, *N. floridana*, *N. leucodon*, and *R. fulvescens* from the historical analysis and *R. montanus* from the contemporary analysis. *Neotoma floridana* was not encountered during the contemporary period and so was also not included in the analysis.

Second, we tested for differences in taxonomic and functional diversity metrics between the two time periods using two-sample t-tests. We assessed change in functional diversity metrics considering all traits, as well as changes for climate response traits and habitat response traits alone (Supplementary Table 1). Life history traits were not used in isolation because they potentially relate to response under both habitat and climate change and therefore cannot be used to inform on specific mechanisms. Because these analyses considered all functional diversity metrics, it was based on sites from both time periods that had at least four species.

RESULTS

Species-specific patterns

We identified a total of 15 species documented during the historical time period and 14 species documented during the contemporary period (Table 2). *Chaetodipus hispidus*, *Peromyscus leucopus*, *P. maniculatus*, and *Sigmodon hispidus* were the most widely distributed species (i.e., found at the greatest proportion of sites) during both time periods, although the order varied slightly (Table 2). Similarly, *S. hispidus* and *C. hispidus* had the greatest increase in the proportion of sites in which they were present between the historical and contemporary time periods (Table 2). In total, seven species increased in the proportion of sites present, whereas five species decreased (Table 2).

The historical CCA accounted for significant variation among species incidence patterns due to environmental characteristics ($F = 2.3$; $P = 0.001$; Fig. 2). The first two CCA axes accounted for 36.04% and 24.12% of the variation, respectively. *Dipodomys ordii* and *O. leucogaster* exhibited strong associations with barren land and cultivated croplands (Fig. 5). *Reithrodontomys montanus* exhibited a strong association with open water (Fig. 5). *Peromyscus*

attwateri and *P. leucopus* exhibited varying relationships with mixed forest habitat (Fig. 5). The

contemporary CCA also accounted for significant variation among species incidence patterns

due to environmental characteristics ($F = 1.8$; $P = 0.001$; Fig. 5). The first two CCA axes

accounted for 32.07% and 21.86% of the variation, respectively. *Dipodomys elator* exhibited a

strong association with cultivated cropland habitat, whereas *D. ordii* and *O. leucogaster*

exhibited strong associations with barren land (Fig. 5).

Table 2. Site-level incidence patterns for the rodent species documented in the study during 1960 – 1970 and 2010 – 2020. The "Sites" column denotes the number of sites a particular species was present in and the "Proportion" column is the number of sites out of the total number of sites for that time period. "Trend" denotes the change in representation within the overall dataset, with a "−" denoting a change of less than 5%.

|	Historical		Contemporary		Trend
	Sites	Proportion	Sites	Proportion	
Baiomys taylori	3	0.02	21	0.15	↑
Chaetodipus hispidus	48	0.32	90	0.63	↑
Dipodomys elator	29	0.19	11	0.08	↓
Dipodomys ordii	29	0.19	37	0.26	↑
Neotoma floridana	3	0.02	0	0.00	−
Neotoma leucodon	5	0.03	11	0.08	↑
Neotoma micropus	46	0.30	14	0.10	↓
Onychomys leucogaster	18	0.12	17	0.12	−
Perognathus merriami	31	0.21	29	0.20	−
Peromyscus attwateri	25	0.17	10	0.07	↓
Peromyscus leucopus	74	0.49	57	0.40	↓
Peromyscus maniculatus	58	0.38	72	0.50	↑
Reithrodontomys fulvescens	3	0.02	17	0.12	↑
Reithrodontomys montanus	23	0.15	4	0.03	↓
Sigmodon hispidus	42	0.28	88	0.62	↑

Taxonomic and functional diversity

Taxonomic diversity, as measured by species richness, increased over time ($t_{98} = 2.13$, $p = 0.04$). Similarly, when considering all traits, FEve increased significantly over time ($t_{98} = 2.99$, $p = 0.003$), whereas FDis shows a decreasing trend ($t_{98} = -1.60$, $p = 0.11$). FEve measures the

evenness of trait distribution in traitspace, whereas FDis summarizes how distant species are on average from the most generalized functional state of an assemblage. Thus, these results suggest that the functional composition of communities is more equitable under modern conditions and that less-specialized functional types are more favorable relative to others. The overall increase in FEve was driven by increases in both climate ($t_{98} = 2.05$, $p = 0.04$) and habitat ($t_{98} = 3.00$, $p = 0.003$) traitspace. Although there was no difference in overall FRic between time periods ($t_{98} = 1.26$, $p = 0.21$), increases in both climate-related FRic ($t_{98} = 4.35$, $p < 0.001$) and FDis ($t_{98} = 3.07$, $p = 0.002$) suggest shifts in incidence toward species with more specialized climate traits that are more distinct from each other on average.

Table 3. Two-sample t-test results comparing diversity metrics for rodents during contemporary (2010-2020) and historical (1960-1970) time periods. For significant metrics, positive t-values indicate an increase in mean values from historical to contemporary time periods.

Metric	t	df	p-value
Spp. Richness	2.13	98	**0.04**
All traits			
FRic	1.26	98	0.21
FEve	2.99	98	**0.003**
FDis	-1.60	98	0.11
FDiv	-0.49	98	0.63
Climate traits			
FRic	4.35	98	**< 0.001**
FEve	2.05	98	**0.04**
FDis	3.07	98	**0.002**
FDiv	-1.48	98	0.14
Habitat traits			
FRic	1.10	98	0.27
FEve	3.00	98	**0.003**
FDis	-1.60	98	0.11
FDiv	0.15	98	0.89

Figure 5. Canonical correspondence analyses based on rodent presence-absence and 16 environmental characteristics across sites for the historical and contemporary time periods. Individual species are denoted by the first letter of the genus and first three letters of the specific epithet (e.g., *Dipodomys elator* = *D. ela*).
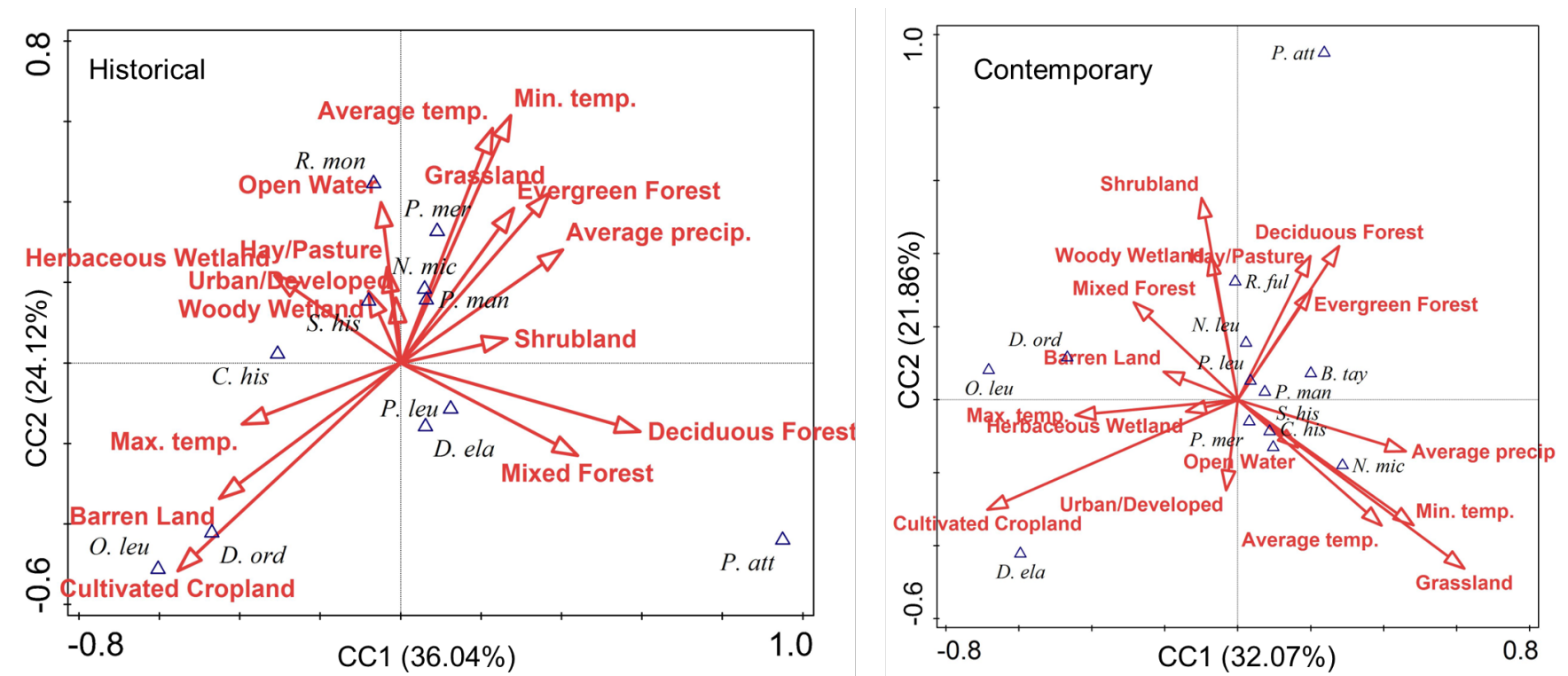
DISCUSSION

Biodiversity is undergoing significant changes due to anthropogenic factors like land cover and climate change (Jarzyna et al. 2015, 2016; Pecl et al. 2017). Understanding responses to environmental change often requires a multifaceted approach (Devictor et al. 2010), including an assessment of TD and FD (Jarzyna and Jetz 2017). We examined relationships among environmental characteristics and rodent species incidence and TD and FD metrics to understand how biodiversity has changed with respect to land cover and climate change over the last half century. We demonstrated 1) variable changes in species incidences and relationships with environmental characteristics and 2) complex diversity changes related to climate and habitat responses. Together, our results demonstrate how trait data can be used to identify causal factors and provide important context for biodiversity change.

Species-specific responses

We documented idiosyncratic changes in species incidence patterns and their relationships with environmental characteristics. The two species with the greatest proportional increase were *C. hispidus* and *S. hispidus* (Table 3), and both species exhibited a relationship with grassland habitat in the contemporary period (Fig. 2). *Sigmodon hispidus* in particular is associated with grass-dominated habitats (Cameron and Spencer 1981). It is believed that the increase of infrastructure like highway rights-of-way has likely provided large tracts of vegetation cover and consequently suitable habitat for dispersal for *S. hispidus* and other mesic species like *B. taylori* (Schmidly and Bradley 2016). Goetze et al. (2016) documented significantly more invasive grass cover (e.g., *Bromus catharticus*, *B. japonicus*, and *Sorghum halepense*) along county roads than in adjacent pasturelands. Even though *C. hispidus* has a xeric

habitat association, it is often found in dry grassland habitat with scattered to moderate stands of herbaceous vegetation (Blair 1954, Paulson 1988, Schmidly and Bradley 2016). Thus, among heteromyid rodents in this region *C. hispidus* may be the most suited to habitats with more vegetation cover, supported by the fact that both *D. elator* and *D. ordii* had strong associations with barren land and/or cultivated croplands (Fig. 2). At the same time, *C. hispidus* can be found in a broader range of soil types (Blair 1937, Paulson 1988, Schmidly and Bradley 2016) than *D. elator* (Roberts and Packard 1973, Carter et al. 1985) and *D. ordii* (Maxwell and Brown 1968, Garrison and Best 1990), and therefore may be more of a generalist in its use of various grassland habitats.

Such findings also have implications for *D. elator*, which is typically found in sparse, short grassland habitat (Roberts and Packard 1973, Stangl et al. 1992, Nelson et al. 2009). The same habitat conditions that may promote incidence of *S. hispidus* could lead to unsuitable habitat conditions for *D. elator*. This species likely uses roadsides and pasture margins as movement and/or dispersal corridors (Roberts and Packard 1973, Stangl et al. 1992). Thus, increasing vegetation cover could have consequences for *D. elator* dispersal which, like other kangaroo rats, is likely to be more dispersal-limited than other rodent species (e.g., Price et al. 1994). This could also explain in part the contemporary association between *D. elator* and cultivated croplands (Fig. 2), as this type of land cover is more likely to maintain open habitat and burrowing locations, particularly along roadsides. Other xeric-adapted species, such as *D. ordii* and *O. leucogaster*, have tracked any potential changes in environmental conditions by maintaining an association with barren lands (Fig. 2).

Taxonomic and functional diversity

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We detected subtle but complex changes in traitspace across rodent communities over the last half-century. First, we identified a significant overall increase in FEve that was driven by increases in both climate- and habitat-related FEve, although the increase was greater for habitat response traits (Table 4). This suggests that widespread species in modern traitspace are less functionally redundant. However, there was a trend towards decreasing FDis among habitat response traits (Table 4), suggesting a decrease in the mean distance of all species to the weighted centroid of communities in trait space (Laliberté and Legendre 2010). This suggests that species are less functionally redundant but over a smaller range of variation, signaling a movement toward functional homogenization and could be due to increasing habitat homogenization across the region (e.g., increasing shrub encroachment and spread of non-native grasses; Nelson et al. 2009, Goetze et al. 2016).

At the same time, in addition to the increase in climate-related FEve, we also detected increases in climate-related FRic and FDis, but no such changes in overall or habitat-related metrics (Table 4). Together, this indicates that rodent communities are responding more strongly to climate filters than habitat filters. In particular, increases in climate-related FRic and FDis suggest that climate response traits are more dispersed and more diverse across rodent communities in the modern time period relative to the historical time period. Future climate projections for this region suggest a warming and drying climate (Kunkel et al. 2013, Modala et al. 2017), with prolonged periods of high temperatures in the region typically coinciding with drought (Hoerling et al. 2014). Thus, these functional changes could be due to increasingly variable climate conditions in the region.

Functional trait ecology

We demonstrated how functional traits can be useful for identifying subtle changes in community-level diversity patterns. In particular, we supplemented patterns of change in species incidence with insight into the complex changes in diversity patterns related to climate and land use. Given the apparent influence of climate-related traits in functional diversity change in this region (Table 4), the inclusion of additional climate response traits could provide further insight into how rodent species are responding to climate change within the region. In addition to the eight craniodental measures used here, Kohli and Rowe (2019) also demonstrated that traits like hair density and relative medullary thickness of the kidney can be used to characterize species adaptations to aridity. Similarly, exploring the utility of novel trait measures, both for climate as well as habitat responses, would be valuable for identifying subtle changes in community diversity that may occur prior to more pronounced changes in metrics like species richness or abundance.

Shareable data on the research project and Texas kangaroo rats (Task 4)

We are presently drafting an article for the Texas Wildlife Association's magazine *Texas Wildlife*. This monthly publication covers a range of wildlife topics of interest to Texans and others with a stake in wildlife management or species conservation. The proposed article will cover our work related to Task 5 and will include images from our camera traps and preliminary findings. Second, our research and general information about *D. elator* was featured in an article written by an undergraduate student at Texas Tech University for online publication on "The Hub", which is a student media environment designed to highlight efforts of the university

community. Finally, are looking into options to disseminate results from this research at a Texas Parks and Wildlife Diversity Webinar, as well as at national meetings.

Patch use, foraging behavior, and daily activity patterns of the Texas kangaroo rat (Task 5)

INTRODUCTION

Patch use, resource acquisition, and timing of activity are all fundamental to organismal fitness and can have important implications for the distribution and abundance of populations (Williams et al. 2017). Understanding how environmental variation shapes activity patterns, such as foraging decisions, may be particularly important amid anthropogenic activities that are leading to rapid changes in habitats around the world. For example, there is evidence that temperature influences timing of activity of animals and that future climate change may shift seasonal activity patterns with negative effects on individual fitness (Schweiger and Frey 2021). Moreover, habitat characteristics can play a fundamental role in shaping antipredator behavior (Guiden et al. 2019) by altering the likelihood of encounter between predators and prey and the ability of prey to detect and escape predators (Lima and Dill 1990, Sheriff et al. 2020). Thus, changes in plant cover, vegetation structure, and species composition affect habitat quality by altering both food availability and susceptibility to predation (Brown 1988), causing shifts in habitat use (Orrock et al. 2003). Because animals forage under multiple constraints (Brown and Kotler 2004), contending with energetic costs, missed opportunity costs, and predation risk (Brown 1988), identifying characteristics that influence habitat use can be important for informing predictions about species susceptibility to environmental change, with implications for developing relevant conservation management strategies.

Characterizing habitat use and the factors that influence it could be of particular importance for the Texas kangaroo rat. There is general agreement that the species requires a sparse, short grassland habitat (Dalquest and Collier 1964, Roberts and Packard 1973, Stangl et al. 1992, Nelson et al. 2009, 2011). However, fire suppression, decreased grazing, and the loss of historical ecological processes have led to increased abundances of shrubs, grasses, and forbs that likely reduce Texas kangaroo rat habitat quality (Stangl et al. 1992; Goetze et al. 2007, 2015; Nelson et al. 2009, 2011; Holt 2018). Ongoing work indicates that the range-wide distribution of *D. elator* is becoming increasingly restricted over time (Stuhler and Stevens *In prep*). Understanding how the species utilizes habitat at smaller scales (e.g., foraging patches) would provide information to predict how it may be responding to site-level habitat changes like shrub or invasive grass encroachment, thus providing additional context about conservation status. Furthermore, as described in the *Background Information* section at the beginning of the report, there is still uncertainty regarding its antipredator behavior and primary predators (Carter et al. 1985, Stangl et al. 2005, Stuhler et al. 2020) as well as its activity patterns (Carter et al. 1985, Jones et al. 1988, Goetze et al. 2008).

We used giving-up densities (GUD; Brown 1988) to study Texas kangaroo rat foraging behavior and patch use. The amount of food remaining in an artificial food patch after a foraging bout (i.e., GUD) reveals how a forager assesses the costs and benefits of remaining in a patch (Brown and Kotler 2004). Thus, it is possible to quantify foraging tradeoffs by using patches with the same properties (e.g., food density, substrate volume) while manipulating foraging costs (e.g., e.g., Brown 1988, Bouskila 1995, Orrock and Danielson 2009, Hinkleman et al. 2012). Differences in GUD among these patches can therefore be attributed to differences in associated costs. For example, among trays where metabolic costs of foraging are similar (e.g., trays on the

same night that experience the same temperature), reduced foraging when predation risk is increased (e.g., open versus covered microhabitats, new moon versus full moon) should be reflected in higher giving-up densities. If trays are identical in predation risk and missed-opportunity costs, increased giving-up densities on nights with cold temperatures suggest that the energetic cost of foraging is higher, thus increasing the marginal value of energy on those nights.

We examined Texas kangaroo rat foraging behavior, patch use, and activity patterns with foraging trays and motion-activated cameras to evaluate how these characteristics were affected by microhabitat, lunar illumination, and thermal costs related to seasonality. We then incorporated a shrub removal experiment to determine how a potential management strategy influenced Texas kangaroo rat patch use. Such an experimental design allowed us to assess whether *D. elator* perceives differences in habitat quality between mesquite-dominated habitat patches relative to those that are more open. Testing for differences in habitat use would enable us to 1) better understand the degree to which *D. elator* is sensitive to shrub encroachment and 2) determine whether mechanical shrub thinning is a viable habitat management strategy to improve habitat quality for the species. Finally, we deployed motion-activated cameras at each site outside of foraging trial events to document site-level activity of mammalian fauna. In doing so, our aim was to contribute important information about the natural history of this species as well as inform habitat-based conservation management strategies for this species moving forward.

METHODS

Study sites

This study was performed at a private ranch in Wichita County, Texas. Sections of this study area have been used extensively for prior TKR research (e.g., Stangl et al. 1992; Goetze et

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al. 2007, 2008; Nelson et al. 2009). The dominant woody vegetation across the study area was honey mesquite (*Prosopis glandulosa*). Soils in this area have been predominantly categorized as clay loam (i.e., Kamay and Asa-Portales soils; Goetze et al. 2007). We initially established 8 sites (see below) during Summer 2021 and added an additional 7 sites in a second pasture during Winter 2022 that differs in recent grazing history: Pasture A has been lightly grazed (i.e., 15.5 acres per unit) continuously for the last five years, whereas Pasture B has not been grazed for over five years. Finally, we added two more sites to Pasture A during Summer 2022, for a total of 17 sites across the study area (Pasture A: 10 sites, Pasture B: 7 sites).

Quantifying TKR foraging behavior

We used foraging trays to quantify giving-up densities to assess foraging behavior and habitat use by *D. elator*. Texas kangaroo rat foraging was assessed over four periods spanning two years: 6 – 13 and 21 – 28 July 2021, 28 January – 4 February and 14 – 21 February 2022, 29 May – 14 June 2022, and 18 October – 3 November 2022. Each session included 12 total nights of data collection; trays were unavailable on nights with rain for logistical reasons. Because rodent foraging can be sensitive to changes in moon illumination (Brown and Kotler 2004, Orrock et al. 2004), data collection initially (i.e., Summer 2021 and Winter 2022) occurred over two non-consecutive periods centered around the new and full moon, respectively. Starting in Summer 2022, we decided to run trays continuously for 12 days and account for the amount of lunar illumination per night in analyses (see below).

Foraging trays were aluminum pans (34 × 24.5 × 7.3 cm) that were filled with 3 L of sand and provisioned with 3 g of millet seeds spread homogenously throughout the tray, a density similar to other studies using the GUD framework with kangaroo rat species (e.g., Brown

1989, Bouskila 1995, Herman and Valone 2000, Emerson et al. 2018). At each site, we placed

one tray directly under a *P. glandulosa* shrub and another tray ≥ 3 meters away from the shrub

out in the open. All sites were separated by at least 50 m to minimize the likelihood that the same

individuals were foraging among multiple pairs of trays. Trays were visited every morning,

remaining seeds were collected with a sieve, and trays were covered with a lid until dusk when

they were recharged with fresh seeds.

We deployed camera traps (Reconyx Hyperfire and Bushnell Core DS) at each tray to 1)

confirm whether foraging was exclusively performed by TKR on a given night and 2) collect

data on TKR activity patterns (i.e., timing, duration, and frequency) as well as the temperature during the foraging bout. Cameras were mounted approximately 1 m above the ground on stands placed 1 m away from each tray.

Fig. 4: Configuration of foraging trays at a site, with one placed under a *P. glandulosa* canopy and the other 3 m away in a more open area. Mounted cameras were placed at each foraging station.

Cameras were set to take photos throughout the night at 1-second intervals whenever motion was

detected, enabling us to capture individual activity patterns at a fine scale. Following each

experimental period, we processed camera trap photos using WildID, a software program for

annotating photos. Observers noted the number of animals in each photo and identified all

animals to species, except where only genus was possible (e.g., *Peromyscus*). We characterized

TKR activity by quantifying the number and length of foraging bouts within a particular tray per night. Independent foraging bouts were characterized as any sequence of photos of *D. elator* at a tray separated by at least 5 minutes.

Vegetation surveys and shrub removal

We quantified microhabitat around each individual tray during the Summer 2021 period. We placed a 2 × 2 m quadrat centered around the location around each tray and estimated the percent cover of bare ground, grass, annual plants, and perennial plants. We also measured the aboveground biomass of each *P. glandulosa* shrub used for cover in the study by measuring the height, length, and width in dm, and multiplying these values together to obtain a volume estimate (dm^3) for each shrub.

On 1 July 2022, we quantified the aboveground biomass of all *P. glandulosa* within a $20m^2$ plot centered around the tray locations at each site by measuring the height, length, and width of each shrub and multiplying these values to obtain a volume estimate (dm^3) for each shrub. We also estimated percent cover of grasses, annual plants, perennial plants, and bare ground within a $2m^2$ quadrat centered around each foraging station. Following vegetation surveys, we removed the canopy of all *P. glandulosa* within the $20m^2$ plot at 9 randomly selected sites distributed between Pasture A and B and cleared the resulting downed woody debris. The remaining 8 control plots were left unmanipulated.

Quantifying site-level activity

Following the post-shrub removal foraging experiment, we deployed cameras at each site from 7 November 2022 to 31 May 2023 to characterize site use by mammalian fauna in thinned

versus unthinned photos. Cameras were mounted 1 m off the ground and placed 10 m away from the center of the site, oriented toward the foraging tray locations. Camera trap settings and photo processing followed the same protocol as for the foraging trials. We quantified the total number of photos of each detected species as a measure of activity intensity. We compared activity levels between thinned and unthinned sites for taxa of interest with paired t-tests.

Statistical analyses

Microhabitat characteristics were compared between covered and open trays using paired t-tests. Foraging tray data were examined using a linear mixed effects model with a normal distribution. We treated cover, percent lunar illumination, and season as fixed effects and site as a random effect. The dependent variable was the proportion of the mass of seeds remaining in each tray, following a logit transformation to improve normality (Warton and Hui 2011). To test how shrub cover and lunar illumination affect spatial patterns of TKR activity, we used a linear model with shrub cover, lunar illumination, and the interaction between shrub cover and lunar illumination as fixed effects and the log-transformed total number of foraging bouts at each site as a response variable.

RESULTS

Microhabitat characteristics

Microhabitat differed between open and covered trays. In particular, there were significant differences in the amount of bare ground cover (Covered: 0.24 ± 0.15 SD, Open: 0.90 ± 0.07; $t_7 = -10.68$, $P < 0.001$), grass cover (Covered: 0.47 ± 0.14, Open: 0.08 ± 0.06; $t_7 = 8.06$, $P < 0.001$), and perennial plant cover (Covered: 0.29 ± 0.13, Open: 0.02 ± 0.02; $t_7 = 5.24$, $P =$

0.001), but no difference in the amount of annual plant cover (Covered: 0.01 ± 0.01, Open: 0.01 ± 0.02; $t_7 < 0.001$, P = 0.99).

Foraging behavior and activity

For foraging periods prior to shrub removal, the proportion of seeds remaining in a tray, a measure of giving up density, was not significantly affected by cover ($F_{1,181} = 0.19$, $P = 0.66$), moon cycle ($F_{1,181} = 0.29$, $P = 0.59$), or the interaction ($F_{1,181} = 0.26$, $P = 0.61$). However, there was a significant effect of season ($F_{1,181} = 3.47$, $P = 0.03$). The average TKR GUD of visited trays was significantly higher during Winter 2022 (Covered: 0.61 ± 0.11; Open: 0.68 ± 0.09) than Summer 2022 (Covered: 0.37 ± 0.17; Open: 0.37 ± 0.17). During the Fall 2022 foraging period (i.e., following shrub removal), there was a significant effect of shrub thinning on giving up density ($F_{1,228} = 4.7$, $P = 0.03$): the average GUD was lower in thinned sites (Covered: 0.26 ± 0.07; Open: 0.22 ± 0.05) relative to unthinned sites (Covered: 0.44 ± 0.14; Open: 0.43 ± 0.12).

Based on data from the Fall 2022 foraging period, there was no significant effect of shrub thinning on the number of tray visits ($F_{1,48} = 0.76$, $P = 0.39$) or the amount of time spent at a foraging tray ($F_{1,48} = 2.04$, $P = 0.16$). Similarly, the number of nightly tray visits was not significantly affected by cover ($F_{1,108} = 0.58$, $P = 0.44$), moon phase ($F_{1,108} = 1.07$, $P = 0.31$), or the interaction ($F_{1,108} = 2.29$, $P = 0.13$). The number of sites visited by foraging rodents varied by session. In Pasture A, 5/8 sites (63%) were used by TKR in Summer 2021, 6/8 sites (75%) were used by TKR in Winter 2022, 8/10 sites (80%) were used by TKR in Summer 2022, and 9/10 sites (90%) were used by TKR in Fall 2022. No sites were used by TKR in Pasture B in any session. Moreover, the number of sites in Pasture B used by other rodent species decreased over time (Winter 2022: 6/7 sites; Summer 2022: 5/7 sites; Fall 2022: 0/7 sites).

Site-level activity patterns

We documented at least 10 mammalian species utilizing our experimental plots, including four species from Order Carnivora (Table 3). Among non-rodents, there was more overall activity in thinned relative to unthinned plots, although this was not consistent across all species (Table 3). There was no significant difference in *C. latrans* ($t_3 = -0.19$, $p = 0.86$), *L. rufus* ($t_3 = -1.25$, $p = 0.30$), or overall carnivore ($t_3 = 0.68$, $p = 0.55$) activity between thinned and unthinned sites.

Order	Species	Thinned	Unthinned
	Canis latrans	32	35
	Lynx rufus	5	23
Carnivora	*Mephitis mephitis*	5	0
	Procyon lotor	75	8
Cetartiodactyla	*Odocoileus virginianus*	60	3
Didelphimorphia	*Didelphis virginiana*	5	0
Lagomorpha	*Lepus californicus*	55	160
	Sylvilagus floridanus	283	78

Table 3. Site-level activity patterns of non-rodent species in Pasture A during Winter 2022.

DISCUSSION

We examined foraging behavior and activity patterns of the Texas kangaroo rat to understand how different environmental characteristics influence habitat use by the species. In general, we did not find evidence that characteristics like lunar phase or shrub cover influenced foraging by *D. elator*. These findings support earlier work by Goetze et al. (2008), who found that Texas kangaroo rats were active throughout the night, regardless of lunar phase. Indeed, results from our camera data suggest that Texas kangaroo rats visited foraging trays as many as 12 times on a given night, although the length of these visits fluctuated widely. Based on preliminary analyses, we also found that shrub removal did not impact TKR activity patterns

(i.e., number and duration of visits), although we did determine that *D. elator* removed more seeds from thinned patches than unthinned patches on a night basis. This is significant because it suggests that *D. elator* perceives thinned patches to be of higher quality than unthinned patches. This indicates that mechanical thinning of *P. glandulosa* could be a necessary and effective way to improve habitat suitability for *D. elator* across its distribution, while also improving the overall quality of rangeland habitat in this region. One possible explanation of this is that *D. elator* foraged more efficiently in thinned patches than in unthinned patches (e.g., spent less time being vigilant in the trays). Further analyses of our photos should aim to determine whether it is possible to differentiate time in the trays spent being vigilant versus time spent foraging. Similarly, future research should continue to look into the impacts of other habitat management techniques, such as prescribed fire, grazing, and herbicide application, to determine whether there are differences in the type of management and how TKR use the resulting habitat based on the overall change to habitat structure and composition. One caveat of our findings is that we only had one foraging experiment following the thinning treatment, and it is possible that the impacts of this experimental manipulation may take more time to have an effect on Texas kangaroo rat foraging. For example, we detected early variation among mammal species in the use of these plots (Table 3). With time, it is possible that the differential use of these plots by certain species (e.g., *L. rufus*) could lead to site-level variation in predation risk, such as direct predator cues like urine (Brinkerhoff et al. 2005), or the presence of non-mammalian predators like snakes (Bouskila 1995).

We did detect more variation in foraging and activity patterns among experimental periods. First, we found that GUD was lower during summer foraging trials than the winter trials. The thermoregulatory costs are likely to be much lower during the summer months than

during the winter months which could affect foraging decisions (Orrock and Danielson 2009).

Second, differences in overall foraging could be related to population dynamics within the

pasture. We documented a steady increase in the number of foraging sites used by Texas

kangaroo rats in Pasture A. It is possible that the lower GUD in summer months could be related

to more TKR individuals present in the study area following breeding events.

Finally, our findings have important implications for habitat management of the species.

While we found mixed results for the impact of shrub removal on *D. elator* foraging and activity

patterns, there was a clear effect of cattle grazing on Texas kangaroo rat habitat use. Importantly,

Pasture A was regularly grazed over the course of this study, and this grazing activity likely

helped maintain suitable habitat for the species. In contrast, Pasture B had not been grazed for

over 5 years and, while the foraging trays were visited by other rodent species, we did not detect

a single Texas kangaroo rat at any point over the course of the study. This is especially notable

because we had detected *D. elator* in that pasture seven years ago and suggests that cattle

grazing is an important management technique for this species and may be important for

promoting site-level persistence of this species throughout its geographic range.

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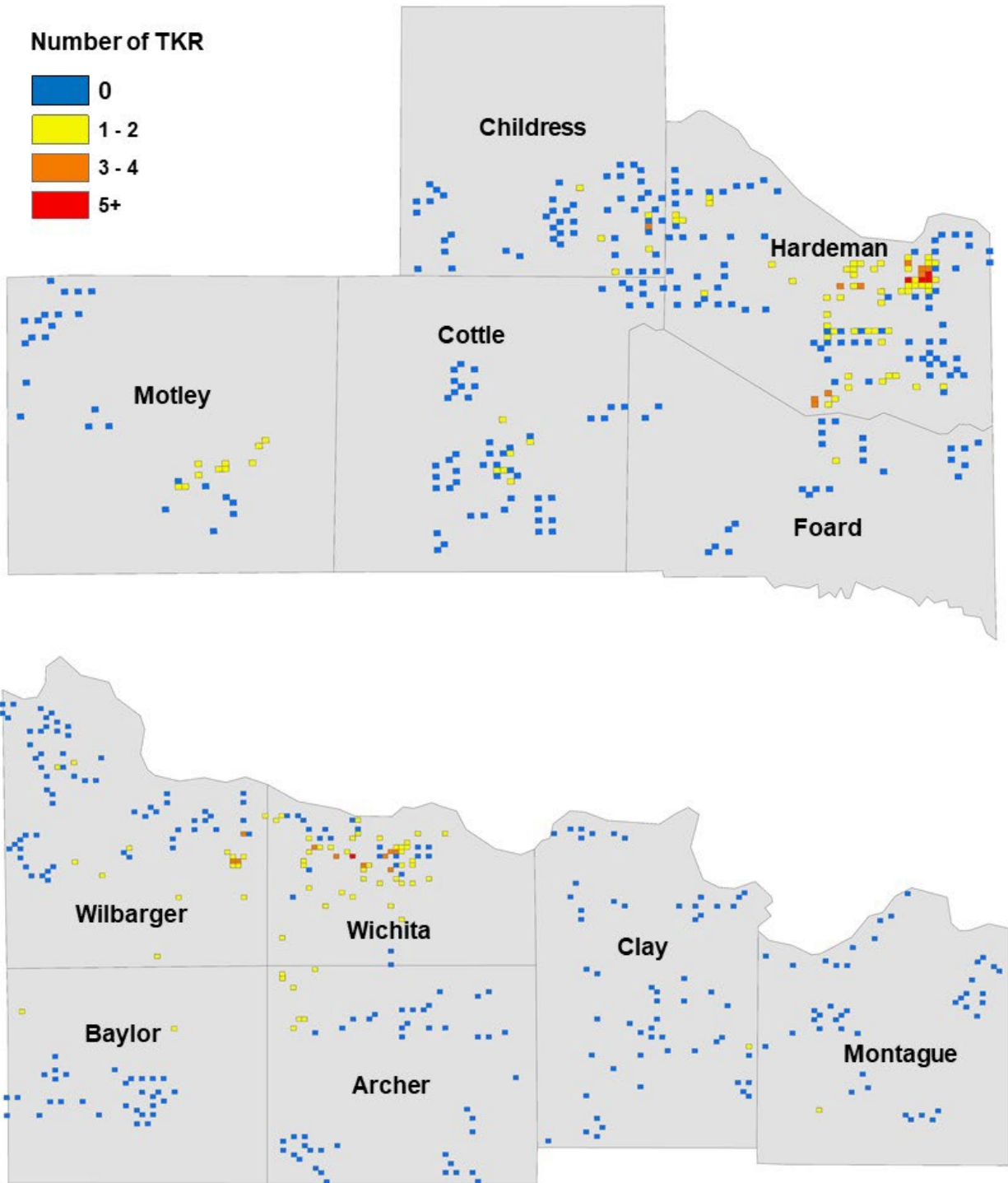
Supplementary Figure 1: Heat map depicting TKR presence in 1km^2 cells across the historical geographic range of the species, based on both historical and recent records. Warmer colors indicate areas with more TKR occurrences. Blue cells indicate cells where the species was surveyed for between 2015 – 2018 but was not encountered.

Table Xz. Results from univariate Multinomial Generalized
Linear Models used to predict persistence categories and
proportions based on each environmental characteristic
separately.

Dependent Variable	Independent Variable	X2	df	P
Persistence Category	BIO1	7.89	1	0.006
	BIO2	1.81	1	0.178
	BIO3	**15.86**	**1**	**<0.001**
	BIO5	1.31	1	0.252
	BIO6	5.36	1	0.021
	BIO7	2.12	1	0.146
	BIO8	2.10	1	0.147
	BIO9	**9.13**	**1**	**0.003**
	BIO10	0.28	1	0.598
	BIO11	1.23	1	0.267
	BIO12	0.11	1	0.745
	BIO13	0.19	1	0.661
	BIO14	1.98	1	0.160
	BIO15	0.10	1	0.923
	BIO16	7.59	1	0.006
	BIO17	0.01	1	0.909
	BIO18	5.28	1	0.022
	BIO19	7.82	1	0.005
	Clay	2.62	1	0.106
	Sand	8.11	1	0.004
	Silt	2.95	1	0.086
Persistence Proportion	BIO1	8.55	1	0.003
	BIO2	1.61	1	0.205
	BIO3	**17.61**	**1**	**<0.001**
	BIO5	1.67	1	0.196
	BIO6	3.38	1	0.066
	BIO7	3.06	1	0.081
	BIO8	2.35	1	0.125
	BIO9	**8.93**	**1**	**0.003**
	BIO10	0.77	1	0.381
	BIO11	1.80	1	0.180
	BIO12	0.45	1	0.500
	BIO13	0.46	1	0.494
	BIO14	3.54	1	0.060
	BIO15	0.14	1	0.709
	BIO16	**11.10**	**1**	**<0.001**
	BIO17	0.14	1	0.704
	BIO18	5.40	1	0.020
	BIO19	**8.86**	**1**	**0.003**
	Clay	2.27	1	0.132
	Sand	7.41	1	0.006
	Silt	2.17	1	0.140

Supplementary Table 1. Description of the 19 traits used to quantify rodent functional diversity, corresponding to one of three niche axes.

Niche Axis	Trait description
Life history	Mean litter size
	Number of litters per year
Climate response	Mean body mass
	Geographic affinity (location of geographic range relative to study area; north, south, equivalent)
	Habitat affinity (mesic, xeric, generalist)
	Daily activity time (nocturnal or crepuscular)
	Terrestriality (fossorial and/or ground dwelling or ground dwelling only)
Habitat response	Locomotion (bipedal or quadrupedal)
	Cheeck pouches (yes or no)
	Condylobasal length
	Upper incisor width
	Upper incisor depth
	Molar toothrow length
	Molar toothrow width
	Rostrum length
	Rostrum width
	Jaw lever length
	Lower incisor width

Supplementary Table 2a. Life history and climate response functional trait values for each species used to calculate functional diversity metrics.

Species	Mean litter size	Litters per year	Body mass	Geographic affinity	Habitat affinity	Daily activity time	Nest location
B. taylori	2.67	10.00	7.43	South	Mesic	2	1
C. hispidus	5.12	1.88	35.70	Equivalent	Xeric	1	1
D. elator	2.91	2.00	105.82	Equivalent	Xeric	1	1
D. ordii	3.15	2.00	49.60	North	Xeric	1	1
N. floridana	2.63	2.25	208.18	Equivalent	Mesic	1	1
N. leucodon	2.14	2.00	190.50	South	Xeric	1	1
N. micropus	2.15	2.00	203.09	South	Mixed	1	1
O. leucogaster	3.84	2.50	32.50	North	Xeric	1	1
P. merriami	4.34	2.00	7.47	South	Xeric	1	1
P. attwateri	3.50	3.70	28.30	Equivalent	Mixed	1	2
P. leucopus	4.35	3.90	22.30	North	Mixed	1	2
P. maniculatus	4.62	3.55	20.50	North	Mixed	1	2
R. fulvescens	3.10	2.00	12.50	South	Mesic	1	2
R. montanus	4.04	3.59	9.95	North	Mesic	1	2
S. hispidus	5.44	2.00	159.60	Equivalent	Mesic	2	1

Supplementary Table 2b. Habitat response functional trait values for each species used to calculate functional diversity metrics. CBL: condylobasal length; UIW: upper incisor width; UID: upper incisor depth; UCTRL: upper check toothrow length; UCTRW: upper check toothrow width; RL: rostrum length; RW: rostrum width; JLL: jaw lever length; LIW: lower incisor width.

Species	Locomotion	Cheek pouches	CBL	UIW	UID	UCTRL	UCTRW	RL	RW	JLL	LIW
B. taylori	Quadrupedal	0	16.49	2.12	1.24	2.78	0.85	6.01	2.60	6.04	1.12
C. hispidus	Quadrupedal	1	27.42	3.36	1.41	4.02	1.43	11.66	3.45	8.81	1.79
D. elator	Bipedal	1	32.43	3.73	2.01	4.72	1.85	13.69	4.27	10.11	2.01
D. ordii	Bipedal	1	30.17	3.82	1.82	4.26	1.83	14.50	3.94	9.43	2.06
N. floridana	Quadrupedal	0	47.48	5.32	2.71	8.93	2.44	18.15	5.85	17.61	4.07
N. leucodon	Quadrupedal	0	42.09	5.29	2.42	8.13	2.32	15.60	5.53	15.77	3.74
N. micropus	Quadrupedal	0	45.89	5.41	2.79	8.51	2.46	17.58	5.31	17.38	4.22
O. leucogaster	Quadrupedal	0	26.40	3.38	1.48	4.29	1.34	11.28	3.33	9.47	2.06
P. merriami	Quadrupedal	1	17.51	2.25	1.23	2.79	1.01	7.22	2.21	5.58	1.18
P. attwateri	Quadrupedal	1	25.75	2.95	1.52	4.09	1.25	10.18	3.11	9.63	1.68
P. leucopus	Quadrupedal	1	23.54	2.66	1.50	3.67	1.11	9.78	2.85	9.16	1.62
P. maniculatus	Quadrupedal	1	22.41	2.62	1.42	3.44	1.04	9.31	2.78	8.54	1.41
R. fulvescens	Quadrupedal	0	18.96	2.23	1.44	3.21	0.94	7.81	2.25	7.24	1.40
R. montanus	Quadrupedal	0	18.72	2.43	1.38	3.09	0.94	6.82	2.56	6.52	1.52
S. hispidus	Quadrupedal	0	33.47	4.19	2.16	6.02	1.96	12.75	4.45	12.89	3.14