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Shrub encroachment, landscape restoration, and intraguild predation

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ABSTRACT

Shrub encroachment into arid grasslands occurs globally with the potential to affect vertebrates and their interactions. In the Chihuahuan Desert of southern New Mexico, shrub encroachment has prompted intensive efforts by land management agencies to remove shrubs and restore historical grassland habitats. We asked if restoration actions involving shrub removal affected dynamics of intraguild predation (IGP) including an IGP predator (coyote, *Canis latrans*), an IGP prey (kit fox, *Vulpes macrotis*), plus their shared lagomorph prey. We used camera traps on 14 sites with paired treated and untreated areas to examine spatial and temporal niche partitioning of coyotes and kit foxes. Shrub removal did not produce straightforward effects on abundances of coyotes, kit foxes, or their prey resources. Instead, abundances of kit foxes were constrained when coyote abundance reached a threshold. Below this threshold, kit foxes were more common on areas with low shrub cover, possibly due to lack of hiding cover for lagomorph prey that increased their predation risk. Our system included two alternative states: IGP predator dominated and coexistence of IGP predator and prey. Coexistence may have been facilitated by temporal niche partitioning as diel activity patterns differed for coyotes and kit foxes. Future research on intraguild predation should integrate spatial and temporal niches to understand species coexistence including on dynamic landscapes undergoing restoration.

1. Introduction

Shrub encroachment into grasslands is widespread in drylands worldwide but with inconsistent effects on diversity and abundance of vertebrates (Eldridge et al., 2011; Stanton et al., 2018). However, shrub encroachment is more likely to negatively affect mammals and herpetofauna especially in regions with low net primary productivity (Stanton et al., 2018). Mechanisms for how shrub encroachment could influence mammalian carnivores include modifying thermal and hiding cover, prey abundances (Blaum et al., 2007), and the landscape of fear for prey (Wagnon et al., 2020). Changes in habitat structure from shrub encroachment may also shape carnivore interactions including intraguild predation (IGP, Robinson et al., 2014).

Intraguild predation is an extreme form of competition in which the IGP predator (dominant predator; i.e. apex predator) and IGP prey (subordinate predator; i.e. mesopredator) compete for shared resources, but the IGP predator also kills the IGP prey (Holt and Polis, 1997). If the IGP prey is a superior exploitative competitor, then three equilibria exist along a productivity gradient (Holt and Polis, 1997; Robinson et al., 2014; Lonsinger et al., 2017). When prey resources are scarce, the IGP prey persists and the IGP predator is excluded. With intermediate resource levels, coexistence of the two species is possible. When prey resources are abundant, the IGP predator persists and the IGP prey is excluded. This shift in dominance from the IGP prey to the IGP predator along a productivity gradient holds when there is an alternative prey (Holt and Huxel, 2007). However, if the IGP predator has exclusive access to the alternative prey then the IGP predator can dominate at lower levels of productivity. In contrast, if the IGP prey has access to alternative resources then it can coexist with the IGP predator over a wider range of productivities (Daugherty et al., 2007; Holt and Huxel, 2007). Intraguild predation could be a component of trophic cascades in arid environments (Gordon et al., 2017) with consequences for state transitions.

In the Chihuahuan Desert in southwestern United States, grasslands have experienced extensive encroachment by creosotebush (*Larrea tridentata*) and honey mesquite (*Prosopis glandulosa*). These grassland-to-shrubland transitions reflect drivers and feedbacks operating at multiple scales including overgrazing by livestock during drought, reduced fire frequency, increased atmospheric CO_2, and increased temperatures and precipitation variability (Bestelmeyer et al., 2018).

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Shrub-dominated states are difficult to reverse, due to hysteresis effects, without intensive management (Bestelmeyer et al., 2018).

The Bureau of Land Management (BLM) has applied herbicides to remove shrubs to >300,000 ha in southern New Mexico starting in the 1980s with a substantial increase in the area treated per year starting in 2007 under the Restore New Mexico Program (Bestelmeyer et al., 2018). These restoration treatments have not shifted diversity of vertebrate taxa, but they have changed abundances (positively and negatively) of multiple species of birds (Coffman et al., 2014) and lizards (Cosentino et al., 2013) and a keystone rodent (Cosentino et al., 2014).

We asked whether landscape restoration via shrub removal in the Chihuahuan Desert affected IGP dynamics. We evaluated abundances of two canid species, an IGP predator (coyote, *Canis latrans*) and an IGP prey (kit fox, *Vulpes macrotis*), plus abundances of their shared lagomorph prey (black-tailed jackrabbit, *Lepus californicus*; desert cottontail, *Sylvilagus audubonii*). Diets of coyotes and kit foxes overlap considerably (Byerly et al., 2018). However, coyotes may consume more lagomorphs, whereas kit foxes may consume more rodents (Byerly et al., 2018). Lagomorphs in the Chihuahuan Desert can reach higher densities in grasslands than in creosotebush shrublands (Lightfoot et al., 2010). In contrast, rodent biomass does not differ on average between grasslands and shrub-dominated habitats (Schooley et al., 2018). Thus, we predicted coyotes would track resources and be more abundant in areas treated for shrub removal where lagomorph prey should be higher. We predicted that kit foxes would spatially avoid coyotes, exploit areas with lower resources, and thus be more abundant in untreated shrublands. Finally, we recognize that predictions about IGP have focused largely on interactions in space (e.g., Robinson et al., 2014; Lonsinger et al., 2017). However, IGP prey also could avoid the IGP predator in time (Monterroso et al., 2013) so we tested for separation in diel activity patterns for kit foxes and coyotes.

2. Materials and methods

Our study region (44,120 km^2) was in the Chihuahuan Desert in southwestern New Mexico (see map in Cosentino et al., 2014). The dominant shrub was creosotebush; other shrubs included tarbush (*Flourensia cernua*) and honey mesquite. Common grasses were dropseeds (*Sporobolus* spp.), bush muhly (*Muhlenbergia porteri*), black grama (*Bouteloua eriopoda*), threeawns (*Aristida* spp.), and burrograss (*Scleropogon brevifolius*).

We selected 14 sites consisting of paired treated and untreated areas spatially matched for soil type (gravelly sandy loams), landform (desert basin), and elevation (mean = 1529 m, range = 1329–1756 m). The mean distance between the 14 sites was 41 km (range = 6–84 km), and treated and untreated areas at a site were within 5.8 km. The BLM aerially applied the herbicide tebuthiuron at a rate of 0.56 kg/ha to target creosotebush on treated areas (mean = 1005 ha; range = 449–1946 ha). Treatments were applied to each area once between 1982 and 2002 (10–30 years before our sampling; mean = 18.4 years). The matched untreated areas were dominated by creosotebush.

We deployed five camera traps on each treated and untreated area ($n = 28$ total areas; $n = 140$ total camera traps). We used three previously established 1-km transects on each area to distribute cameras (Coffman et al., 2014; Cosentino et al., 2014). Transects within an area were 300–1500 m apart and ≥100 m from roads. We then randomly placed camera traps at the start, middle, or end of a transect (i.e., we used 5 out of the possible 9 positions on the 3 transects) with the constraint that the five camera traps within an area were >500 m apart from each other. For analysis, we combined the data from the array of five cameras within an area.

At each camera trap location, we attached a camera with a passive infrared motion sensor (Bushnell Trophy Cam, model no. 119436) to a fencepost 0.5 m aboveground. Cameras were programmed to take three photographs in a short burst with a 30-sec delay before triggering again. We baited camera traps by staking a fatty acid scent lure (Pocatello Supply Depot, Pocatello, ID) and a punctured can of wet cat food (Robinson et al., 2014) 3 m in front of the camera. We sampled each site for one month between September 2012 and January 2013. We sampled three or four sites during each of four sampling periods. The paired treated and untreated areas within a site were always sampled concurrently.

We considered photographs of a given species from each site to be independent if separated by ≥ 60 min. We used photographic rate (no. of independent photographs at an area) as a measure of relative abundance (Palmer et al., 2018; Andreoni et al., 2021). In our statistical models, we included sampling effort (no. trap-nights camera operated). We used time stamps from independent photographs to compare diel activity patterns for coyotes and kit foxes.

To determine if predator and prey abundances reflected changes in vegetation from restoration actions, we measured cover of shrubs and grasses (perennial and annual) on treated and untreated areas. Vegetation cover was measured using line-point intercept sampling on two 50-m transects associated with each of the three 1-km transects (for details see Coffman et al., 2014). For analysis, we averaged estimates of shrub and grass cover from the six vegetation transects within each treated and untreated area. We assessed whether treatments altered vegetation cover with separate linear mixed models with shrub cover or grass cover as the response variable. The models included treatment as a fixed effect and site as a random effect.

We tested for effects of shrub removal treatments on abundances of the focal mammal species using generalized linear mixed models (GLMMs) with a negative binomial response distribution and log link function. For each model, photographic rate was the response variable, log (sampling effort) was an offset variable, treatment and sampling period were fixed effects, and site was a random effect. We chose this approach instead of occupancy modeling (Robinson et al., 2014) because naïve occupancy was so high for two species (coyote = 0.893, jackrabbit = 1.00) that focusing on occurrence would have been uninformative.

Biodiversity responses to shrub removal can include time lags (Cosentino et al., 2014), but differences in photographic rates between treated and untreated areas within a pair were unrelated to time since treatment for all species (Table S1). Thus, we did not include time since treatment in our GLMMs to reduce model complexity.

We next examined how the four mammal species responded to shrub cover and potential trophic interactions. We used the same response variables and GLMM structure as before but included shrub cover as a fixed effect instead of treatment. For coyotes, we also included lagomorph abundance (summed photographic rates for jackrabbits and cottontails) as a measure of prey resources. For kit foxes, we included lagomorph abundance plus photographic rate of coyotes as a measure of IGP pressure. For jackrabbits and cottontails, we included canid abundance (summed photographic rates for coyotes and kit foxes) as a measure of predator pressure. All photographic rates used as predictors were corrected for sampling effort (no. independent photographs divided by no. trap-nights).

Because photographic rates for kit foxes and coyotes suggested a nonlinear response in which coyotes suppressed foxes only beyond a threshold for coyote abundance (see Results), we conducted a post hoc change-point analysis to confirm this threshold. The change-point analysis integrated cumulative sum charts with bootstrap analysis (Taylor, 2000). We then examined photographic rate of kit foxes versus shrub cover, but only for areas below the threshold with low coyote abundances, using a negative binomial model without a random effect for site.

To test for differences in diel activity patterns of coyotes and kit foxes, we combined data from all sites and applied the nonparametric Watson's U^2 test (Batschelet, 1981). We also measured overlap in activity patterns between coyotes and kit foxes using the kernel density estimation procedure in the 'overlap' package in R (Ridout and Linkie, 2009) to estimate an overlap coefficient that ranges from 0 (no overlap) to 1 (complete overlap).

3. Results

Restoration treatments changed vegetation cover as expected (Fig. 1a). Shrub cover decreased on treated areas relative to untreated areas ($F = 51.39$, df = 1,13, $P < 0.001$), and grass cover increased on treated areas ($F = 8.99$, df = 1,13, $P = 0.01$).

Our sampling effort of 3320 trap-nights produced 167 independent photographs for coyotes, 174 for kit foxes, 671 for black-tailed jackrabbits, and 83 for desert cottontails (Fig. S1). Treatments to remove shrubs did not have a simple, direct effect on any of the four mammal species (Table S2, Fig. 1b). Photographic rates for kit foxes increased across the four sampling periods, whereas photographic rates for jackrabbits decreased across periods (Table S3).

None of the mammal species responded to shrub cover overall (Table S2). Photographic rates for the two canid predators were unrelated to abundances of their lagomorph prey. Likewise, photographic rates for the two lagomorph species were unrelated to abundances of the canid predators (Table S2).

Photographic rate for kit foxes was related negatively to coyote abundance (Table S2). However, the pattern indicated a threshold response in which foxes were constrained only beyond a threshold for coyote photographic rate (Fig. 2a). Our change point analysis confirmed this threshold with 96% confidence. At areas where kit foxes were not suppressed by coyotes, fox abundances were related negatively to shrub cover (Fig. 2b; $\beta = -0.083$, SE = 0.041).

Diel activity patterns of coyotes and kit foxes differed ($U^2 = 0.219$, df = 170, $P < 0.05$) with an overlap of 0.74 (95% CI = 0.66–0.81). Kit foxes had a crepuscular activity peak (17:00–20:00) before coyotes became active (Fig. 3). Coyotes were also more active during the day.

4. Discussion

Large-scale efforts to remove shrubs and restore grasslands in the Chihuahuan Desert affected IGP dynamics. However, shrub removal did not produce simple responses in abundances for canid predators or their

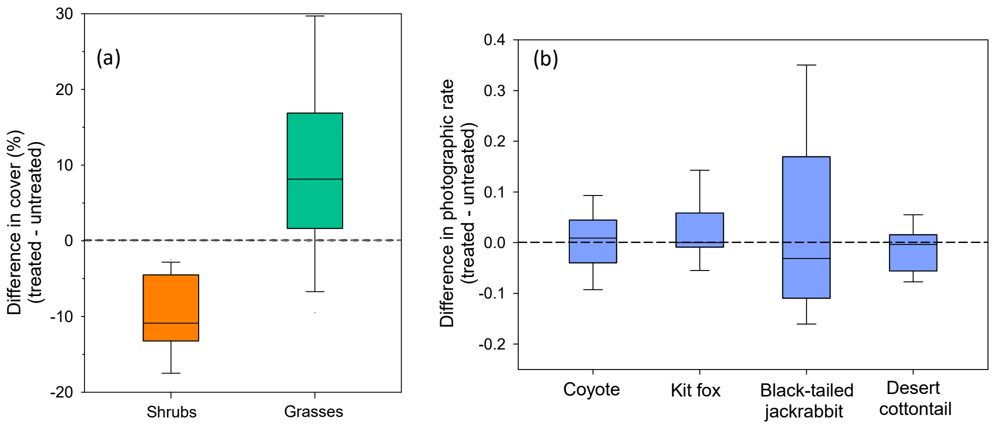

Fig. 1. Responses to shrub removal efforts in southern New Mexico for (a) cover of dominant vegetation types, and (b) photographic rate for canid predators and lagomorph prey. Photographic rates are corrected for sampling effort. Each box plot represents the difference between a paired treated area and an untreated reference area (n = 14 site pairs). Values > 0 indicate positive effects of shrub removal treatments. Box plots include medians (horizontal line), 25th and 75th percentiles (top and bottom of box), and 10th and 90th percentiles (whiskers).

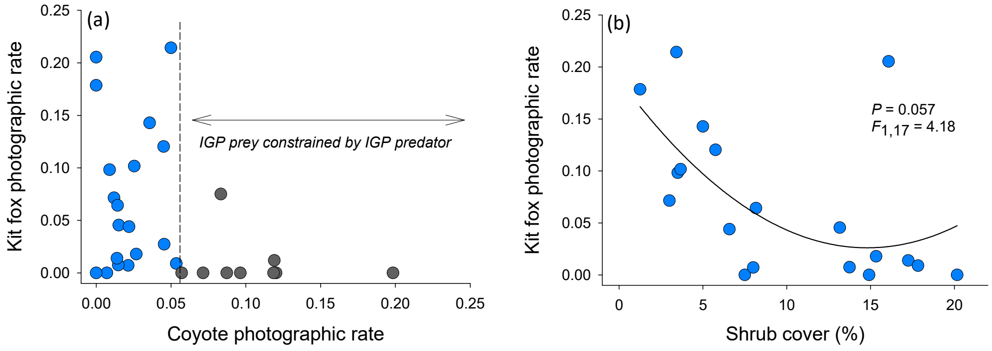

Fig. 2. Interactions between intraguild predation (IGP) and shrub cover in a landscape under restoration. (a) Relationship between photographic rates (corrected for sampling effort) of kit foxes and coyotes on 28 study areas in the Chihuahuan Desert in New Mexico, 2012–2013. The threshold where coyote abundance begins to constrain kit fox abundance (vertical dotted line) was estimated by change-point analysis (96% confidence). (b) Response of kit foxes to shrub cover on areas where their abundances were not constrained by coyotes (n = 19; areas denoted by blue circles in panel A). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

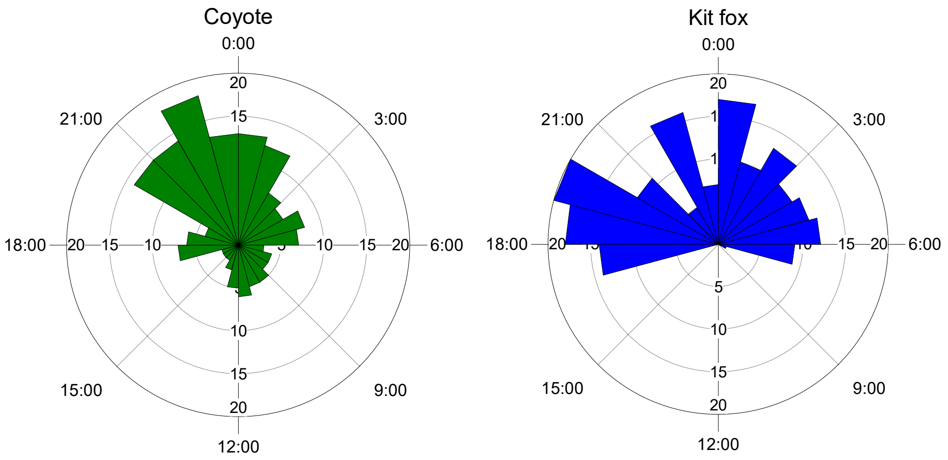

Fig. 3. Diel activity patterns differed for coyotes and kit foxes on 28 study areas in southern New Mexico, 2012–2013. Each petal of the rose diagram displays the number of independent photographs (>60 min apart) in 1-hr intervals.

shared lagomorph prey. Instead, where kit foxes (IGP prey) were not constrained by coyotes (IGP predator), foxes were more abundant on areas with low shrub cover. Temporal niche partitioning may also promote species coexistence.

Surprisingly, our prediction of increased lagomorph abundances on treated areas was not supported. We found no evidence of an underlying prey productivity gradient that should influence IGP outcomes (Holt and Polis, 1997; Robinson et al., 2014). Long-term monitoring showed that densities of black-tailed jackrabbits and desert cottontails were consistently higher on a grassland site than on a creosotebush site (Lightfoot et al., 2010). Although restoration treatments effectively remove shrubs (Fig. 1a), they produce savannah states with shrub cover intermediate to shrublands and remnant grasslands (Coffman et al., 2014). Lagomorphs may not distinguish strongly between these savannah states and encroached shrublands.

Although coyote abundance was unrelated to treatments or lagomorph abundance, pressure from this IGP predator varied considerably across areas. Kit foxes were unlikely to occur on areas beyond a threshold of coyote abundance (Fig. 2a). Below this threshold, complete exclusion of foxes was rare and finer-scale avoidance of coyotes in space seemed possible. Thus, our system included two alternative states: IGP predator dominated and coexistence of IGP predator and prey (Lonsinger et al., 2017).

When foxes were not suppressed by coyotes, they reached higher abundances on low-shrub areas that often had received a restoration treatment. Why were kit foxes more common in open habitats? First, we might not have adequately quantified the prey productivity gradient. We were unable to sample rodents, an important component of fox diets (Byerly et al., 2018). Although average biomass of Chihuahuan Desert rodents is insensitive to shrub encroachment, rodent biomass is higher on unencroached grasslands during dry periods (Schooley et al., 2018). In this study, sampling occurred following four years with below-average summer precipitation (Schooley et al., 2018). More generally, our snapshot survey might have missed predator-prey dynamics that could be revealed by long-term monitoring.

Second, kit foxes may have chosen habitats based on the likelihood of capturing prey after an encounter instead of on prey abundance. The landscape of fear for desert lagomorphs is altered by shrub encroachment, and they perceive open habitats to be riskier than shrublands (Wagnon et al., 2020). Higher abundances of kit foxes in low-shrub areas could reflect greater hunting success in habitats lacking adequate hiding cover for prey.

Third, kit foxes may have responded to their own landscape of fear. Their ability to visually detect coyotes should be reduced in areas with high shrub cover, increasing their risk of predation (Thompson and Gese, 2007).

Investigations of IGP, including for coyotes and kit foxes (Robinson et al., 2014; Lonsinger et al., 2017), have focused on spatial interactions. The IGP prey also can avoid the IGP predator via temporal niche partitioning. Such avoidance in time might not lessen competition for resources, but it reduces mortality risk for the IGP prey. We showed that diel activity patterns differed for kit foxes and coyotes. In particular, foxes were active in early evening before coyotes became active. Coyotes might have avoided being active in the evening when nocturnal desert rodents were inactive in burrows and when lagomorphs could still visually scan for predators. Kit foxes may have tolerated this window of time when capturing prey could be difficult because the IGP predator was scarce.

Future directions for IGP research should include integration of spatial and temporal niches (Farris et al., 2020). Such merging will further our understanding of species coexistence on arid landscapes including those undergoing restoration.

CRediT authorship contribution statement

Robert L. Schooley: Conceptualization, Formal analysis, Writing – original draft, Funding acquisition. **Brandon T. Bestelmeyer:** Resources, Funding acquisition, Writing – review & editing. **Casey J. Wagnon:** Formal analysis, Data curation, Writing – review & editing. **John M. Coffman:** Methodology, Investigation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2021.104588.

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