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RESEARCH ARTICLE

Dryland state transitions alter trophic interactions in a predator–prey system

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Abstract

1. Environmental change is expected to alter trophic interactions and food web dynamics with consequences for ecosystem structure, function and stability. However, the mechanisms by which environmental change influences top-down and bottom-up processes are poorly documented.
2. Here, we examined how environmental change caused by shrub encroachment affects trophic interactions in a dryland. The predator–prey system included an apex canid predator (coyote; *Canis latrans*), an intermediate canid predator (kit fox; *Vulpes macrotis*), and two herbivorous lagomorph prey (black-tailed jackrabbit, *Lepus californicus*; and desert cottontail, *Sylvilagus audubonii*) in the Chihuahuan Desert of New Mexico, USA.
3. We evaluated alternative hypotheses for how shrub encroachment could affect habitat use and trophic interactions, including (i) modifying bottom-up processes by reducing herbaceous forage, (ii) modifying top-down processes by changing canid space use or the landscape of fear experienced by lagomorph prey and (iii) altering intraguild interactions between the dominant coyote and the intermediate kit fox. We used 7 years of camera trap data collected across grassland-to-shrubland gradients under variable precipitation to test our a priori hypotheses within a structural equation modelling framework.
4. Lagomorph prey responded strongly to bottom-up pulses during years of high summer precipitation, but only at sites with moderate to high shrub cover. This outcome is inconsistent with the hypothesis that bottom-up effects should be strongest in grasslands because of greater herbaceous food resources. Instead, this interaction likely reflects changes in the landscape of fear because perceived predation risk in lagomorphs is reduced in shrub-dominated habitats. Shrub encroachment did not directly affect predation pressure on lagomorphs by changing canid site use intensity. However, site use intensity of both canid species was positively associated with jackrabbits, indicating additional bottom-up effects. Finally, we detected interactions between predators in which coyotes restricted space use of kit foxes, but these intraguild interactions also depended on shrub encroachment.

5. Our findings demonstrate how environmental change can affect trophic interactions beyond traditional top-down and bottom-up processes by altering perceived predation risk in prey. These results have implications for understanding spatial patterns of herbivory and the feedbacks that reinforce shrubland states in drylands worldwide.

KEYWORDS
canid predators, Chihuahuan Desert, intraguild predation, lagomorph prey, landscape of fear, shrub encroachment, structural equation modelling, trophic interactions

1 | INTRODUCTION

Predicting how global change will modify top-down and bottom-up processes across food webs is a key challenge in ecosystem ecology (La Pierre & Hanley, 2015; Whalen et al., 2013). Drivers of global change are expected to disrupt predator–prey dynamics and trophic interactions (Tylianakis et al., 2008), with consequences for the organization of ecological communities (Deguines et al., 2017; Estes et al., 2011; Wong & Candolin, 2015). However, it remains unclear how global change will affect the relative importance, variability and interdependence of top-down and bottom-up processes (La Pierre & Hanley, 2015). Therefore, understanding how global change will impact trophic interactions is necessary to predict how ecosystems will respond to novel conditions and to guide conservation efforts (Tylianakis et al., 2008).

The conversion of grasslands to shrub-dominated states in arid and semi-arid landscapes (hereafter drylands) is a significant form of ecosystem change globally (Eldridge et al., 2011). Although the effects of shrub encroachment on biodiversity have been investigated (e.g. Blaum et al., 2007; Stanton et al., 2018; Whitford, 1997), few studies have focused on how dryland state transitions affect trophic interactions. Consequently, ecologists have a limited understanding of how changes in trophic processes (e.g. spatial patterns of herbivory) may reinforce shrubland states (Bestelmeyer et al., 2007; Gordon et al., 2017). Improved understanding of how shrub encroachment affects trophic relationships should illuminate feedback mechanisms that control shrub expansion (Roth et al., 2009).

Shrub encroachment may strengthen or weaken trophic interactions through multiple mechanisms. For example, drylands experience strong bottom-up effects through rainfall-driven pulses of plant productivity, triggering population irruptions at higher trophic levels (i.e. the pulse-reserve paradigm; Letnic & Dickman, 2010; Reynolds et al., 2004; Schooley et al., 2018). However, shrub encroachment decreases the productivity of nutrient-rich plants such as graminoids and forbs (Huenneke et al., 2002; Ratajczak et al., 2012), which is expected to diminish the availability and quality of food for herbivore prey (Hopcraft et al., 2010; Riginos & Grace, 2008). This reduction of forage in shrublands could disrupt bottom-up control in herbivore populations, with knock-on effects for higher trophic levels and the potential to modify energy exchange in dryland food webs (Goeke & Armitage, 2021).

Alternatively, shrub encroachment may affect top-down control by altering predator pressure or perceived predation risk in prey (i.e. landscape of fear; Gaynor et al., 2019). For example, increases in shrub cover can alter predator abundances (Blaum et al., 2007), potentially intensifying or diminishing direct top-down effects for prey. Shrub encroachment could also modify the landscape of fear that prey experience (Atuo & O'Connell, 2017; Loggins et al., 2019; Wagnon et al., 2020), indirectly affecting prey abundance patterns by eliciting changes in their behaviour and habitat use (Laundré et al., 2014). Indeed, behavioural adjustments by prey to perceived predation risk often manifest through habitat shifts to less risky areas, even if those areas are of low resource value (Hopcraft et al., 2010). Consequently, a key prediction generated by the landscape of fear model is the aggregation of prey in habitats perceived as less risky, irrespective of resource availability (Gaynor et al., 2019; Palmer et al., 2022). Whether from direct or indirect processes, such shifts in top-down interactions caused by shrub encroachment could trigger trophic cascades in drylands (Fisher et al., 2021; Gordon et al., 2017; Henke & Bryant, 1999) altering ecosystem functions such as primary production and nutrient cycling (Monk & Schmitz, 2022).

Lastly, intraguild competition and predation are common biotic interactions between predators (Holt & Polis, 1997), and shrub encroachment could alter predator–predator relationships because of changes in habitat structure (Janssen et al., 2007) or productivity gradients (Greenville et al., 2014). For example, apex predators can select habitats with high shrub cover because of preferred thermal cover or greater prey availability, displacing subordinate predators to less favourable and unproductive areas (Lonsinger et al., 2017; Thompson & Gese, 2007). Conversely, subordinate predators may find refuge or be able to exploit resources in shrublands better, thereby escaping competition with apex predators (Goldberg et al., 2022). In either case, changes in intraguild interactions caused by shrub encroachment could influence lower trophic levels with consequences for food web dynamics (Finke & Denno, 2006).

Here, we evaluated how shrub encroachment affects predator–prey and predator–predator dynamics, focusing on a canid-lagomorph community in the Chihuahuan Desert. Specifically, we examined trophic interactions between an apex canid predator (coyote; *Canis latrans*), an intermediate canid predator (kit fox; *Vulpes macrotis*), and two herbivorous lagomorph prey (black-tailed jackrabbit;

Lepus californicus, and desert cottontail; *Sylvilagus audubonii*) across shrub encroachment gradients. Lagomorphs can play a critical role in the Chihuahuan Desert by changing composition and diversity of plant species through selective herbivory on grasses (Abercrombie et al., 2019; Havstad et al., 1999), and canids can indirectly influence the structure of faunal communities through top-down processes (Henke & Bryant, 1999). Therefore, knowledge of how shrub encroachment modifies trophic interactions between canid predators and lagomorph prey should improve our understanding of processes affecting ecological state dynamics and the recovery of perennial grasses (Gordon et al., 2017; Roth et al., 2009). We tested a priori hypotheses on how shrub encroachment affected trophic interactions (see Figure 1) by analysing 7 years of camera trap data collected across grassland-to-shrubland gradients under variable precipitation within a structural equation modelling (SEM) framework.

2 | METHODS

2.1 | Study area

Our study area was within the Jornada Basin Long Term Ecological Research (LTER) site located in the Chihuahuan Desert of southwestern New Mexico, USA (32°35′ N, 106°51′ W) (Figure S1a) and encompassed ~200 km^2 of the Jornada LTER site. The area is a warm, high elevation (1334 m a.s.l.) desert with a long-term mean annual precipitation of 250 mm. Precipitation occurs mainly as monsoonal rain during summer (July–October) with high spatial and annual variability (Huenneke & Schlesinger, 2006).

The Jornada LTER site has experienced widespread changes in ecosystem state caused by shrub invasion (Peters et al., 2006, 2012) and is an ideal system for studying the effects of state transitions on trophic processes. The extent of historical grasslands at the Jornada LTER site has declined sharply over the past 150 years because of the encroachment of honey mesquite (*Prosopis glandulosa*), a native shrub (Grover & Musick, 1990; Peters et al., 2006). Grassland-to-shrubland transitions were triggered by overgrazing by cattle during prolonged drought interacting with multiple feedback mechanisms (Bestelmeyer et al., 2018; Peters et al., 2006).

Our study was conducted on the basin floor sand sheet geomorphic unit where honey mesquite is the dominant shrub species (Monger et al., 2006). Other shrubs included creosotebush (*Larrea tridentata*), tarbush (*Flourensia cernua*) and yucca (*Yucca* spp.). Common perennial grasses included black grama (*Bouteloua eriopoda*), dropseed (*Sporobolus* spp.), threeawn (*Aristida* spp.) and tobosa (*Pleuraphis mutica*). We obtained permission to conduct this

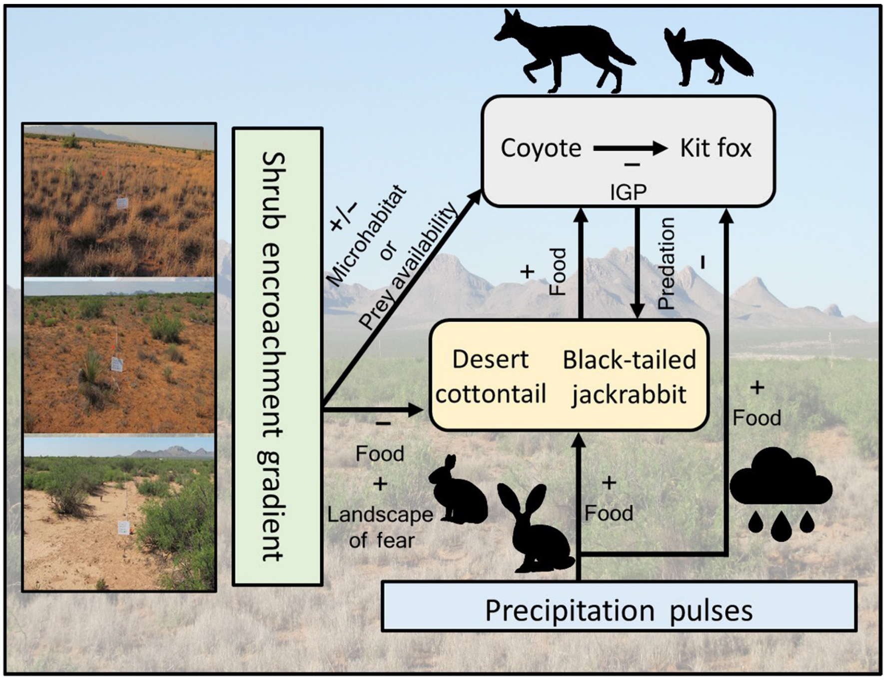

FIGURE 1 Conceptual path model describing how shrub encroachment and precipitation affect trophic interactions of lagomorphs and canids at the Jornada Basin Long Term Ecological Research site, New Mexico, USA. 'Precipitation pulses' represent bottom-up effects predicted under the pulse-reserve paradigm (Reynolds et al., 2004). 'Predation' represents top-down effects of canid predators on lagomorph prey. The 'shrub encroachment gradient' represents different ecological states (grasslands, ecotones and shrublands), which could modify bottom-up effects by altering food availability for lagomorphs (Hopcraft et al., 2010). Alternatively, shrub encroachment could modify top-down effects through changes in abundances or habitat use of canid predators (Blaum et al., 2007) or by altering the landscape of fear that lagomorph prey experience (Wagnon et al., 2020). 'IGP' represents intraguild predation between the dominant coyote and the subordinate kit fox (Robinson et al., 2014). Expected positive and negative effects are indicated with '+' and '−', respectively. The background photo shows the landscape of our study system in the Chihuahuan Desert.

research at the Jornada Basin LTER site from the program manager. Ethical approval for this study was provided by the Institutional Animal Care and Use Committee at New Mexico State University (#2309000636).

2.2 | Sampling design and photographic data

We modelled trophic interactions between canid predators and lagomorph prey using photographic data collected from a network of 24 sites (Figure S1b). Each site was 3 ha (100 × 300 m), monitored with two camera traps and represented various degrees of shrub encroachment. Hence, we used photographic data collected from 48 camera traps distributed across 24 3-ha sites for our investigation. All study sites are currently or were formerly dominated by perennial grasses that have been invaded to varying degrees by honey mesquite. Thus, the 24 sites represented natural habitat transitions from perennial grasslands to mesquite shrublands (Bestelmeyer et al., 2007; Schooley et al., 2018; Svejcar et al., 2019).

We implemented camera surveys in 2014 by establishing 15 sites within five core pastures (three sites per pasture). The pastures were 5–10 km apart. Within each pasture, we selected sites representing three ecological states based on the percentage of shrub and grass cover (grassland, ecotone and shrubland; Bestelmeyer et al., 2007). In 2015, we expanded our survey effort to include nine additional sites that also represented varying degrees of mesquite encroachment. Collectively, these 24 sites offered a wide range of grass cover (mean = 14.5%; range: 1.7%–50.2%) and shrub cover (mean = 12.3%; range: 1.5%–27.1%). The minimum distance between the centre of a 3-ha site and the centre of its nearest neighbour varied from 185 to 3062 m (mean = 1084 m; median = 522 m). Because some sites were not far apart relative to the movement capacities of our focal species, we tested for spatial autocorrelation in residuals from our statistical models (see below).

We deployed two motion-triggered cameras (Trophy Cam models, Bushnell) at each site separated by 187 m ($n = 48$ camera traps at 24 sites; Figure S1c). We treated the paired cameras on each site as a single sampling unit for our analyses by combining data from both camera traps, which were located in similar vegetation. We affixed camera traps to fenceposts 0.5 m above-ground, and programmed cameras to take three photographs in a short burst with a 30-s delay before rearming. All camera sites were unbaited. Cameras were active from July through October or November each year from 2014 to 2020 (Table 1).

All photographs were relabelled, sorted and stored using the procedures and software programs described by Sanderson and Harris (2013). We considered photographs to be independent if sequential photographs of a species at a camera site were separated by >60 min. To assess if using a 60-min threshold for independence potentially altered results compared to using a narrower time window, we measured the correlation between the number of photos for species from datasets using 60 and 30-min thresholds. We used photos from all years, sites and our four focal species for comparisons. The 60 and 30-min datasets were strongly correlated ($r = 0.99$ and $p < 0.001$ for all species comparisons), so our choice of a 60-min threshold is unlikely to have influenced the results.

We used photographic detection data to describe patterns of site use intensity for species. Specifically, we divided the number of independent photos of a species at a site by the total number of trap nights (i.e. the number of 24-h cycles cameras were active at a site) multiplied by 100. This index accounts for variation in sampling effort and represents the number of independent photo events per 100 camera trap nights (O'Brien, 2011). We used the intensity of site use for each species as the response variable in our modelling effort.

Site use intensity derived from camera traps have been mechanistically linked to abundances in multiple taxa (Kays et al., 2020; Palmer et al., 2018), including canids and lagomorphs (Jensen et al., 2022; Kenney et al., 2024). Given the spatial scale of our sampling, however, our intent was to use this measure to explore how relative habitat use changes across shrub encroachment and precipitation gradients for canids and lagomorphs. Site use intensity by a species can reflect changes in the number of individuals in the area (demographic response), how often individuals use that site (habitat choice) or both (Sollmann, 2018). However, the net result is the same

TABLE 1 Annual survey periods, number of trap nights and number of independent photographs for camera trap surveys conducted at the Jornada Basin Long Term Ecological Research site, New Mexico, USA, 2014–2020.

Year	Survey dates	Survey length (days)	Total trap nights (site-level mean ± SD)	No. of independent photos			
				Jackrabbit	Cottontail	Coyote	Kit fox
2014	July 13–October 31	111	2753 (184 ± 38)	2014	131	129	55
2015	July 14–October 13	92	3540 (148 ± 42)	3324	945	85	50
2016	July 16–October 26	103	3763 (157 ± 44)	3049	1356	119	78
2017	July 13–October 31	111	4547 (189 ± 43)	5572	2655	255	18
2018	July 16–October 20	97	4035 (168 ± 29)	6201	1966	554	61
2019	July 13–November 07	118	4910 (205 ± 33)	5453	736	345	34
2020	July 14–November 10	120	4901 (204 ± 29)	2450	304	315	29
Total	–	752	28,449 (4064 ± 730)	28,063	8093	1802	325

Note: The number of sites surveyed was 15 in 2014 but was increased to 24 for all subsequent years.

in terms of potential increases in herbivore pressure or top-down pressure by carnivores. Therefore, site use intensity should be a dependable proxy for capturing spatiotemporal variation in trophic interactions between predator and prey species (Keim et al., 2019).

2.3 | Vegetation cover and precipitation

We quantified vegetation cover at camera sites in 2017 using line-point intercept methods (Herrick et al., 2005). We established five 50-m transects within each 3-ha site that were offset from each other in a staggered formation of 20 m (Figure S1c). We measured vegetation cover at 25-cm intervals along each transect (200 points) and then averaged values across all transects to estimate shrub cover for sites.

Our snapshot sampling may have missed slight changes in vegetation cover during the 7-year study. However, changes in canopy cover of mesquite, the dominant shrub, were expected to be marginal because of its long-lived nature (i.e. 200 years), slow growth rates and low population turnover (Huenneke & Schlesinger, 2006; Peters & Gibbens, 2006). Hence, we used measurements of shrub cover collected in 2017, at the midpoint of our study, to quantify structural characteristics of the ecological state at each site.

We characterized the grassland-to-shrubland gradient in our modelling using the percentage of shrub cover instead of grass cover for several reasons. First, shrub cover is the dominant indicator of ecological state on this landscape (Bestelmeyer et al., 2016, 2018). Second, shrub cover determines the amplitude of spatiotemporal variation in grass cover; grass cover is constrained by shrubs (Bestelmeyer et al., 2018). Third, it would be uninformative to use grass cover collected from a single year because of strong annual variation in grass cover driven by rainfall (Huenneke & Schlesinger, 2006; Peters & Gibbens, 2006). Finally, model selection procedures confirmed that the SEM with shrub cover outperformed alternative SEM structures using different vegetation indicators (Table S1).

Although we did not have annual measurements of herbaceous vegetation on all 24 sites, above-ground net primary production (ANPP) for grasses and forbs is measured annually on a subset of sites (nine of the 24; Bestelmeyer & Schooley, 2024). A complementary analysis revealed that annual summer precipitation explained a considerable amount of variation in herbaceous ANPP on these sites ($R^2 = 0.76$; Figure S2), supporting extensive research linking local rainfall with annual biomass production of grasses and forbs at the Jornada LTER site (Huenneke & Schlesinger, 2006; Lightfoot et al., 2011; Peters et al., 2012; Schooley et al., 2018). Thus, we evaluated bottom-up responses in our system by including precipitation (mm) as a proxy for food resources for herbivores, which is a more suitable measure than the 1-year measurement of grass cover collected during the midpoint of the study. We measured precipitation using the closest rain gauge to each site (mean distance = 0.93 km; range: 0.16–2.31 km). Annual precipitation was variable ranging from 174 mm in 2016 to 301 mm in 2017 (Figure S3).

We included summer precipitation (May–October) during the current year as a predictor of bottom-up effects for all species. We chose a single period because the inclusion of different lag times (e.g. $t-1$, $t-2$) would have made our SEM increasingly complex. Furthermore, complementary analyses revealed that summer precipitation for the current year was a strong predictor of jackrabbits and there was competitive support for cottontails (Table S2). Finally, including different time lags in models did not outperform the SEM with current year summer precipitation (Akaike's information criterion [AIC]: current year summer precipitation = 1468.26, 1-year lag precipitation = 1493.84, and 2-year lag precipitation = 1481.67).

2.4 | Statistical approach and conceptual path model

To evaluate our hypotheses of how shrub encroachment could affect trophic interactions among predators and prey (Figure 1), we used a piecewise SEM framework (Lefcheck, 2016; Shipley, 2009). Piecewise SEM translates casual pathways in a directed graph to a set of linear equations, which are then individually assessed to optimize the solution for the response variable (i.e. local estimation, Grace et al., 2015). Piecewise SEM allows for fitting a wide range of variance structures and the inclusion of random effects. Moreover, the direction, sign and relative strength in our SEM allow us to test alternative hypotheses on how shrub encroachment affects trophic processes. We created a conceptual model (Figure 1) to represent the hypothesized relationships between shrub encroachment (per cent shrub cover), precipitation pulses (summer rainfall) and lagomorph and canid site use. We incorporated bottom-up and top-down processes in our SEM because their interaction can impact dryland ecosystems (Holmgren et al., 2006; Meserve et al., 2003).

We hypothesized positive relationships among rainfall, lagomorph prey and canid predators if simple bottom-up processes drive trophic relationships as predicted by the pulse-reserve-paradigm (Reynolds et al., 2004). However, it may take 1–2 years after increases in prey populations to detect a demographic response in canid predators (Bartel et al., 2008; Prugh et al., 2005). Thus, we also evaluated lagged bottom-up responses in canids using data for lagomorph site use from the previous year. Bottom-up processes are represented by pathways from precipitation to lagomorphs and canids and an additional pathway from lagomorph prey to canid predators. The direct pathway from precipitation to canid predators corresponds to bottom-up pulses that affect food resources other than lagomorphs (e.g. insects and honey mesquite fruits). However, shrub encroachment is hypothesized to reduce high-quality forage available for herbivores and, therefore, influence bottom-up effects (Hopcraft et al., 2010; Riginos & Grace, 2008). In accordance with the nutrient-availability hypothesis, we predicted that bottom-up effects would be strongest in grasslands where forage quality is highest (i.e. graminoids and forbs; Peters et al., 2012).

In contrast, canid predators can limit abundances of lagomorph prey by exerting direct top-down effects through predation (Henke & Bryant, 1999; Krebs et al., 2001). We therefore included a pathway from canids to lagomorphs and expected a negative association between predators and prey. Additionally, indirect top-down effects on prey abundance and primary producers may result from prey responding to spatial variation in perceived predation risk (Gaynor et al., 2019). The landscape of fear hypothesis predicts that prey should shift habitat use to less risky patches, even if those patches are of low resource value. A previous study at the Jornada Basin LTER site clearly demonstrated that perceived risk in both lagomorph species declined in shrubbier habitat (Wagnon et al., 2020), which were characterized by low grass and forb cover (i.e. low resource value for herbivore prey). Accordingly, if lagomorphs make habitat choices based on variability in perceived predation risk, we expect intensity of site use to be higher in shrub-dominated habitats perceived as less risky. This pattern may be particularly pronounced during wet years when forage production is less limiting but attenuated in dry years when high quality forage is more abundant in grasslands (Schooley et al., 2018). To test the nutrient availability and landscape of fear hypotheses, we included an interaction pathway between shrub cover and precipitation on lagomorph prey. Support for either hypothesis will depend on the strength and sign of the interaction pathway.

Finally, we tested intraguild interactions between the dominant coyote and the subordinate kit fox (Robinson et al., 2014; Schooley et al., 2021). Coyotes decrease survival and alter habitat use in kit foxes through intraguild interference and predation (Nelson et al., 2007; White & Garrott, 1997). Hence, we included a direct path from coyotes to kit foxes and expected a negative relationship between predators. However, kit fox habitat use may depend on coyote densities and changes in shrub cover (Nelson et al., 2007; Schooley et al., 2021; Thompson & Gese, 2007). Therefore, we tested if the effect of coyote on kit fox depended on shrub cover by including an interaction pathway from both variables to kit foxes.

2.5 | Linear mixed modelling

As an initial step to support our conceptual path model, we fit separate component models for jackrabbits, cottontails, coyotes and kit foxes using linear mixed-effects models (Deguines et al., 2017). We included site identity (categorical variable with 24 levels) as a random effect for all models to account for our repeated measures design (6–7 measures per site). We graphically checked the assumptions of the model by assessing the variance of residuals against fitted values, covariates and sampling year. Subsequently, to meet model assumptions and improve model fit for all species, we log-transformed site use intensity and included a variance structure with year as a covariate (i.e. each year was allowed to have a different variance; Zuur et al., 2009). We used AIC to select the structure that best improved the fit of the model (Burnham & Anderson, 2002). We also checked for spatial autocorrelation among sites by performing a Global Moran's *I* test on the residuals of the best-supported model for each species using inverse distance weighting.

For all linear mixed models, we specified a full model for each species containing all hypothesized predictor variables (Figure 1; Table S3). We also included 'shrub cover × predictor' interaction terms to evaluate whether the strength of trophic interactions depended on the ecological state. Shrub cover and precipitation were standardized to improve interpretations of interactive effects. We then simplified each model by performing a stepwise removal of two-way interactions with weak evidence ($p > 0.05$) using marginal *F*-tests (Pinheiro & Bates, 2000). We kept all fixed effects in each component model for further evaluation in the SEM. We used maximum likelihood estimation to compare models and restricted maximum likelihood to estimate coefficients for the final model (Zuur et al., 2007). We assessed multicollinearity in each component model using variance inflation factors (VIF). All component models had VIFs <3. The sample size for each model was 159.

2.6 | Structural equation modelling

We developed an initial piecewise SEM by combining the four component models from our mixed-effects modelling stage. We tested the overall fit of the SEM and whether unspecified paths should be included by applying the Shipley *d*-separation test (i.e., Fisher's *C* statistic; Lefcheck, 2016). A Fisher C score with $p > 0.05$ indicates that there are no missing paths and that the SEM structure was correctly specified. The original SEM had an inadequate fit (Fisher's $C = 70.56$, $p < 0.001$), and a path was missing between jackrabbit and cottontail (i.e. significant, non-zero coefficient: $\beta = 0.59$). Therefore, we included correlated errors between jackrabbit and cottontail site use intensity to account for unresolved correlations (Grace et al., 2010).

We optimized the model by removing paths with little evidence ($p > 0.05$), starting with the path with the highest *p* value, continuing stepwise and evaluated the effect of path removal on AIC (Deguines et al., 2017; Elliot Noe et al., 2022). We selected the model with the lowest AIC score. Our final SEM met the recommendation that the ratio of sample size to the number of estimated paths is >5 (Grace et al., 2015). We provided standardized and unstandardized path coefficients for each component model.

Finally, we tested for a 1-year response lag in canids to lagomorphs by conducting a separate SEM using a truncated dataset (2015–2020). The SEM structure was identical to the final model without lag effects (i.e. all other fixed and random effects were the same), except we used lagomorph site use intensity from the previous year as a predictor for canid site use intensity in the current year. We could not directly compare the SEMs with and without lags because the response variable for lagomorphs differed between model structures (i.e. current versus previous year site use intensity data). We therefore used AIC to compare univariate linear mixed-effects models with previous year or current year lagomorph site use intensity as predictors of canid site use intensity. This test allowed for a direct assessment of whether canid responses to prey were lagged.

We conducted all statistical analyses using R 4.2.1 (R Core Team, 2022). We used the package *nlme* (Pinheiro et al., 2022) to fit individual mixed models and the package *piecewiseSEM*

(Lefcheck, 2016) to fit component models in a SEM framework. To aid in interpretation of interaction effects, we generated plots using marginal means calculated using the package *ggeffects* (Lüdecke, 2018).

3 | RESULTS

3.1 | Camera trap surveys

Our survey effort resulted in 28,449 trap nights (Table 1). We detected jackrabbit the most frequently, followed by cottontail, coyote and kit fox (Table 1). There was marked spatiotemporal variation in patterns of species site use intensity, with use of both prey species and coyotes peaking in 2017 or 2018 coinciding with high rainfall (Figure 2 and Figure S3).

3.2 | Structural equation modelling

Our final SEM indicated a good fit to the observed data (Fisher's $C=0.82$, $p=0.66$) and explained moderate variation in site use intensity of jackrabbits ($R^2=0.27$), coyotes ($R^2=0.19$) and kit foxes ($R^2=0.19$), with lower explanatory power for cottontails ($R^2=0.05$). Compared to our initial SEM, a non-significant path was removed (cottontails to coyotes), which improved the model fit (Table S4). There was weak evidence for interaction effects between shrub cover, precipitation and lagomorph prey on canid predators and those interaction terms were dropped from component models (Table S3). Finally, the model residuals showed weak evidence of spatial autocorrelation for all species during most years (see Table S5), indicating that spatial dependencies were not an issue after accounting for covariates.

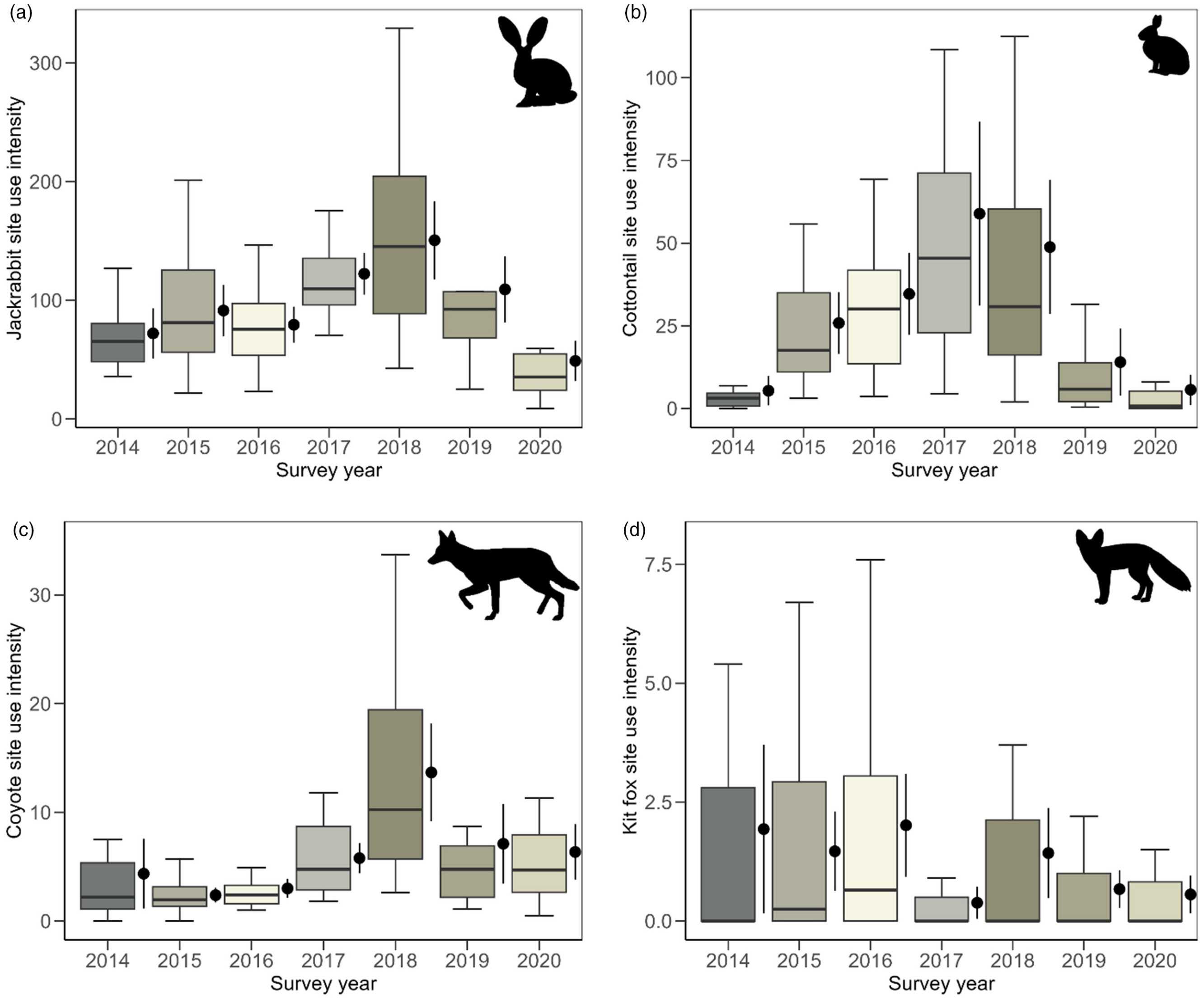

FIGURE 2 Boxplots of site use intensity for (a) jackrabbit, (b) cottontail, (c) coyote and (d) kit fox at the Jornada Basin Long Term Ecological Research site, New Mexico, USA, 2014–2020. The boxplots represent the median and 25th and 75th percentiles. The whiskers represent the 10th and 90th percentiles. The black-filled circles are means with 95% confidence intervals.

We did not find strong support for a direct negative effect from canids to lagomorphs, indicating that predators were not limiting prey. Instead, we identified a strong positive relationship between canids and lagomorphs, suggesting that lagomorph prey influences canid site use patterns. Hence, the final SEM did not include a direct pathway from canids to lagomorphs.

Both lagomorphs responded positively to the direct effects of summer rainfall, although the evidence for cottontails was not as strong (Figure 3; Table 2). We found strong evidence for the interactive effect between precipitation and shrub cover on site use intensity of both lagomorphs, indicating lagomorph response to precipitation depended on ecological state. Specifically, lagomorphs responded strongly to bottom-up pulses during years of high summer precipitation, but only on sites with moderate to high shrub cover (Figure 4a,b). However, the relationship reversed during dry years, when site use intensity of lagomorphs was highest in grasslands (Figure 4a,b).

As expected, there was a positive relationship between site use intensity of jackrabbits and canids, with coyote site use responding more strongly to changes in jackrabbit site use (Figure 3; Table 2). Canid predators did not respond to variation in cottontail site use, although a direct positive effect of cottontail on kit fox was marginally supported (standardized path coefficient $= 0.10$, $p = 0.13$). The direct effect of shrub cover (0.12) on coyote was inconclusive ($p = 0.18$), and there was marginal evidence for a direct, positive effect of precipitation on coyote site use (0.11, $p = 0.11$; Table 2).

There was strong evidence for the interactive effect between shrub cover and coyote site use on kit foxes (Figure 3), suggesting kit fox habitat use was influenced by intraguild interactions. Specifically, a clear positive relationship was expressed between site use intensity of kit foxes and shrub cover when coyotes were relatively uncommon (Figure 4c). However, during years when coyote site use intensity was moderate or high, the relationship was attenuated or decoupled, and kit foxes used grasslands more frequently (Figure 4c).

The SEM with lagged responses of canids to lagomorphs also fit the data well (Fisher's $C = 10.17$, $p = 0.25$) and supported a 1-year response lag for coyotes but not kit foxes (Figure S4 and Table S6). Specifically, the SEM indicated that site use intensity of jackrabbits in the previous-year positively affected site use of coyotes in the current year. Comparisons of linear mixed-effects models with and without prey lags did not support a lag response for kit foxes, and there was competing support for a lag response by coyotes to jackrabbits (Table S7). Neither canid responded to 1-year lags in cottontail site use intensity. Importantly, the SEM with lag effects also supported the previously identified interaction among lagomorphs, ecological state and summer precipitation (Figure S4; Table S7).

4 | DISCUSSION

Our investigation of trophic interactions across shrub encroachment gradients revealed complex dynamics in which outcomes of productivity pulses depended on ecological state and the landscape of fear for prey. Specifically, lagomorph site use intensity was linked to summer precipitation, but these bottom-up pulses were strongest

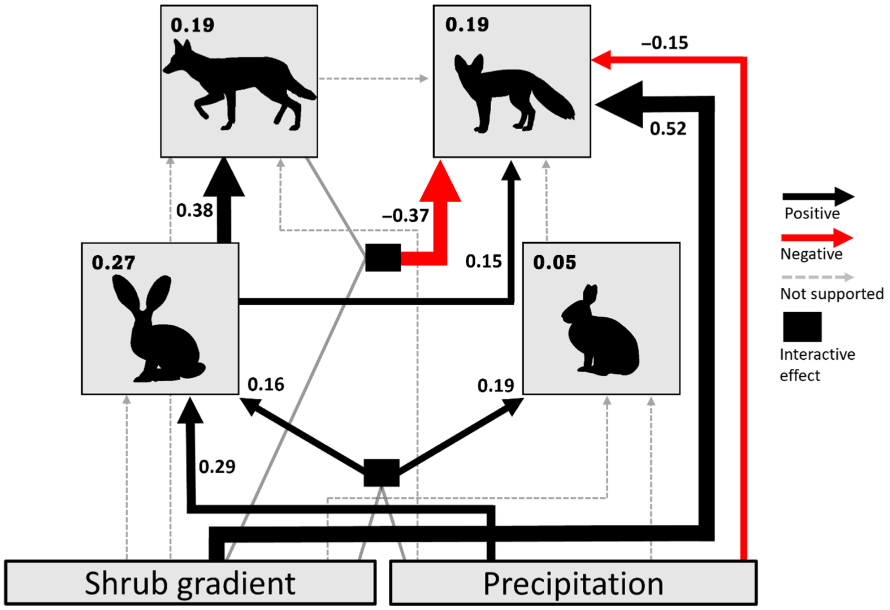

FIGURE 3 Final structural equation model estimating trophic effects for desert lagomorphs and canids at the Jornada Basin Long Term Ecological Research site, New Mexico, USA, 2014–2020. The final model did not include lagged predator responses. The data revealed moderate to strong evidence ($p > 0.05$) for trophic effects represented by solid arrows. Dashed arrows represent effects not supported by the model. The black arrows show positive effects, and the red arrows show negative effects. The black squares connecting variables represent the interaction pathways (i.e. two-way interaction terms). The thickness of the pathway is scaled to the magnitude of the standardized coefficients, which are provided along arrows. R^2 values are displayed for response variables. Correlated errors between jackrabbits and cottontails are not shown for clarity.

TABLE 2 Unstandardized (estimate) and standardized (std. estimate) path coefficients and unresolved correlations for the final structural equation model (SEM).

Response	Predictor	Estimate	SE	p	Std. estimate
Jackrabbit	Shrub	0.071	0.063	0.276	0.105
	Precip	**0.192**	**0.039**	**<0.001**	**0.286**
	Shrub × Precip	**0.118**	**0.043**	**0.007**	**0.158**
	Marginal $R^2=0.12$				
	Conditional $R^2=0.27$				
Cottontail	Shrub	0.127	0.109	0.253	0.092
	Precip	0.160	0.093	0.089	0.116
	Shrub × Precip	**0.285**	**0.103**	**0.007**	**0.185**
	Marginal $R^2=0.02$				
	Conditional $R^2=0.05$				
Kit fox	**Shrub**	**0.350**	**0.116**	**0.006**	**0.519**
	Precip	**−0.099**	**0.040**	**0.013**	**−0.147**
	Coyote	−0.047	0.059	0.432	−0.052
	Jackrabbit	**0.149**	**0.069**	**0.033**	**0.148**
	Cottontail	0.050	0.032	0.127	0.102
	Shrub × Coyote	**−0.130**	**0.049**	**0.010**	**−0.369**
	Marginal $R^2=0.06$				
	Conditional $R^2=0.19$				
Coyote	Shrub	0.091	0.067	0.184	0.122
	Precip	0.080	0.050	0.110	0.107
	Jackrabbit	**0.419**	**0.085**	**<0.001**	**0.375**
	Marginal $R^2=0.12$				
	Conditional $R^2=0.19$				
Unresolved correlations					
Cottontail~~Jackrabbit[a]		**0.591**	–	**<0.001**	**0.591**

Note: 'Shrub' is per cent shrub cover and 'Precip' is summer precipitation (mm) for the current year. The bold font denotes the effects with moderate to strong statistical support ($p<0.05$).

[a] Indicates missing path added to the final SEM.

in shrublands. This outcome cannot be explained by the nutrient-availability hypothesis because herbaceous biomass is reduced with shrub encroachment (Peters et al., 2012; Schooley et al., 2018), and instead it is consistent with changes in the landscape of fear tied to shrub cover (Wagnon et al., 2020). Intraguild interactions between the apex and intermediate predators, in which coyotes constrained the space use of kit foxes, also depended on shrub encroachment. Collectively, these findings extend our understanding of species interactions in drylands and underscore how environmental change can affect trophic interactions by altering perceived predation risk in prey.

If simple bottom-up forces were driving secondary production in our system, we would expect lagomorph response to precipitation to be strongest in grasslands where resources are greatest (Brown & Ernest, 2002). However, we detected the opposite pattern in which site use intensity of lagomorphs was negatively (cottontail) or weakly (jackrabbit) related to rainfall in grasslands, providing minimal evidence for the nutrient-availability hypothesis. This finding is similar to other research at the Jornada LTER site that found no connections between lagomorph densities and annual rainfall or plant production in a grassland for 10 years (Lightfoot et al., 2011). Thus, declines in key food resources caused by shrub encroachment may be less consequential than other factors in determining lagomorph dynamics.

A top-down hypothesis explaining positive associations between lagomorphs and precipitation in shrublands is that canid site use declines with shrub encroachment, releasing lagomorphs from predation pressure (Henke & Bryant, 1999). For example, increases in shrub cover reduced carnivore abundance and richness in the Kalahari Desert because of decreases in prey availability (Blaum et al., 2007). In our study, however, coyote site use did not vary consistently across shrub gradients and site use intensity of kit foxes can be higher in shrublands when coyotes are uncommon. Thus, shrub encroachment does not reduce canid predators, and predator release is not a likely driver of lagomorph dynamics at our study site.

The landscape of fear is a final explanation for the observed interaction between shrub cover and precipitation affecting lagomorphs. The hypothesis predicts that prey abundance will be greater in habitats perceived as safe because of shifts in habitat selection to avoid predation, even if safer habitats have lower food resources (Riginos, 2015; Riginos & Grace, 2008). In a recent study in this system, perceived predation risk in jackrabbits and cottontails was quantified with >200 trials of flight initiation distances, and for both species, their perceived risk was negatively related to shrub cover (Wagnon et al., 2020). Therefore, lagomorphs likely responded to variation in safe and risky habitats by proactively shifting their use to areas of minimal perceived risk following resource pulses (Riginos, 2015; Schmitz et al., 2004), when food was not as limiting, resulting in higher use of shrublands.

Lagomorphs were relatively more common in grasslands in dry years; however, and lagomorphs may tolerate greater risk when resources are limited. During droughts, herbivores may be forced to trade-off risk in favour of more abundant forage. For example, African ungulates select low quality habitats with lower perceived predation risk during periods of average rainfall but shift to riskier but nutrient-rich habitats in drought (Davies et al., 2021; Riginos, 2015). Our study extends these trade-offs of foraging risk to herbivores in the Chihuahuan Desert. Furthermore, our findings indicate strong spatiotemporal variation in trophic processes driven by interactive effects of state transitions and weather-driven fluctuations in resources on the nature and strength of top-down and bottom-up pathways (Maron et al., 2022). Our research confirms the

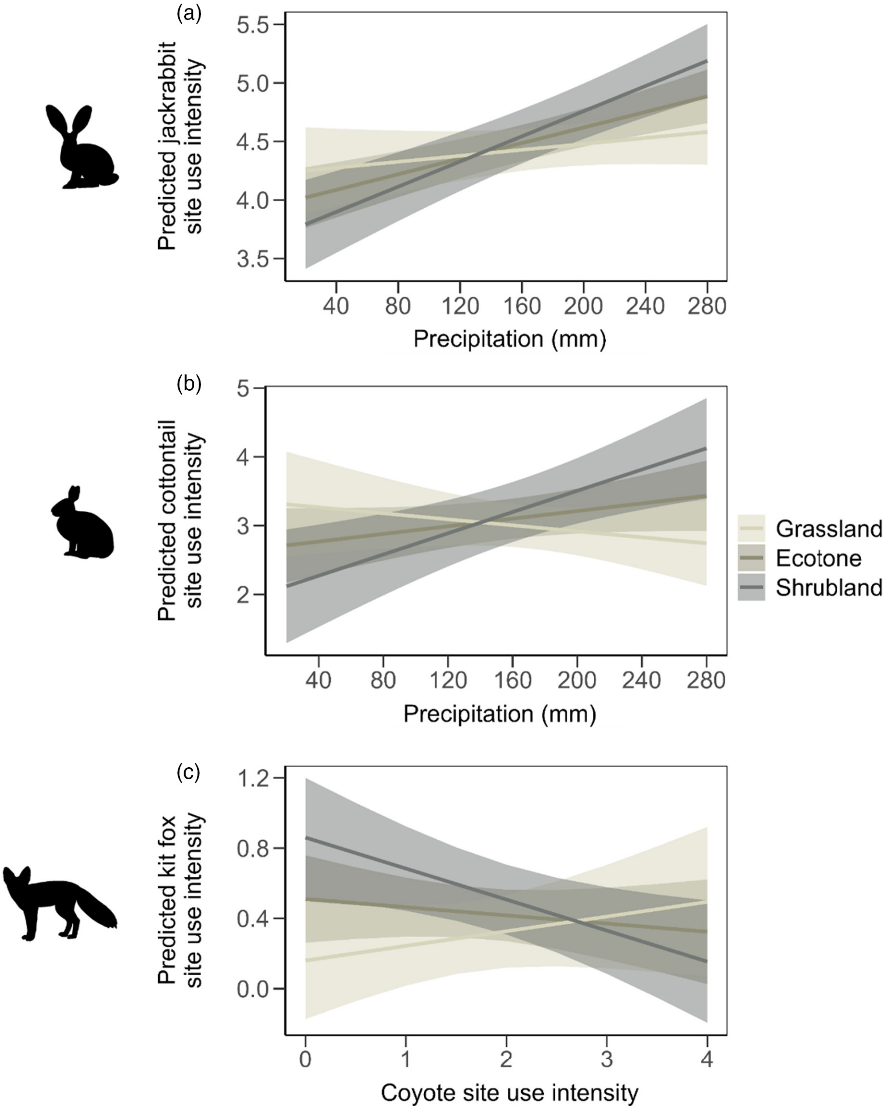

FIGURE 4 Interactive effects of shrub cover and summer precipitation on predicted site use intensity of (a) jackrabbit and (b) cottontail and (c) interactive effects of shrub cover and coyote site use on the site use intensity of kit fox at the Jornada Basin Long Term Ecological Research site, New Mexico, USA, 2014–2020. Coloured ribbons denote 95% confidence intervals. Note that site use intensities are on the logarithmic scale ($\log_{10}$).

importance of varying trophic interactions in drylands (Holmgren et al., 2006; Letnic et al., 2011; Meserve et al., 2003) but is novel in that we link variability in trophic processes to perceived predation risk altered by landscape-level habitat transitions.

We showed that site use intensity for lagomorphs is highest in shrublands during wet periods but greater in grasslands during dry periods. Rodent dynamics across shrub encroachment gradients are similar to lagomorphs (Schooley et al., 2018), and these two herbivore groups can substantially alter plant communities (Abercrombie et al., 2019; Brown & Heske, 1990; Maron et al., 2022). Thus, our findings have implications for understanding state transition dynamics in the Chihuahuan Desert because they may indicate how herbivory changes with ecosystem productivity (i.e. temporal variability) and ecological state (i.e. spatial variability). For example, shrublands may experience intensified herbivory during wet periods because of higher local abundances and increased foraging activity (Abu Baker et al., 2015; Longland, 1991; Schooley et al., 2018). This, in turn, could suppress grass recruitment and establishment (Abercrombie et al., 2019), reinforcing shrub dominance through positive feedbacks (D'Odorico et al., 2012; Kerley & Whitford, 2009). Although we did not measure herbivory rates, previous research indicates that small mammal herbivory in the Chihuahuan Desert can be greater in shrub-dominated versus grass-dominated states (Abercrombie et al., 2019; Bestelmeyer et al., 2007). During droughts, however, herbivory pressure may shift to areas with greater grass cover when forage is scarce in shrubland habitats, increasing impacts to grassland states during periods of stress (Archer et al., 2017; D'Odorico et al., 2012). Confirming such patterns of herbivore pressure could guide management and restoration efforts focused on the recovery of perennial grasslands (Holmgren & Scheffer, 2001).

Coyotes and kit foxes responded positively to jackrabbit site use, indicating bottom-up effects. In contrast, we found little evidence for canids responding to cottontail site use, perhaps because the availability of cottontail prey was relatively low compared to jackrabbit prey throughout the study (Figure 2, Table 1). Accordingly, site use intensity for coyote and kit fox may be driven by jackrabbit site use (Bartel et al., 2008; Clark, 1972; Cypher & Spencer, 1998) because jackrabbits are primary prey for both predators (Byerly et al., 2018; Lonsinger et al., 2020). Moreover, cyclical dynamics between coyotes and hares are well documented in boreal ecosystems

(Krebs et al., 2023) and, to a lesser extent, the Great Basin Desert (Bartel et al., 2008; Clark, 1972). Given the link between jackrabbit prey and canid predators in our system, if jackrabbits undergo cyclic dynamics similar to other systems, then over longer time scales than our study, predator–prey dynamics might be governed by coupled population cycles strongly modulated by climate (Bowler et al., 2014; Peers et al., 2020). Continued long-term monitoring of canids and lagomorphs at the Jornada Basin LTER site should shed light on whether coyotes and jackrabbits exhibit cyclical dynamics, highlighting the importance of long-term ecological research.

Our analyses did not support a 1-year lag response by kit foxes to lagomorph prey, and we found mixed evidence of a potential lagged response by coyotes to jackrabbits. The response of canids to lagomorphs in this study may not be as delayed as in previous time series analyses (Bartel et al., 2008; O'Donoghue et al., 1997; Prugh et al., 2005) because the patterns likely reflect both spatial and temporal processes. A lag by a predator would reflect a demographic response to prey abundance. However, if predators spatially redistribute themselves across the landscape to habitat with greater lagomorph activity, then changes in canid site use patterns could occur without a delay. Indeed, both processes can simultaneously drive species abundance patterns (Kéry & Royle, 2016), and what we captured with our camera trap data likely reflected demographic changes over time as well as spatial shifting within a year.

We were unable to conduct a complete analysis of the response of canids to rodent prey (i.e. we collected rodent biomass annually on only nine of the 24 sites; Bestelmeyer & Schooley, 2022), which is a limitation of our study. However, an analysis of the subset of sites indicated that canids did not respond to changes in rodent biomass (Table S8). We also lacked data on raptors, which is a further limitation because raptors might impact lagomorph site use. Although these two potential pathways could not be incorporated into our SEM, our study on canid-lagomorph dynamics still provides valuable insights into the underappreciated role that perceived predation risk plays in mediating herbivore responses to climate and environmental change in drylands.

Spatial use patterns of kit foxes also were influenced by intraguild interference with the dominant coyote (Lonsinger et al., 2017; Robinson et al., 2014). Kit foxes expressed a strong positive association with shrub cover when coyotes were relatively uncommon, probably because foxes were tracking prey when the threat of intraguild predation was low (Nelson et al., 2007; Thompson & Gese, 2007). However, when site use intensity of coyotes increased, the association between kit foxes and shrub cover decoupled, suggesting that coyotes were excluding kit foxes from shrublands (Kozlowski et al., 2012; Nelson et al., 2007). Increases in coyote-caused mortality of kit fox and swift fox (*Vulpes velox*) are related to increases in shrub cover, likely because changes in habitat structure increase exposure to predation risk or change the distribution of prey, requiring foxes to forage in areas used by coyotes (Lonsinger et al., 2017; Nelson et al., 2007; Thompson & Gese, 2007). Therefore, during periods of high coyote abundance, kit foxes may maximize fitness by spatial niche partitioning in which they select habitats that reduce the threat of intraguild killings (Kozlowski et al., 2012; Nelson et al., 2007; Thompson & Gese, 2007). However, site use intensity was consistently higher for coyotes than for kit foxes, even in 'low' coyote years, suggesting spatial overlap always occurs to some extent. Temporal niche partitioning may also promote the coexistence of carnivores (Palomares & Caro, 1999). Therefore, below a threshold of coyote abundance, kit foxes may shift their temporal activity patterns to exploit prey-rich habitats despite the presence of coyotes (Kozlowski et al., 2012; Schooley et al., 2021).

In conclusion, shrub encroachment represents a significant form of environmental change in drylands that can disrupt trophic interactions. Our results indicate ecological state changes in drylands may mediate herbivore responses to productivity pulses by altering perceived predation risk. Specifically, grassland–shrubland regime shifts may indirectly weaken the strength of top-down processes by creating safer habitat for herbivore prey, which may influence herbivory pressure and reinforce shrubland states and their spread (Kerley & Whitford, 2009). Therefore, the landscape of fear that herbivores experience must be considered when assessing how shrub encroachment impacts the dynamics of food webs in global drylands.

AUTHOR CONTRIBUTIONS

Conceptualization: Casey J. Wagnon, Robert L. Schooley and Brandon T. Bestelmeyer; *Data curation*: Casey J. Wagnon; *Methodology*: Casey J. Wagnon, Robert L. Schooley and Brandon T. Bestelmeyer; *Software and visualization*: Casey J. Wagnon; *Funding acquisition*: Robert L. Schooley and Brandon T. Bestelmeyer; *Project administration*: Robert L. Schooley; *Writing—original draft*: Casey J. Wagnon; *Writing, review and editing*: Casey J. Wagnon, Robert L. Schooley and Brandon T. Bestelmeyer. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interest.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2547d7wz8 (Wagnon et al., 2024a). Raw camera trap data are available from the Environmental Data

Initiative: https://doi.org/10.6073/pasta/bf6aea9b4ff8656d6a7d3b0a1e5f9f30 (Wagnon et al., 2024b); net primary productivity data are available from the Environmental Data Initiative: https://doi.org/10.6073/pasta/3fcf0fee94238b6f1c1673636ed6e90f (Bestelmeyer & Schooley, 2024); and rodent biomass data are available from the Environmental Data Initiative: https://doi.org/10.6073/pasta/083c12a1452105f7e10bd53861e2e4e3 (Bestelmeyer & Schooley, 2022).

STATEMENT OF INCLUSION

Our study was conducted at a field site in New Mexico that is part of the Long-Term Ecological Research Network. Our research team includes scientists and technicians from the region. We will share outcomes from the research with land managers and local ranchers through the Las Cruces Office of the Bureau of Land Management and the Malpai Borderlands Group. We also share results with the Asombro Institute for Science Education who then creates curriculum material for regional K-12 schools that primarily serve students from underrepresented groups.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Map of (a) Jornada Basin Long Term Ecological Research (LTER) site in New Mexico, USA, (b) the 24 sites monitored with camera traps within the Jornada Basin LTER site, and (c) an example of the spatial arrangement of paired camera traps and line-point intercept transects across ecological states.

Figure S2. Relationship between annual aboveground net primary production (ANPP; g/m^2 per year) for grasses and forbs and summer precipitation at the Jornada Basin LTER site in New Mexico, USA.

Figure S3. Annual patterns of summer (May–October), winter (November–April), and total (November–October) precipitation at the Jornada Basin Long Term Ecological Research site, 2014-2020.

Figure S4. The structural equation model testing for 1-year lagged responses in canids to lagomorph prey at the Jornada Basin Long Term Ecological Research site, New Mexico, USA, 2014-2020.

Table S1. Comparison of structural equation models (SEMs) testing the effects of different vegetation indicators (shrub cover, forb cover, grass cover, bare ground) on site use intensity of lagomorphs and canids.

Table S2. Model selection statistics for linear mixed-effects models evaluating the response of lagomorphs and canids to total (Tot; November–October), summer (Sum; May–October), and winter (Win; November–April) precipitation (ppt) with time lags at Jornada Basin Long Term Ecological Research site, 2014-2020.

Table S3. Results of the preliminary mixed-effects models and marginal *F*-tests evaluating interactive effects between shrub encroachment and predictor variables on site use intensity for lagomorphs and canids.

Table S4. Model comparison statistics examining the removal of non-significant paths from component models using AIC.

Table S5. Associated *p*-values from Global Moran's *I* test for spatial autocorrelation of model residuals from the best supporting linear mixed-effects model used for each species.

Table S6. Unstandardized (Estimate) and standardized (Std.estimate) path coefficients and unresolved correlations for the structural equation model evaluating lagged predator responses to prey.

Table S7. Model comparison using AIC to evaluate support for canid response to previous-year lagomorph site use intensity.

Table S8. Model comparisons testing whether canid site use intensity responded to rodent biomass.

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