

## RESEARCH ARTICLE

## Incorporating temporal dynamics to enhance grazing management outcomes for a long-lived species

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## Abstract

1. Identifying successful management strategies for long-lived species is challenging, especially in fluctuating environments, because the response of individual vital rates and overall growth rates to management action can vary over time. A demographic approach that isolates the impact of management and environment on individual vital rates, and assesses their importance for growth rate over time, can indicate whether and why a management strategy is successful.
2. Here we take a demographic approach to assess the success of grazing management for the perennial grass *Stipa pulchra*, California's state grass and a focus on conservation efforts. We tracked *S. pulchra* populations in paired grazed and ungrazed plots over 6 years, which included a historic drought and an El Niño rain year, and calculated summary transition matrices for the main effects of year, grazing and year  $\times$  grazing interaction for each site. We averaged these summary transition matrices to calculate population growth rates,  $\lambda$ , for the main effects of year, grazing and year  $\times$  grazing and used life table response experiment (LTRE) analysis to compare how individual vital rates contributed to differences in  $\lambda$  between grazed and ungrazed plots over time.
3. Overall we found that grazing was a successful management strategy; grazed populations maintained a positive average population growth rate whereas ungrazed populations declined. We found that grazing had a larger positive effect on growth rates in wet years than drought years. This was because grazed populations benefited from a greater contribution of adult growth immediately following the end of the drought compared with ungrazed populations and from adult survival thereafter.
4. *Synthesis and applications.* Although *Stipa pulchra* is the focus of many management efforts, the use of grazing for management is contentious, and there have been few studies that take a demographic approach to understanding *S. pulchra* responses over time. Our results indicate that conservation and restoration efforts should move beyond recruitment to focus on adult growth and survival for overall population success. To this end, moderate grazing can be a successful

strategy to maintain *S. pulchra* populations and is particularly important in wet years to promote plant growth.

#### KEYWORDS

California grasslands, drought, life table response experiment, plant demography, population growth, rainfall variability, *Stipa pulchra*

## 1 | INTRODUCTION

Successful conservation efforts require understanding species population dynamics, and if necessary, identifying interventions that shift these dynamics to increase species' average growth rate (Menges, 2000). Long-lived species pose a particular challenge for conservation, as persistence depends on a positive average growth rate, but their annual growth rates and underlying vital rates may vary widely in relation to environmental conditions (Buckley et al., 2010; Morris et al., 2008). Furthermore, the same management action may alter individual vital rates differently depending on the environment, and management actions may alter multiple vital rates at the same time (Li et al., 2013; Thorson et al., 2015). Consequently, understanding how management efforts modulate different vital rates over time, coupled with understanding the relative importance of different vital rates for population viability, is key for developing effective practices to conserve long-lived species (Chirakkal & Gerber, 2010; Frederiksen et al., 2014).

Variation in vital rates (survival, growth, reproduction and recruitment) can be key to the persistence of long-lived plant species (Villellas et al., 2015), but can also complicate management (Shea et al., 2010). For example, high recruitment or growth in favourable years, coupled with high adult survival in otherwise unfavourable years, can maintain the viability of long-lived species populations (Hilde et al., 2020). Thus, while a population that is in decline due to persistently low recruitment may benefit from seed addition, a common restoration strategy, it must coincide with a period favourable for recruitment to be successful (Fehmi et al., 2014). The effect of management actions on other vital rates may also depend on environmental conditions (Davison et al., 2010; Frederiksen et al., 2014). For example, grazing is a common grassland management strategy to promote the growth of target species by reducing their competitors (Brys et al., 2004; Vitt et al., 2009). This effect is likely most beneficial under high resource conditions, however; under low resource conditions, such as a drought, grazing may reduce growth by increasing stress on the target species (Souther et al., 2020). Assessing performance across a wide range of conditions and over time is, therefore, essential for predicting population trajectories in changing and managed environments.

Identifying which vital rates to target is key to long term management success. For example, while restoration efforts often focus on recruitment (Palma & Laurance, 2015), adult survival is often the vital rate to which long-term population persistence is most sensitive (Morris et al., 2008). Increasing adult survival may require

ongoing management actions, such as annual mowing or grazing to reduce competitors (Li et al., 2013), or periodic management to bolster adult populations after an extreme event, such as planting adult plugs after a large drought (Mordecai et al., 2015). Importantly, management actions may have opposing effects on different vital rates. For example, grazing may promote adult survival through competitor reduction but lower recruitment by consuming seedlings (Brys et al., 2004; Li et al., 2013). As such, the efficacy of management actions should be assessed in terms of how they affect overall population growth rather than individual vital rates. This requires an integrative approach to assess the relative contribution of each vital rate to growth under different environmental conditions and on average over time.

*Stipa pulchra* (purple needlegrass, hereafter *Stipa*, species nomenclature follows Baldwin et al., 2012) exemplifies the challenges of managing long-lived species in a variable and changing world. *Stipa* is a long-lived native perennial which is thought to have dominated many areas of California now dominated by non-native annual grasses (Heady, 1977). As a relict species of native Californian grasslands, *Stipa* is often incorporated in restoration outplantings and is a focal point of management if any relict populations remain on the landscape (D'Antonio et al., 2002). California's high climate variability has complicated efforts to assess *Stipa* population dynamics (Dyer, 2002; Hamilton et al., 2002; Marty et al., 2005). Grazing has been posited as a management tool to reduce *Stipa* competitors, providing microsites for recruitment and enhancing adult growth (Menke, 1992). At the same time, the combination of grazing and drought has been implicated in the conversion of California grasslands to an annually dominated state (Jackson, 1985; Stromberg & Griffin, 1996), and the effect of grazing may, therefore, depend on rainfall conditions. To date the majority of *Stipa* management studies have focused on the seedling phase, on the basis that annual grasses are mostly likely to suppress *Stipa* individuals at this life stage (Lulow, 2008; Moyes et al., 2005; Young et al., 2015). At the same time, it is estimated that *Stipa* can live up to 100 years (Hamilton et al., 2002), and a few studies have highlighted the potential for longevity to buffer perennial populations across low recruitment years (Mordecai et al., 2015; Seabloom et al., 2003).

Here, we use a long-term demographic data set to assess the effectiveness of sheep and cattle grazing as a management tool for relict *Stipa* populations in highly variable California grasslands. We tracked the dynamics of *Stipa* populations in paired grazed and ungrazed plots across 6 years, a period which included both an historic drought and an extremely wet year. We used matrix models

to calculate population growth and conducted a life table response experiment (LTRE) to assess which demographic processes contributed to population growth over the study. We hypothesized that the effect of grazing on individual vital rates and overall population growth would differ by rainfall conditions. Specifically, we expected that grazing would have a positive effect on population growth by enhancing recruitment and growth in wet years via competitor reduction, but a negative effect on population growth in dry years by reducing the survival of drought-stressed plants. Second, we hypothesized that, although most restoration efforts focus on recruitment, adult survival would be most critical management determinant of long-term population viability. Although *Stipa* is the focus of extensive conservation efforts in California, our study is one of the first demographic studies to assess *Stipa* response to rainfall and grazing management in a holistic way.

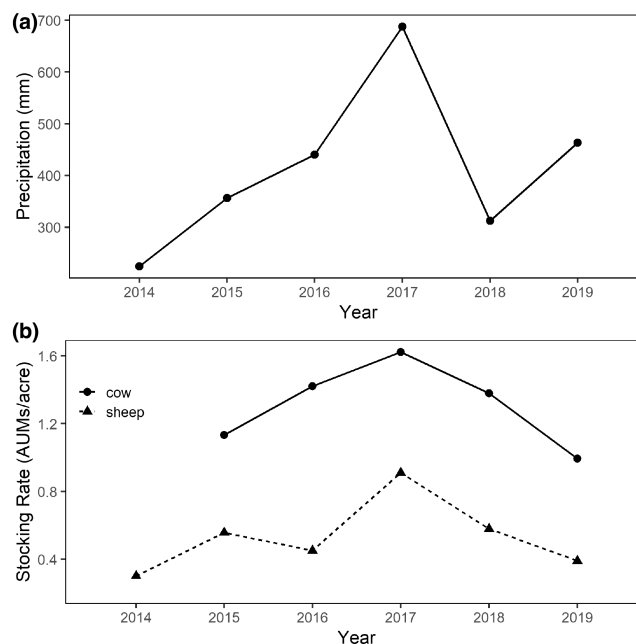
## 2 | MATERIALS AND METHODS

### 2.1 | Study site

We conducted our study from 2014 to 2019 at the Vasco Caves Regional Preserve (37°48'17.95"N, 121°41'13.15"W, Byron, CA; Vasco Caves hereafter) and in the Los Vaqueros Watershed (37°48'30.43"N, 121°44'55.49"W) with approval from the East Bay Regional Park District. These sites are reflective of the valley grassland vegetation type, which extends across the Central Valley from the foothills of the Sierra Nevada to the east and the California coast ranges to the west (Bartolome et al., 2007; Heady, 1977). The valley grasslands in these preserves are dominated by non-native annual grasses (e.g. *Avena fatua*, *Festuca perennis*, *Bromus diandrus*), but the preserve has several patches of remnant native perennial bunchgrasses (e.g. *S. pulchra*, *Melica californica*; species nomenclature follows Baldwin et al., 2012). The bunchgrass *Stipa* is among the 10 most common species at Vasco Caves, although its abundance varies considerably both spatially and temporally (Bartolome et al., 2012). The site has a Mediterranean climate, with cool-wet winters and hot-dry summers, with the growing season constrained from September to May. *Stipa* seedlings germinate following the fall rains and juveniles and adults set seed in late spring. The average growing season rainfall from 1981–2019 was 395.7 mm and average growing season temperature over the same period was 13.2°C (PRISM Climate Group, 2012). The first years of sampling, 2014 and 2015, were the last years of a historic multi-year drought for the state of California (growing season precipitation from 2012–2015 was 258.8, 279.1, 224.5, 356.6 mm; respectively), and rainfall varied considerably over the study period (Figure 1a).

### 2.2 | Grazing study

At six sites, we set up grazed and ungrazed paired 10 m × 15 m plots (Figure S2). Ungrazed plots were fenced with 4-ft high wire mesh



**FIGURE 1** (a) Growing season (September–May) precipitation over the course of the study. (b) Stocking rates (animal unit months AUMs per acre) of cow and sheep over the course of the study (records are missing for cattle in 2014, but grazing was comparable with subsequent years). Cattle were grazed in the Los Vaqueros Watershed primarily from November to May, and sheep were grazed in Vasco Caves Regional Preserve primarily from January to July.

that excluded sheep and cattle but not native consumers (e.g. rodents). When possible, we included sites established by Bartolome et al. (2012), such that one of our plots was ungrazed since 2005 and another since 2008; in 2013 we added new paired grazed controls adjacent to these plots (Table S1). A third ungrazed plot from Bartolome et al. (2012) experienced marked declines in *Stipa* abundance, with too few *Stipa* remaining to measure in this study, suggesting potential survival bias in the retained ungrazed plots. Consequently, in 2014 we established four new ungrazed plots and paired grazed controls, targeting areas in which *Stipa* was abundant (Table S1). One of the new sites was in Los Vaqueros Watershed, which is cattle grazed, whereas the other five sites were in Vasco Caves which is sheep grazed.

Vasco Caves has a long history of sheep grazing from mid-winter (January/February) through spring and early summer, while Los Vaqueros Watershed has a history of cattle grazing primarily from November through May with summer grazing in wet years. Given this legacy, our experiment can be thought of as a test of grazing management compared with grazing removal rather than to permanently ungrazed management. During our study, Vasco Caves had a yearly average stocking rate of 0.49 AUMs/acre and Los Vaqueros had a yearly average stocking rate of 1.31 AUMs/acre (Figure 1b). In 2018 we measured aboveground net primary productivity in the ungrazed plots as 499 ( $\pm 68$ ) g/m<sup>2</sup> (Figure S4B) and Vasco Caves grazing records indicated a residual dry matter of 263 ( $\pm 42$ ) g/m<sup>2</sup> (D. Bell, pers. comm.), suggesting a utilization rate of around 50%. Grazing

and animal care was operated by third party lessees and overseen by the East Bay Regional Park District.

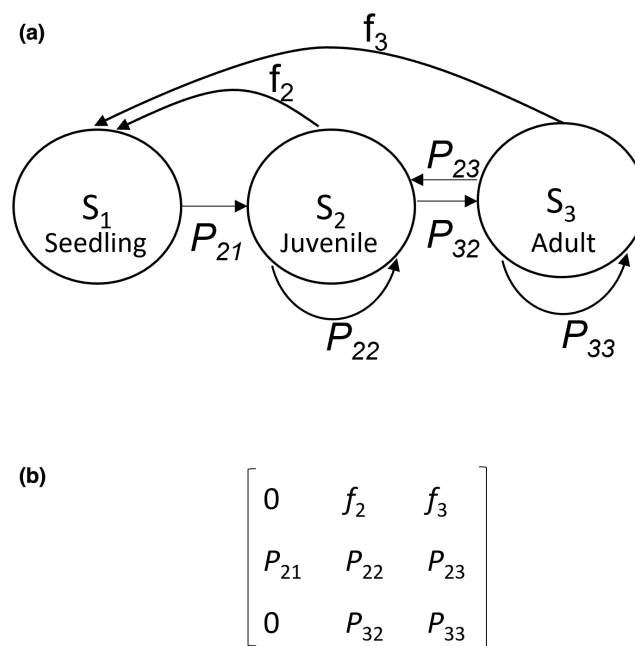
In each 10 m × 15 m plot, we set up replicate 0.5 m × 0.5 m subplots to sample *Stipa* individuals. Along the 10 m side we set out at least three transects spaced every 3 m, setting a subplot every 2 m along the transect, for a total of five subplots per transect (Figure S2). We continued adding transects as needed until at least 50 *Stipa* individuals were censused with the 100m<sup>2</sup>. Thus, we sampled at least 15 subplots (three transects with five subplots) in every plot; in two plots it was necessary to increase sampling intensity to meet our quota (Table S1). Within a subplot we marked each *Stipa* individual with an aluminium tag and measured basal circumference by wrapping a soft measuring tape around the base of the individual. For any individuals that were oblong shaped, we measured length and width instead of circumference. For individuals that died back into distinct clumps due to drought or gopher activity we took multiple smaller circumference measurements. For individuals less than 3 cm in circumference we counted the number of ramets and scaled circumference allometrically. We noted when an individual was clearly a new recruit (e.g. seed husk still visibly attached to plant or little to no standing dead biomass). We converted basal circumference measurements and length and width measurements to area to estimate the size of an individual, which we used to demark the life stages described below, with the largest individuals estimated at 389.9 cm<sup>2</sup> (Figure S3).

Because we marked each individual, our design allows us to track changes in *Stipa* population structure. From 2015 to 2019, we revisited all plots yearly in April, noted and removed tags from dead individuals, re-measured live individuals and noted and marked new seedlings. For each subplot, we created a map of all the tagged individuals to help ensure resampling success. We also counted intact reproductive culms on any flowering juvenile or adult, as a measure of reproductive output. In 2019, we additionally bagged a reproductive culm on 10–20 individuals in each ungrazed plots to get an estimate of seeds per reproductive culm. The bags were set in early April and resampled in late May after seed set. We only sampled seeds per culm within ungrazed areas because grazers would preferentially target the seed bags out of curiosity, making it challenging to get an accurate estimate.

In 2018, we sampled aboveground plant vegetation at each of the 12 plots. Within each 10 m × 15 m plot we sampled all aboveground plant material within five 25 cm × 25 cm quadrats haphazardly placed within the sampling area. We sorted the biomass into litter (plant material from a previous year) or live biomass (growth from that growing season).

## 2.3 | *Stipa* life cycle

For our study, we specified a *Stipa* life cycle that included three life stages: seedling, juvenile and adult (Figure 2a). We defined a seedling as a new recruit less than 1 cm basal circumference (i.e. <0.08 cm<sup>2</sup>), a juvenile as an individual between 1 and 3 cm in basal circumference



**FIGURE 2** (a) Life cycle diagram of perennial bunchgrass, *Stipa pulchra*.  $S_1$ – $S_3$  represent key life stages evaluated in this project: Seedling (<1 cm basal circumference), ‘juvenile’ (1–3 cm basal circumference) and adult (>3 cm basal circumference), respectively. Arrows connecting life stages indicate the probability of transition from one stage to the next or remaining at that life stage, with the first subscript denoting the transition stage and second the initial stage. (b) Transition probabilities used to populate a transition matrix that corresponded to the life cycle. Zeroes in the matrix indicate transitions that are not observed. The time step for this analysis is 1 year.

(i.e. 0.08–0.72 cm<sup>2</sup>), and an adult as anything larger than 3 cm (i.e. >0.72 cm<sup>2</sup>) in basal circumference (Figure S3). Our spring census allowed us to begin with the seedling stage where an individual can transition to a juvenile if it survives its first year, with summer survival a primary barrier to this transition ( $P_{21}$ ). An individual can remain a juvenile ( $P_{22}$ ) or transition to an adult ( $P_{32}$ ). We used the term juvenile because many of these individuals were transitioning from seedlings, however they should be thought of as ‘apparent juveniles’ as an adult can remain an adult ( $P_{33}$ ) or regress back to a juvenile ( $P_{23}$ ), due to splitting or an overall reduction in size. We assumed based on field observations that seedlings are not reproductive but juveniles ( $f_2$ ) and adults ( $f_3$ ) are.

We used our measured vital rates to populate transition matrices (Figure 2b). We estimate the transition from seedling to juvenile ( $P_{21}$ ) as the proportion of all seedlings in a plot in the previous year that transitioned to juveniles, and the transition from juvenile to adult ( $P_{21}$ ) as the proportion of all juveniles in the previous year that transitioned to adults. We estimated juvenile ( $S_2$ ) and adult ( $S_3$ ) survivorship as the proportion of surviving individuals of their respective class surviving in a plot since the previous year. Adults periodically regressed to juveniles ( $P_{23}$ ), which we estimated as the proportion of adults in a plot that decreased in size class from the previous year. We estimated the fecundity of juveniles ( $f_2$ ) and adults ( $f_3$ ) as the

product of the probability that an individual reproduced the previous year (calculated as the number of individuals with reproductive culms/the total number of individuals sampled in the plot), the average number of culms for a reproductive individual the previous year, the average number of seeds per reproductive culm (measured on bagged culms in 2019; Table S2), and a recruitment rate. The recruitment rate was estimated as the proportion of seedlings found in the plot relative to the total plot-level seed production the previous year (estimated as the total number of reproductive culms  $\times$  average number of seeds per culm). Both seedling and seed estimates were scaled by area to account for the different sampling area in some plots.

We assembled summary transition matrices for each of the main effects of year, grazing and the year by grazing interaction for each site (Figure 2b). For each summary matrix we pooled the data from all plots within the focal treatment and then estimated the transition probabilities and fecundity using the pooled data. For example, to estimate the effect of grazing we pooled across all individuals sampled from 2014 to 2019 in the grazed versus ungrazed experimental plot, respectively. This approach allowed us to minimize the impact of stochastic changes in the other treatments on our calculations of transition probabilities for the main effects (Horvitz & Schemske, 1995). This approach resulted in 12 summary transition matrices to test grazing effects, (2 grazing treatments  $\times$  6 sites), 30 summary transition matrices to test year effects (5 years  $\times$  6 sites), and 60 transition matrices to test a grazing by year interaction (2 grazing treatments  $\times$  5 years  $\times$  6 sites). In these instances, each year represents the changes in vital rates between 2 years (e.g. 2015 represents changes from 2014 to 2015). We did not pool across sites as we observed variable responses in the subpopulations to the treatments that we wanted to account for in our analysis. This by-site summary matrix approach allowed us to best account for these site-level differences while also minimizing the impacts of one treatment on the transition probabilities of another.

## 2.4 | Analyses

We first characterized plot-level density patterns within each of the four life stages to assess trends in grazing response over time. We conducted linear mixed effects models, with the average density/ $\text{m}^2$  of a focal life stage as the response variable, year as the fixed effect and site as a random effect. Due to large differences in initial density between grazed and ungrazed areas, we ran the models separately for grazed and ungrazed populations. To evaluate how grazing treatments impacted vegetation, using data collected in 2018 we conducted linear mixed effects models with either litter or live biomass as the response variable, grazing treatment as the fixed factor and biomass sample replicate nested within grazing treatment and site as a random factor. All analyses were conducted in Rv4.0.2; mixed-effect models were conducted using library('nlme') (Pinheiro et al., 2013) and contrasts were assessed using library('multcomp') (Hothorn et al., 2008).

We calculated population growth rate using the library('popbio') in R for the main effects of year, grazing and their interaction

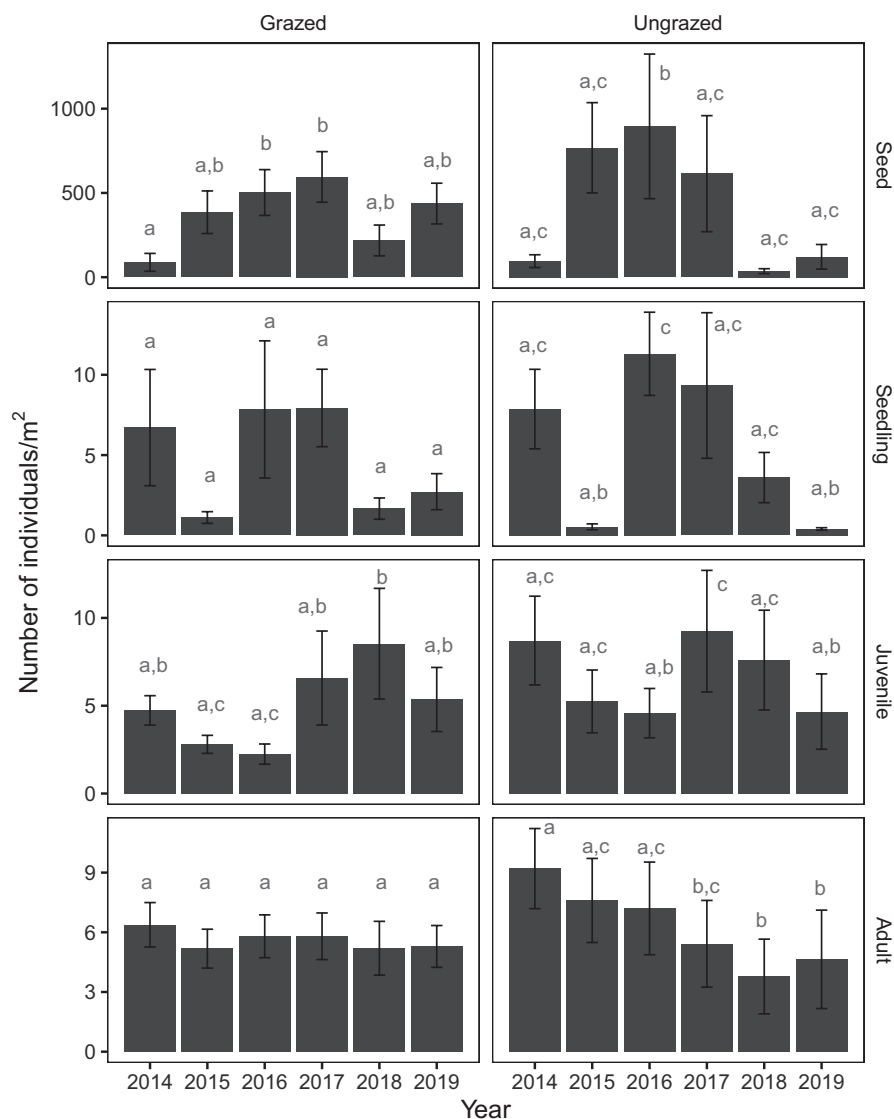
(Stubben & Milligan, 2007). To calculate lambda for the main effects of year and grazing we first averaged the summary matrices across our sites to generate an average transition matrix and used this average matrix to calculate the population growth rate,  $\lambda$ . We estimated the population growth rate as the dominant eigenvalue of the averaged transition matrix. We compared differences in  $\lambda$  by calculating 95% confidence intervals via bootstrapping (Caswell, 2000). We randomly resampling individuals with replacement within a treatment to generate a bootstrapped data set of equal size for each plot. We then recalculated our transition probabilities and transition matrices as described above for each respective factor (year, grazing, year  $\times$  grazing) and averaged our bootstrapped matrices to recalculate  $\lambda$ . For example, for confidence intervals around grazed and ungrazed  $\lambda$ , we calculated 12 transition matrices (i.e. 2 grazing treatments  $\times$  6 sites) from the bootstrapped dataset. We averaged the six site matrices within each treatment to get an average transition matrix that we used to calculate  $\lambda$ . We repeated this process 999 times from which we calculated the mean lambda and 95% confidence intervals. To determine whether lambda was significantly different between grazing and among years, we compared overlapping confidence intervals.

To quantify how different matrix elements may have contributed to the observed differences in  $\lambda$ , we additionally conducted a LTRE retrospective analysis (Caswell, 2000; Horvitz et al., 1996), using the library('popbio') (Stubben & Milligan, 2007). For the LTRE analysis, we compared an observed matrix with a pooled referenced matrix. We estimated the reference matrix by calculating transition probabilities from the entire data set ( $N = 4974$ ). The LTRE analysis for the main effects of year and grazing were estimated using the same average summary matrices used to estimate lambda. The LTRE for the interactive effects of year and grazing were estimated by first calculating the LTRE effects for each of the 60 transition matrices. From each of these matrices we then subtracted the main effects of year and grazing, leaving us with the net interactive effects of year and grazing. To assess contributions by demographic processes we grouped and summed across matrix elements into growth ( $P_{10}$ ,  $P_{21}$ ,  $P_{32}$ ), survival ( $P_{22}$ ,  $P_{33}$ ), regression ( $P_{23}$ , adult reducing to size of a juvenile) and fecundity ( $f_2$ ,  $f_3$ ). To assess contributions by life stage for the LTRE, we grouped and summed across matrix elements for a given life stage. Within the same bootstrapping efforts described above for lambda we additionally ran the LTRE analysis on the bootstrapped data set to generate 95% confidence intervals around our estimates.

## 3 | RESULTS

### 3.1 | Life stages and vital rates

Over the course of the study, we tagged almost 5000 individuals across all life stages. Density tended to vary over time, but the extent of the variation was dependent on the life stage and grazing treatment (Figure 3; Table S3). For example, in both grazed and ungrazed areas, estimated seed density varied over time, peaking in 2016 for grazed areas and in 2017 for ungrazed areas (Table S3).



**FIGURE 3** Average number of *Stipa pulchra* individuals across different life stages observed within experimental plots over time ( $\pm$ SE). Interannual density varied more for seed and seedling stages, and grazing impacted adult density over time. Letters indicate post-hoc significant differences between years within a given grazing treatment at  $p < 0.05$ . Model summary statistics are reported in Table S3.

Seedling density did not significantly differ among years in grazed plots but did differ significantly between years in ungrazed plots, where seedling density was greater in 2016 compared with 2015 and 2019 (Table S3). Juvenile density also varied among years in grazed and ungrazed areas, with peak density in 2018 for grazed areas versus 2017 in ungrazed areas (Table S3). Adult density did not vary over time in the grazed plots, but it did slowly decrease over time in the ungrazed areas (Table S3).

The removal of grazing resulted in litter accumulating in ungrazed plots. In 2018, litter biomass was almost three times that of ungrazed areas ( $F_{1,5} = 17.12$ ,  $p < 0.01$ ; Figure S4A). Aboveground live biomass, however, did not differ between grazed and ungrazed areas ( $F_{1,5} = 3.22$ ,  $p = 0.13$ ; Figure S4B).

### 3.2 | Population growth

We observed that *Stipa*  $\lambda$  varied over the course of the study and ranged from 0.70 to 1.24. For 3 of the 5 transition year periods, it

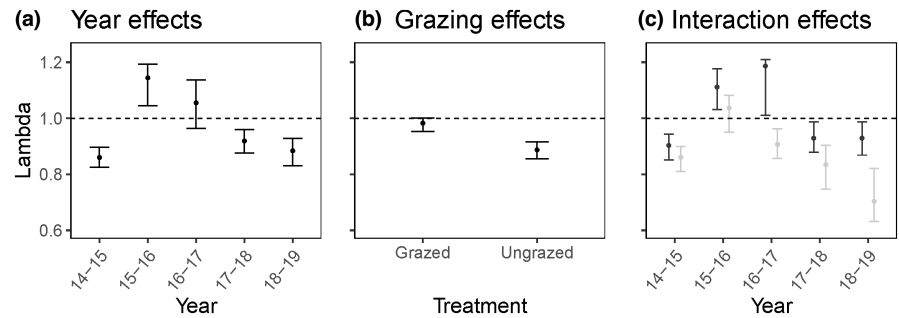
was significantly less than 1 (i.e. 95% CI did not overlap 1; Figure 4a). Ungrazed areas had a lower  $\lambda$  than grazed when pooled across years (i.e. 95% CI did not overlap; Figure 4b). However, within a given year this trend was more nuanced, where  $\lambda$  for grazed areas was greater than ungrazed only in 2017 and 2019 (Figure 4c). The magnitude of the difference between lambdas under grazed compared with ungrazed conditions was greatest in our wettest year (2017) and lowest under drought (2015–2016), suggesting that grazing was more favourable for population growth in wetter conditions (Figure 4c).

### 3.3 | Vital rate contributions to population growth

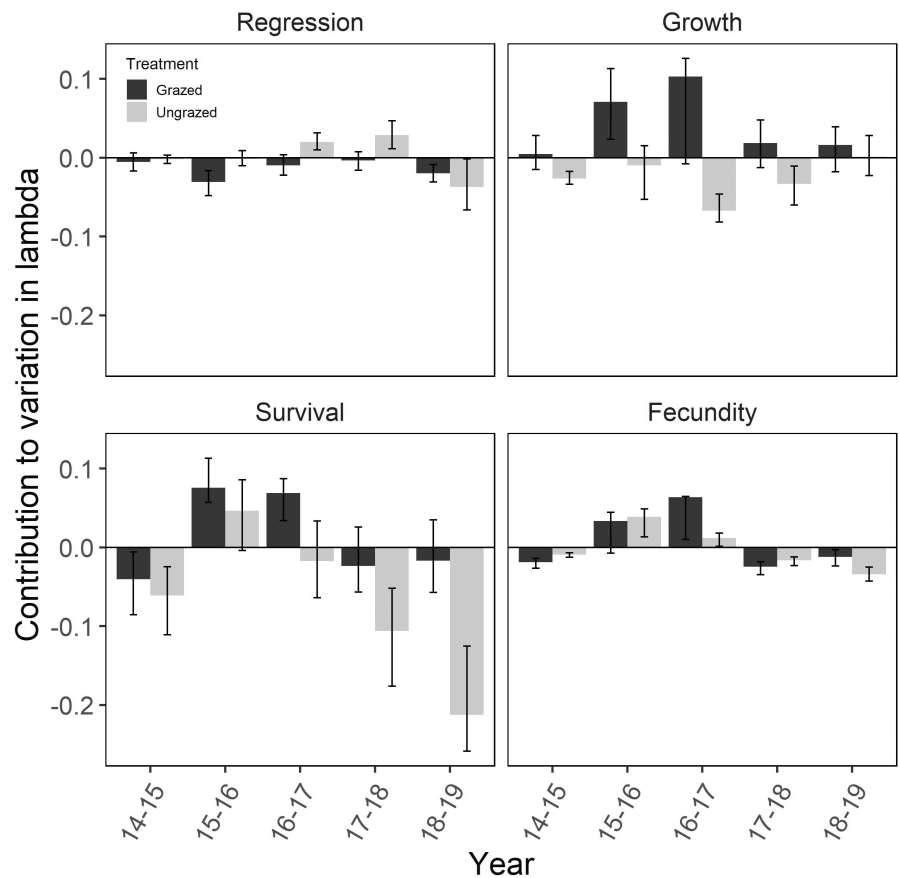
Our LTRE analysis indicated that greater  $\lambda$  in grazed versus ungrazed areas was due to a combination of different demographic responses over time (Figure 5; Figure S5). For example, in the 2015–2016 and 2016–2017 years, the positive values of  $\lambda$  were due to strong responses in growth for *Stipa* individuals (i.e. transitions from one stage to the next) and higher survivorship in the grazed areas (Figure 5).



**FIGURE 4** Lambda for *Stipa pulchra* populations across (a) year, (b) grazing treatments and (c) grazing and year interaction (dark is grazed, light is ungrazed). Note that year indicates the timestep between the 2 years listed (e.g. 14–15 is transition from 2014 to 2015).



**FIGURE 5** Summary of life table response experiment of contributions of matrix elements representing regression ( $P_{23}$ ; adult reducing to size of a 'juvenile'), growth ( $P_{10}$ ,  $P_{21}$ ,  $P_{32}$ ; transition from one life stage to the next), survival ( $P_{22}$ ,  $P_{33}$ ; survival for 'juveniles' and adults) and fecundity ( $f_2$ ,  $f_3$ ; seedlings produced by 'juveniles' and adults) to annual differences in population growth in grazed and ungrazed populations of *Stipa pulchra*. Errors bars indicate bootstrapped 95% confidence intervals. Note that year indicates the timestep between the 2 years listed.



Conversely the increasingly lower  $\lambda$  for ungrazed populations was associated with lower survivorship (Figure 5). On average, the demographic dynamics of juveniles and adults made the largest contributions to  $\lambda$  in the grazed and ungrazed populations (Figure S5).

## 4 | DISCUSSION

Long-lived species pose a challenge for ecosystem management, as their vital rates can fluctuate over time, and the effect of management actions may not be consistent from 1 year to the next (Schweiger et al., 2020). Our demographic study of long-lived *Stipa* populations underscores this challenge, as individual vital rates and overall population growth rates varied considerably over time. Grazing, however,

was a consistently effective management tool; grazed populations maintained a positive average growth rate, whereas ungrazed populations were in decline. Importantly, the degree to which grazing benefited annual population growth, as well as the vital rates that contributed to growth, varied from year to year. Grazing had a larger positive effect on growth rates in wet years, and this pattern was associated with a greater contribution from adult growth immediately following the drought, and from adult survival thereafter. Although the majority of *Stipa* restoration efforts focus on recruitment, it was these two vital rates—adult growth and survival—that had the largest effect on population success. Our results suggest that ongoing management, such as moderate sheep and cattle grazing, can be an important tool to maintaining *Stipa* populations and is particularly necessary to support population growth in wet years.

Grazing was critical to maintain *Stipa* populations at our site and had a positive or neutral effect across all rainfall conditions. Grazing may directly benefit *Stipa* growth rates by reducing previous year's litter within the adult bunches, creating space for new growth. It also may indirectly benefit *Stipa* by reducing the effect of non-native annual grasses, which both compete with *Stipa* and generate litter that suppresses *Stipa* recruitment and growth (Dyer, 2003; Menke, 1992). Annual grasses are highly responsive to annual rainfall (Dudney et al., 2017; Hallett et al., 2019), and we found that the positive effect of grazing on  $\lambda$  was most pronounced in wet years. This supports our hypothesis that reducing competition via grazing supports viable *Stipa* populations in already invaded landscapes, especially in wet years that are expected to be favourable to annual grass competitors. There has been considerable concern about grazing management in California grasslands because the combination of heavy grazing and drought have been implicated in the system's initial conversion to an annually-dominated state (Jackson, 1985; Stromberg & Griffin, 1996). Although we had expected grazing to negatively affect *Stipa* in dry years by compounding plant stress (Souther et al., 2020), populations in grazed and ungrazed plots had comparable growth rates under drought. This is likely because the park actively reduced stocking rates under drought to a quarter of their typical rate. Had stocking rates been kept consistent over the course of the study we may have observed negative effects of grazing. Future studies that manipulate grazing intensity may be able to identify when and how the benefits of grazing may shift. Our observed neutral to positive effects of grazing suggest that management has heeded lessons from the past and that contemporary grazing practices that vary stocking rates with rainfall are beneficial, and in this case essential, for *Stipa* population viability.

Although the overall effect of grazing was beneficial for *Stipa* population growth, the vital rates contributing to this effect changed over time. Shifts in vital rate contributions to population growth may be a product both of concurrent and legacy rainfall effects (Evers et al., 2021; Sala et al., 2012). For example, grazing increased population growth by promoting adult growth immediately following the drought, during a time when rainfall was available to *Stipa* but annual grass seedbanks were likely depleted (Dudney et al., 2017; Love, 1944). Subsequently, adult survival contributed to the differences between grazed and ungrazed plots, likely due to both a legacy effect of previous growth, resulting in more robust adults in grazed plots, and to greater annual grass competition in ungrazed plots following a renewal of their seedbank. Similar legacies are likely for other vital rates, such as previous-year seed production influencing subsequent-year fecundity or recruitment. Notably other studies have observed strong lagged effects of climate on vital rates (Evers et al., 2021; Tenhumberg et al., 2018). For example, perennial forb *Astragalus scaphoides* exhibited reduced flowering if the previous year's spring was particularly wet (Crone et al., 2009; Tenhumberg et al., 2018). Reproductive vital rates were less critical for overall population growth in our model, although it is possible we did not observe a series of years in which conditions favourable for seed production were followed by conditions favourable for

high recruitment. Other grazing studies have observed that grazing reduced seed production and recruitment but similar to our study these vital rates had minimal to no impacts on population growth (Aschero et al., 2016; Johansen et al., 2016; Li et al., 2013). The combination of legacy growth effects and the impacts of the invaded grassland matrix in our system may have created conditions under which grazing is more prone to impact population growth. Moreover, these dynamics may lead to frequent nonlinearities in the grazing effect and its mechanism and highlights the importance of long-term monitoring. Grazing can be strategically applied to enhance native diversity within invaded systems, but successful outcomes are contingent on balancing resource conditions with grazing dynamics such as intensity and season (Firn et al., 2013). Our multi-year study gave us insights into the interactions between grazing and climate, and future studies that take an experimental approach to manipulating water availability, invader competition and grazing could further disentangle these synergies.

For long-lived species the persistence of certain age or stage classes—such as adults that can survive otherwise unfavourable years—can buffer a population from negative impacts on population growth (Morris et al., 2008). Our LTRE analysis indicated that juveniles and adults were two key life stages that mediated *Stipa*'s population growth dynamics, with their growth and survival contributing the most to differences in grazed versus ungrazed population growth. Mordecai et al. (2015) also found that *Stipa* adult survival is a key demographic process that should be a focus for land managers, underscoring the importance of maintaining adults and indicating that adult density would a good restoration target to monitor. Yet grazing as a management strategy is often studied and implemented in relation to recruitment rather than persistence. For example, early spring grazing has been suggested to reduce annual grasses and open space for native perennial seedlings, which germinate later (Dyer et al., 1996; Langstroth, 1991). Similarly, grazing has been emphasized in wet years to increase seedling density by mitigating competition and litter (Dyer et al., 1996; Marty et al., 2005). While some studies report grazing effects on a variety of life stages, few compare the importance of vital rates for the overall goal of population persistence. Our integrated demographic approach highlights that there is a disconnect between the critical life stages that regulate population growth and those that have been historically targeted for grazing management.

Understanding the impact of grazing management across variable conditions has become more pressing in light of changing precipitation regimes. Within California, ranchers have expressed concerns that their current management strategies are insufficient to cope with climate uncertainty (Macon et al., 2016). Modelling approaches that are able to integrate information that captures the spatial and temporal heterogeneity of a system can provide key insights that can guide seasonal management actions to achieve long-term management goals. For example, Behrendt et al., 2013 were able to identify different optimal stocking rates for sheep grazed rangeland in New South Wales, Australia across a variety of seasons, as well as seasons less optimal for grazing for desired management



species. Here we found that the low-moderate grazing intensity overall benefited the stability of *Stipa* populations across a period of variable precipitation; however, our results also highlighted that some populations are more vulnerable to local extinction if grazing were to be removed. Our ungrazed populations varied in how long grazing had been removed. One site had been ungrazed since 2005 and continued to have a stable population of *Stipa*; however, in two of the populations where we removed grazing at the onset of our study, we observed high overall declines in population growth. Careful monitoring of populations will be important to ensure the successful management of vulnerable populations. Taken together, these results highlight the importance of monitoring treatments across spatial and temporal gradients to improve management outcomes (Grman et al., 2013; Stuble et al., 2017).

Grazing has emerged as a powerful management strategy to help landowners meet conservation objectives (Brunson & Huntsinger, 2008; Toombs et al., 2010), with striking results for increasing diversity in annual dominated systems (Weiss, 1999). For long-lived species management actions such as grazing can affect multiple demographic processes (e.g. growth, survival, recruitment), and these effects may be contingent on underlying spatial and temporal heterogeneity. Demographic modelling such as the approach presented here has a rich history of use in conservation biology (Crone et al., 2011; Frederiksen et al., 2014), and we present an example of how this approach can be similarly used to enhance ecosystem management to disentangle spatial and temporal effects on population dynamics of a species of management concern. Moreover, this approach helped identify key life stages and transitions (i.e. juvenile and adult; growth and survival) that strongly mediate the efficacy of grazing as a management strategy. This work demonstrates that there are many more opportunities by which demographic monitoring with modelling approaches can continue to inform management in a spatially and temporally heterogeneous landscape.

## AUTHOR CONTRIBUTIONS

Loralee Larios and Lauren M. Hallett jointly designed and conducted the field study; Loralee Larios conducted the population modelling; Loralee Larios and Lauren M. Hallett conducted additional statistical analyses, created figures, and co-wrote the manuscript.

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## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

Data are available via Dryad Digital Repository <https://doi.org/10.6086/D1KD6R> (Larios & Hallett, 2022).

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## SUPPORTING INFORMATION

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

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