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Declines in rodent abundance and diversity track regional climate variability in North American drylands

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Abstract

Regional long-term monitoring can enhance the detection of biodiversity declines associated with climate change, improving future projections by reducing reliance on space-for-time substitution and increasing scalability. Rodents are diverse and important consumers in drylands, regions defined by the scarcity of water that cover 45% of Earth's land surface and face increasingly drier and more variable climates. We analyzed abundance data for 22 rodent species across grassland, shrubland, ecotone, and woodland ecosystems in the southwestern USA. Two time series (1995–2006 and 2004–2013) coincided with phases of the Pacific Decadal Oscillation (PDO), which influences drought in southwestern North America. Regionally, rodent species diversity declined 20%–35%, with greater losses during the later time period. Abundance also declined regionally, but only during 2004–2013, with losses of 5% of animals captured. During the first time series (wetter climate), plant productivity outranked climate variables as the best regional predictor of rodent abundance for 70% of taxa, whereas during the second period (drier climate), climate best explained variation in abundance for 60% of taxa. Temporal dynamics in diversity and abundance differed spatially among ecosystems, with the largest declines in woodlands and shrublands of central New Mexico and Colorado. Which species were winners or losers under increasing drought and amplified interannual variability in drought depended on ecosystem type and the phase of the PDO. Fewer taxa were significant winners (18%) than losers (30%) under drought, but the identities of winners and losers differed among ecosystems for 70% of taxa. Our results suggest that the sensitivities of rodent species to climate contributed to regional declines in diversity and abundance during 1995–2013. Whether these changes portend future declines in drought-sensitive consumers in the southwestern USA will depend on the climate during the next major PDO cycle.

KEYWORDS
biodiversity, climate change, *Dipodomys*, *Onychomys*, *Peromyscus*, small mammal, Standardized Precipitation Evapotranspiration Index

1 | INTRODUCTION

Anthropogenic climate change can influence biodiversity (Bellard et al., 2012; Butchart et al., 2010; Wiens, 2016), making understanding how climate affects species abundances an important step to predict the future composition of ecological communities and improve conservation efforts (Smith et al., 2018). Drylands, regions constrained by water scarcity, are critical for understanding how changes in climate affect biodiversity because they cover 45% of terrestrial land surface (Pravalie, 2016). In North American drylands, future climate predictions include nearly 100% probability of decadal drought, the impacts of which will be amplified by climate warming (Cook et al., 2015, 2019). Aridity has already intensified with climate change in dry ecosystems (Maurer et al., 2020; Meehl et al., 2016), and variability in climate has increased during the past century at both seasonal and interannual time scales (Petrie et al., 2014; Rudgers et al., 2018).

Regional long-term monitoring has strong potential to detect relationships between biodiversity and climate variables, thereby improving future projections on changes in biodiversity (Counihan et al., 2018; Schmeller et al., 2018). First, time-series data will support better predictions on species responses to climate change than commonly used species distribution models in cases where space cannot be substituted for time; these cases occur when spatial differences among sites in climate cannot be decoupled from other spatial patterns, such as community composition or geologic history (Harris et al., 2018; Kazenel et al., 2019). Second, time-series data can be used to predict when the influence of a climate variable depends on its mean state and whether the mean state changes directionally over time (Lawson et al., 2015), as is occurring with anthropogenic climate change. For example, a 10% decrease in precipitation may cause a smaller ecological response in a wetter mean climate than in a drier mean climate (Rudgers et al., 2018). Indeed, past research predicts that arid communities will be less sensitive to extreme drought than mesic communities because dryland species are adapted to aridity (Lloret et al., 2012; Thoma et al., 2019; Tielboerger et al., 2014); however, it is difficult to separate aridity from other sources of spatial variation in these space-for-time studies. In an alternative scenario, species may respond most strongly to climate change in the driest climates, if they are already near their physiological limits (Huxman et al., 2004; Knapp et al., 2015; Maurer et al., 2020; Somero, 2010). Finally, time series may be especially useful for identifying climate drivers of biodiversity in regions with large temporal variability in climate, such as drylands (Maurer et al., 2020; Rudgers et al., 2018).

Climate sensitivity functions (CSFs) provide a tool for understanding ecological correlations to climate using time series from multiple locations (Rudgers et al., 2018). A CSF depicts the complex relationship between an ecological variable (e.g., species abundance) and its climate driver (e.g., drought index) by capturing nonlinearity in the functional response. Sensitivity is characterized by the shape of the function, rather than solely by a linear slope. When a CSF is nonlinear, such as concave or convex, then increases in the *variance* of a climate variable are predicted to alter the long-term ecological outcome, even if mean climate does not change (Lawson et al., 2015; Vazquez et al., 2017). For example, an asymptotic concave function predicts net negative effects of increasing variance in climate, because low values of the climate variable, such as extreme drought, cause large declines in species abundance, whereas large values of the climate variable (e.g., wet conditions) cause only small increases. In contrast, a convex function (e.g., exponential curve) predicts net positive effects of increasing variance in climate. The magnitude of a species sensitivity to *variance* in climate is predicted, in part, by the degree of nonlinearity in the CSF. For example, Rudgers et al. (2018) documented differences among grasslands and shrubland in nonlinear CSFs for plant productivity. Recent efforts have improved detection of linear relationships between species abundances and climate variables (e.g., Munson, 2013; Platts et al., 2019; Prugh et al., 2018), but even studies that incorporate more complex functions to predict winners and losers under climate change (e.g., Domisch et al., 2011; Kafash et al., 2018; Thuiller et al., 2009) typically do not explore the shapes of the nonlinearities to infer sensitivity to changing *variance* in climate (reviewed by Lawson et al., 2015; Vazquez et al., 2017).

Rodents are dominant mammalian consumers (Heske et al., 1993; Kelt et al., 1996; Kerley et al., 1997) that contribute important community diversity to drylands globally (Ernest, 2005; Ojeda et al., 2000; Yarnell et al., 2007). Losses of rodent diversity can affect key ecological processes, plant diversity, and food web structure. Rodents influence plant communities through their resource preferences, large systems of engineered burrows, or extensive seed caches (Brown & Heske, 1990; Brown et al., 2001; Davidson et al., 1985; Prugh & Brashares, 2012). Rodents also constitute important food resources as prey for terrestrial and avian predators (Kotler, 1984; Longland & Price, 1991; Meserve et al., 2003).

Drought or other extreme climate conditions may define "winner" and "loser" species—taxa that, respectively, increase or decrease with changes in climate (O'Brien & Leichenko, 2003; Prugh et al., 2018). Climate affects rodent community composition and diversity in drylands because the amount and timing of precipitation are key drivers of food plant availability (Beatley, 1969; Brown & Ernest, 2002; Dickman et al., 1999; Greenville et al., 2012; Kelt, 2011; Kelt et al., 2008; Previtali et al., 2009; Schooley et al., 2018; Shenbrot et al., 2010; Thibault & Brown, 2008; Thibault et al., 2010). Air temperature and precipitation can also directly affect rodent physiology, behavior, survival, and reproductive success (Brown & Harney, 1993; Brown & Zeng, 1989; Conley et al., 1977; Lightfoot et al., 2012; Moses et al., 2012) or indirectly alter trophic interactions with predators or parasites (Davidson et al., 1985; Dickman et al., 2010; Kotler, 1984; Letnic et al., 2011; Meserve et al., 2003; Yunger et al., 2007). Despite these documented influences of climate, studies on terrestrial consumers, including those on rodents, have not yet explored the nonlinearities that can predict susceptibility to climate variability or sought cases where the effects of climate variability depend on the climate mean.

In addition, if a species is a winner or loser with climate change in one location or ecosystem type, it is unclear how well this climate sensitivity generalizes to other ecosystems across a region or over a species range. Because prior studies have examined long-term patterns in rodent communities from a single location (e.g., Ernest et al., 2000; Lightfoot et al., 2012; Schooley et al., 2018) or spatial patterns lacking temporal resolution, such as from species occurrence records (e.g., Baltensperger & Huettmann, 2015), we lack information on how much ecosystem type imposes a filter on species sensitivity to climate, for example, through the structure or composition of the vegetation and the availability of specific food resources (Platts et al., 2019). Populations may differ in climate sensitivity among locations within a species range, with populations at species geographic range edges more sensitive to climate variables than those in range centers (Cahill et al., 2014; Pearson et al., 2009), particularly if range edges mark physiological limits (Heinrichs & Schmidt, 2017; Somero, 2010). Regional-scale, long-term data can improve generalizations by merging inference across both space and time to determine whether there are local differences in which species are winners versus losers in response to drought or other climate variables, supporting the hypothesis that the geographic location or ecosystem-type modulates a species' climate sensitivity.

Here, we combined 12 concurrent long-term (9+ years) datasets encompassing sites from the northern Chihuahuan Desert to the southern Great Plains in western North America to examine temporal patterns in rodent diversity, composition, and species abundances at a regional scale that included eight ecosystem types. Mean annual precipitation spanned 230–380 mm, and mean annual temperature ranged from 9 to 17°C (Table S1 gives site details). Datasets extended over two decade-long periods that differed in phase of the Pacific Decadal Oscillation (PDO), with wetter conditions prevailing during the 1990s (1995–2006 time series) and drier conditions dominating the second time series (2004–2013; Cayan et al., 1998; Pascolini-Campbell et al., 2019). The PDO is a natural cyclic pattern of Pacific sea surface temperatures (Zhang et al., 1997) that modifies the El Niño Southern Oscillation to influence precipitation in the southwestern US (Chen et al., 2017; Gutzler et al., 2002; Milne et al., 2003). The time series differed by 45 mm in mean annual precipitation, with 315 mm during 1996–2006 and 270 mm during 2004–2013, enabling us to compare rodent sensitivities to climate at the same location, but under contrasting temporal windows that differed in the climate mean. We addressed the following specific questions. (1) Do temporal dynamics in rodent species diversity and abundance diverge among ecosystems, or are they regionally concordant? (2) Does ecosystem type modulate which species are “winners” or “losers” under climate change (spatial context dependency)? (3) Does the importance of climate to rodent abundance depend on a temporal shift in mean climate (temporal context dependency)? Specifically, within an ecosystem type, we predicted that the importance of climate, and its importance relative to plant productivity, would increase in magnitude during the drier mean climate of the PDO, because species would be more likely to approach physiological thresholds.

2 | METHODS

2.1 | Focal ecosystem types

We combined data across 12 independently designed long-term rodent monitoring sites in Arizona, New Mexico, and Colorado (Appendix S1: Table S1 gives site details; Figure S1 provides a map). The full data package, including R scripts, is available through the Environmental Data Initiative (Rudgers et al., 2021).

Datasets were divided into two decadal periods: 1995–2006 spanned the warm phase of the PDO with wetter conditions, whereas 2004–2013 was drier (cool phase). The transition back to the wet phase for the southwestern US occurred during 2013–2015 (Meehl et al., 2016). Information on specific methods for each site are reported previously for Portal, AZ (Brown & Zeng, 1989), Sevilleta Long-term Ecological Research (SEV LTER) program (Ernest et al., 2000), Jornada Basin (JRN LTER; 1995–2006: [Lightfoot et al., 2012], 2004–2013 [Schooley et al., 2018]), and Colorado shortgrass steppe (SGS LTER; Stapp et al., 2008). Because trapping in Colorado sites ended in 2013, we used this year for the endpoint, so all sites spanned equivalent time periods. We overlapped the middle years (2004–2006) of each time series to span a full decade and to maximize temporal resolution because Jornada added new locations in 2004 (Table S1). This approach also ensured that analyses of temporal trends or climate predictors were not confounded by differences among sites in the number of years examined.

For the period 1995–2006, there were nine sites. These included two ecosystems at JRN LTER in southern New Mexico: black grama (*Bouteloua eriopoda*)-dominated grassland and creosote bush (*Larrea tridentata*)-dominated shrubland; four SEV LTER ecosystems in central New Mexico: piñon-juniper woodland (*Pinus* and *Juniperus* spp.), black grama grassland, and two creosote bush shrubland sites; one site at a temporally variable grass–shrub ecotone in Arizona (POR); and two ecosystems at SGS LTER in Colorado: blue grama (*B. gracilis*)-dominated grassland and mixed saltbush (*Atriplex* spp.) shrubland (Table S1). For 2004–2013, there were eight sites: three JRN LTER ecosystems (black grama grassland, mesquite (*Prosopis glandulosa*) shrubland, and their ecotone), two of the four previously monitored SEV LTER ecosystems (black grama grassland and creosote bush shrubland), the same Portal site as the first time series, and the same two SGS LTER ecosystems (Table S1).

2.2 | Rodent monitoring

At each site, rodent abundance was quantified using live trapping primarily during September–October (Table S2). Trapping protocols differed somewhat among sites (additional details in Appendix S1, Table S1). To create consistency across datasets, during each sampling period, we estimated abundance as the number of unique animals caught per trap per night, excluding any recaptures. Rodent species are listed in Table S2.

2.3 | Climate data

We obtained monthly climate data from the PRISM database (PRISM Climate Group, 2019) for mean temperature, maximum temperature, and cumulative precipitation. We then averaged monthly mean and maximum temperatures for the fall monsoon growing season (July–October) or the primary spring growing season (March–June) and summed precipitation over the same windows. We chose these seasonal time windows to match methods for climate sensitivity functions in Rudgers et al. (2018). We used monthly mean temperature and precipitation data together with latitude to calculate the Standardized Precipitation Evapotranspiration Index (SPEI; a drought index) across all sites within each time series (Vicente-Serrano et al., 2010), using the Thornthwaite method for potential evapotranspiration (cran.r-project.org/web/packages/SPEI/index.html). We calculated 6-month integrated SPEI for each season (ending in June or October) as well as 12-month integrated SPEI (ending in December). We also created a seasonal and yearly time lag to evaluate whether immediate weather or weather from the prior season (spring, 6-month lag) or prior year (12-month lag) better explained variation in rodent diversity or abundance. Time lags can influence desert consumers differently due to specific life histories; for example, prior climate conditions may affect current abundance through differential lifespans and reproductive outputs (Jaksic et al., 1997; Meserve et al., 2011).

2.4 | NDVI plant productivity

To compare the relative importance of climate against that of plant productivity, we obtained data on the Normalized Difference Vegetation Index (NDVI) from the U.S. Geological Survey's Landsat program (Masek et al., 2006). NDVI is a commonly used surrogate for plant productivity that works effectively in cross-site comparisons (Pettorelli et al., 2005) and is the only available vegetation metric measured consistently across the rodent monitoring sites. Landsat satellite images were available at a 30 m spatial resolution and 16-day temporal resolution. Using Google Earth Engine (Gorelick et al., 2017), we obtained all Landsat images for the time series, extracted data pixels within a 1000 m radius from the center of each rodent trapping site, and averaged NDVI values within this radius to obtain a single NDVI value for each trapping site and time point. We discarded any data points where >25% of the area was covered by cloud, as determined by the pixel_qa layer included with Landsat data. Finally, we averaged these time points to obtain a monthly time series of NDVI for each trapping site. We calculated the average 6-month NDVI for each season (ending in June or October).

2.5 | Statistical analysis

To understand the differences among rodent communities in relationships with climate, we made cross-site comparisons of rodent community structure, including composition, diversity, and abundance. All analyses included the random effect of replicate trapping grid (or web) identity to account for the non-independence of repeated measures on the same grid through time. For community composition, we used perMANOVA on a matrix of community data in which each column was a rodent species and each cell was the number of animals caught per trap per night for each year (Primer v. 6, Clarke & Gorley, 2009). PerMANOVA models included site, year, and the random effect of trapping grid (nested within site) using the Bray–Curtis distance metric with 9999 permutations under a reduced model with Type III SS. We tested which sites differed significantly in rodent composition using pairwise tests with false discovery rate (FDR) correction and visualized compositional differences with nonlinear multidimensional scaling (NMDS) analysis with 500 restarts on the Bray–Curtis distance metric. We used SIMPER analysis to explore which rodent taxa contributed most to variation in composition among ecosystem types and locations (Primer v. 6, Clarke & Gorley, 2009). We examined heterogeneity in rodent community composition by testing divergence among grids within each site using permDISP, and pairwise tests with FDR correction to adjust P values for multiple comparisons. Then, we used general linear mixed-effects models to evaluate differences among ecosystem types in rodent diversity (Shannon H' index), richness, and total rodent abundance. Models used the fixed effects of year and site and the random effect of replicate trapping grid nested within site, using function *lme* in the <nlme> package (Pinheiro et al., 2016).

1. Do temporal dynamics in diversity and abundance diverge among ecosystems, or are they regionally concordant?

We used the general linear mixed-effects models described above to evaluate temporal patterns in diversity, focused on the year and year × site effects. We applied model selection procedures based on the second-order Akaike information criterion (*AICc*, Burnham & Anderson, 2002) to compare a simple model with a linear trend against models with temporal autocorrelation (either autoregressive 1 or autoregressive 2) using function *lme* in the <nlme> package (Pinheiro et al., 2016). *AICc* values were obtained with the MuMIn package (Bartoń, 2013), and results taken from the model with the lowest *AICc*. We determined marginal R^2 values using *rsquared* in piecewiseSEM (Lefcheck, 2015).

2. Spatial context dependency: Does ecosystem type modulate which species are "winners" or "losers" under climate change?

Our model selection approach was similar to Prugh et al. (2018) in which the abundance of each rodent taxon (species, genus, or family) was regressed against each climate variable or NDVI to evaluate their relative importance as predictors. However, we additionally evaluated potential for sensitivity to *variance* by including nonlinearities in these relationships using CSF analysis (Rudgers et al., 2018). "Winner" taxa under drought were indicated by a significantly positive relationship between abundance and the inverse of SPEI, indicating greatest abundance under drier conditions (i.e., negative SPEI values).

During initial model selection, candidate models evaluated the relative importance of the following variables: the SPEI drought index integrated over the preceding 6-month or 12-month period, annual or monsoon precipitation, annual or monsoon mean temperature, or NDVI in spring or fall. For each predictor, we also evaluated its influence with a 6-month or a 12-month time lag. General linear mixed-effects models (lme4, Bates et al., 2015) took the form: rodent response ~predictor variable × site and included the repeated, random effect of replicate grid to account for repeated measures structure. Only sites where the rodent taxon was present were included in the analysis for each taxon. Because some rodent species were rare or did not occur across sites in the region, we binned some taxa by genus (e.g., *Chaetodipus*) to enable inclusion of climate variable × site interactions. Across our candidate model set, we then used the *AICc* to choose the best predictor of abundance for each rodent taxon (Burnham & Anderson, 2002).

Next, to evaluate whether climate or NDVI predictors were similar among dryland ecosystem types, we compared four models, all of which used the best climate predictor identified during initial model selection. These models included *regional* models, which did not have an interaction between the climate variable and site, or *ecosystem-specific* models that had the climate × site interaction to test the hypothesis that abundance–climate relationships vary among ecosystem types. To explore potential sensitivity to climate *variance*, for each model, we also compared *quadratic nonlinear* models to *linear* models. We did not use more complex models than quadratic due to the relatively short length of each time series (~10 years). In all cases, ecosystem-specific models outranked regional models, and we decomposed significant interactions involving sites using post-hoc Tukey HSD tests to compare nonlinear regression parameters. We present results of model selection via *AICc* (Bartoń, 2013), as well as statistical results from the best model for each rodent taxon in each time series.

3. Temporal context dependency: Does the importance of climate to rodent abundance depend on a temporal shift in mean climate?

Within an ecosystem type, we compared results between the two time series to examine whether the magnitude or direction of relationships between rodent abundance and climate or vegetation differed between the phases of the PDO. Model selection procedures cannot be used to directly compare different datasets (Burnham & Anderson, 2002). Therefore, rather than comparing model *AICc* values as metrics of performance, we determined model weights for the best climate or vegetation predictor within each PDO phase to assess the degree to which the relative importance of the predictors of rodent abundance changed temporally, concordant with the PDO.

3 | RESULTS

3.1 | Setting the stage: How rodent communities vary among ecosystems

3.1.1 | Composition

Rodent community composition strongly depended on ecosystem type, more so than on geography (Figure 1; Table 1: Composition). Among ecosystems, the piñon-juniper woodland had the most distinctive community, and piñon-juniper woodland and blue grama grassland ecosystems differed the most (Figure 1a), even though blue grama grass dominates the woodland understory. Blue grama grassland and mixed saltbush shrubland were the next most divergent ecosystems, despite their close geographic proximity; both differed from each other and from all other sites (all $p < 0.05$, Figure 1a). The three sites representing creosote bush shrubland clustered together with similar species composition (all $p > 0.09$; Figure 1; Table 1), despite their geographic distance (Table S1). Likewise, the black grama grassland ecosystems had more similar composition to each other than to any other ecosystem types ($p > 0.10$, Figure 1; Table S1). The genus *Dipodomys* occurred in all sites, highlighting its dominance in the southwestern USA. Shrublands were generally more dominated by *Dipodomys* species than grasslands, and two species (*D. merriami* and *D. ordii*) contributed up to 50% of the differences in composition between grassland versus shrubland sites, according to SIMPER analysis. The desert pocket mouse (*Chaetodipus penicillatus*) contributed to a distinctive community at Portal, Arizona, but it was absent from almost all the other sites. The smallest heteromyid in our datasets, the silky pocket mouse (*Perognathus flavus*), caused compositional divergence among ecosystems in New Mexico, where it was one of the most frequently captured species and explained 24% of the dissimilarity among grassland ecosystem types at SEV and JRN. In contrast, the northern grasshopper mouse (*Onychomys leucogaster*) dominated grassland (~98%) and shrubland (53%) ecosystems in Colorado (additional details in Appendix S2).

Ecotones had greater dispersion in rodent composition than sites representative of a single ecosystem type (Figure 1; Table 1: Dispersion $p = 0.0001$), supporting the expectation that rodent communities vary more among years and trapping grids at transition zones between ecosystem types than at core ecosystem types. The ecotone in southeastern Arizona (POR) had the greatest dispersion (1995–2006: dispersion = 42.7; 2004–2013: dispersion = 41.4) followed by the ecotone between mesquite shrubland and black grama grassland in southern New Mexico (2004–2013: JRN2 dispersion = 36.7). Not surprisingly, ecotones had communities characteristic of both grassland and shrubland assemblages (Figure 1).

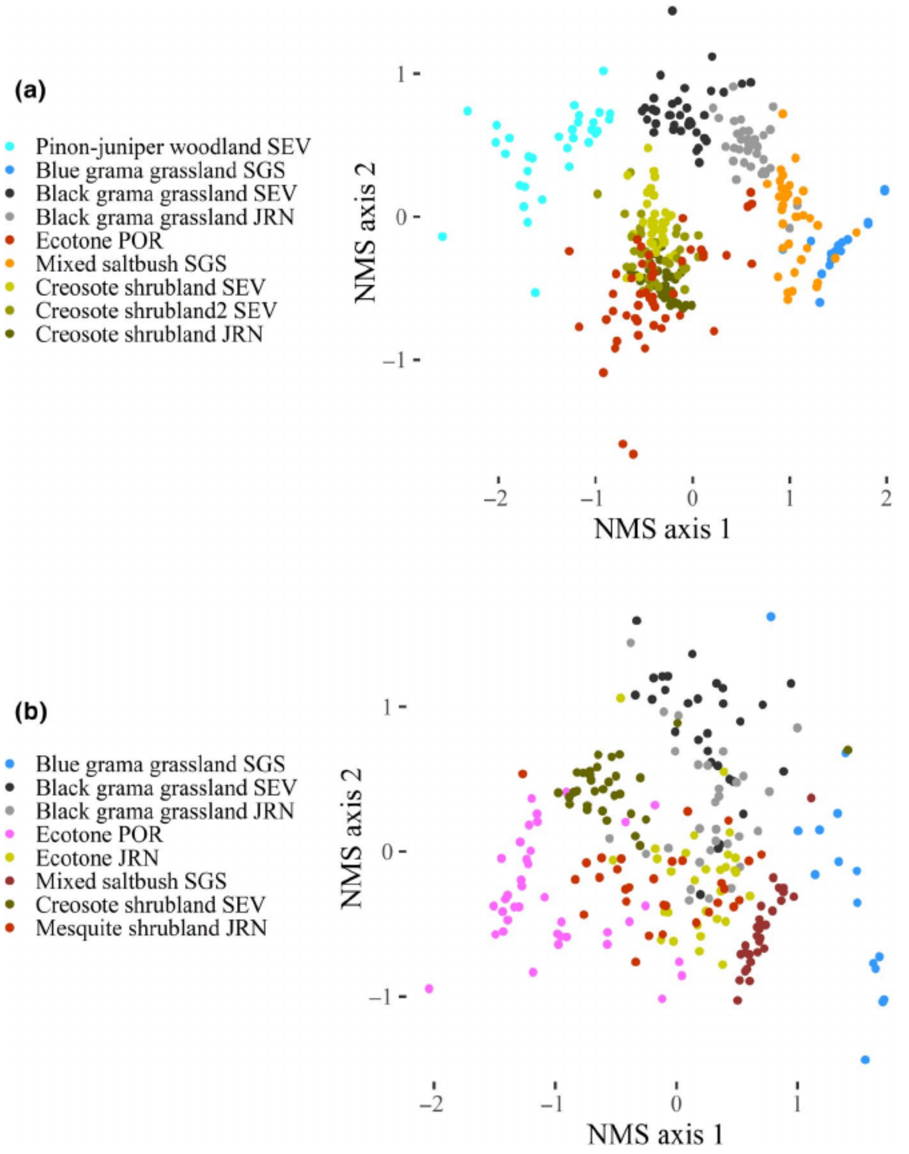


FIGURE 1 Nonmetric multidimensional scaling plots depicting differences in rodent community composition among ecosystem types with codes for each site: (a) during 1995–2006 (2D stress = 0.12) or (b) during 2004–2013 (2D stress = 0.18). Each point represents a replicate trapping web × year combination. Site codes are described in Table S1

TABLE 1 Statistical results from analysis of rodent community composition (perMANOVA), beta-diversity (Dispersion), diversity (Shannon *H′* Index), species richness and total rodent abundance for each time series (1995–2006, 2004–2013)

	Composition		Dispersion		Diversity		Richness		Abundance	
	pseudo-*F*	*p*	pseudo-*F*	*p*	X^2	*p*	X^2	*p*	X^2	*p*
1995–2006										
Year	5.57	**0.001**	0.93	0.7516	5.83	**0.0158**	4.44	**0.0350**	0.42	0.5158
Site	41.27	**0.001**	13.41	**0.0001**	180.20	**<0.0001**	285.56	**<0.0001**	376.39	**<0.0001**
Year × Site	4.69	**0.001**	4.57	**0.0388**	18.87	**0.0156**	13.49	0.0962	31.37	**0.0001**
2004–2013										
Year	5.70	**0.001**	1.14	0.4593	18.41	**<0.0001**	11.73	**0.0006**	9.35	**0.0022**
Site	12.45	**0.001**	5.04	**0.0001**	151.13	**<0.0001**	83.46	**<0.0001**	97.25	**<0.0001**
Year × Site	2.88	**0.001**	3.83	0.0870	6.54	0.4787	3.22	0.8639	6.49	0.4840

Note: $p < 0.05$ are in bold.

3.1.2 | Diversity and abundance

Species diversity varied among ecosystem types, with up to 900% differences between the most and least diverse rodent communities (Table 1; Table S3). Blue grama grassland had the lowest species diversity (letters indicate significant differences among means via post-hoc Tukey HSD tests: mean = 0.12a CL = −0.025 to 0.261), followed by piñon-juniper woodland (mean 0.77b CL = 0.625–0.908) and mixed saltbush shrubland (mean = 0.89b CL = 0.743–1.028; Table S3). Generally, creosote bush and mesquite shrubland ecosystems had similarly high species diversity, followed by black grama grassland and ecotones, which often did not differ from shrublands (Table S3). Species richness tracked diversity patterns, with ~400% greater richness in the most versus least species-rich ecosystems and 16- to 125-fold differences in abundance among ecosystem types (Table 1; Table S3). Total abundance (i.e., community size) was similarly low among blue grama grassland (mean = 0.008a CL = −0.0024 to 0.0186), piñon-juniper woodland (mean = 0.021a CL = 0.0101–0.0312), and mixed saltbush shrubland ecosystems (mean = 0.040a CL = 0.0297–0.0509), followed by grassland (mean = 0.054b CL = 0.0438–0.0648) and shrubland (mean = 0.069bc CL = 0.0587–0.0797) in central New Mexico, with the greatest abundance in the southern and ecotone sites (JRN mean = 0.101c CL = 0.094–0.1114, POR mean = 0.091c CL = 0.0821–0.1002; Table S3).

1. Do temporal dynamics in diversity and abundance diverge among ecosystems, or are they regionally concordant?

During 1995–2006, species diversity declined across the region by ~20%, with ~2% loss of diversity per year (Regional slope (β) with 95% CI = −0.016 [−0.029, −0.003], marginal R^2 = 0.44; Table 1: Year). However, total rodent abundance did not change during this period (β = −0.005 [−0.001, 0.0005], Table 1: Year). Taxa that declined over time, regionally in abundance included *Peromyscus* (β = −0.0004 [−0.0005, −0.0002]), *Onychomys* (β = −0.0002 [−0.0004, −0.00003]), and *Neotoma* (β = −0.0004 [−0.0005, −0.0003]). Beyond the regional trends, the magnitude of declines in rodent diversity diverged among ecosystem types (Figure 2a; Table 1: Year × Site). Piñon-juniper woodland had ~7.5% per year declines, and mixed saltbush declines were 7% per year. In piñon-juniper woodland, *Neotoma* contributed to declines in diversity (β = −0.0005 [−0.001, −0.0001]), whereas cricetids dominated the decline in mixed saltbush ecosystem, particularly *Peromyscus* (β = −0.0018 [−0.0022, −0.0014]) and *Onychomys* (β = −0.0009 [−0.0015, −0.0002]). Estimates of species richness tracked results for diversity (marginal R^2 = 0.48) but with weaker year × site interactions (Table 1). While there was no region-wide decline in rodent community size during 1995–2006, abundance decreased in some sites (Figure 2b; Table 1: Year × Site). The strongest temporal change occurred in southern New Mexico (JRN) in both black grama grassland and creosote bush shrubland, with yearly losses of 3%–5% of rodents caught per trap per night (Figure 2b). In contrast, abundance increased ~4% per year in the ecotonal ecosystem of southeastern Arizona (POR).

During 2004–2013, regional diversity declined more strongly than in the prior time series, with ~35% loss over the time period and ~4% loss per year (Regional slope (β) with 95% CI = −0.040 [−0.059, −0.021], marginal R^2 = 0.50; Table 1, Year). In contrast to the first time period, total rodent abundance also declined across the region during 2004–2013, with losses on the order of 4.5% of rodents caught per trap per night per year (β = −0.003 [−0.006, −0.001], marginal R^2 = 0.31; Table 1: Year). Taxa that declined over time, regionally (all p < 0.04), included *D. spectabilis* (β = −0.0005 [−0.0081, −0.0002]), *D. ordii* (β = −0.0008 [−0.0016, −0.00005]), *P. flavus* (β = −0.0004 [−0.0008, −0.00004]), *Onychomys* (β = −0.0005 [−0.0008, −0.0002]), and *Peromyscus* (β = −0.0002 [−0.0003, −0.00002]). Declines in diversity and abundance varied among ecosystem types, similar to the first time series (Figure 3; Table 1: Year × Site), with the greatest diversity declines in mixed saltbush ecosystem (Figure 3a, ~10% diversity loss per year). Sizable losses of both diversity (6% decline per year, Figure 3a) and abundance (10% decline per year, Figure 3b) also occurred in creosote bush shrubland of central New Mexico, and several taxa contributed: *D. merriami*, *D. spectabilis*, *P. flavus*, and *Peromyscus*.

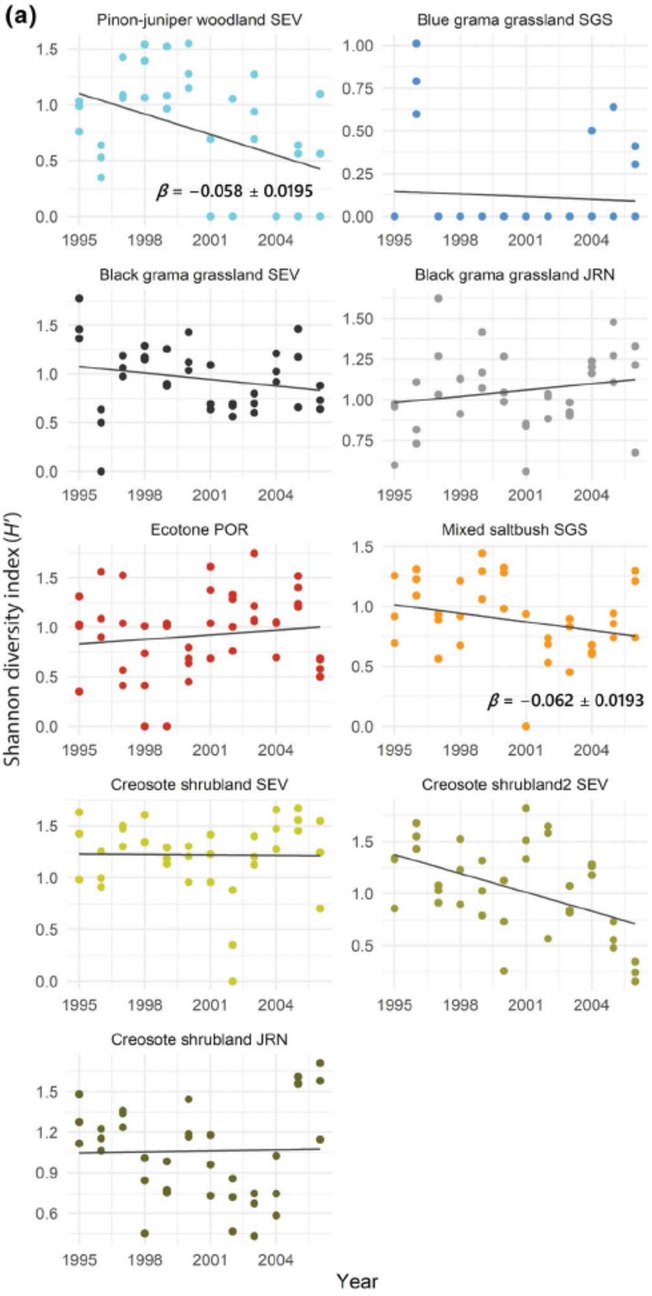


FIGURE 2 Temporal trends in (a) diversity (Shannon H') and (b) abundance of rodents during 1995–2006. Sites with significant temporal changes show the value of the slope (β) ± SE

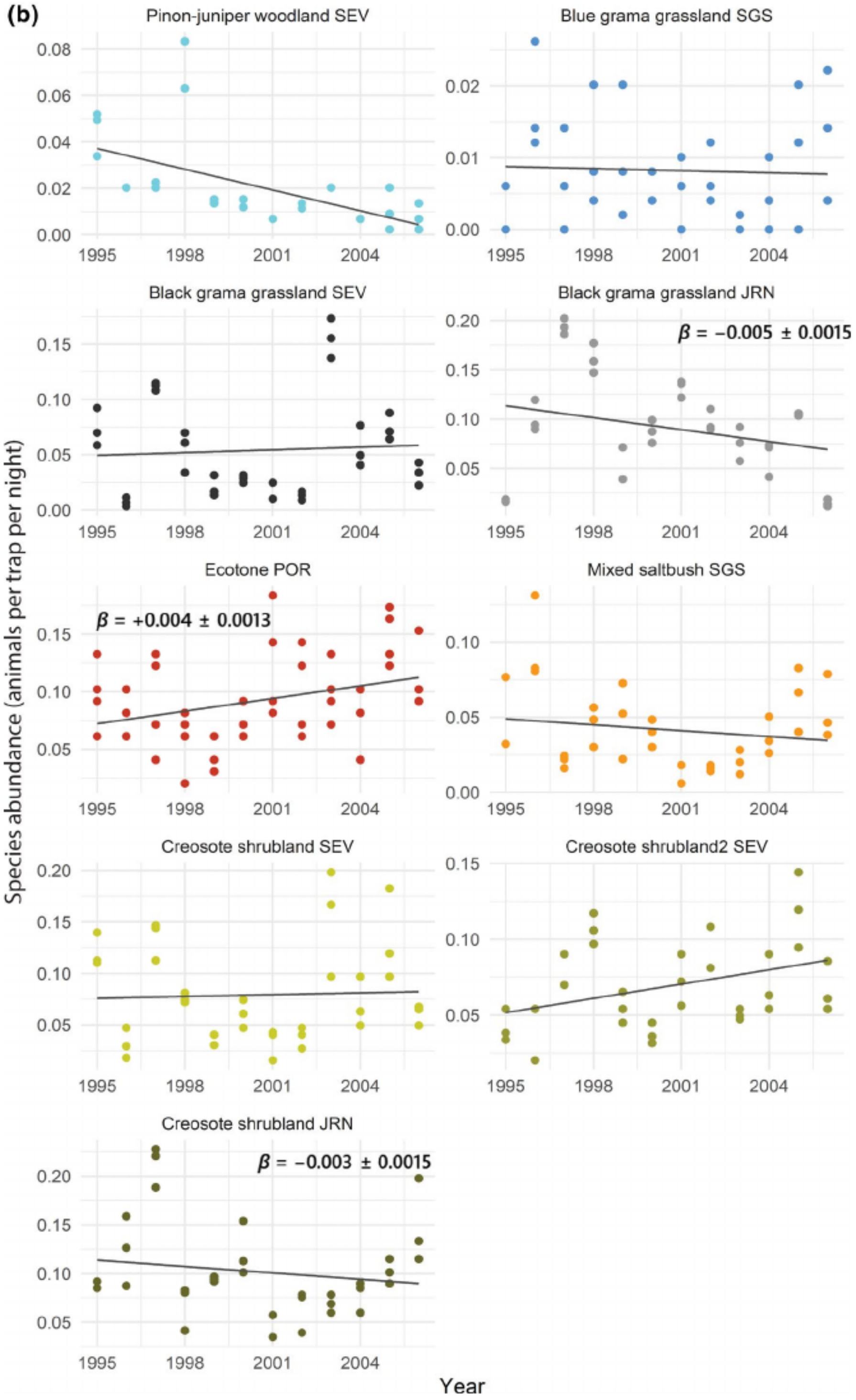


FIGURE 2 continued

2. Spatial context dependency: Does ecosystem type modulate which species are "winners" or "losers" under climate change?

3.1.3 | Sensitivity to mean drought

Ecosystem type modulated which rodent taxa were winners or losers under drought conditions. Linear relationships between abundance and the drought index diverged among ecosystems in 60% of all rodent taxa and time-series combinations, in 80% of rodent taxa below the family level, and in 75% of single species analyses in which ecosystem differences could not be conflated with rodent species identity due to lumping of species within a genus (Table S4; SPEI × Site; Figure 4a). Within a taxon, status flipped from winner to loser among ecosystems in 55% of significant cases (Figure 4a, full results in Table S5), and ecosystems differed in the magnitude, but not the direction, of sensitivity to drought in the remaining 45% of significant cases. Across all comparisons, fewer

FIGURE 3 Temporal trends in (a) diversity (Shannon H') and (b) abundance of rodents during 2004–2013. Sites with significant temporal changes show the value of the slope (β) ± SE

taxon–ecosystem combinations were winners (18%) than losers (30%) under drought.

The strongest winners under drought, as predicted by their linear relationships to SPEI (Figure 4a), were in the family Heteromyidae: *P. flavus* in central New Mexico grassland (SEV), *D. merriami* in creosote bush shrubland of southern New Mexico (JRN) and in the Arizona ecotone (POR), and *D. ordii* in southern New Mexico grassland (JRN). The losers, ranked by magnitude, were *Peromyscus* spp. in piñon-juniper woodlands, *Chaetodipus* spp. in the Arizona ecotone (POR) during the second time series, and *D. merriami* in creosote shrubland of central New Mexico (SEV2, Figure 4a). Other loser cases included *D. ordii* in most ecosystems during the second time series, *P. flavus* in southern New Mexico grassland (JRN) and

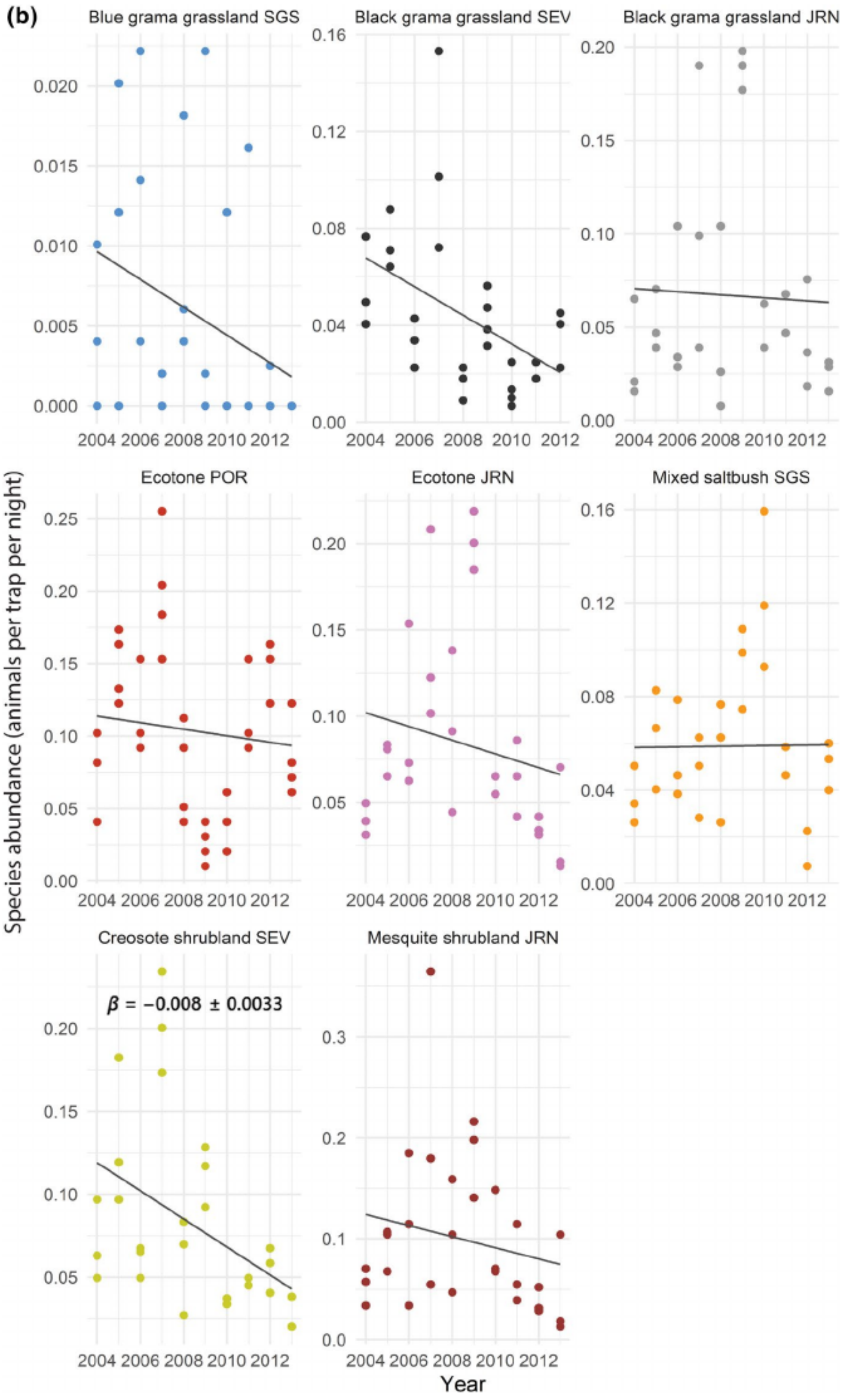


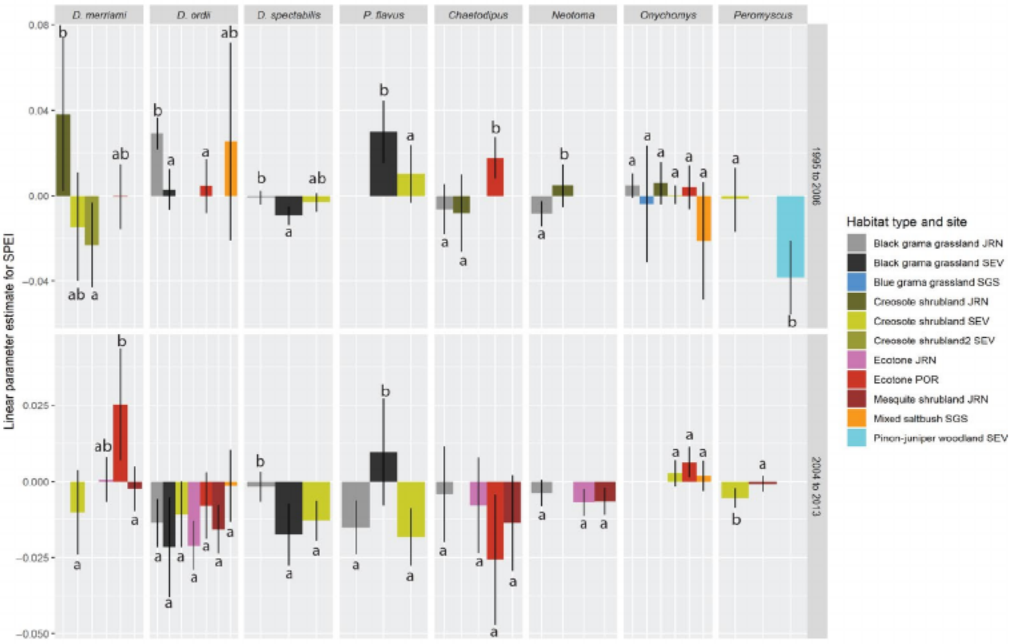
FIGURE 3 continued

central New Mexico shrubland (SEV) during the second time series, and *D. spectabilis* in central New Mexico grassland and shrubland (SEV, Figure 4a). Some taxa co-varied little with the drought index, even when time lags were considered. In most ecosystems where they occurred, *Onychomys*, *Neotoma*, and *Chaetodipus* were neutral with drought during both time series (Figure 4), although *Neotoma* (*N. albigula* and *N. micropus*) were losers in southern New Mexico grasslands (JRN) during the first time series, and *Chaetodipus* (four species) closely tracked the drought index in Arizona (POR).

3.1.4 | Sensitivity to variability in drought

Nonlinear CSFs between abundance and drought diverged among ecosystem types in 80% of rodent taxa with significant nonlinearities

(a) Population increase/decrease under greater mean drought



(b) Population increase/decrease under greater variability in drought

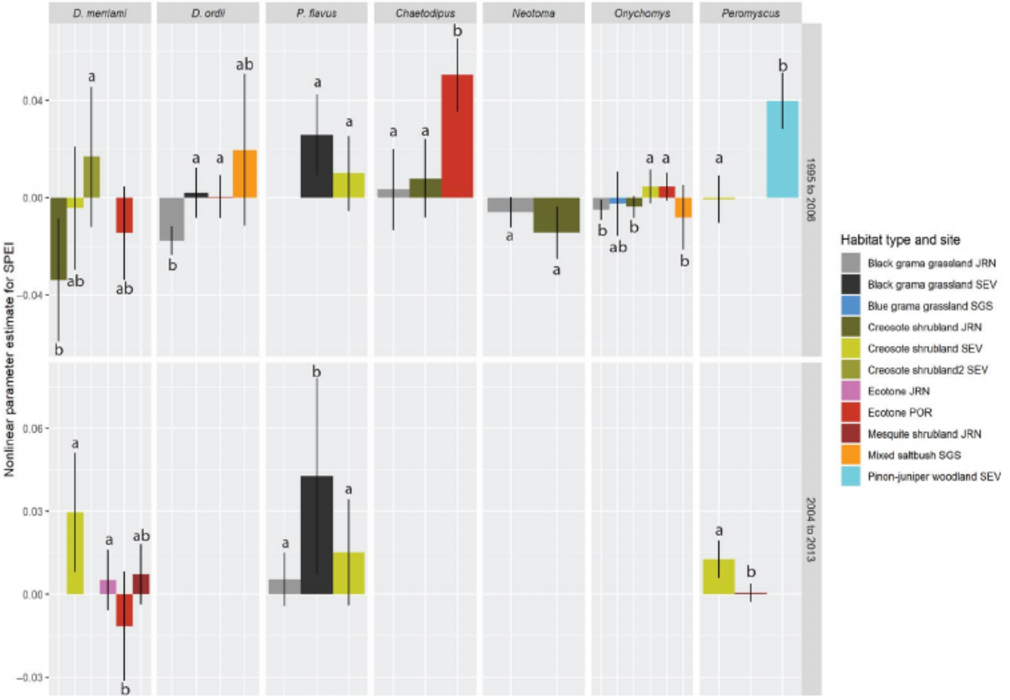


FIGURE 4 Parameter estimates from climate sensitivity functions (CSFs) for rodent abundance during 1995–2006 or 2004–2013 time series, using the inverse of the Standardized Precipitation Evapotranspiration Index (SPEI). (a) Linear relationships of rodent abundance with SPEI. Here, the bar shows the slope (β) ± 95% confidence interval. Confidence intervals that do not overlap zero indicate relationships significantly different from zero at $p < 0.05$. Winners under drought had positive slopes—their abundances increased when the drought index was more severe, and losers under drought had negative slopes. (b) If the relationship between abundance and SPEI was significantly nonlinear, the bar shows the estimate of the quadratic term (γ) ±95% confidence interval. *D. spectabilis* had no significantly nonlinear parameters and is not included. Negative values indicate concave (hump-shaped) relationships, which predict abundance should decline if the drought index becomes more variable from one year to the next. Positive values indicate convex (bowl-shaped) relationships, which predict abundance should increase if the drought index becomes more variable from one year to the next. On each panel, different letters indicate statistically significant differences in climate sensitivity among the populations in different ecosystem types within each rodent taxon, following post-hoc Tukey HSD tests

(8 of 10 taxa in Figure 4b, full results in Tables S4 and S5). Predicted losers under increasing climate variability were all in ecosystems in southern New Mexico (JRN); these were the hottest sites after Portal, AZ (Table S1; Figure 4b). In rank order, losers were *D. merriami* in creosote bush shrubland, *D. ordii* in black grama grassland, *Neotoma* in creosote bush shrubland, and *Onychomys* in black grama grasslands. The taxon predicted most likely to win under increasing variability in drought was *Chaetodipus* in the Arizona ecotone (POR), which had a convex CSF. Other taxon–ecosystem combinations with convex nonlinearities occurred in central New Mexico (SEV): *P. flavus* in black grama grassland, *Peromyscus* in the piñon-juniper woodland and creosote bush shrubland, and *D. merriami* in creosote bush shrubland.

Some rodent taxa were insensitive to variance in drought, at least over the observed climate windows of our time series. For *D. spectabilis*, abundance was never nonlinearly related to drought (absent from Figure 4b). *Neotoma* was predicted to decline with variability in drought only in creosote shrubland of southern New Mexico (JRN) during the first time series, and similarly for *Onychomys* in JRN grassland during the first time series (Figure 4b).

3. Temporal context dependency: Does the importance of climate to rodent abundance depend on a temporal shift in mean climate?

The detection of winner and loser rodent taxa differed between the two time series, indicating temporal inconstancy in rodent sensitivity to climate. During the wetter phase of the PDO (1995–2006), 29% of rodent populations were winners under drier conditions, and just 10% were losers (Figure 4a, linear relationships). During the drier phase (2004–2013), only 7% of populations were winners, and 50% were losers. Of the 18 populations continuously monitored during both time series, more than twice as many (39%) were losers during the second interval than during the first interval (17%), and 22% had status changes from neutral in the first time series to loser in the second (Figure 4a; Tables S4 and S5). For example, *D. ordii* in southern New Mexico black grama grasslands was a winner under drought during the first time series, but a loser in the second interval (Figure 4a). *Chaetodipus* spp. in the ecotone site in Arizona (POR) also flipped from being winners during the first time series to losers during the second. For *Chaetodipus*, *Peromyscus*, and some other cricetids, it was not possible to resolve species-level relationships with climate due to the lack of overlap in species-level identity across sites in the region (see Table S2). Thus, reordering of the relative abundances of species that differ in their drought tolerances could underlie some of these differences between PDO time periods.

In contrast to the increased detection of drought-losers during the second time series, ecosystem-modulation of winners and losers instead weakened during the dry phase of the PDO (2004–2013). Ecosystem type modified which rodent taxa were winners or losers under drought in nearly all cases during 1995–2006 (Figure 4; Table S4; SPEI × Site, exceptions were nearly significant: *Neotoma*, $p = 0.056$, *Peromyscus*, $p = 0.058$). While some ecosystem types still diverged during the second time series, these SPEI × site interactions were only significant for 30% of taxa (Figure 4; Table S4; SPEI × Site, Heteromyidae, $p = 0.057$; *D. ordii*, $p = 0.106$; *Chaetodipus*, $p = 0.398$; Cricetidae, $p = 0.553$; *Neotoma*, $p = 0.537$; *Onychomys*, $p = 0.383$).

Lastly, climate was relatively more important to abundance than plant productivity during the time series that covered the drier phase of the PDO (2004–2013). During 1995–2006, drought was often not the best predictor of rodent abundance, even though 40% of relationships between taxon abundance and drought were statistically significant (Table S5). Instead, plant productivity, as estimated by NDVI, outranked climate variables as the best regional predictor for 70% of rodent taxa in the first time series (Table S6, Model selection results). During the second time series (2004–2013), however, abundance was best explained by climate variables for 60% of rodent taxa, and in about half of these, climate variables lagged by 1 year were better predictors than current year's climate (Table S6), indicative of legacy effects. Model weights for the best vegetation or climate predictor for each rodent taxon effectively quantified these patterns. During 1995–2006, when the climate was wetter, models predicting abundance as a function of vegetation (NDVI) had mean model weights of 0.67, whereas model weights for climate variables averaged 0.29. During 2004–2013, the reverse occurred as the mean weight of models with the best climate predictor (0.54) was more than double the mean weight of models with the best vegetation predictor (0.24).

4 | DISCUSSION

We revealed three novel patterns in the dynamics of rodent communities across the Chihuahuan Desert-Southern Great Plains region of North America. First, rodent diversity and species richness declined at the regional scale over the two decades spanned by our monitoring programs. Second, whether a rodent species was a winner or loser under drought was strongly modulated by ecosystem type and the temporal phase of the Pacific Decadal Oscillation (wet or dry phase). Third, we provided the first analysis to rank small mammal species not only as winners or losers under drought but also as winners or losers under the increasing climate uncertainty caused by rising interannual variability in drought. Together, these results demonstrate the importance of considering both ecosystem type and temporal climate trends, such as major climate oscillations, when investigating the sensitivity of consumers to anthropogenic climate change.

4.1 | Declines in rodent diversity

Our results demonstrate that regional dynamics in rodent species diversity tracked climate and its impact on plant production, even while rodent community composition was predominantly influenced by ecosystem type (Figure 1). The losses in rodent species diversity documented here are consistent with prior studies on rodents in single dryland sites, in which rodent diversity or abundance declined under drought (Ernest et al., 2000; Greenville et al., 2012; Lima et al., 2008; Meserve et al., 1995, 2011; Yarnell et al., 2007; Zarybnicka et al., 2017). In addition, prior results of a geographic survey using space-for-time substitution (Brown & Ernest, 2002) correspond with the temporal patterns in our study in linking declines in rodent diversity and abundance with declines in taxa that were losers under drought. Losses in rodent diversity, and the clearly nonlinear temporal patterns in rodent abundance across the region (Figures 2b and 3b), reflect a prevailing regional influence of the Pacific Decadal Oscillation (PDO) on consumer community dynamics. Due to the PDO, the 1995–2006 period was a 15% wetter decade than 2004–2013. With the recent shift back to the warm (wet) phase of the PDO (Meehl et al., 2016), continued monitoring will be required to resolve whether regional declines in rodent diversity will continue into the future, or rebound, if the PDO brings a decade of increased precipitation to the region.

4.2 | Overriding influences of ecosystem type and time period on the sensitivity of consumers to climate

Whether a particular rodent species was a winner or loser under drought was greatly modulated by space (ecosystem type) and time. Spatial variation ranged from dry grasslands and shrublands to conifer woodland, and temporal variation reflected the phase of the PDO (Figure 4). Ecosystem type is likely to be a common filter on consumer responses to climate because features that differ, such as the identity of foundation plant species, vegetation structural complexity, seed resource availability, and fraction of bare ground, influence the distribution of microsites suitable for rodent breeding, foraging, thermoregulating, and escaping from predators (Kotler, 1984; Kotler & Brown, 1988; Longland & Price, 1991; Milling et al., 2017; Scheffers et al., 2014). Differences between grasslands and shrublands in rodent communities and their drought sensitivities are consistent with known ecological differences between dry grasslands and shrublands. Desert grasslands differ from shrublands in soils, plant species composition, vegetation structure, and responsiveness to precipitation pulses (Le Houreu, 1984). For example, shallow-rooted grasses respond quickly to small rain events, whereas deep-rooted shrubs respond more to heavy rains that infiltrate deep soil layers (Reynolds et al., 2004; Schlesinger et al., 1990). In addition, the productivity of C_4-dominated grasslands can be driven primarily by summer rains, whereas C_3-dominated shrublands, such as the creosote bush shrubland studied here, typically respond more to winter precipitation than summer rains (Muldavin et al., 2008). Such dynamics in seasonal precipitation and plant productivity should shape the spatiotemporal patterns of rodent granivory and herbivory, even for geographically adjacent plant community types. Furthermore, ecosystem heterogeneity can increase rodent species richness by increasing the patchiness of food resources or predator-free space, particularly for rodent species that specialize on different microhabitats (Abramsky, 1988; Kraft & Stapp, 2013). Habitat structure can also influence how climate variables, such as precipitation or extreme heat, generate stress (Nowakowski et al., 2018; Sears et al., 2016) and constrain suitable foraging conditions for consumers (Murray & Smith, 2012). Habitat differences in the form of microhabitats can be exploited by fossorial rodents living in drylands. Underground burrowing systems offer a buffering zone which can help small mammals living in warming and drying conditions to adapt to climate stress (Riddell et al., 2021).

While some rodent species had relatively consistent responses to drought across ecosystems (Figure 4, *D. ordii*, *D. spectabilis*, *Onychomys*), 55% of cases flipped from winner to loser status among ecosystem types, likely due to their documented microhabitat preferences or ability to retreat to refugia during drought (Lemen & Rosenzweig, 1978; Price & Waser, 1985; Schooley et al., 2018). For example, kangaroo rats (*Dipodomys*) prefer large areas of bare ground with little canopy cover, whereas *P. flavus* prefer grass cover (Bock et al., 2006; Jones et al., 2003; Lemen & Rosenzweig, 1978). If drought opens bare ground in some habitats more than others, this could drive stronger positive relationships between *Dipodomys* abundance and drought in those ecosystems. Similarly, ecosystem-specific differences in the influence of drought on seed resources, such as from annual plants (Beatley, 1969; Lightfoot et al., 2012; Yeakel et al., 2020), may explain winner–loser flips, as may proximity of the monitored population to the species' range edge. For example, *D. merriami* was a winner under drought near the center of its latitudinal range within shrubland ecosystems of southern New Mexico, but it was a loser in central New Mexico shrublands, where it approaches its northern range limit. Additionally, while *P. flavus* was a winner under drought in central New Mexico grassland with mean annual temperature of 14.0°C, it flipped to a loser in the warmer grassland of southern New Mexico (mean annual temperature of 15.6°C). Thus, species sensitivity to climate will depend on how the ecosystem modulates thermal or desiccation thresholds. Future work to characterize fine-scale differences among ecosystems could generate new hypotheses on which aspects of the ecosystem most strongly influence species' climate sensitivities.

4.3 | Consumer sensitivity to increasing unpredictability in climate

Climate sensitivity functions yield predictions on how species will respond to amplified variance in climate (Rudgers et al., 2018), an element of climate change projected to increase for most regions (Cook et al., 2019; IPCC, 2013; Singh et al., 2013). As with winner–loser status under increasing drought, rodent sensitivities to increasing variance in drought were also strongly ecosystem-specific (80% of the significant relationships), although there was less divergence between the PDO time periods. Interestingly, predicted losers under increasing climate variability were not constrained to a single rodent family. However, all cases occurred in ecosystems located in southern New Mexico, which were among the warmest sites in our region.

This finding could be explained by a reduction in grass productivity caused by increased precipitation variability reported by previous studies conducted in this region (Gherardi & Sala, 2015). In addition, our results predicted that some rodents may benefit as climates become more variable, in particular *Chaetodipus* spp. in Arizona, *P. flavus* in black grama grasslands of central New Mexico, *Peromyscus* in piñon-juniper woodlands, and both *D. merriami* and *Peromyscus* in creosote bush shrublands of central New Mexico. To our knowledge, these results provide the first predictions on how rodent community structure may respond to future increases in interannual climate variability.

4.4 | An increasingly important role of climate

The relative importance of climate versus plant productivity in predicting rodent abundances strengthened during the second time series, suggesting an increasing role for the direct effects of climate in explaining rodent abundances during the dry phase of the PDO. Specifically, the Normalized Difference Vegetation Index (NDVI) was the best predictor of rodent abundance for 70% of rodent taxa during the first time period (1995–2006), whereas climate variables outranked vegetation for 60% of taxa during the second time period (2004–2013). In most cases, the drought index better explained variation in rodent abundance when it was lagged by at least a season. These results are consistent with previous studies on rodents, documenting influences of climate conditions from the previous year (Baez et al., 2006; Jaksic et al., 1997; Meserve et al., 2011). Indeed, rodent populations are known to increase in pulses after a season of high rainfall, and heteromyids, specifically, rely on seeds produced during times of greater primary production, thus driving spikes in abundance in the following year (Ernest et al., 2000; Hernandez et al., 2005; Lightfoot et al., 2012; Previtali et al., 2009; Schooley et al., 2018).

4.5 | Study limitations

It is often the case with ecological field research that perfect replicates are complicated by real-world variation. First, across the region, sites differed somewhat in trapping methods and timing of trapping (Table S1). However, it is unlikely that these small differences affected the detection of ecosystem-based context dependency, because all sites had designs that adequately estimated local rodent community composition over time and because rodent composition clearly converged within ecosystem types (Figure 1), despite any site-scale differences in methodology. Second, our study capitalized on the high natural variability in climate and rodent abundance in dryland ecosystems to draw predictions from observational data. However, experiments conducted at the scale of rodent territories, such as rain-out shelters or water additions, would be the best solution to pinning changes in rodent abundance or diversity on changes in climate.

Third, our results for rodent abundances and NDVI overlooked fine-scale species-specific interactions between rodents and plants. We used NDVI because it was the only vegetation variable measured consistently across the diverse sites. However, fine-scale plant species composition data would improve the ability to rank the relative importance of climate and plant predictors of rodent abundance. Desert rodent species do not respond to plant production booms uniformly, but rather specific rodent taxa track particular plant species. For example, at JRN, rodent densities correlated positively with annual grasses (e.g., *Bouteloua barbata*, *B. aristoides*) after 6–18 month time lags, rather than to any other plant species or to all plants combined (Lightfoot et al., 2012). In contrast, an analysis of other sites from that region, found that total plant biomass was the best predictor of heteromyid abundance (Schooley et al., 2018). In addition to the complexity introduced by plant species composition, proximity of sites to drought refugia could create site-specific climate sensitivities by affecting rodent core-transient dynamics (Schooley et al., 2018; Stevens & Tello, 2012).

Fourth, the weaker relationships between rodents and NDVI detected during the second time series could be improved by adding resolution of individual plant species responses to our datasets; however, temporal variation may also indicate temporal changes in rodent food preferences, rather than food plant responses to climate. For example, while heteromyids are largely granivores, they also consume leaves (Kerley et al., 1997). Cricetids, such as *Peromyscus*, regularly feed on plant seeds and foliage; *Neotoma* feed mostly on leaves, while *Onychomys* feed largely, but not exclusively, on insects (Hope & Parmenter, 2007; Price & Joyner, 1997). In addition, *Onychomys* abundances are the hardest to estimate accurately because these species forage at large spatial scales (Frank & Heske, 1992; Stapp, 1999). Similarly, heteromyids prefer large-sized seeds when foraging (Dylewski et al., 2020; Price, 1983) but that preference can vary with rodent species richness and interspecific competition (M'Closkey, 1978, 1980). Better resolution of the linkages between specific rodent diets and plant species dynamics (e.g., Yeakel et al., 2020) will improve the ability to predict rodent declines under changing plant communities and climates.

4.6 | Future directions

Expanding the time series to a third decade (2013–2022) to capture the warm phase of PDO would improve predictions on how rodent diversity, composition, and abundance track ongoing climate change. During 2013–2016, the PDO began to transition back to the warm phase, which delivers more precipitation to the southwestern US (Meehl et al., 2016). Continued monitoring would enable the first opportunity to replicate the warm phase of the PDO. Other research avenues include detailed rodent physiology in relation to diet (reliance on seeds versus leaves and C_3 versus C_4 plants, Yeakel et al., 2020) as well as coupling rodent data to climate change experiments to better understand how landscape resources will change for rodent communities under no-analog climates of the future. Finally, we suggest linking rodent traits to climate sensitivities. For example, a recent modeling study (Yeakel et al., 2020) identified 50 g as a key threshold for body mass at which caching rodents become less sensitive to increasing variability in food resources caused by stochastic precipitation regimes. In our study, the large-sized *D. spectabilis* (115 g) was a loser under drought in central New Mexico grasslands (see also Moses et al., 2012) and not significantly sensitive to variability in drought (Figure 4). This finding is also supported by previous research in which a congener, the giant kangaroo rat (*D. ingens*), declined in abundance during a single severe drought event in California (Prugh et al., 2018).

Variation in the reproductive potential of rodent species that occupy different ecosystems is likely a key factor underlying differences in rodent population responses to rainfall and plant production (Brown & Harney, 1993; Dickman et al., 1999; Letnic et al., 2011; Lightfoot et al., 2012; Perrin & Kotler, 2005; Reichman & van de Graaff, 1975). Linking population traits, such as body size and natality, or species traits, such a range size and range limits, may help to explain intraspecific differences in climate sensitivities and resolve why some populations (even within the same species) are winners versus losers under drought.

5 | CONCLUSION

Regional long-term monitoring of 12 sites across the southwestern US revealed declines in the abundance and biodiversity of small mammals (1995–2013). Our climate sensitivity function approach developed novel metrics to identify winners and losers under drought and to newly predict how consumers respond to future changes in the variability of climate. We revealed novel patterns of spatial context dependency, in which ecosystem type modulated whether species were winners or losers under climate change, as well as temporal context dependency, in which species climate sensitivities depended on the temporal phase of a major climate oscillation. Together, these results highlight the importance of incorporating spatial variation in ecosystem type as well as temporal differences in average climate into our understanding of how consumers respond to climate change.

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DATA AVAILABILITY STATEMENT

The full data package that supports the findings of this study, including R scripts, is openly available through the Environmental Data Initiative (Rudgers et al., 2021) at https://doi.org/10.6073/pasta/f183393c8060f407f32d323491247f35.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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