RESEARCH ARTICLE

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Rodent, snake and raptor use of restored native perennial grasslands is lower than use of unrestored exotic annual grasslands

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Abstract

1. In California's Central Valley, most native grasslands have been destroyed or degraded due to invasion, farming and development. Grassland restoration is often assumed to provide improved wildlife habitat, ostensibly increasing the abundance and diversity of at least some native wildlife species relative to unrestored, invaded annual grasslands.

2. We compared rodent, snake and raptor activity and species richness at paired unrestored and restored grasslands across four blocked locations in the Central Valley using trapping and observational surveys in up to four seasons per guild from 2014 to 2015. Restored treatments were planted with native perennial grasses 13–24 years prior to study initiation but were partially re-invaded by Mediterranean annual grasses and forbs. Unrestored treatments contained similar non-native plant species assemblages as restored treatments, but did not contain any native grass.

3. Rodent, snake and raptor activity was generally higher in unrestored relative to restored treatments. For rodents, the non-native *Mus musculus* (house mouse) showed the greatest disparity in abundance, while greater raptors and snakes likely responded to greater rodent abundance.

4. Within treatments, species-specific rodent responses were related to structure of physical vegetation. In particular, *Peromyscus maniculatus* (native deer mouse) was associated with more bare ground and shorter vegetation, while the house mouse was associated with less bare ground and taller vegetation, regardless of treatment type. Substantial changes in rodent species composition were observed over short periods of time (<3 months) after unplanned manipulation of vegetation structure via livestock grazing, with patterns reflecting the species-specific response to physical vegetation structure.

5. *Synthesis and applications.* Our results reveal that while grassland restoration may promote persistence of native plant communities, restoration may not be beneficial to some higher trophic levels, and in fact may reduce habitat value for some native predators in grasslands invaded by Mediterranean plant species. Changes in vegetation structure can strongly impact wildlife species composition, suggesting a more nuanced approach is required for the restoration of desired wildlife communities. Thus, species-specific goals should be carefully considered to ensure improved alignment of restoration methods with expected restoration outcomes.

1 | INTRODUCTION

One of the central goals of habitat restoration and management is enhancement of wildlife habitat and biodiversity (Bradbury, 2009). Many studies have shown that managing systems from the top-down (e.g. via restoration of native predators) can lead to cascading impacts on prey behaviour, wildlife communities, plant communities and hydrology (Beschta & Ripple, 2009). However, causal mechanisms underlying wildlife responses to plant restoration (or invasion) are not frequently studied, yet plants are known to directly and indirectly influence wildlife by provisioning food and habitat (Terborgh, Holt, & Estes, 2010). By directly manipulating plant communities, restoration can potentially cause a bottom-up ripple of effects throughout wildlife communities. While "wildlife restoration" generally assumes an increase in suitable habitat for wildlife, it is not clear how many wildlife communities respond to plant restoration (Majer, 2009).

California's diversity of climates and habitats confers one of the most diverse assemblages of wildlife in the United States, but these are now greatly reduced in abundance (Vander Zanden, Olden, & Gratton, 2006) largely due to habitat destruction and fragmentation (Didham, Tylianakis, Gemmell, Rand, & Ewers, 2007). At a global scale, habitat loss is considered a greater immediate threat to biodiversity than climate change (Jetz, Wilcove, & Dobson, 2007). Pristine or relict native grasslands are one of the most threatened ecosystems in the world, and wildlife species utilizing grasslands have decreased drastically over the last 200 years (Samson & Knopf, 1994).

California's grasslands in particular are some of the most invaded ecosystems globally, with native plant cover replaced almost entirely with annual Mediterranean forbs and grasses (Hamilton, Griffin, & Stromberg, 2002). Grassland restoration is currently undertaken to restore biodiversity and ecosystem services—such as habitat for native floral and faunal species, forage for livestock, and aesthetic value—that have been lost due to invasion by exotic weedy species and other anthropogenic influences (Seabloom, Harpole, Reichman, & Tilman, 2003). For example, mitigation efforts have been implemented in the Central Valley of California to support the nesting and foraging habitat requirements of the state-threatened *Buteo swainsoni* (Swainson's hawk) ([CDFW] California Department of Fish and Wildlife, 2016). Woodbridge (1998) reported that the primary impact of weedy invasions on *B. swainsoni* is a reduction in prey abundance, such that grassland restoration could provide better quality foraging habitat, although little is known about this link. While the restoration of historic plant community assemblages is assumed to provide increased resource availability for other trophic levels, how well this objective is met is rarely quantified (Boyd & Svejcar, 2009). As budgets constrict and demands for accountability and results heighten, it becomes imperative

that the presumed positive relationship between restoration and ecosystem services be tested (Benayas, Newton, Diaz, & Bullock, 2009).

One approach to understanding the effects of grassland restoration on species not targeted by restoration is to monitor community responses throughout the food web. Rodents are an important group to monitor for assessing impacts of restoration on biological communities: they are a critical food resource for predators, and thus might exert bottom-up control of predator populations, and influence top-down control on plant communities and vegetation (Howe & Lane, 2004). Such wildlife might be expected to respond positively or negatively to grassland restoration, depending on their habitat preferences and availability of resources. Using structural equation models (SEMs) (Grace, 2006) we can assess the impacts of restoration from a community perspective, testing whether patterns in wildlife distribution and abundance could be predicted based on habitat parameters and the distribution and abundance of prey.

1.1 | Objectives

Paired unrestored and restored grasslands can yield powerful, albeit inherently non-random, replicated natural experiments (Majer, 2009), allowing a linkage to be made between structural and compositional differences in plants to wildlife abundance. Within four paired unrestored and restored grasslands, we monitored plant communities, as well as rodent, snake and raptor activity, for up to four consecutive seasons. Specifically, this research addresses:

1. Spatial structural differences in plant communities.
2. Concomitant rodent species-specific responses to physical structure.
3. Differences in relative abundance of rodents, snakes and diurnal raptors between unrestored and restored grasslands.

2 | MATERIALS AND METHODS

2.1 | Geographic and temporal replication

We chose four locations (B1–B4, hereafter "blocks") in the Central Valley of California, United States, that contained paired unrestored (UR) exotic annual and restored (R) native perennial grassland fields (hereafter "treatments"), with each treatment being at least seven hectares (ha) and having similar soil types, topography, land-use history and management within each block. Paired treatments were nested within each block and had similar historical livestock grazing regimes (Table 1 and Table S1). Owners removed livestock (if any) at

least 30 days prior to monitoring periods. We sampled in up to four seasons to elucidate seasonal changes in physical vegetation structure and wildlife responses (Barbour, Keeler-Wolf, & Schoenherr, 2007). We monitored rodents and snakes over 30-day periods in the first three seasons, and over a 2-month period in the final season (due to logistical constraints): April (Spring 2014), July (Summer 2014), November (Autumn 2014) and February/March (Winter 2015). Due to limited availability of raptor experts, we monitored raptors over 30-day periods in only three seasons: July (Summer 2014), November (Autumn 2014) and July (Summer 2015) (Table S2).

2.2 | Sampling design

We established four 150-m transects within each treatment to monitor vegetation and rodents, with transects running parallel to each other and separated by at least 50-m. Rodent traps were placed along transects at approximately 15-m intervals to yield 11 traps per transect. We placed 0.61-m × 1.22-m sheets of untreated CDX plywood and galvanized corrugated metal (hereafter, "coverboards") on the ground to monitor snake populations; the two materials provided different structures, and different species may prefer different materials (Grant et al., 1992). Three coverboard points were located at 75-m intervals along a separate transect running parallel to and approximately 5-m from each rodent transect, with an adjacent pair of coverboards (one of each material) at each point, for a total of 198 coverboards (Figure 1). We installed coverboards in January 2014 to allow wildlife to become accustomed to them prior to initial monitoring the following Spring. Trapping and survey order were randomly assigned to treatments and blocks each season, subject to logistical constraints.

2.3 | Monitoring

2.3.1 | Vegetation

We monitored vegetation along rodent transects immediately prior to trapping each season in 0.5-m² quadrats placed immediately adjacent to each rodent trap. We visually estimated per cent cover of bare ground, litter, native and exotic grasses, and native and exotic forbs

for a total of 100% per quadrat following Werner, Vaughn, Stuble, Wolf, and Young (2016). For annual plants, we counted only live tissues; for perennial grasses we recorded all cover, including dormant tissues. Litter was comprised of desiccated annual grasses and forbs. We visually estimated plant canopy height using a visual obstruction method, in which we placed a meter stick *c.* 1 m from the observer; the observer recorded visual obstruction of the meter stick at a height of 1 m from the soil surface (sensu Holechek, 2011).

2.3.2 | Rodents

We conducted live trapping to monitor rodent populations each season. We baited live traps (8.9 cm × 7.6 cm × 22.9 cm; H.B. Sherman Traps, FL, USA) with oats and peanut butter at dusk and checked them at dawn to minimize time in traps, reduce stress and minimize exposure to extreme temperatures. We sexed, weighed and identified individuals to species by inspecting teeth and markings, and eartagged with a small self-piercing tag (Nietfeld, Barrett, & Silvy, 1994).

Due to unavoidable cattle interference at B4 in Spring 2014, we trapped in only three blocks; we trapped in all four blocks in the subsequent three seasons. Unplanned sheep grazing occurred at B3 during the first three days of trapping in Summer 2014; sheep were removed on day four of trapping, and returned again for several weeks after we completed trapping for the season. We continued trapping during grazing, but did not include these data in final rodent abundance analyses due to potential changes in rodent detection probability. However, we did utilize these data to provide insight into potentially correlated rodent responses to rapid changes in vegetative cover. Collectively, we operated traps for seven trap nights for the first three seasons and five trap nights for the final season.

2.3.3 | Snakes

We surveyed coverboards for snake activity across all blocks in the mornings up to eight times per block, treatment and season, identifying snakes to species. A total of 48 coverboards were located in each block (two boards per point, three points per transect, four transects per treatment and two treatments per block), with 3,216 coverboard surveys recorded over the course of the study.

TABLE 1 Wildlife survey blocks. Geographic information, approximate area of treatments and year of native perennial grass restoration at four blocks in the Central Valley, CA, USA

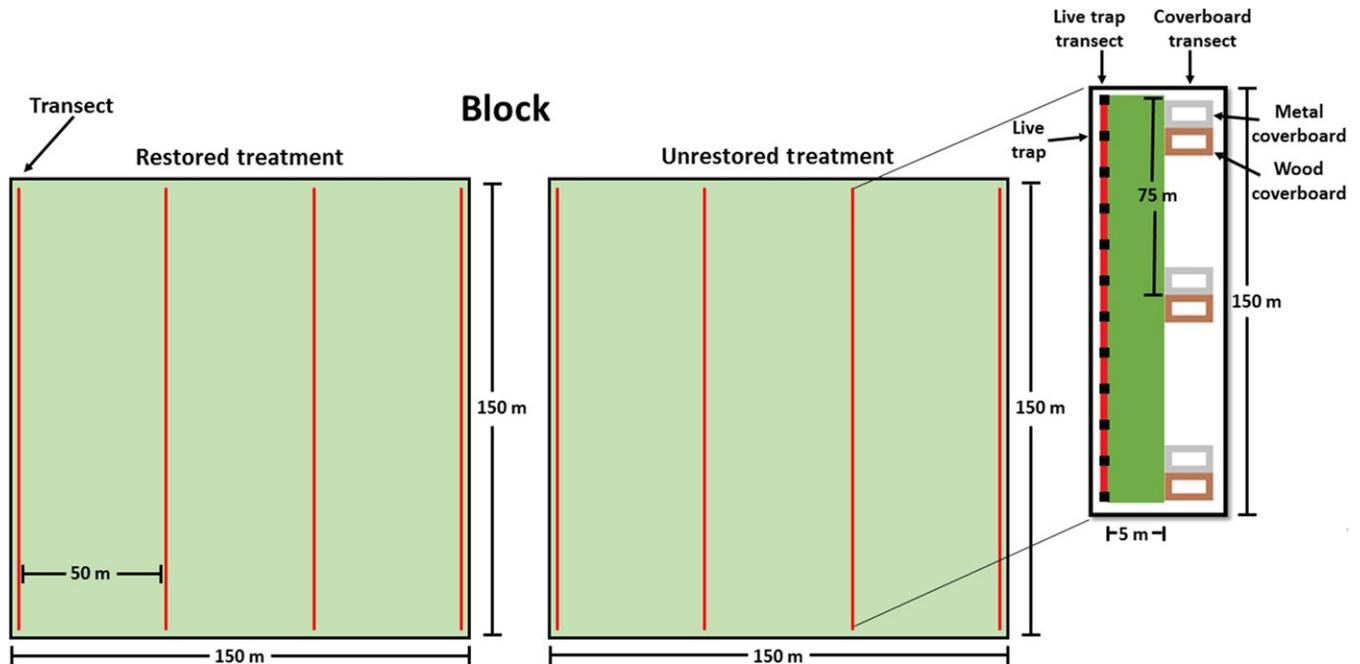| Block ID	City	County	GPS coordinates	Hectares (UR/R)	Restoration year
B1	Elk Grove	Sacramento	38°26′0.46″N 121°28′47.93″W	11.3/7.2	2003
B2	Winters	Yolo	38°38′6.42″N 122°00′54.80″W	7.2/7.4	1992
B3	Zamora	Yolo	38°49′23.26″N 121°55′46.00″W	7.0/10.7	2003
B4	Esparto	Yolo	38°36′49.43″N 122°3′33.58″W	7.3/8.0	1992

UR, unrestored, invaded; R, restored.

FIGURE 1 Experimental design for one blocked location. Sampling schematic of monitoring treatments in a block, which is comprised of one location with nested, paired unrestored and restored grassland treatments in the Central Valley, CA, USA. Four blocks were monitored for differences in vegetation, rodents, snakes and raptors over the course of up to four seasons for each wildlife group from Spring 2014 to Winter 2015 [Colour figure can be viewed at wileyonlinelibrary.com]

2.3.4 | Raptors

We monitored diurnal raptor activity using an all-animal sampling approach where we recorded individual raptors within the treatment boundaries (Gaibani & Csermely, 2007). We conducted surveys for 1 hr per treatment for a period of 5 days in Summer 2014 and Autumn 2014. In Summer 2015, we conducted surveys for 1.5 hr per treatment for a period of 7 days. Captive falconry exercises interfered with raptor surveys at B3 in Summer 2014, and these data were omitted.

We assigned at least two observers to each raptor survey; surveyors used 10 × 42 binoculars, and utilized natural cover of trees and shrubs when possible. Surveys began approximately 30 min after sunrise, and were not conducted during high wind or heavy rainfall, although they occurred on sequential days when possible. We recorded species, time spent within the treatment area, number of attacks (an aggressive stoop where the bird made contact with the ground) and the result of each attack (considered successful if prey was observed in talons or feeding was recorded).

All aspects of animal handling and monitoring were approved by the University of California, Davis's Institutional Animal Care and Use Committee (protocol no. 18026).

2.4 | Statistical analyses

2.4.1 | Vegetation

We used a linear mixed effects model (Bates, Maechler, Bolker, & Walker, 2015) to assess differences in eight vegetation metrics

(height, total cover, bare ground, litter, native grass, native forb, exotic grass, exotic forb) between treatments within and across seasons, with a random intercept for block, and with treatment nested in block, and transect in treatment. We included the interaction of treatment × season if the model fit was better than an additive-only model based on likelihood ratio tests, using transformations as needed to meet model assumptions (see Table 2).

2.4.2 | Wildlife abundance

We used a general indexing approach (Engeman & Whisson, 2006) to make relative comparisons of wildlife abundance within each treatment. Thus, while we did not estimate actual abundance, we operationally defined relative standardized wildlife *activity* within each treatment as "abundance," acknowledging that detection probability was not addressed in this study. Abundance was calculated as the number of unique tagged individuals captured per transect, treatment and season for rodents, and total number of observed individuals per treatment for snakes across two wet (Winter and Spring) seasons. Abundance was standardized by number of days of surveys or trapping days for viable boards and traps (to account for traps and boards damaged or closed by wild pigs [*Sus scrofa*] overnight) respectively. We assumed independence of rodent transects, as our trapping data revealed that only 1.4% of unique individuals (25 of 1,738) travelled between transects (50 m apart).

We used generalized linear mixed effects models to assess relative wildlife abundance, followed by bootstrapping across all seasons combined as described for vegetation analyses. We conducted

TABLE 2 Vegetation parameters by season and grassland treatment. Means (±1 SE) of vegetation metrics at four blocks in the Central Valley, CA, USA; superscript letters within a parameter column and season row indicate a significant difference between treatments within a season at α = 0.05; some variables were transformed for analysis

Identifiers		Vegetation metric							
Season (year)	Treatment	Canopy height (cm)*,†	Bare ground (%)*,†	Total litter (%)†,‡,§	Native grass (%)†,‡,§	Native forb (%)*,†	Exotic grass (%)†,§	Exotic forb (%)*,†	Total cover (%)*,†
Spring (2014)	Unrestored	13 (0.76)[a]	3.5 (0.66)[a]	31 (1.6)[a]	0 (0)[a]	2.2 (0.75)[a]	37 (1.9)[a]	27 (2.0)[a]	96 (0.66)[a]
	Restored	13 (0.65)[a]	6.6 (0.85)[b]	21 (1.6)[b]	12 (1.3)[b]	6.7 (0.97)[b]	36 (1.9)[a]	18 (1.4)[b]	93 (0.85)[b]
Summer (2014)	Unrestored	15 (0.85)[a]	5.6 (1.1)[a]	93 (1.1)[a]	0 (0)[a]	0.006 (0.005)[a]	0 (0)[a]	1.4 (0.23)[a]	94 (1.1)[a]
	Restored	16 (0.82)[b]	5.2 (0.80)[a]	77 (1.6)[b]	17 (1.6)[b]	0 (0)[b]	0 (0)[a]	0.89 (0.32)[b]	95 (0.80)[b]
Autumn (2014)	Unrestored	6.3 (0.54)[a]	9.1 (1.4)[a]	91 (1.4)[a]	0 (0)[a]	0.003 (0.003)[a]	0 (0)[a]	0.062 (0.020)[a]	91 (1.4)[a]
	Restored	9.2 (0.65)[b]	7.4 (0.89)[b]	74 (1.9)[b]	18 (1.8)[b]	0 (0)[a]	0 (0)[a]	0.35 (0.26)[a]	93 (1.1)[b]
Winter (2015)	Unrestored	8.9 (0.70)[a]	15 (1.8)[a]	26 (1.7)[a]	0 (0)[a]	2.0 (0.40)[a]	35 (1.8)[a]	23 (2.0)[a]	86 (1.8)[a]
	Restored	6.8 (0.49)[b]	11 (1.3)[b]	19 (1.3)[b]	11 (1.1)[b]	6.3 (0.99)[b]	35 (1.8)[a]	18 (1.5)[a]	89 (1.3)[b]

Transformations for each parameter: canopy height = sqrt; bare ground = $1/\sqrt{x + 0.005}$; total litter = none; N.Grass = log(x + 0.01); N.Forb = log + 0.001; E.Grass = none; E.Forb = log(x + 0.001); total cover = cube root.

*Significant treatment × season interaction.

†$p < .01$.

‡Significant treatment factor.

§Significant season factor.

these analyses for all rodents combined (*M. musculus* [house mouse], *Peromyscus maniculatus* [native deer mouse], *Reithrodontomys megalotis* [native Western harvest mouse] and *Microtus californicus* [native California meadow vole]), and for each rodent species separately; we did not capture enough *M. californicus* individuals to calculate estimates for this species.

We applied bootstrapping with 1,000 iterations to the final model (Canty & Ripley, 2015; Davison & Hinkley, 1997) to obtain estimates of the mean, *SE*, and 95% confidence intervals (CIs) for relative abundance in each treatment, using Efron's nonparametric bias-corrected and accelerated bootstrap method to assess statistical significance at α = 0.05. If the CI for the difference in activity between treatments or seasons did not contain zero, then this was a significant factor for each analysis.

We used a generalized linear mixed effects model (Bates et al., 2015) to individually assess total number of captures of the three most commonly trapped rodent species, *M. musculus*, *P. maniculatus* and *R. megalotis* as they related to variations in physical vegetation structure. Initial full models included two- and three-way interactions of bare ground × height × season, and treatment × season with a Poisson (log link) family distribution; we reduced the model stepwise and selected candidate models based on likelihood ratio tests (chi-square; Bates et al., 2015).

We utilized the effects of unplanned grazing by sheep at B3 in Summer 2014 to assess changes in rodent species composition in response to changes in physical vegetation structure. We used glmer models with a Poisson distribution, similar to those described above individually for only *M. musculus* and *P. maniculatus*, as we did not trap any *R. megalotis* in Summer or Autumn in that block. The initial full model included the two-way interactions of season × rodent species, bare ground × canopy height, rodent species × bare ground and rodent species × height; we reduced the model stepwise as previously described.

For raptor responses, we standardized by total hours of survey effort within each survey season. We assumed independence of treatments for snakes and raptors, based on the assumption that they would preferentially utilize one treatment or another based on availability of desired resources and meeting of physiological needs in the preferred habitat (e.g. Huey, 1991). Thus, sample units per treatment, block and season were transect (nested within treatment) for live-trapped rodents (*n* = 4) and the entire treatment for raptors and snakes (*n* = 1).

We conducted similar univariate analyses for snakes combined and raptors combined, but we did not analyse within these groups by species because we did not observe sufficient numbers of each species for individual analysis (see Table S2 for list of species). For raptors, we used the same linear mixed effects modelling approach to assess time spent in habitat, number of attempted prey attacks and number of successful prey attacks, with all values standardized by survey effort. Because hunting behaviour varies substantially by species, we counted the number of individuals who attempted at least one attack, and standardized by the total number of raptors observed in the treatment; we did the same for successful prey attacks, as some species have higher

TABLE 3 Wildlife activity in paired unrestored and restored grasslands. Total and unique captures or observations, means, and SEs (±1 SE of the mean) of wildlife activity totalled across up to four seasons (Spring, Summer, Autumn, Winter) from 2014 to 2015 at paired treatments in four blocks in the Central Valley, CA, USA; responses were standardized by live trapping or survey effort

Group/species	Survey method	Metric (standardized)	Treatment	Count (total/unique)	Sample mean/mean estimate*	Sample SE/SE estimate*
All rodents[†,‡]	Live trapping	Live captures	Unrestored	1,585/1022	0.40/0.44	0.03/0.05
			Restored	1,147/716	0.30/0.33	0.03/0.05
Microtus californicus	Live trapping	Live captures	Unrestored	1/1	0.0002/NE	0.0002/NE
			Restored	7/7	0.002/NE	0.0009/NE
Peromyscus maniculatus	Live trapping	Live captures	Unrestored	470/234	0.13/0.14	0.02/0.02
			Restored	338/164	0.10/0.11	0.02/0.02
Reithrodontomys megalotis	Live trapping	Live captures	Unrestored	62/41	0.02/0.01	0.005/0.004
			Restored	28/19	0.007/0.007	0.002/0.002
Mus musculus[†]	Live trapping	Live captures	Unrestored	1,025/721	0.25/0.23	0.033/0.024
			Restored	759/513	0.19/0.26	0.032/0.020
Escapes[†,‡]	Live trapping	Live captures	Unrestored	27/15	0.007/0.006	0.002/0.002
			Restored	25/13	0.003/0.003	0.001/0.001
All snakes[†,§]	Coverboard surveys	Number observed	Unrestored	33/NA	0.92/0.92	0.27/0.24
			Restored	3/NA	0.09/0.09	0.07/0.05
All raptors[†,§]	Timed surveys	Number observed	Unrestored	295/NA	3.7/3.6	0.90/0.54
			Restored	196/NA	1.8/1.7	0.74/0.44
All raptors[§]	Timed surveys	Minutes in treatment	Unrestored	8668/NA	1.8/1.7	0.61/0.45
			Restored	6493/NA	1.2/1.1	0.48/0.32
All raptors[†,§]	Timed surveys	Proportion of individuals attacking	Unrestored	267/118[¶]	0.38/0.37	0.05/0.05
			Restored	130/65[¶]	0.25/0.23	0.08/0.06
All raptors[†,§]	Timed surveys	Proportion of successful individuals	Unrestored	89/60**	0.21/0.20	0.03/0.03
			Restored	27/26**	0.11/0.10	0.04/0.03

NA, not applicable; NE, not estimable due to low sample size.

*Mean and SE estimates obtained using bootstrapping.

[†] Groups/species with treatment estimates that were significantly different at α = 0.05 across all seasons.

[‡] Includes "escapes".

[§] Snake data evaluated for Spring 2014 and Winter 2015 together, as one snake was observed in the UR treatment in Summer and Autumn 2014 combined; raptor data evaluated for all seasons combined (Summer 2014, Autumn 2014, Summer 2015).

[¶] Values are "total number of attack attempts across all raptors"/"total number of raptors that made at least one attack attempt".

**Values are "total number of successful prey captures across all raptors"/"total number of raptors that make at least one successful attack".

success rates than others. This avoided biasing our results towards treatments with a higher number of observations of species that have relatively higher attack or success rates.

For all analyses, when normality of residuals was a model assumption, we performed a Shapiro–Wilk normality test and assumed normality if $W \geq 0.95$.

2.4.3 | Structural equation modelling

We explored relationships among treatments, vegetation parameters and wildlife observations in two separate SEMs, combining Spring and Winter seasons in a "wet season" submodel and Summer and Autumn seasons in a "dry season" submodel. We separated the analysis this way because (1) raptors were only monitored in Summer and Autumn seasons, despite being present in other seasons, while snakes were only observed in Spring and Winter, and (2) vegetation parameters were similar within but not between dry and wet seasons (Figure S1) signalling distinct periods of growth and litter accumulation.

We hypothesized that grassland restoration would directly impact only vegetation, and therefore influences of restoration on wildlife would be entirely mediated by vegetation (Figure S2). We similarly hypothesized that effects of vegetation parameters on snakes and raptors would be indirect, mediated by the abundance of their rodent prey. Thus, our hypothesized model describes a food web under strong bottom-up control with potentially rippling influences of human intervention.

We linked synthetic vegetation parameters (e.g. total plant cover and canopy height) to wildlife to simplify model structure and because we generally found stronger relationships between wildlife and total cover than individual vegetation functional groups (e.g. exotic grasses, native forbs). Total plant cover was modelled as a fixed composite variable, defined as the sum of individual vegetation components. We assumed that canopy height was driven by total plant cover, and that height did not reciprocally influence total cover. Conceptually, canopy height could increase in response to increasing plant cover through light competition and sampling effects of diversity, while cover could increase with canopy height through facilitation. The entire range of canopy heights in our dataset was common at 100% plant cover, while canopies were only taller than 30% of the maximum (15 cm) when cover was over 75%, providing some support for our assumption (Figure S3).

Structural equation models were fitted using local estimation, and claims of independence were assessed using d-separation tests (Grace et al., 2012; Pearl, 2000; Shipley, 2009). We began with hypothesized relationships and considered alternative paths using a cut-off of $\alpha = 0.05$. Canopy height and rodent counts were modelled as Poisson variables (log link), while individual vegetation parameters (logit transformed) and standardized predator abundances (snakes, raptors) were modelled as Gaussian variables (identity link). Regression coefficients were estimated using generalized linear mixed effects models (Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2013) to allow for different family distributions and random terms.

All statistical analyses were performed in R (R Core Team, 2016).

TABLE 4 Confidence intervals for differences in rodent activity by season in paired unrestored and restored grasslands. Estimated 95% confidence intervals (CI) for differences in rodent activity between unrestored and restored treatments in four blocks in the Central Valley, CA, USA; all values standardized by trapping or survey effort. NE = not estimable due to low sample size; overall positive values indicate higher activity in unrestored treatments

| Sampling metric | | | CI for difference | | | | |
Group/species	Survey method	Metric (standardized)	Across seasons	Spring (2014)	Summer (2014)	Autumn (2014)	Winter (2015)
All rodents*†	Live trapping	Unique captures	0.05, 0.18†	−0.09, 0.10	−0.05, 0.10	0.03, 0.15†	−0.03, 0.10
Microtus californicus‡	Live trapping	Unique captures	NE	NE	NE	NE	NE
Peromyscus maniculatus	Live trapping	Unique captures	−0.05, 0.10	−0.08, 0.10	−0.05, 0.10	−0.03, 0.15	−0.03, 0.10
Reithrodontomys megalotis	Live trapping	Unique captures	−0.0002, 0.02	−0.01, 0.03	−0.007, 0.01	−0.0001, 0.06	−0.02, 0.01
Mus musculus	Live trapping	Unique captures	0.01, 0.13†	−0.009, 0.32	−0.12, 0.16	−0.05, 0.17	−0.07, 0.16
Escapes	Live trapping	Unique captures	0.0003, 0.007†	−0.01, 0.004	−0.002, 0.01	0.001, 0.02†	−0.002, 0.008

*Includes "escapes".
†The difference between treatments is significant at $\alpha = 0.05$ if the interval does not contain zero.
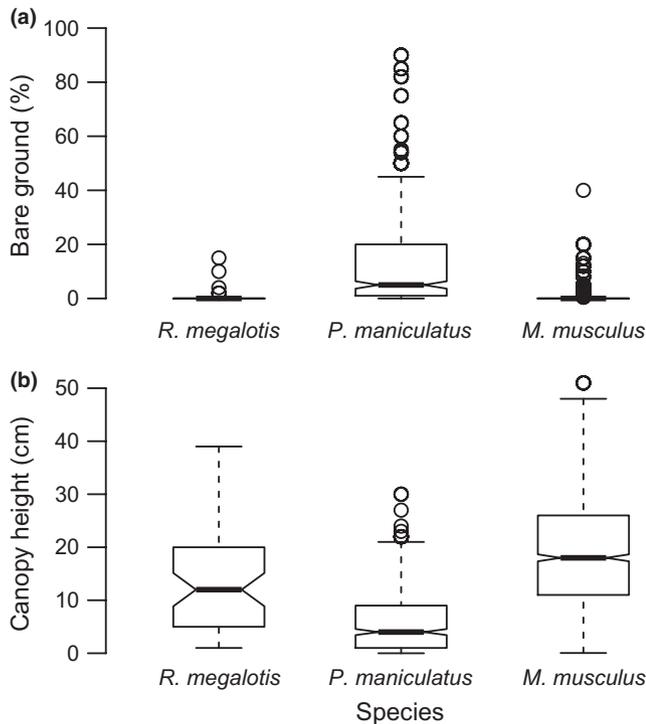‡Only eight individuals trapped, with seven in restored treatments.

FIGURE 2 Bare ground and canopy height near commonly trapped rodent species. Notched boxplots of (a) per cent bare ground and (b) canopy height of vegetation adjacent to live traps for the most commonly trapped rodent species across treatment types and four blocks in the Central Valley, CA, USA in four seasons from Spring 2014 to Winter 2015

FIGURE 3 Canopy height and rodent community composition each season in an unrestored grassland grazed in Summer. Mean (±1 *SE*) (a) canopy height and (b) total number of rodents of each species captured in an unrestored grassland at one Central Valley, CA, USA block across four seasons from Spring 2014 to Winter 2015. Grazing by sheep occurred during the summer season, substantially altering canopy height for the subsequent two seasons

3 | RESULTS

3.1 | Vegetation

Nearly all vegetation parameters differed between UR and R treatments, but these differences were often contingent on season (Table 2 and Tables S3–S5). Treatment and season were significant factors for native grass cover ($p < .001$ and $p = .005$ respectively); we did not detect any native grasses in UR treatments. Native grass cover was highest in Autumn, followed by Summer, Spring and Winter. While cover of native forbs was generally low, we found the interaction of treatment × season to be significant for average native forb cover ($p < .001$), with greater cover in R treatments in Spring and Winter, but no significant difference between treatments in Summer and Autumn.

Treatments had similar exotic annual grass cover ($p = .983$), with cover of live annual grasses depending almost entirely on season ($p < .001$); they were common in Spring and Winter but absent in Summer and Autumn. We found the interaction of treatment × season to be significant for exotic forb cover ($p < .001$), with greater exotic forb cover in UR treatments in Spring and Summer, but no significant difference between treatments in Autumn and Winter.

Treatment and season were significant factors for litter cover ($p < .004$ and $p < .001$ respectively), with more litter in UR treatments across all seasons. Litter cover peaked in all treatments in Summer
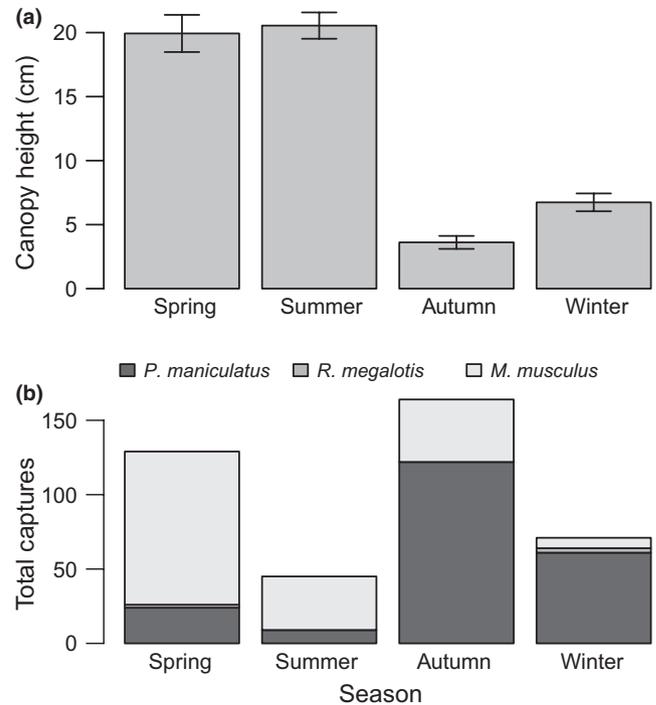
and Autumn signalling seasonal senescence of annual grasses and forbs. The interaction of treatment × season was significant for canopy height ($p < .001$) such that there was no significant difference between treatments in Spring, but was higher in R treatments in Summer and Autumn, and higher in UR treatments in Winter.

We found the interaction of treatment × season to be significant for bare ground ($p < .001$), but there was no consistent trend between the two treatments: R treatments had significantly more bare ground in Spring, UR treatments had significantly more bare ground in Summer and Winter, and we detected no significant difference between treatments in Autumn.

3.2 | Wildlife abundance

Treatment and season were significant factors for rodent abundance, with greater abundance in UR treatments ($p = .0175$; Tables 3 and 4), and higher abundance in Spring, followed by Autumn, Summer and Winter ($p < .0001$; Tables 3 and 4). While native rodent species did not respond significantly to restoration, non-native *M. musculus* was more abundant in UR treatments ($p = .0408$; Tables 3 and 4).

Across treatments, we found the most commonly trapped rodent species in areas with different physical vegetation structure (Figure 2). We caught significantly more *M. musculus* in areas with taller canopy heights ($p < .001$) and less bare ground ($p < .003$),

TABLE 5 Confidence intervals for differences in snake and raptor activity in paired unrestored and restored grasslands. Estimated 95% confidence intervals for differences in standardized wildlife activity between unrestored and restored treatments across up to four seasons from 2014 to 2015 across four blocks in the Central Valley, CA, USA; overall positive values indicate higher activity in unrestored treatments

Group	Survey method	Metric	CI for difference
Snakes	Coverboard surveys	Number observed	0.32–1.7[a]
Raptors	Timed surveys	Number observed	0.51–3.3[a]
Raptors	Timed surveys	Minutes in treatment	−0.20–1.9
Raptors	Timed surveys	Per cent attacks	0.29–0.71[a]
Raptors	Timed surveys	Per cent successes	0.14–0.43[a]

[a]Difference between treatments significant at α = 0.05.

significantly more *P. maniculatus* in areas with lower canopy heights ($p < .001$) and more bare ground ($p < .01$), and significantly more *R. megalotis* in areas intermediate to previous two rodent species, where both canopy height ($p < .001$) and bare ground were low (although not significant, $p = .356$).

We compared spatial vegetation structure and the total number of *M. musculus* and *P. maniculatus* in the UR treatment before and after sheep grazing at B3. Prior to grazing the area was dominated by *M. musculus*. Grazing increased bare ground and reduced litter, but the main impact was a substantial reduction in canopy height (decreased from a mean of 20.5 cm in Summer to 3.6 cm in Autumn). After grazing, the UR treatment was dominated by *P. maniculatus* (Figure 3), such that the interaction of species × season was significant ($p < .0001$). This rapid change in rodent species composition did not occur in any other season, treatment, or block.

We observed significantly more snakes ($p < .003$) and raptors ($p < .007$) in UR treatments. While time spent by raptors in UR treatments was higher, treatment was not significant ($p = .207$; Tables 3 and 5). Attack and success rates varied by species, with the total proportion of raptors attacking at least one prey item ($p = .034$) and successfully capturing at least one prey item significantly higher in UR treatments ($p < .05$; Tables 3 and 5).

3.3 | Structural equation modelling

Structural equation modelling revealed indirect effects of restoration on wildlife in both wet and dry season submodels (Table S6). After testing for the importance of omitted paths in each model, we determined that no additional paths were needed. Restoration treatment had strong, lasting impacts on plant communities, and the results of the SEMs corroborate those for the univariate responses of individual vegetation parameters to treatment and season. More importantly, however, structural equation modelling revealed that wildlife responses were generally more strongly correlated with variables internal to the models (i.e. variables that were both predictors and responses) than with restoration treatment, revealing how restoration influenced patterns of wildlife distribution and abundance (Figure 3).

The two most abundant rodent species responded differently to total plant cover and canopy height (Figure 4), in agreement with univariate analyses. However, even after accounting for the influences of vegetation on these two species, there remained a strong

and significant ($p < .001$) negative correlation between these species in both submodels, which we retain as an unexplained correlation. This correlation may reflect some unmeasured relationship between rodents and the plant community or, perhaps more likely, competitive interactions between rodent species.

Snakes and raptors both responded to the abundance of rodent prey. Snakes were positively associated with *M. musculus* abundance, yet there remained a negative effect of restoration treatment despite no association with either total plant cover or canopy height, possibly revealing large-scale habitat preference resulting from combined effects of vegetation structure and prey availability. Raptors were also positively associated with *M. musculus* abundance, and we detected a negative association with canopy height that may reflect some aspect of habitat patch quality related to foraging success.

4 | DISCUSSION

Less than 2% of historic native grasslands currently exist in the Central Valley of California, which has driven interest to restore native grassland biodiversity and associated ecosystem functions. However, grassland restoration requires substantial resource investment, has variable success, and is rarely followed with monitoring to determine if stated goals were met. Ideally, grassland restoration would improve habitat quality for native wildlife and restoration success would be measured throughout the food web.

Our results in the Mediterranean climate of the Central Valley reveal that grassland restoration was successful in establishing long-term presence of native grasses not seen in invaded, annual grasslands. This change in plant composition from restoration altered the physical structure and native diversity of vegetation, which are likely to influence wildlife composition (Gill et al., 2006; Goerrissen, 2005). We observed greater utilization of UR treatments by native predator populations, likely in response to significantly more non-native rodents. Rodent abundance was higher overall in UR than R treatments. Even when the difference was not statistically significant for a season or species, total captures, unique captures and standardized abundance were strongly skewed towards higher abundance in UR treatments for all species. However, the overall difference in rodent abundance was largely driven by greater abundance of non-native *M. musculus* in UR treatments.
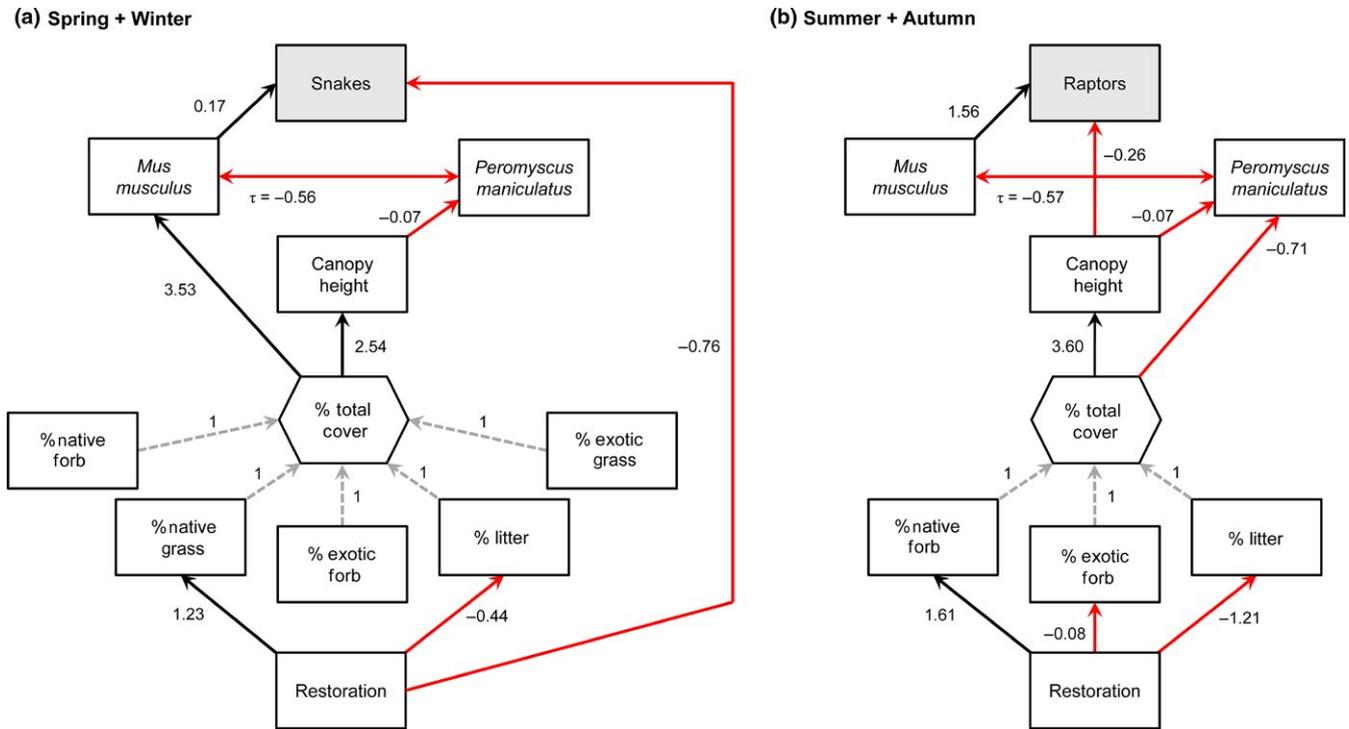
FIGURE 4 Final structural equation models for (a) Spring + Winter and (b) Summer + Autumn season submodels. Structural equation models for wildlife in unrestored and restored grassland treatments in four blocks in the Central Valley, CA, USA from 2014 to 2015. Hexagonal variable for total plant cover is a composite variable defined as the sum of individual vegetation groups (i.e. path coefficient ≡ 1, dashed arrows). Standardized snake and raptor abundance are shown in grey to signify that models involving these variables used median values of explanatory variables by location, treatment and season. Black arrows represent significant positive regression coefficients and red arrows represent significant negative coefficients. Individual vegetation components (e.g. native grass cover) were logit transformed before running linear models. Unstandardized path coefficients are shown, along with Kendall rank correlation coefficients between mouse species (τ). Linear regressions predicting canopy height and rodent abundances used Poisson error distributions and all others used Gaussian error distributions. We used $\alpha = 0.05$ as a threshold for determining whether paths should be added or removed from the model [Colour figure can be viewed at wileyonlinelibrary.com]

It is likely that differences in rodent abundance were driven by changes to micro-habitat availability and physical structure of the landscape. In particular, differences in the amount of litter between UR and R treatments might help explain this pattern. Greater litter in UR treatments can act as protective cover for species like *M. musculus*, which was more abundant in UR treatments and appears to prefer greater cover in comparison with native mice. Additionally, the presence of native bunch grasses might have decreased habitat quality for dominant non-native mice, although the mechanism underlying this potential effect remains unclear. Nevertheless, like the R treatments in our study, many grassland restorations seed with native bunchgrasses, and management to reduce invasive vegetation and keep interspaces open might allow for increased diversity of subordinate plant species (Bond, Baumann, Lanell, Thackston, & Bowman, 2005) and discourage colonization by non-native rodents.

While UR treatments harboured more rodents than their R counterparts on average, the two most abundant rodent species showed habitat-use differences related to physical structure that were consistent across treatments. We trapped more *P. maniculatus* in areas with more bare ground and shorter vegetation, and more *M. musculus* in areas with less bare ground. These preferences appear to be so strong that an abrupt alteration to grassland physical structure can result

in a rapid shift in rodent species composition, as we found with the shift in dominance from *M. musculus* to *P. maniculatus* following summer sheep grazing in one UR grassland. This finding is corroborated by previous research showing that these two species' distributions overlapped in vegetated floodplains but not in heavily grazed uplands of grasslands in Iowa, USA, which were dominated by *P. maniculatus* (Geier & Best, 1980).

We estimated mean abundance of snakes and raptors to be ten and two times higher, respectively, in UR than R treatments which is likely reflective of greater availability of prey resources in UR treatments (Galushin, 1974; Luiselli, 2006). Furthermore, we observed more than twice as many predatory attacks by raptors and almost twice as many successful raptor attacks in UR treatments, while SEMs revealed positive impacts of *M. musculus* abundance on both snakes and raptors and negative effects of restoration that are likely mediated by vegetation structure. Treatment areas were clearly too small to serve as entire home or foraging ranges; nevertheless, most reserves would also be too small to act as home ranges, and the focus for raptor conservation could instead be on those factors that make smaller habitats preferred and how degraded habitats can be improved or made more attractive to raptors (Widén, 1994) (also see Appendix S1 for other caveats). If a goal of restoration is the establishment of foraging grounds for native

snakes and raptors, practitioners should consider whether their methods will result in increased prey abundance.

5 | CONCLUSIONS

Grasslands are among the most threatened habitats in the United States (Vickery & Herkert, 2001). Weed invasions by annual grasses in California represent a sweeping change to plant species composition and spatial structure, displacing native vegetation and ultimately affecting faunal communities and habitat utilization (D'Antonio, Dudley, & Mack, 1999). While invasive plants are thought to have little impact on biotic communities relative to pathogens and predators (Meiners, Pickett, & Cadenasso, 2001), we found clear and consistent differences in abundance of rodents, snakes and raptors in unrestored and restored grasslands across four blocks in the Central Valley, despite obvious differences in history, management, topography and surrounding land-use. Management and conservation of existing exotic annual grasslands may thus provide better raptor foraging grounds than restored grasslands.

Restoration ecology is a rapidly evolving discipline, but still lacks theory integrating multi-trophic interactions into large-scale experiments (Kardol & Wardle, 2010). Monitoring of organismal responses to grassland restoration—and changes to multi-trophic interactions—is necessary to inform management and better appropriate funds available for restoration and conservation. Our results will inform land management in grasslands for a number of taxa, and give scientists and managers a better grasp of the variety of impacts that grassland restoration, community composition and physical structure may have on wildlife. Such evidence-based assessments provide better tools for developing vegetation and wildlife management plans in restored and invaded landscapes.

AUTHORS' CONTRIBUTIONS

K.M.W. and R.A.B. designed the study; K.M.W. implemented the study and conducted univariate analyses and wrote and edited the manuscript, and M.A.W. conducted structural equation modelling; R.P.B. conducted and supervised raptor surveys; M.A.W., R.P.B., and R.A.B. edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Additional Supporting Information may be found online in the supporting information tab for this article.