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UNIVERSITY OF CALIFORNIA SANTA CRUZ

**LONG-TERM EFFECTS OF MANAGEMENT AND CLIMATE ON
CALIFORNIA'S GRASSLAND FLORA AND RARE PLANT SPECIES**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ENVIRONMENTAL STUDIES

By

Josephine C. Lesage

December 2020

The Dissertation of Josephine C. Lesage is
approved:

Professor Karen D. Holl, chair

Professor Michael E. Loik

Professor Daniel M. Press

Professor Susan P. Harrison

Quentin Williams
Acting Vice Provost and Dean of Graduate Studies

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ABSTRACT

LONG-TERM EFFECTS OF MANAGEMENT AND CLIMATE ON CALIFORNIA'S GRASSLAND FLORA AND RARE PLANT SPECIES

The California floristic province is home to a rich diversity of plant species, and the ecosystems they compose have a long and complex history of human management and anthropogenic disturbance. This is especially true of native grassland habitats, which have been burned, grazed, and replaced by agriculture and housing, and are now present in only a small fraction of the area they once covered. More recently, restoration and management activities increasingly seek to maintain and improve the plant diversity of California grasslands, but the effectiveness of typical strategies may alter under a changing climate. In this dissertation, I examined evidence of climate change effects on California grassland communities, the long-term effectiveness of livestock grazing as strategy to conserve native species, and the lessons that several decades of rare plant reintroductions have for future projects.

In the first chapter, I used eight datasets collected over periods of 12 to 33 years to examine whether global climate change has altered California grassland vegetation communities. I used a metric known as the Community Temperature Index (CTI), which draws on historical species distribution records and spatial climate data to measure the relative dominance of species adapted to warmer and cooler temperatures within a location. I found evidence of long-term (1950-2019) increases in temperature and vapor pressure deficit at the sites I analyzed, though shorter-term study-period weather patterns were more variable. Six of the eight sites showed significant shifts in community composition towards warmer-climate species over

time, and these increases occurred at faster rates than has been measured in other systems. Overall, the results suggest that some California grassland communities are shifting towards greater dominance by species adapted to warmer climates, but that these changes must be understood and interpreted within the history of abiotic conditions, long-term climate and weather history, and past land-use context of a site, as shorter-term weather patterns may not align with longer-term climate change and site conditions and past land management may exert a strong influence over community trajectory.

My second chapter is focused on long-term grazing as a management strategy to maintain the diversity of native annual forbs in California coastal prairies in light of a recent historic drought and increasing temperatures. I resampled paired transects in eleven grazed and ungrazed sites from Monterey to Sonoma counties, California, 15 years after the original study. I found evidence to support the continued use of grazing to maintain higher native annual forb richness in coastal prairies, but also found that native annual forb richness had declined over 15 years in grazed prairies. Grazing continued to maintain low vegetation heights and thatch depths, and prevented shrub encroachment. I used circumstantial evidence from wetland indicator status and specific leaf area to support the hypothesis that severe drought and increasing aridity may be driving the declines in native annual forb richness that I measured, and explore how management and climate may interact to affect plant communities.

In my third chapter, I synthesized lessons learned from reintroduction efforts for 14 listed plant species in California. Introductions and reintroductions of listed plant species are likely to be increasingly necessary in the future, so understanding how practitioners view their work and identifying persistent resource mismatches are key to the long-term viability of listed species. I interviewed practitioners to understand their definitions of recovery; how likely they felt recovery was; the advice they would share with other practitioners; and the resources they thought were lacking but that could make future projects more successful. I found that practitioners were generally guided by sound ecological theory and wanted to invest significant time and resources into understanding species biology and ecology, but that there were often barriers to success in the form of funding, time, and social constraints. Rare plant reintroductions are complicated by mismatches in timing and goals, but some individuals have been able to successfully navigate these challenges.

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CHAPTER 1

CALIFORNIA GRASSLANDS SHIFT TOWARDS WARMER-CLIMATE SPECIES

Abstract

Global climate change can alter ecological communities over time, resulting in shifts towards species that are better adapted to warmer climates. Community Temperature Index (CTI) can track these changes by measuring the relative dominance of species adapted to warmer and cooler temperatures within a community. I analyzed eight California grassland datasets spanning 12 to 30 years from 1983 to 2018 to examine whether there had been a region-wide shift in native species richness and cover, as well as a shift towards species adapted to warmer climates as indicated by increasing CTI. There was strong evidence of long-term (1950-2018) increases in temperature and vapor pressure deficit at the sites I analyzed, though shorter-term study-period weather patterns were more variable. At six out of eight sites, I found evidence of significant community shift towards warmer-climate species over time, and at faster rates than has been measured in other systems. Thermophilization was not consistently driven by the replacement of native by non-native species, though native species richness did decline at multiple sites. I was unable to draw out consistent correlations between increases in CTI and concurrent changes weather or community composition. The results of my study indicate the importance of framing shifts in ecological communities within larger historical landscape and climate contexts, because short-term weather patterns may

not align with longer-term climate change trajectory, and abiotic factors such as soil and landscape management can exert a strong influence over community trajectory. Overall, the results of this work suggest that some California grassland communities are shifting towards greater dominance by species adapted to warmer climates while species adapted to colder climates decline.

Introduction

Global climate change and anthropogenic disturbance can cause ecological communities to shift over time due to differing niche tolerances and competitive abilities (Magurran 2016; Stuart-Smith et al. 2018). Warming-driven changes in species distributions have varied across regions and taxa (Chen et al. 2011), and evidence suggests that many factors, such as an area's land-use history, soil type, water availability, and baseline community composition, can all mediate how a species responds to climate change (Brown et al. 1997; Perring et al. 2016, 2018; Qin et al. 2020). Assessing community-level responses to climate change is thus complicated by both the challenge of understanding the varied responses of individual species within a community, and the ways that commonly-used community metrics, such as species richness or cover, may obscure responses to climate (Dornelas et al. 2014; Jones et al. 2017; Hillebrand et al. 2018).

The community temperature index (CTI) offers a straightforward method to measure the relative dominance of species adapted to warmer and cooler temperatures within a community, based on historical climate data and known species occurrence

records (Devictor et al. 2008; Feeley et al. 2013). CTI has been used in birds (Godet et al. 2011; Auffret and Thomas 2019), forest ecosystems (Duque et al. 2015; Fadrique et al. 2018; Dietz et al. 2020), and in multi-taxa, high-elevation studies (Roth et al. 2014; Freeman et al. 2020) to show that species adapted to warmer climates have increased in relative dominance over time, though there have also been studies where CTI has not changed despite apparent changes in weather patterns (Savage and Vellend 2015). In vegetation studies, CTI has most often been used to analyze resurveys of forest plots to evaluate changes in groups of relatively long-lived trees over large spatial domains. For communities where the potential for turnover is high and generation times are short, such as grasslands in California, community-level CTI responses to climate change may occur more rapidly than in habitats dominated by long-lived vegetation, but this has not been tested *in situ*.

In this chapter, I analyze eight California grassland datasets for periods of 12 to 30 years in length from 1983 to 2018 to test whether there is evidence of a region-wide shift towards species adapted to warmer climates, as indicated by increasing CTI. Additionally, I ask whether increasing temperatures have favored non-native species adapted to high temperatures to the detriment of native diversity and abundance. Because California's grasslands are annual-dominated ecosystems that range from highly diverse communities dominated by native species on unique soils to highly invaded systems comprised entirely of non-native annual vegetation (Bartolome et al. 2007; Ford and Hayes 2007; Harrison and Viers 2007), an analysis

of multiple sites across a region provides a more complete picture of potential changes that are occurring than single site studies.

Methods

Study sites

I analyzed datasets from eight California grasslands collected between 1983 and 2018 (Table 1-1). Datasets varied in duration and start/end dates, as well as in the data collection methods: some were sampled as point-intercept transects or quadrats, and others were collected as aerial cover estimates along transects or within quadrats. To standardize across datasets, data were converted to relative cover by summing all cover or intercepts within a quadrat or transect and calculating the relative contribution of each species to the sum. Data for most sites were collected once annually during peak spring growth, except at McLaughlin, where data were collected once in spring and once in summer each year.

The sites vary with respect to climate, land use history, and soil type. The northernmost and wettest site, Angelo Coast Range Reserve, receives between 2-10 times the mean annual precipitation as the other sites (Suttle and Thomsen 2007). All sites but Angelo Reserve are known to have been grazed historically by cattle but were released from grazing prior to data collection. At three sites (Swanton Ranch, UCSC, and Elkhorn Slough), the same data collection methods were also used in continuously grazed plots. I primarily present results from the ungrazed plots, except to examine whether the release from grazing may have driven the change in CTI. The

length of time between grazing release and data collection varied across sites, from 20 years to immediate data collection following release (Hobbs and Mooney 1995; Hayes and Holl 2011; Harrison et al. 2015). Small mammals (voles, kangaroo rats, mice) were not excluded at any of the sites. Six of the eight grasslands were dominated by non-native annual grass and forb species, though some had a high richness of native species. At two of the sites, all plots are located on serpentine soils (Jasper Ridge and McLaughlin – Serpentine), and these were the only sites with >60% mean native cover.

Climate and weather variables

I obtained modelled monthly interpolated weather data for all sites from 1950-2019 from the PRISM Climate Group (<https://prism.oregonstate.edu/>). I included mean annual and mean winter (Dec-Feb) minimum temperature, annual and winter precipitation, and annual and growing season (Dec-Apr) minimum and maximum vapor pressure deficit weather variables in my analyses. I included both seasonal means and annual means of weather variables in my analyses because for many annual plants, the seasonal variables are most critical to determining survival and reproductive success. I include vapor pressure deficit (VPD), which is closely correlated with temperature, because it reflects the evapo-transpirative demand that plants experience at higher temperatures, and therefore the severity of potential water stress. Plants that keep their stomata open during periods of high VPD are more likely to experience hydraulic failure and drought-associated mortality, while plants that

close their stomata during high VPD periods can experience carbon starvation if photosynthesis is reduced for extended periods of time (Grossiord et al. 2020).

Community Temperature Index

I followed methods described in Feeley *et al.* (2011) to calculate the community temperature index (CTI) of each plot over time. For each site, I generated a list of all species present, and then gathered all geo-located occurrence records within the state of California from the Global Biodiversity Information Facility for this species list. I limited occurrence records to the state of California to make the dataset more manageable; because of the extensive breadth of temperature and precipitation values within California, these values are unlikely to be biased by unintentionally sampling from a narrow range of possible climate values. Duplicate records and those with incorrect or impossible coordinates were removed using the *CoordinateCleaner* and *scrubr* packages (Chamberlain 2020; Zizka et al. 2020). To generate a species thermal index (STI) for each species, I associated the occurrence records with mean temperature values from WorldClim data, available through the *Raster* package (Hijmans et al. 2020). I then calculated the STI as the mean of the temperatures for each occurrence. To ensure that this STI was representative of the distribution of temperatures at which the species occurs, I checked that the distribution of temperatures values for species was normal. Each species' temperature index was then weighted by its relative abundance within the community to calculate plot-level CTI values.

Data Analysis

Data were processed and analyzed in R. To calculate community turnover, I used the CoDyn R package (Hallett et al. 2020). I tested for directional changes in weather and CTI at each site using generalized linear models of focal variables over time in the lme4 package (Bates et al. 2020). I tested the correlation between changes in CTI and key weather variables using linear models. I tested for changes in native richness, relative cover and community turnover over time using linear mixed models with plot as a random factor, using a Poisson distribution for the richness tests. I used t-tests to compare whether native and non-native species had different mean species temperature and precipitation index values. To correct for multiple tests across sites, I adjusted p-values using the Bonferroni correction based on the number of explanatory variables in the models.

Results

Overall, there were more significant weather changes over the 50-year period than during the study periods, and the shorter study period trends did not always match the longer-term trends. Six out of seven sites warmed significantly in terms of both mean annual and mean winter minimum temperatures over the last 70 years (1950-2019) with rates of warming between 0.005°C and 0.02°C per year (Table 1-2, Figure 1-1). The only significant increase in mean temperature during the study periods was mean winter minimum temperature at Jasper Ridge. There was no

significant change in either annual or winter precipitation at any site over the long-term period or the study periods, except a significant decline in winter precipitation during the study period at one site (Angelo Reserve). Mean annual minimum vapor pressure deficit (VPD) increased significantly since 1950 at five sites, and annual minimum or growing season minimum VPD increased significantly at three sites during the study periods. Maximum VPD did not increase significantly at most sites during the longer 1950-2019 period, and during the study periods, only a few sites experience significant increases in maximum VPD.

Community Temperature Index (CTI) values increased significantly at six of the eight sites over the study periods (Figure 1-2, Table S1-1) and estimated rates of thermophilization (CTI increase) were between $0.008^{\circ}\text{C y}^{-1}$ to $0.094^{\circ}\text{C y}^{-1}$. Increases in CTI occurred through several mechanisms: the loss of low-STI species (darker blue colors), the arrival of high-STI species (darker red and purple colors), and changes in the dominance of low- and high-CTI species (Figure 1-2). Where I was able to compare plots released from grazing and plots that continued to be grazed (Swanton Ranch, UCSC, and Elkhorn Slough), the CTI trends were the same across grazing treatments (Table S1-2, Figure S1-1). At every site where CTI increased significantly over time, CTI was correlated with at least one weather variable over the study period such as mean temperature, minimum annual temperature, mean annual minimum VPD, and growing season (Dec-Apr) minimum VPD (Table 1-3).

Five out of the eight grasslands in this study experienced small but significant declines in native species richness over time, with between 0.01 and 0.15 species lost

per year (Figure 1-3, Table 1-4). Relative native cover declined significantly at three sites at rates of 0.4 to 1.2% per year and increased significantly at one site by 1% per year. At five out of eight sites, there was no significant difference between the STI of native and non-native species (Figure 1-3, Table 1-4). The rate of species turnover increased significantly at two sites, though the rate of change was very small.

Discussion

The long-term temperature trends at the sites I analyzed align with observed records and modelled predictions of a warming climate due to anthropogenic greenhouse gas emissions (IPCC 2014). The rates of temperature change at sites estimated in this study ($0.005^{\circ}\text{C year}^{-1}$ to $0.020^{\circ}\text{C year}^{-1}$) are similar to the mean rates found in an analysis of multiple global datasets ($0.014^{\circ}\text{C year}^{-1}$ to $0.018^{\circ}\text{C year}^{-1}$; Foster & Rahmstorf 2011). VPD, which is fundamentally determined by temperature, also increased over the long-term, indicating that plants at these sites have experienced increasing evaporative demand since 1950. The lack of a trend in changing precipitation quantity is unsurprising, given inconsistent model predictions in the direction and magnitude of precipitation change (Pierce et al. 2013; Neelin et al. 2013), and California's known high inter-annual precipitation variability (Cowling et al. 1996; Vaughn and Young 2010).

Though all but one site showed significant changes in weather variables over the long-term (1950-2019), study-period weather patterns did not always reflect these trends (Table 1-2, Figure 1-1). For instance, at Angelo Coast Range Reserve,

precipitation declined significantly during the study period, but there was no significant change over the long-term. Similarly, mean temperature at Swanton Ranch and UCSC was stable during the study periods but has increased over the longer time scale. These differences between study period trends illustrate the importance of examining any short-term changes within the larger context of longer-term historical trends.

I found evidence of significant community shift towards warmer-climate species over time at six out of eight sites (Figure 1-2, Table S1-1), but no consistent correlations between CTI and study-period weather (Table 1-3). The widespread increase in CTI measured at my sites occurred despite minimal significant concurrent changes in study-period weather, and for some sites where there were significant weather trends, there were no significant changes in CTI (Table 1-5). This may be due to my use of interpolated weather data, which may not accurately reflect site or microsite weather. Alternatively, the significant change in CTI may reflect the significant long-term trends as opposed to the shorter-term weather patterns. The shift towards warmer climate adapted species is an expected result of rising temperatures and VPD since 1950, and it is possible that the study period weather does not provide the historical context necessary to see weather as the driving factor for these changes in CTI. Furthermore, the rates of thermophilization (CTI increase) for the sites in this study were between $0.008^{\circ}\text{C y}^{-1}$ and $0.094^{\circ}\text{C y}^{-1}$, similar to the changes in observed temperature from 1950-2019 ($0.005^{\circ}\text{C y}^{-1}$ to $0.029^{\circ}\text{C y}^{-1}$). Though both observed temperature and CTI changes were only fractions of a degree, these may reflect

significant ecological changes in community composition, considering that the total spread in observed mean temperature at sites is only 3.4°C.

The rates of thermophilization for these sites are faster than those measured in other systems. Studies of bird communities have reported thermophilization rates between 0.004-0.010°C yr⁻¹ (Devictor et al. 2008; Kampichler et al. 2012), whereas rates in tropical and subtropical forests have ranged from 0.0065°C yr⁻¹ to 0.027°C yr⁻¹, with variation between juvenile and adult trees (Feeley et al., 2011; Duque, Stevenson and Feeley, 2015; Fadrique et al., 2018). The faster rates of community warming measured at the grassland sites in my study could be explained by the high proportion of annual species in California grasslands (Cleland et al. 2013), and relatively high rates of turnover in these grasslands (Figure 1-3, Table 1-4). With their faster generation times and high community dominance, annuals would allow for plant communities to shift more rapidly in response to rising temperatures, potentially leading to a faster conversion of these communities towards new species over time.

Thermophilization at the sites I analyzed was not consistently driven by the replacement of native by non-native species, though native species richness did decline at multiple sites. CTI can increase through multiple independent or concurrent mechanisms: new, high-STI (species temperature index) species can arrive; historically present low-STI species can be lost; and high-STI species can increase in relative abundance while low-STI species decline. If there is a strong relationship between STI and species provenance, increasing CTI values would be especially

concerning. I found that five of the eight grasslands declined in native species richness over time, but that non-native species had significantly warmer STI values than native species at only three sites (Figure 1-3, Table 1-4). At some sites, such as Elkhorn Slough, the change in CTI was in large part due to the decline and eventual loss of low-STI native species (*Danthonia californica*) and arrival and increased abundance of high-STI non-native species (*Brachypodium distachyon*). However, a global meta-analysis supports the hypothesis that non-native and native vegetation respond similarly to warming temperatures (Sorte et al. 2013), and at other sites I analyzed, thermophilization was largely due to shifts in the dominance within groups of non-native or native species. Thus, changes in CTI are not necessarily linked to changes in native or non-native species richness or cover, but a complex set of changes that are not necessarily related to species provenance.

Though it is logical that increases in CTI are due to increased temperatures, soil type could potentially confound the results. Soils vary substantially with respect to fertility and water holding capacity, which can play an important role in determining community composition, how impactful drought and dry periods are on vegetation, and a vegetation community's ability to resist drought periods and potentially climate change (Hulshof and Spasojevic 2020; Werner et al. 2020). Though some studies suggest low-nutrient serpentine soils with high levels of endemism may be more resistant to climate change (Grime et al. 2008; Damschen et al. 2012), my analyses show mixed evidence of this resistance. Both the serpentine and non-serpentine plots at McLaughlin Reserve lost native annual species over time

(Harrison et al. 2015), but the CTI in the serpentine plots was stable while CTI in the annual grassland plots increased. The increase in the non-serpentine plots CTI can be partially attributed to a swaps among the non-native annual species: colder-STI *Taeniatherum caput-medusae* (13.6°C) declined over time, while warmer-STI *Avena fatua* (15.6°C) and *Vicia villosa* (15.0°C) increased. Unlike the serpentine plots at McLaughlin, the other serpentine grassland site at Jasper Ridge increased significantly in CTI over time. This may be because Jasper Ridge is located in a region of high nitrogen deposition, making serpentine invasion by non-serpentine endemic species more likely, and reducing its overall resistance to climate change (Weiss 1999). There are also additional soil-related factors which may affect community response to climate, such as water-holding capacity, nutrient levels, and microbial community (Classen et al. 2015; McLaughlin et al. 2017), for which I am unable to make comparisons but which could be important.

The land use and management history of a site also potentially influences community trajectory under climate change, and therefore could confound interpretation of CTI. All but one site in my study were released from cattle grazing prior to data collection, and this change in land management regime may be driving the change in CTI or altering the effect of weather patterns on CTI. For instance, if some low-STI species (such as *Danthonia californica*) benefit from grazing (Hatch et al. 1999), then the cessation of grazing may accelerate their disappearance from the community, and therefore increase CTI at a site if they are replaced with higher STI species. To test this hypothesis, I compared the changes in CTI at three sites where

long-term vegetation composition data were collected in both ungrazed plot and plots with ongoing cattle grazing (Hayes and Holl 2011). I found that CTI trends were consistent in both treatments at these three sites, suggesting that land management technique and the release from grazing was not the primary driver of CTI change, but instead, that changes that were shared across treatments, such as weather or climate trends, are more likely to have been the drivers of the increase in CTI (Table S1-2, Figure S1-1).

Overall, the results of this work suggest that some California grassland communities are shifting towards greater dominance by species adapted to warmer climates. Though I found evidence of native species decline over time at several grasslands, thermophilization also occurred at sites where native species richness or cover remained stable or increased. The results of my study indicate the importance of framing community changes within larger historical landscape and climate contexts, as short term weather patterns may not align with the longer-term climate change history of a site, and landscape history may exert a strong influence over community trajectory.

Table 1-1. Datasets included in analyses. Mean annual temperature, precipitation, and relative native cover are calculated for each site based on the study years from PRISM monthly data. For the McLaughlin sites, only presence-absence data were collected for the first six years.

Site name	Location	Mean annual temp. (°C)	Mean precip. (mm)	Study Period	No. Years	No. Reps	Grassland Classification	Mean native relative cover (%)	Data collection method
Angelo Coast Range Reserve	39°43'02.5"N 123°39'11.1"W	12.9	1882	2002-2015	14	5	Annual	30.6 ± 1.5	Cover in 0.09 m ² quadrats
McLaughlin Reserve	38°52'11.2"N 122°25'15.6"W	15.3	886	2000 (2006)-2018	13 (19)	38	Serpentine	14.9 ± 0.6	Cover in 1 m ² quadrats
						42	Annual	68.3 ± 1.0	
Jasper Ridge	37°24'22.4"N 122°14'31.8"W	15.2	576	1983-2015	33	12	Serpentine	89.6 ± 0.9	Cover in 1 m ² quadrats
Swanton Ranch	37°02'43.1"N 122°13'16.1"W	13.1	803	1999-2012	14	3	Coastal prairie	3.3 ± 1.6	5x5 point-intercept in four 1 m ² quadrats per replicate
University of California, Santa Cruz (UCSC)	36°59'11.1"N 122°03'09.2"W	13.5	961	1999-2012	14	3	Coastal prairie	5.1 ± 1.0	5x5 point-intercept in four 1 m ² quadrats per replicate
Elkhorn Slough	36°52'02.4"N 121°44'27.5"W	13.7	478	1999-2018	18	3	Coastal prairie	5.6 ± 1.3	5x5 point-intercept in four 1 m ² quadrats per replicate
Carrizo Plain	35°11'20.6"N 119°51'45.2"W	16.3	183	2007-2018	12	20	Annual	43.3 ± 1.3	9x9 point intercept in 1 m ² quadrats

Table 1-2. Linear models of change in weather variables over time at each site, during the period from 1950-2019 and site-specific study periods. ‘Growing season’ refers to Dec – Apr, VPD = vapor pressure deficit. Bold text indicates significance after Bonferroni correction for multiple hypothesis tests ($p \leq 0.00625$), while italics show values of $0.00625 < p < 0.05$.

1950-2019 Weather Trends						
Site	Mean annual temperature			Mean winter (Dec-Feb) minimum temperature		
	Est.	z	P	Est.	z	P
Angelo	0.005	1.60	0.114	0.013	1.87	0.066
McLaughlin	0.008	3.60	<0.001	<i>0.020</i>	2.73	<i>0.008</i>
Jasper	0.018	6.20	<0.001	<i>0.016</i>	2.13	<i>0.037</i>
Swanton	0.005	3.44	0.001	0.023	3.96	<0.001
UCSC	0.008	6.34	<0.001	0.029	4.44	<0.001
Elkhorn	0.012	3.85	<0.001	0.024	3.64	<0.001
Carrizo	0.020	5.43	<0.001	0.028	4.18	<0.001
Site	Annual precipitation (water year)			Winter (Dec-Feb) precipitation		
	Est.	z	P	Est.	z	P
Angelo	-1.88	-0.53	0.599	-1.40	-0.52	0.607
McLaughlin	-0.03	-0.02	0.987	0.04	0.03	0.980
Jasper	-0.62	-0.44	0.659	-0.21	-0.22	0.829
Swanton	0.58	0.31	0.761	0.70	0.50	0.617
UCSC	-0.23	-0.11	0.913	0.18	0.12	0.907
Elkhorn	0.53	0.47	0.637	0.50	0.65	0.518
Carrizo	0.65	1.18	0.242	0.65	1.18	0.075
Site	Mean annual minimum VPD			Growing season mean min. VPD		
	Est.	z	P	Est.	z	P
Angelo	<i>0.003</i>	2.19	<i>0.032</i>	-0.002	-1.11	0.271
McLaughlin	0.017	6.01	<0.001	0.009	3.56	<0.001
Jasper	0.009	5.76	<0.001	<i>0.003</i>	2.01	<i>0.048</i>
Swanton	0.007	4.68	<0.001	0.005	3.16	0.002
UCSC	0.011	8.49	<0.001	0.007	5.76	<0.001
Elkhorn	<i>0.005</i>	2.65	<i>0.010</i>	<i>0.004</i>	2.25	<i>0.028</i>
Carrizo	0.021	7.02	<0.001	0.010	4.59	<0.001
Site	Mean annual maximum VPD			Growing season mean max. VPD		
	Est.	z	P	Est.	z	P
Angelo	-0.022	-2.80	0.007	-0.008	-1.09	0.280
McLaughlin	<i>0.033</i>	2.78	0.007	0.032	3.14	0.003
Jasper	0.017	1.89	0.063	0.024	2.88	0.005
Swanton	-0.005	-0.82	0.414	0.008	1.21	0.229
UCSC	-0.030	-4.53	<0.001	-0.003	-0.34	0.736
Elkhorn	-0.003	-0.47	0.637	0.009	1.30	0.198
Carrizo	0.008	0.75	0.456	<i>0.024</i>	2.27	<i>0.027</i>

Study Period Weather Trends

Site	Mean annual temperature			Mean winter (Dec-Feb) minimum temperature		
	Est.	z	P	Est.	z	P
Angelo	0.025	0.57	0.579	-0.028	0.05	0.732
McLaughlin	0.056	1.16	0.268	0.147	2.09	0.059
Jasper	0.019	1.49	0.147	0.070	3.58	0.001
Swanton	-0.017	-0.52	0.614	-0.006	-0.01	0.911
UCSC	-0.028	-0.93	0.373	-0.031	-0.49	0.631
Elkhorn	<i>0.052</i>	<i>2.50</i>	<i>0.023</i>	0.019	0.46	0.650
Carrizo	<i>0.132</i>	<i>3.10</i>	<i>0.011</i>	<i>0.203</i>	<i>2.84</i>	<i>0.017</i>
Site	Annual precipitation (water year)			Winter (Dec-Feb) precipitation		
	Est.	z	P	Est.	z	P
Angelo	-60.87	-2.01	0.068	-69.07	-3.48	0.004
McLaughlin	14.07	0.60	0.558	6.54	0.37	0.716
Jasper	-6.40	-1.47	0.151	-1.86	-0.63	0.536
Swanton	-4.84	-0.37	0.721	-14.45	-1.73	0.109
UCSC	-8.31	-0.53	0.604	-15.69	-1.59	0.138
Elkhorn	3.05	0.46	0.653	-0.41	-0.09	0.930
Carrizo	4.61	9.12	0.624	0.03	0.04	0.970
Site	Mean annual minimum VPD			Growing season mean min. VPD		
	Est.	z	P	Est.	z	P
Angelo	0.011	0.55	0.592	<i>0.025</i>	2.28	<i>0.042</i>
McLaughlin	0.062	1.47	0.168	0.031	0.78	0.450
Jasper	0.018	3.86	<0.001	0.006	1.31	0.201
Swanton	0.068	8.10	<0.001	0.058	6.23	<0.001
UCSC	0.058	6.15	<0.001	0.048	4.77	<0.001
Elkhorn	<i>0.030</i>	<i>2.57</i>	<i>0.019</i>	<i>0.031</i>	<i>3.03</i>	<i>0.007</i>
Carrizo	0.048	0.91	0.386	0.029	0.59	0.566
Site	Mean annual maximum VPD			Growing season mean max. VPD		
	Est.	z	P	Est.	z	P
Angelo	0.032	0.34	0.743	0.156	1.84	0.090
McLaughlin	-0.201	-1.47	0.166	-0.039	-0.26	0.799
Jasper	-0.035	-1.22	0.233	0.013	0.42	0.675
Swanton	0.098	1.76	0.103	0.150	3.95	0.002
UCSC	0.073	1.09	0.297	<i>0.128</i>	<i>2.69</i>	<i>0.020</i>
Elkhorn	<i>0.102</i>	<i>2.79</i>	<i>0.012</i>	0.138	3.65	0.002
Carrizo	0.116	0.83	0.426	0.083	0.48	0.640

Figure 1-1. Trends in selected weather variables for each site from 1950 to 2019. The study period is shown in blue within the total period. Linear models for both change during the overall period and the study period are shown as red lines. VPD = vapor pressure deficit.

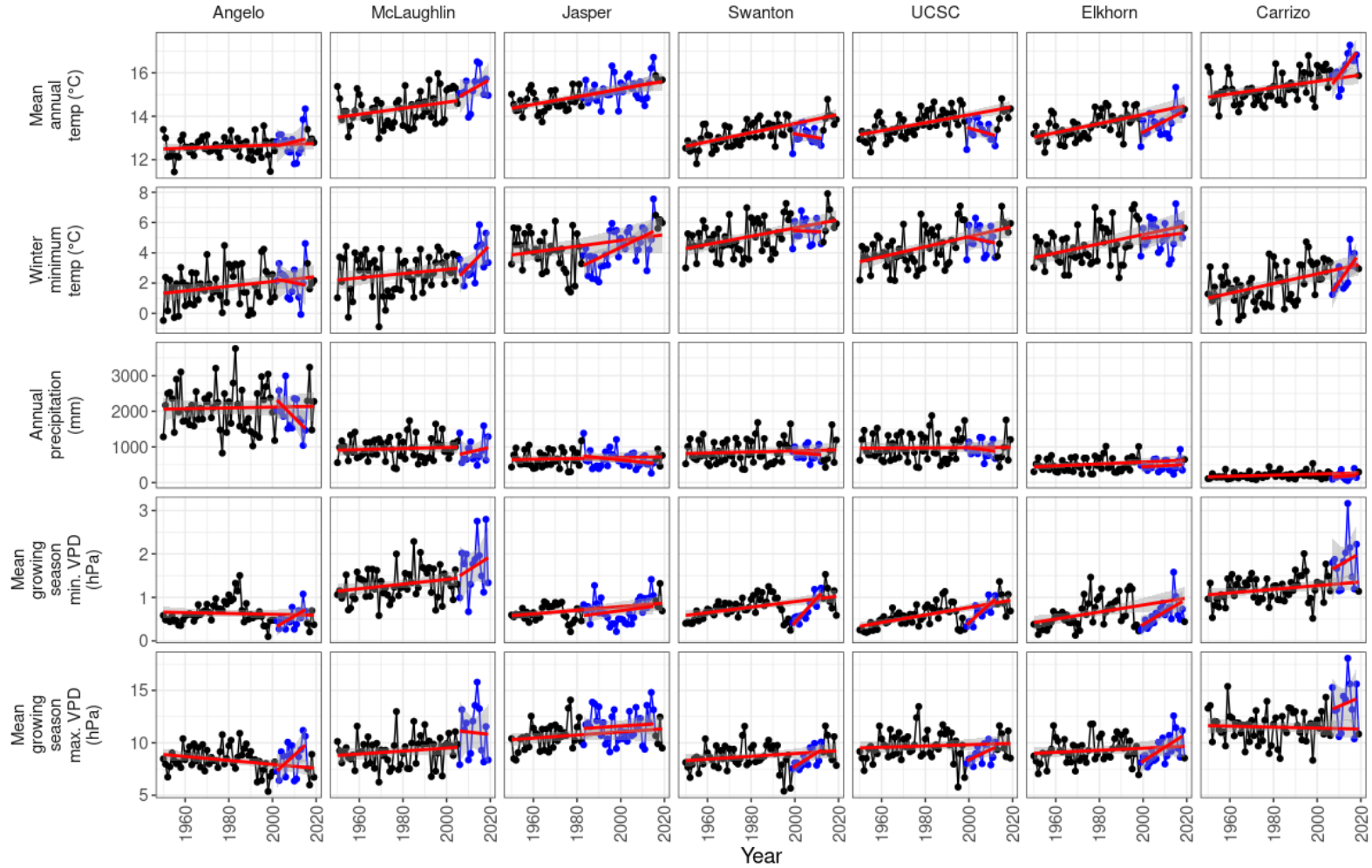


Figure 1-2. Mean Community Temperature Index (CTI, line charts) and relative cover of species by Species Temperature Index (STI, colored bar charts) of each site over time ordered from coolest to warmest sites. Error bars represent 1 SE. Y-axes of the CTI plots vary across sites. Stars in the lower-right corner indicate significant increases in CTI over time. The STI figures show the contributions of each species to total relative cover for all plots at a site, color coded by STI.

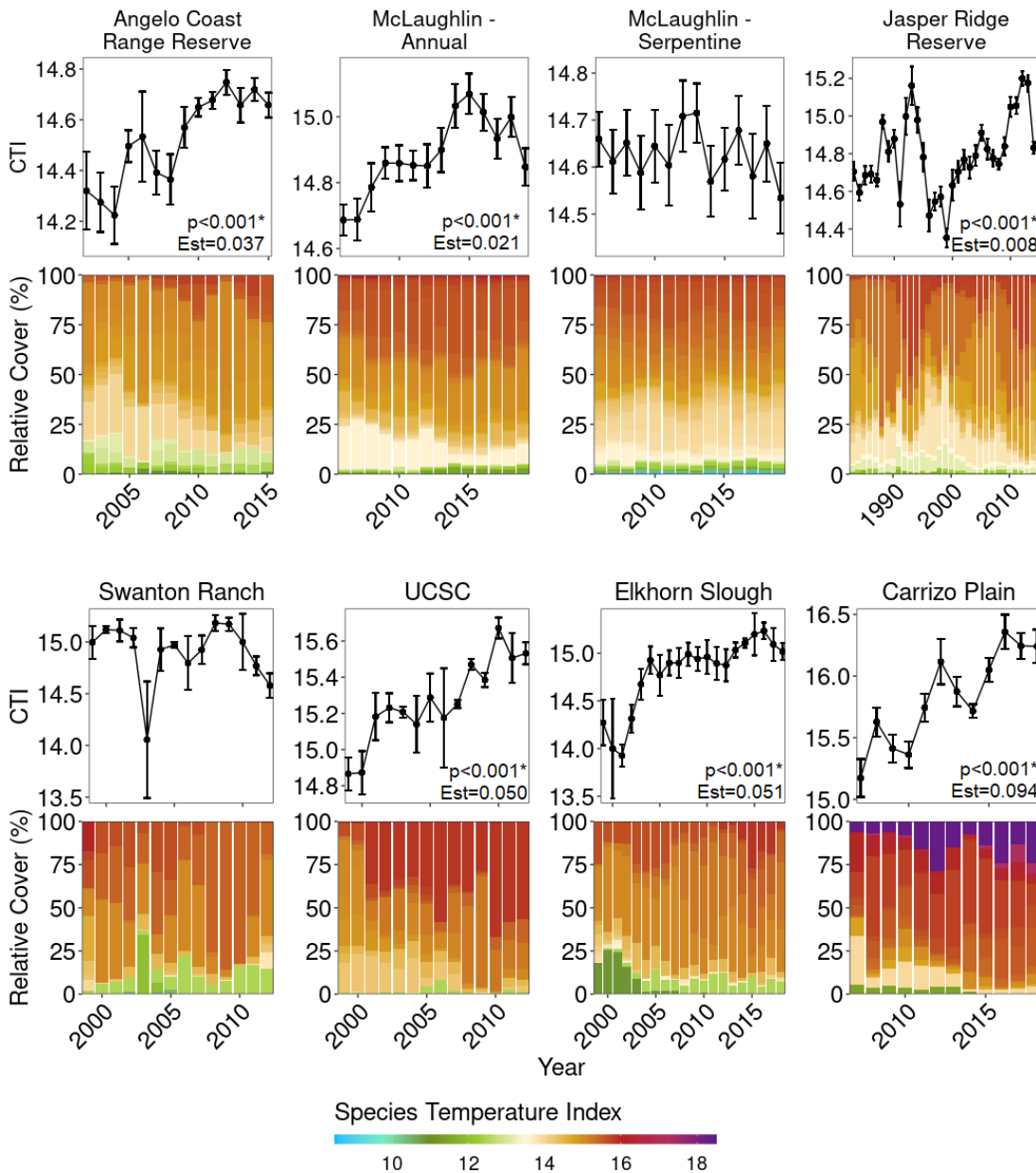


Table 1-3. Correlations between values for CTI and key study period weather variables. Bold lines are significant after Bonferroni correction for multiple hypothesis tests ($p = 0.0125$); italics show values of $0.0125 < p < 0.05$.

Site	CTI vs. annual mean temp.			CTI vs. annual min. temp		
	Est.	<i>z</i>	P	Est.	<i>z</i>	P
Angelo	-0.013	-0.28	0.781	0.040	0.78	0.437
McLaughlin – Annual	0.098	4.24	<0.001	0.090	4.67	<0.001
McLaughlin – Serpentine	-0.002	-0.06	0.956	-0.020	-0.86	0.393
Jasper	-0.003	-0.12	0.902	0.050	2.57	0.011
Swanton	-0.151	-0.97	0.340	-0.205	-1.32	0.196
UCSC	-0.133	-1.39	0.174	-0.079	-0.79	0.435
Elkhorn	0.282	3.12	0.003	<i>0.209</i>	2.25	<i>0.028</i>
Carrizo	0.335	5.59	<0.001	0.385	7.41	<0.001
Site	CTI vs. annual min. VPD			CTI vs. growing season (Dec-Apr) min. VPD		
	Est.	<i>z</i>	P	Est.	<i>z</i>	P
Angelo	0.010	0.09	0.929	<i>0.333</i>	<i>2.44</i>	<i>0.017</i>
McLaughlin – Annual	0.077	3.04	0.002	0.081	2.91	0.004
McLaughlin – Serpentine	-0.007	-0.22	0.824	-0.002	-0.09	0.932
Jasper	0.295	6.81	<0.001	0.245	5.02	<0.001
Swanton	-0.013	-0.06	0.954	-0.069	-0.28	0.784
UCSC	0.646	5.06	<0.001	0.654	3.91	<0.001
Elkhorn	0.595	2.83	<0.001	0.700	3.96	<0.001
Carrizo	<i>0.152</i>	<i>2.19</i>	<i>0.030</i>	0.032	0.41	0.685

Figure 1-3. From top to bottom: Native species richness, relative cover of native species, community turnover, and mean STI of native and non-native species at each site over time. Error bars represent standard error; stars indicate significance after Bonferroni correction ($p < 0.0167$) for richness, cover and turnover plots, and significance at $p < 0.05$ for t-test comparisons.

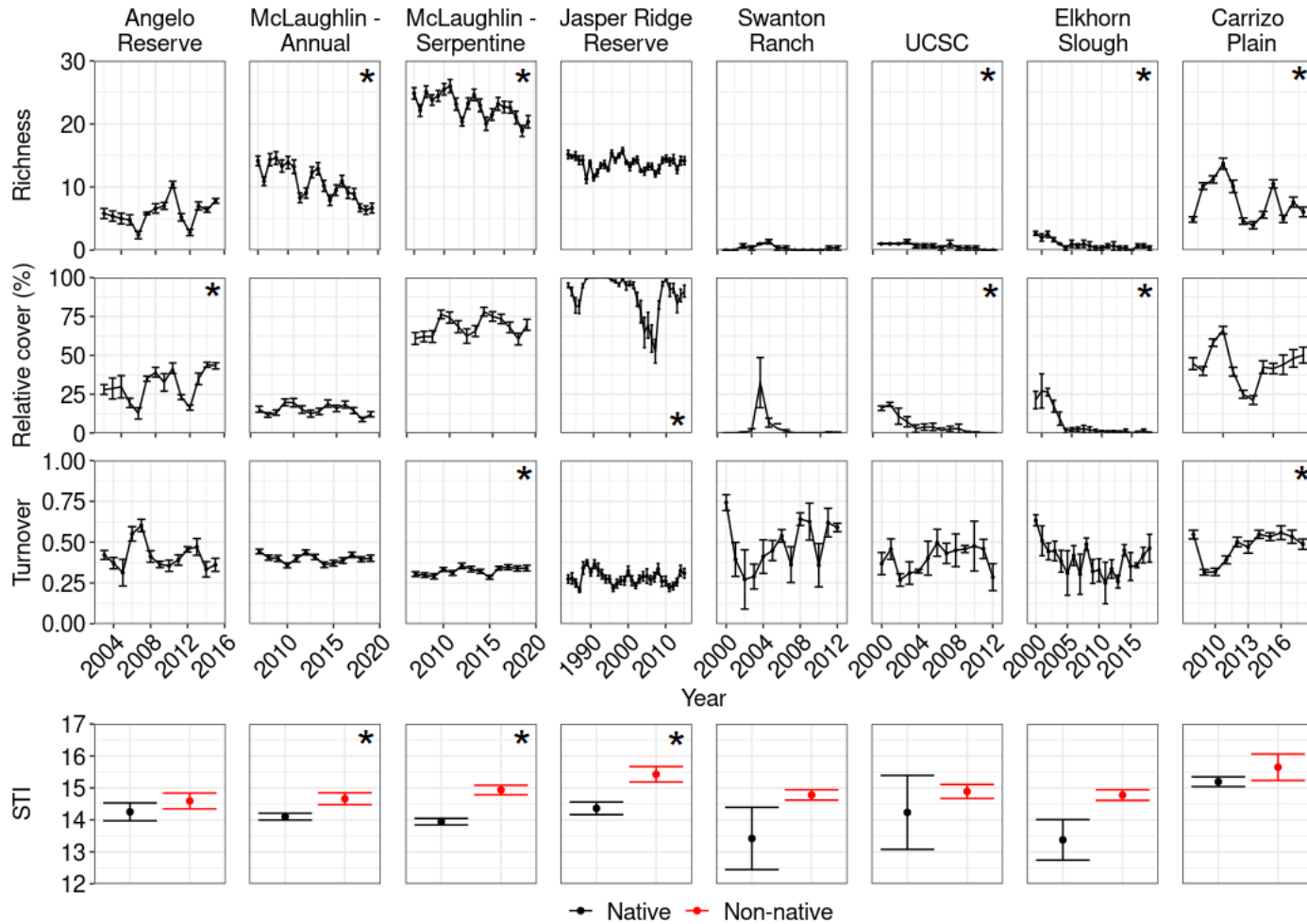


Table 1-4. Results for a) Poisson linear models of native species richness over time, b) linear models of relative cover of native species over time, c) linear models of community turnover over time, and d) t-tests comparing average STI of native and non-native species at each site. For the linear models, bold text indicates significance after Bonferroni correction for multiple hypothesis tests ($p < 0.0167$); italics show significance prior to correction ($0.05 > p > 0.0167$).

Sites	A) Native Species Richness			B) Native Species Relative Cover		
	Est	<i>z</i>	P	Est.	<i>z</i>	P
Angelo	<i>0.026</i>	<i>2.11</i>	<i>0.035</i>	1.003	2.858	0.006
McLaughlin – Annual	-0.036	-19.36	<0.001	-0.170	-1.233	0.218
McLaughlin – Serpentine	-0.010	-7.386	<0.001	0.362	1.512	0.131
Jasper	-0.001	-0.453	0.650	-0.433	-4.634	<0.001
Swanton	-0.062	-0.092	0.356	-0.418	-1.034	0.307
UCSC	-0.148	-2.792	0.005	-1.225	-7.223	<0.001
Elkhorn	-0.117	-4.278	<0.001	-1.129	-6.746	<0.001
Carrizo	-0.035	-5.08	<0.001	-0.356	-0.919	0.359
Sites	C) Community Turnover			D) Native vs. Non-native Species Temperature Index		
	Est.	<i>z</i>	P	t	df	P
Angelo	-0.003	-0.965	0.338	-0.917	33.84	0.366
McLaughlin – Annual	-0.001	-1.106	0.269	-2.612	99.62	0.010
McLaughlin – Serpentine	0.003	2.897	0.004	-5.494	93.17	<0.001
Jasper	-0.001	-1.272	0.204	-3.432	5.39	0.017
Swanton	0.011	1.247	0.220	-1.379	4.22	0.237
UCSC	0.000	0.058	0.954	-0.556	2.15	0.631
Elkhorn	-0.006	-1.864	0.068	-2.141	6.85	0.070
Carrizo	0.015	4.655	<0.001	-1.032	16.78	0.317

Table 1-5. Summary of selected variables that changed significantly over time at each site. Values shown are modeled estimates of change per year. Bold text indicate that values were significant following Bonferroni correction ($p < 0.00625$ for weather variables, $p < 0.0167$ for community composition variables), while values in italics were significant at $p < 0.05$. Empty cells indicate no significant change over time.

Site		Angelo	McLaughlin – Annual	McLaughlin – Serpentine	Jasper	Swanton	UCSC	Elkhorn	Carrizo
CTI		0.037	0.21		0.008		0.05	0.051	0.094
1950-2019 Weather	Mean temp. (°C)		0.008		0.018	0.005	0.008	0.012	0.020
	Mean Dec-Feb min. temp. (°C)		<i>0.020</i>		<i>0.016</i>	0.023	0.029	0.024	0.028
	Annual min. VPD (hPa)	<i>0.003</i>	0.017		0.009	0.007	0.011	<i>0.005</i>	0.021
	Dec-Apr min. VPD (hPa)		0.009		<i>0.003</i>	0.005	0.007	<i>0.004</i>	0.010
	Dec-Apr max. VPD (hPa)		0.032		0.024				<i>0.024</i>
Study Period Weather	Mean temp. (°C)							<i>0.052</i>	<i>0.133</i>
	Mean Dec-Feb min. temp. (°C)				0.070				<i>0.203</i>
	Annual min. VPD (hPa)				0.018	0.068	0.058	<i>0.030</i>	
	Dec-Apr min. VPD (hPa)	<i>0.025</i>				0.058	0.048	<i>0.031</i>	
	Dec-Apr max. VPD (hPa)					0.150	<i>0.128</i>	0.138	
Community Composition	Native Richness	<i>0.026</i>	-0.036	-0.01			-0.148	-0.117	-0.035
	Native relative cover	1.003			-0.433		-1.225	-1.129	
	Turnover			0.003					0.015

Supplemental Tables and Figures

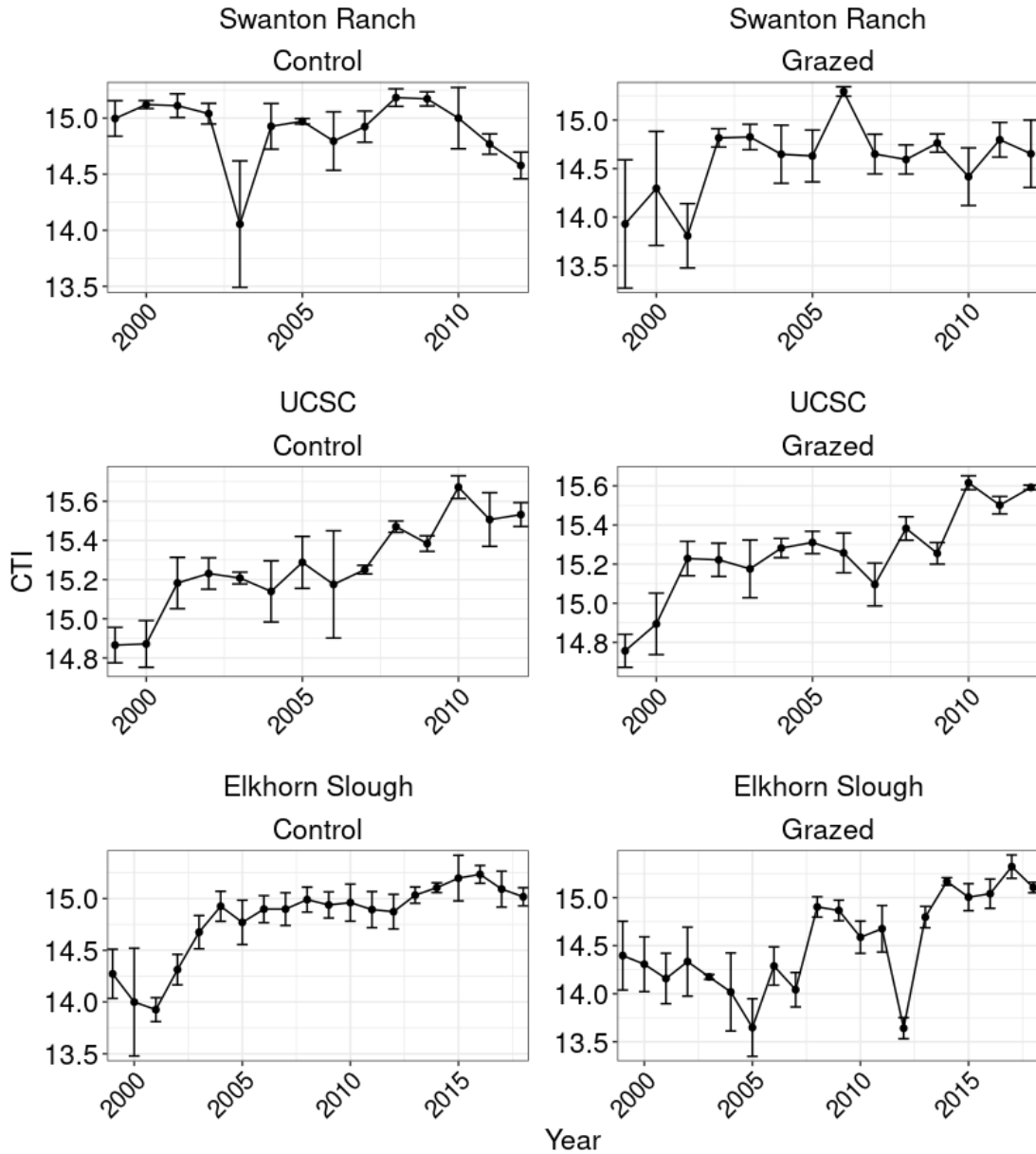
Table S1-1. Results of linear models of CTI over time for each site. Bold text indicates significance.

Site	CTI		
	Est.	t	P
Angelo	0.037	5.845	<0.001
McLaughlin - Serpentine	0.021	5.286	<0.001
McLaughlin - Annual	0.003	-0.591	0.555
Jasper	0.008	5.654	<0.001
Swanton	-0.009	-0.541	0.591
UCSC	0.050	6.573	<0.001
Elkhorn	0.051	6.639	<0.001
Carrizo	0.094	8.778	<0.001

Table S1-2. Models for change in CTI over time across grazing treatments at Elkhorn Slough, Swanton Ranch, and UCSC. Bold text indicates significance after Bonferroni correction for multiple hypothesis tests ($p < 0.0167$).

Site	Treatment	CTI		
		Est.	t	P
Swanton Ranch	Control	-0.009	-0.541	0.591
	Grazed	0.038	1.945	0.057
UCSC	Control	0.050	6.573	<0.001
	Grazed	0.047	6.890	<0.001
Elkhorn Slough	Control	0.051	6.639	<0.001
	Grazed	0.059	5.491	<0.001

Figure S1-1. The CTI of both grazing treatments at Swanton Ranch, UCSC, and Elkhorn Slough. Error bars represent standard error.



CHAPTER 2

NATIVE ANNUAL FORBS DECLINE IN CALIFORNIA COASTAL PRAIRIES OVER 15 YEARS DESPITE GRAZING

Abstract

Grazing, a common management strategy in grasslands worldwide, has been shown to benefit the diverse and threatened guild of native annual forbs in California coastal prairies, but recent drought and increasing aridity could alter this relationship. In 2016 and 2017, I sought to examine the long-term effects of grazing and climate on native annual forbs by resampling paired transects in eleven grazed and ungrazed sites from Monterey to Sonoma counties, California, originally measured in 2000 and 2001. I found that grazed sites continued to have higher native annual forb richness (5.2 species per plot) than ungrazed sites (3.2 species per plot), but that native annual forb richness declined by 2.9 species/plot in grazed prairies and 0.1 species/plot in ungrazed prairies over 15 years. Grazed prairies continued to have lower vegetation height and thatch depth than ungrazed prairies, and shrub encroachment was significantly greater in ungrazed prairies. I suggest that severe drought and increasing aridity may be driving the declines in native annual forb richness that I measured. This hypothesis was supported by the finding that the species lost were disproportionately wetland-associated and had higher average specific leaf area than species that persisted to 2016-2017. Though grazed grasslands continue to have a higher diversity of native annual forbs, I recommend further study to understand mechanisms driving richness declines, modulation of grazing impacts under varying

weather, and possible post-drought recovery.

Introduction

Many human activities alter the diversity of native species in natural communities (Vellend et al. 2013; Dornelas et al. 2014). One of the most widespread human activities in grass-dominated landscapes is managed grazing, which occurs in roughly half of the Earth's savanna, grassland, and steppe biomes (Asner et al. 2004). In some arid and semi-arid regions, overgrazing has resulted in widespread grassland degradation and diversity loss (Fleischner 1994; Painter 1995; Lund 2007; Hilker et al. 2014). However, human activities, including well-managed grazing, can also benefit a diversity of native species in an ecosystem.

Livestock grazing has been shown to benefit vegetation diversity in many grass-dominated ecosystems (Olf and Ritchie 1998; Rambo and Faeth 1999; de Bello et al. 2006; Wilson et al. 2012; Beck et al. 2015). At moderate stocking rates in mesic grasslands, large mammal grazing increases the floral diversity of South American steppe (Lezama et al. 2014), Mediterranean-climate grasslands (Montalvo et al. 1993; Beck et al. 2015), midwestern United States tallgrass prairies (Collins 1998), and northern European semi-natural grasslands (Pykälä 2003). Furthermore, livestock grazing can reduce the spread of woody shrubs and trees into grasslands, precluding conversion to shrubland or forest in the absence disturbance (Lauenroth 1979; Van Auken 2000; Castro and Freitas 2009; Bugalho et al. 2011; Lyseng et al. 2018).

In Mediterranean climates, grazing generally benefits short-statured species

(Hayes and Holl 2003; Kimball and Schiffman 2003; Stahlheber and D'Antonio 2013; Borer et al. 2014), though the strength and direction of this effect can vary depending on annual precipitation (Fuhlendorf et al. 2001; Jonas et al. 2015; Gornish and Ambrozio dos Santos 2016). Grazing is promoted as a conservation strategy in California grasslands to enhance the diversity of native species (Ford et al. 2013; Bartolome et al. 2014), as it serves to reduce the cover, biomass, and litter of fast-growing, tall-statured exotic annual grasses.

Climatic drying due to global climate change will also impact native species diversity. Climate models predict increasingly 'extreme' precipitation, wherein rainfall events occur less frequently, but in larger magnitudes; increasing 'whiplash' weather, when exceptionally dry and wet periods follow one another with minimal change in net precipitation; and rising temperatures globally (Kharin et al. 2007; Smith 2011; IPCC 2014; Swain et al. 2018). Over the last few decades, California grasslands have experienced increasing temperatures and aridity (Williams et al. 2015) and a 1-in-1200-year drought from 2012-2014 (Griffin and Anchukaitis 2014). Both of these climatic anomalies have impacted the species composition of California grasslands, leading to declines of some drought-sensitive species (Copeland et al. 2016; Harrison et al. 2018). Understanding the interactive effects of common land management practices, such as grazing, and climate anomalies will help land managers make better informed decisions about future management strategies.

I wanted to know whether grazing continues to benefit native annual forbs in California's coastal prairies, particularly given the extreme drought and temperature

conditions in the years preceding the study. I focus on northern coastal prairies, which are highly diverse grassland systems along California's coast stretching from Santa Barbara county into Oregon, where winter precipitation is relatively high and coastal fog alleviates summer drought (Ford and Hayes 2007). These grasslands are exceptional for their high native species richness, of which a large proportion are annual forbs (Stromberg et al. 2001; Ford and Hayes 2007), and for maintaining higher native species cover than other California grassland types (Stromberg et al. 2001). I focus on native annual forbs in these prairies because they represent between 25-60% of the recorded species richness (Stromberg et al. 2002; Hayes & Holl 2003; Ford & Hayes 2007; Lulow & Young 2009), and because they benefit from cattle grazing (Hayes and Holl 2003; Stahlheber and D'Antonio 2013). In 2000-2001, the two authors of the precursor to this study surveyed paired grazed and ungrazed coastal prairies and found that grazing favored small-statured native annual forbs (Hayes and Holl 2003).

I hypothesized that native annual forb richness and cover would have declined in these grasslands since 2001 due to the recent severe drought and overall increasing aridity, but that declines in richness and cover would be less severe in grazed grasslands because grazing reduces the competitive dominance of non-native annual grasses. To evaluate whether potential declines were related to changes in weather and/or changes in the surrounding vegetation structure, I analyzed climate-relevant traits of the native annual forb species in my sites and changes in vegetation structure over time. I compared the wetland indicator status of species that were recorded in the

earlier but not recent surveys, which should reflect whether those species were more adapted to mesic environments. I also examined species' specific leaf area (SLA), which has been shown to be associated with drought tolerance (Westoby et al. 2002; Kimball et al. 2012; Harrison et al. 2018), and compared species' seed weights, which are associated with higher survival under drought stress (Westoby et al. 2002; Hallett et al. 2011). I hypothesized that the native annual forb species missing in the recent survey would be less likely to have stress and drought-tolerant traits than those that persisted.

Methods

Site description and climate data

In 2000 and 2001, the authors of the original study (Hayes & Holl 2003) surveyed 26 paired grazed and ungrazed coastal prairie sites between San Luis Obispo and Mendocino counties in California, USA. At all sites, cattle were the only domestic grazing animals, there was no evidence of prior mechanical disturbance, and soils were deeper than 40 cm and not ultramafic (serpentine). In 2016 and 2017, I revisited all sites between Monterey and Sonoma Counties, the central area of the prior survey, where I could obtain access and grazing patterns had been maintained since 2000-2001. I sampled eleven sites and only included data from these sites in my analyses. I gathered grazing regime information from conversations with landowners and internal reports. Sites were typically grazed in the early spring or year-round by cow-calf or dairying operations. In many cases, specific data on the intensity or

timing of grazing for each of my sites in each year was not available, given the nearly 20-year time span of my study. Based on my conversations, grazing pressure in 2016-2017 was maintained at or slightly below 2000-2001 levels.

California's Mediterranean ecosystems have high interannual variability in rainfall quantity and timing, though precipitation generally falls between October and April. Therefore, the most ecologically relevant measure of annual precipitation is a "water year", measured from 1 October to 30 September of the following year. I gathered precipitation and temperature information from weather stations in Santa Cruz, Monterey, San Francisco, and Marin counties from NOAA's Climate Data Online archive (<https://www.ncdc.noaa.gov/cdo-web/>). Precipitation was near the 100-year average (449 to 1328 mm) and below average (416 to 912 mm) in the 2000 and 2001 water years at my study sites, respectively. Precipitation was close to average (511 to 1085 mm) in 2016 and substantially greater than average (673 to 1958 mm) in 2017. Growing season precipitation (November-March) followed similar trends, and temperatures were similar in both sets of sampling years (Figure S1-1). However, my second set of sampling years occurred just following the 1-in-1200 year drought experienced in California from 2012-2014 (Griffin and Anchukaitis 2014), which was accompanied by above-average temperature (Figure S2-1).

Community composition and forb presence

Data collection followed methods described in Hayes and Holl (2003). I

sampled from April through May, traveling from southern sites to northern sites to follow the peak flowering phenology of most species. At each site, I relocated the 2000-2001 50-m line transects using a Garmin eTrex 20 GPS. There were five transects each in the grazed and ungrazed portions (hereafter “plots”) at each site.

I quantified community composition by recording the identity of each species that intersected a 1.8-mm-diameter pin at 1-m intervals. I recorded each species that intercepted the pin once. Nomenclature and species origin information follow the Jepson Manual and online Jepson eFlora database (Baldwin et al. 2012; Jepson Flora Project 2019). I carefully searched for and quantified the cover (to nearest cm^2) of all native annual forbs present within a 1-m belt transect centered over the 50-m transect. I measured vegetation height using a piece of paper dropped onto foliage and the recording the lowest point, and thatch depth (build-up of dead plant biomass) by pushing a 1.8-mm pin to the soil surface and measuring the tallest standing dead biomass, at 5-m intervals. I calculated the number of intercepts of woody shrub cover along each transect in one sampling year during each sampling period (2001 and 2016).

Native annual forb trait data

I compiled seed weight and specific leaf area (SLA, leaf area/leaf dry mass) for native annual forbs identified in my study from several sources. Seed weight data were obtained for a total of 55 of the 60 species from the TRY Plant Trait Database (Kattge et al. 2011), the Kew Millennium Seed Bank Seed Information Database

(Royal Botanic Gardens Kew, 2018), and weighing stored seed at the UCSC Arboretum. SLA data were obtained for a total of 43 of the 60 species from the TRY Plant Trait Database and data collected by others (Kattge et al. 2011; Sandel et al. 2011; Wright et al. 2017; Harrison et al. 2018), and from species present in and near sites during spring and summer 2018. When data for a single species were available from multiple sources, I averaged the values. I used the United States Army Corps of Engineers National Wetland Plant List to determine the wetland indicator status of all native annual forbs found in my sites (Lichvar et al. 2016).

Data analysis

Most variables were averaged across transects in the same plot (site \times treatment combination) prior to analyses; species richness was summed across all five transects in a plot. I used linear mixed models to compare native annual forb richness and cover in the 11 sites resampled over time, using treatment and year as fixed effects and site as a random factor. Native annual forb cover data were $\log(x+1)$ transformed prior to analysis. Differences in mean vegetation height and thatch cover in 2016 and 2017 were compared in grazed and ungrazed prairies using one-tailed t-tests. I tested whether changes in native annual forb richness were related to changes in vegetation factors by comparing the net change in richness to net change in vegetation height, thatch height, and shrub cover. I did this by averaging variables within each plot at each sampling period (2000-2001 and 2016-2017) and calculating the change in each variable between time points. I used a generalized linear mixed

effects model to test for the effects of these factors (fixed effects = vegetation height, thatch depth, and shrub cover; random effect = site) on native annual forb richness. Trait data for native annual forb species were averaged by those found in each category of time periods (*i.e.*: lost, observed in only 2000-2001; still present, observed in both time periods; and new, observed in only 2016-2017) and compared using one-way ANOVAs. In the case of significant differences, I used Tukey Honest Significant Difference tests to compare group means. Data were analyzed in R version 3.5.1 using the base statistics and lme4 packages (Bates et al. 2020).

Results

I recorded a total of 60 annual forb species (over 5,500 m²) in 11 grazed and ungrazed prairies during the four survey years. The total number of native annual forb species declined in both grazed (50 to 27 species) and ungrazed (34 to 22 species) prairies from 2000-2001 to 2016-2017. Likewise, the mean number of annual forb species per site declined in both grazed (by 2.9 species 250 m⁻²) and ungrazed (by 0.1 species 250 m⁻²) prairies between the sampling periods, though I found the same positive effect of grazing on native annual forb richness as in the earlier study (Time: $F=3.9$, $p = 0.013$; Treatment: $F = 25.3$, $p < 0.001$; Time \times Treatment: $F=1.9$, $p = 0.146$; Figure 2-1A). Native annual forb cover was also higher in grazed than ungrazed sites (Treatment: $F = 12.0$, $p = 0.0010$, Time: $F = 1.1$, $p = 0.363$, Time \times Treatment: $F = 0.39$, $p = 0.762$; Figure 2-1B). In 2017, native cover in a single outlier site was more than ten times the mean of the remaining sites (1733 m² ha⁻¹), which

resulted in a doubling of mean native cover from $157.0 \pm 83.3 \text{ m}^2 \text{ ha}^{-1}$ to $300.7 \pm 161.9 \text{ m}^2 \text{ ha}^{-1}$ (Figure S2-1). Nonetheless, the effect of grazing treatment on native annual forb cover was still significant when this outlier site was excluded (Treatment: $F = 8.5$, $p = 0.005$, Time: $F = 1.1$, $p = 0.3539$, Time \times Treatment: $F = 0.36$, $p = 0.781$).

Vegetation height and thatch depth were lower in grazed than ungrazed plots in both sampling periods. Vegetation measured on average 5.3 cm taller in 2016-2017 than in 2000-2001 across both plot types (Table 1). Vegetation continued to be significantly taller in ungrazed prairies in 2016-7 (16.2 cm taller; $t = -4.52$, $p < 0.001$), as it had been in 2000-2001 (12.0 cm taller; $t = -6.63$, $p < 0.001$). Ungrazed prairies also continued to have significantly deeper thatch than grazed prairies in both sampling periods (2000-2001: 3.2 cm thicker, $t = -6.00$, $p < 0.001$; 2016-2017: 3.6 cm thicker, $t = -2.53$, $p = 0.030$; Table 2-1). Woody shrub cover, primarily of the native species *Baccharis pilularis*, *Rubus ursinus*, and *Toxicodendron diversilobum*, increased significantly more in ungrazed prairies (from 7% to 29%) than in grazed prairies (from 1% to 4%) between the two sampling periods (Time: $F = 16.5$, $p < 0.001$; Treatment: $F = 15.2$, $p = 0.002$; Time \times Treatment: $F = 5.0$, $p = 0.044$). In ungrazed prairies, shrub cover increased by an average of $1.5\% \text{ year}^{-1}$. The changes in vegetation structure between sampling periods did not explain a significant amount of the difference in native annual forb richness (GLMM: vegetation height: $p = 0.3962$, thatch depth: $p = 0.5863$, shrub cover: $p = 0.6304$).

The majority of species observed in both sampling periods are classified as

upland or facultative upland species (Figure 2-2). The proportion of species classified as ‘obligate wetland’, ‘facultative wetland’, or ‘facultative’ by the US Army Corps of Engineers was greater in 2000-2001 (30%) than in 2016-2017 (23%)(Figure 2-2) and the proportion of facultative upland and upland species increased by the same amount. The mean seed weights of species observed only in 2000-01, both time periods, and only in 2016-17 did not differ significantly, even when I excluded two outlier *Lupinus* species with exceptionally high seed weights ($n = 53$ species, $F = 1.4$, $p = 0.11$, Figure 2-3A, Figure S2-3). The average SLA of species observed only in 2000-2001 was greater than those found in both periods or only in 2016-2017 ($n = 43$ species, $F = 3.3$, $p = 0.020$, Figure 2-3B).

Discussion

Grassland structure and native annual forbs in grazed and ungrazed prairies

Grazing had similar effects on vegetation structure and the richness and cover of native annual forbs in 2016-17 as in 2000-2001. Plot-level species richness of native annual forbs was higher in grazed than ungrazed prairies, but the richness of grazed prairies declined substantially over time. The decline of native annual forb species richness in ungrazed prairies was significantly lower than in grazed prairies, probably because these prairies had much lower richness to begin with, which includes a subset of species that can tolerate competition with tall-stature exotic grasses.

Consistent with earlier results, grazed prairies had shorter standing living

canopies and reduced standing dead biomass in 2016-2017 (Table 2-1), likely benefitting small-statured annual forbs. Though vegetation was slightly taller (by roughly 5.9 cm) in both plot types in 2016-2017 than in 2000-2001, the net difference between grazed and ungrazed plots was consistent over time. Greater light at the soil surface increases native annual forb germination and growth when competition with exotic annual grasses is high (Coleman & Levine 2007). Reducing the canopy height and dominance of exotic annual grasses through grazing is an important grassland management technique, as these exotic species have faster growth rates and are competitively dominant to many native species in their early stages, reducing native species establishment (Carlsen et al. 2000; Corbin & D'Antonio 2004; Marushia & Allen 2011; Seabloom 2011; Brandt & Seabloom 2012).

I also found further support for the use of cattle grazing to reduce the rate of shrub encroachment into California coastal prairies. Many native coastal prairie species are adapted to disturbance regimes that prevent shrub encroachment, having evolved under grazing by Pleistocene megafauna (Wigand et al. 2007), and later, frequent burning by Native peoples (Anderson 2007; Cuthrell et al. 2007). Ungrazed plots sites experienced significantly greater increases in shrub species cover than grazed prairies over a 15-year period. The most common shrub species and their rate of spread are similar to those found at other coastal California sites, and include mostly native species (McBride and Heady 1968; Russell and McBride 2003; Zavaleta and Kettley 2006).

Potential causes of declines in native annual forb richness

The species richness of native annual forbs declined significantly over time, despite the previously demonstrated beneficial effects of grazing on native annual forbs (Hayes and Holl 2003; Stahlheber and D'Antonio 2013). I was unable to directly attribute this decline to changes in grazing regime or climate. However, I use circumstantial evidence to evaluate whether richness declines are consistent with concurrent changes in grazing patterns and grassland vegetation structure, or if there is evidence that climate or weather could have been a driver of the reductions that I measured between the two sampling periods.

I found minimal evidence that changes in grazing, and therefore changes in vegetation structure factors (shrub cover, vegetation height, or thatch depth) in grazed prairies drove the decline in native annual forb richness I measured. Thatch depth did not differ in grazed plots between the sampling periods. Vegetation was slightly taller (5.9 cm) in the later sampling period, but this was true in both grazed and ungrazed plots and is more likely driven by the greater growing season precipitation in 2016-2017 than in 2000-2001 (Figure S2-1). There was a small increase in shrub cover (1 to 4%) in grazed sites, but it was not statistically significant and was much smaller than in ungrazed plots (7 to 29%). These results are consistent with my conversations with landowners who indicated that the sites were grazed at similar or slightly lower intensities in 2016-2017 as in 2000-2001, though I do not have detailed historical grazing. Moreover, my generalized linear mixed effects model did not show a significant relationship between changes in vegetation structure variables and changes

in cover and native annual forb richness between the two sampling periods.

Several lines of evidence support the hypothesis that recent climate and weather factors explain the decline in native annual forb richness, though I did not conduct manipulative experiments to directly link specific climate variables and species composition. Between the sampling periods, California experienced an exceptionally severe 1-in-1200 year drought (Griffin and Anchukaitis 2014), and the years just preceding my second sampling period were both exceptionally dry and warm (Figure S2-1). Evidence from wetland indicator status indices and SLA data suggest that increasing climatic water deficit may be an important contributor in the richness declines I measured. Nearly half of native annual forbs measured in 2000-2001 were not observed in 2016-2017 (Figure 2-2), and the species I did not observe in the second sampling period were disproportionately those adapted to mesic environments according to their wetland indicator status. Likewise, average SLA decreased between the two sampling periods, and high SLA is associated with drought-intolerance and low water use efficiency (Poorter et al. 2009; Tucker et al. 2011; LaForgia et al. 2018), physiological factors that would have been critical during the historic 2012-2014 drought. The SLA data should be treated cautiously because I used SLA data from different sources and lacked data for some species, as not all annual species were present to take measurements from during the later sampling period. Hence, additional manipulative experiments would be helpful to test the drought tolerance of native annual forbs, particularly those of conservation concern.

The declines in species richness I observed in grazed prairies might be caused

by an inversion of the relationship between grazing and native annual forb richness during extreme drought. Species richness generally increases under grazing in mesic environments, but richness often declines under grazing in arid environments (Schultz et al. 2011; Stahlheber and D'Antonio 2013; Lezama et al. 2014). Continued grazing at historical stocking levels during the extreme drought of 2012-2014 may have directly reduced native annual forb species richness. The only way to tease these effects apart, however, is with a manipulative experiment that controls both grazing pressure and weather.

Looking forward: native annual forbs in the future

Both my results and those of Harrison et al. (2018) at an interior grassland site show a pattern of extinction and declining native annual forb richness in California. It is impossible, however, to determine whether I observed a short-term response to the 2012-2014 drought or what could become a longer-term trend. Heavy winter rainfall in 2017 did not result in increased site-level native annual forb species richness, which would be expected if high precipitation stimulated the persistent seedbanks typical of many species in this group, though a single high precipitation year may not be enough for all species to recover following severe drought. I observed an increase in native annual forb cover but not richness in 2017 as compared to 2016 (an average rainfall year), suggesting that the high precipitation in 2017 benefitted species that persisted through the drought in both grazed and ungrazed prairies. Research on the dynamics of annual forbs and annual grasses suggests that annual forbs persist

alongside exotic annual grasses in part due to precipitation variability and drought (Levine and Rees 2004; Hallett et al. 2019). More time is necessary to determine whether the decline in richness I observed are due to local extinction, or only temporary responses to drought.

In conclusion, I find that grazed grasslands continue to have a greater richness of native annual forbs than ungrazed grasslands, but that the gap between grazed and ungrazed prairies diversity has declined. My study provides additional evidence that drought and rising temperatures affect community composition in managed grasslands globally (Gaitán et al. 2014; Khishigbayar et al. 2015). Finally, my study suggests that species adapted to mesic microhabitats where aridity is increasing may need alternative conservation strategies, such as assisted migration to climate refugia and *ex situ* collections, beyond *in situ* grazing landscape management.

Acknowledgements

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Tables and Figures

Table 2-1. Vegetation and thatch height in grazed and ungrazed plots during all sampling years.

	Treatment	2000	2001	2016	2017
Vegetation Height (cm)	Grazed plots	14.0 ± 2.6	13.5 ± 2.0	20.6 ± 4.4	18.7 ± 3.1
	Ungrazed plots	27.6 ± 2.1	24.1 ± 2.2	28.9 ± 2.0	32.0 ± 2.0
	Δ Grazed – Ungrazed	13.6	10.6	8.6	13.3
Thatch Height (cm)	Grazed plots	1.4 ± 0.9	1.6 ± 0.6	2.1 ± 1.0	1.6 ± 0.6
	Ungrazed plots	4.5 ± 1.6	5.0 ± 1.0	5.6 ± 1.2	5.1 ± 0.3
	Δ Grazed – Ungrazed	3.1	3.4	3.5	3.5

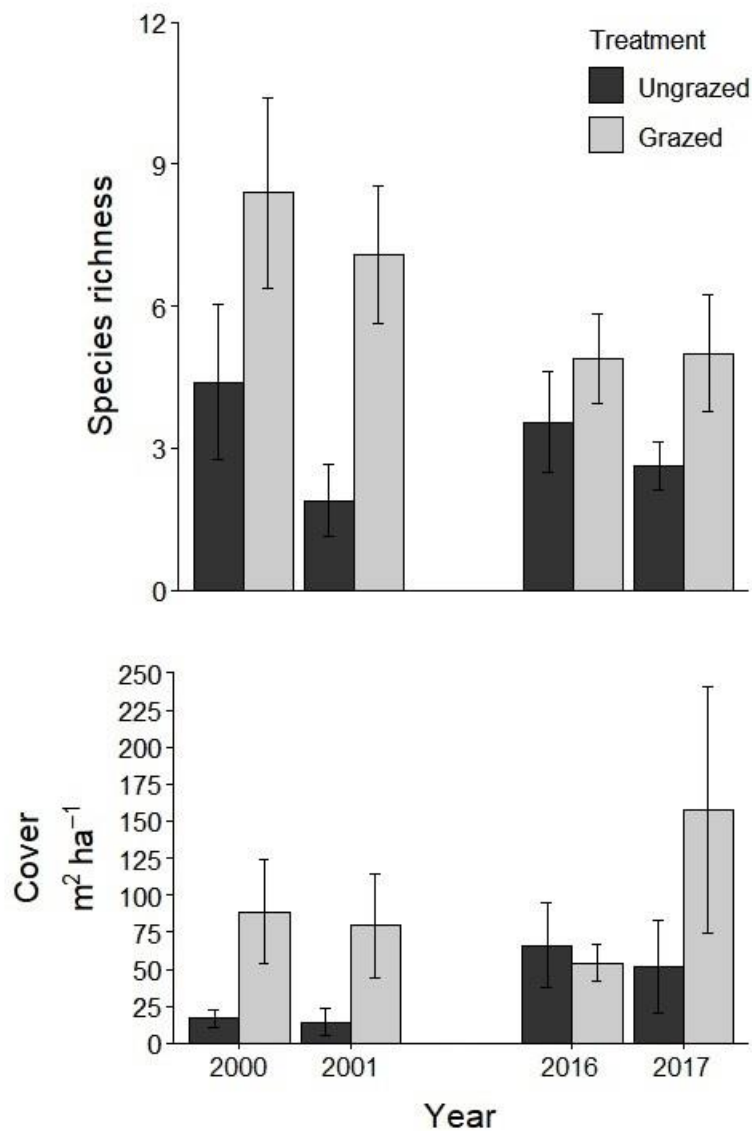


Figure 2-1. Plot-level richness (a) and cover (b) of native annual forbs in grazed and ungrazed prairies in four survey years (n=10 in 2000 and 2016, n=11 in 2001 and 2017). Error bars represent 1 standard error (SE). The exceptionally high cover at a single outlier grazed plot in 2017 has been excluded from (b); Figure S2-2 includes this site.

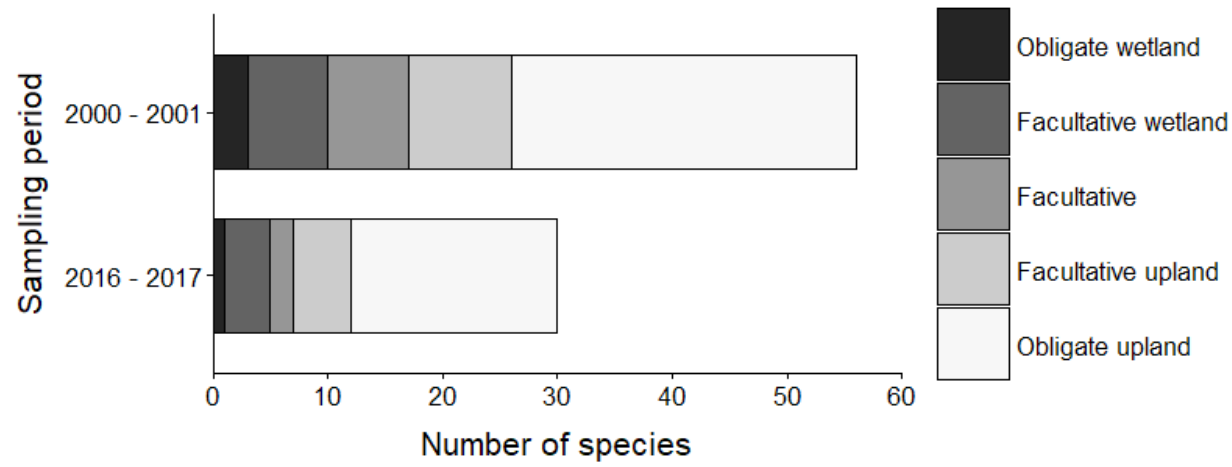


Figure 2-2. Wetland indicator status of native annual forbs observed in 2000-2001 and in 2016-2017.

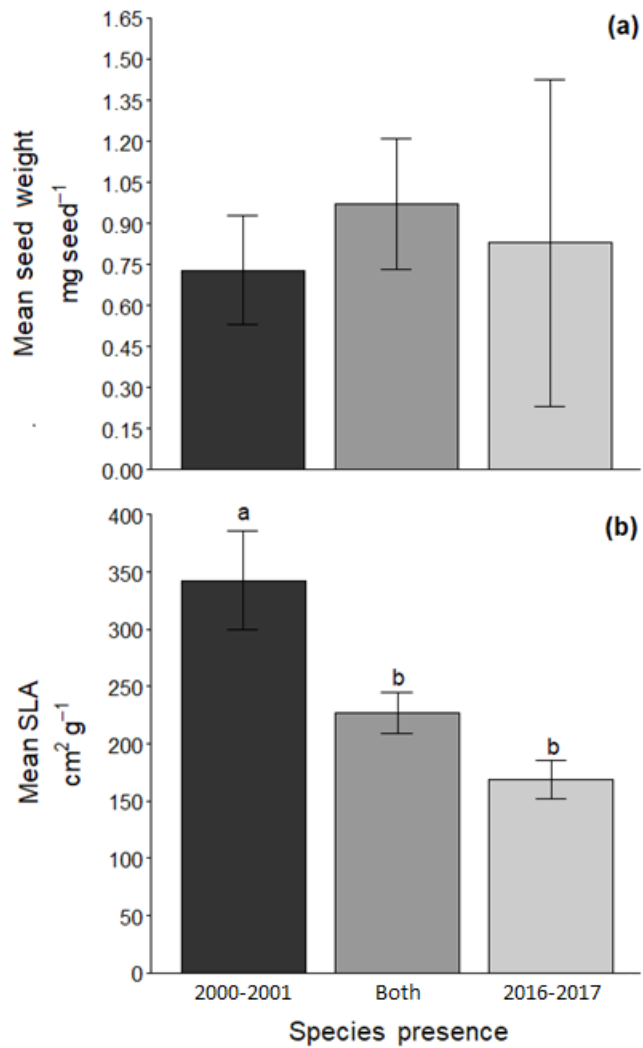


Figure 2-3. Mean (± 1 SE) of dry seed mass (A, $n=53$) and specific leaf area (SLA, B, $n=43$) for native annual forbs that were observed in 2000-1, both sampling periods, or only in 2016-7. Two outlier *Lupinus* species were omitted from (a) but are shown in figure S2-3. Letters represent significant differences between categories.

Supplemental Tables and Figures

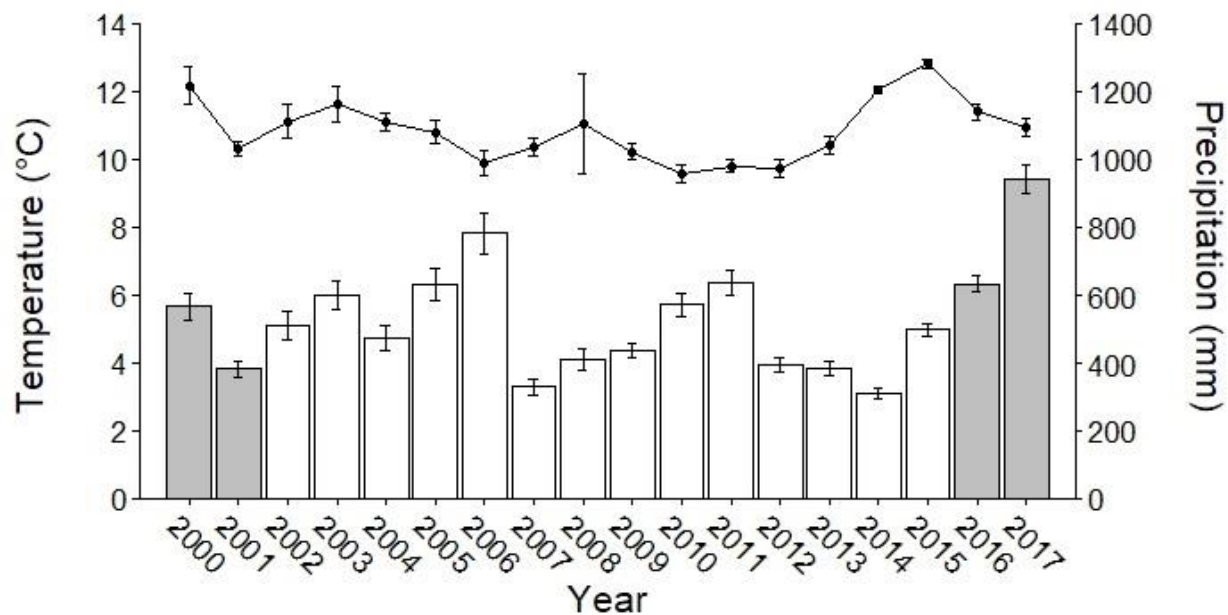


Figure S2-1. Growing season (November – April) temperature (points) and precipitation (bars) for meteorological stations in the sampling region (including Monterey, Santa Cruz, San Francisco, and Marin counties). The sampling years are shaded.

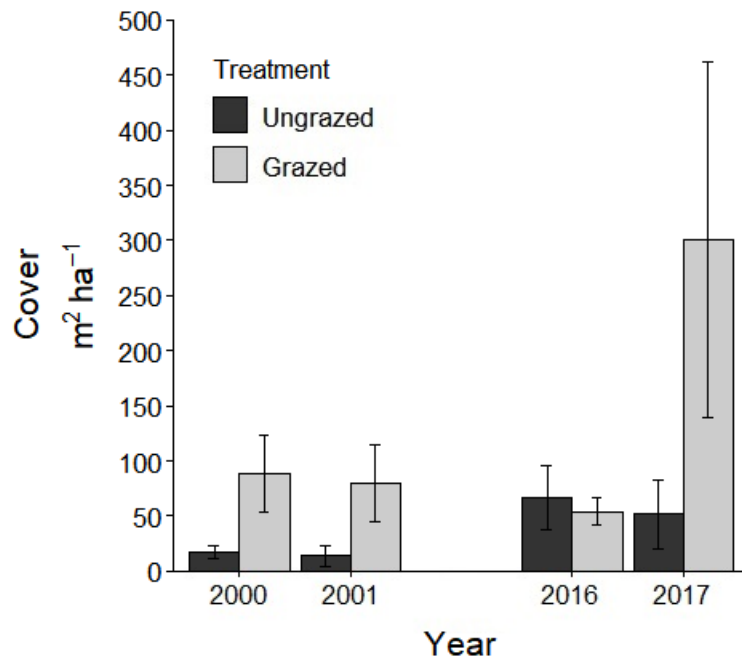


Figure S2-2. Site-level cover of native annual forbs in grazed and ungrazed prairies in four survey years (n=10 in 2000 and 2016, n=11 in 2001 and 2017). The exceptionally high cover at a single outlier site in 2017 is included here.

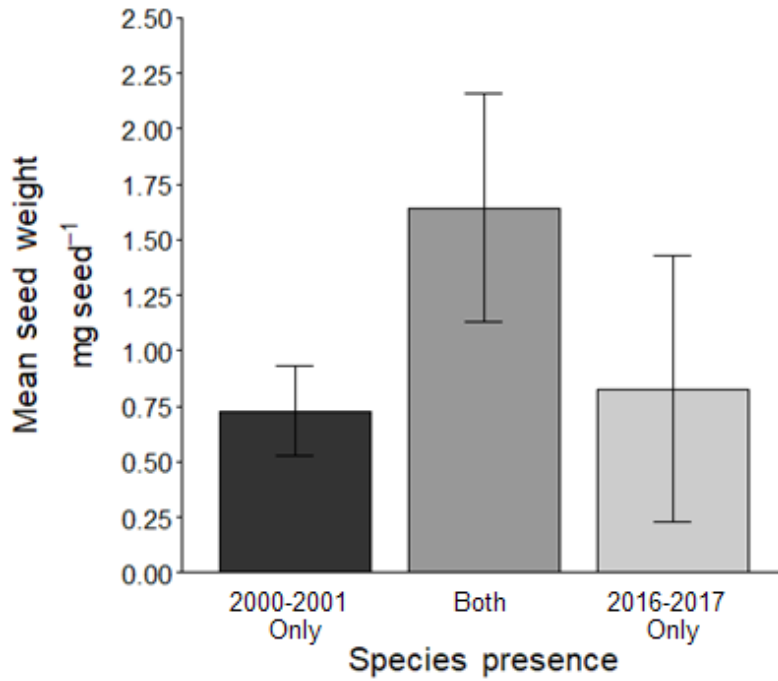


Figure S2-3. Mean (± 1 SE) of dry seed mass ($n=55$) for native annual forbs that were observed in 2000-1, both sampling periods, or only in 2016-7. Two outlier *Lupinus* species are included.

CHAPTER 3

LESSONS FROM THE REINTRODUCTION OF LISTED PLANT SPECIES IN CALIFORNIA

Abstract

Reintroduction is an increasingly common practice to conserve and recover threatened and endangered plant species, so understanding how practitioners view their work and identifying persistent resource mismatches are key to the long-term viability of these listed species. I interviewed practitioners involved in reintroduction projects for 14 species in the state of California to understand 1) how they defined recovery; 2) their assessment of the likelihood of recovery; 3) what advice they would share with other practitioners to improve reintroduction efforts; and 4) what resources could make future projects more successful. Practitioners' definitions of recovery aligned with ecological theory and emphasized the importance of self-sustaining populations and large populations, as well as the presence of multiple populations. However, most practitioners felt that recovery was unlikely or did not think the species they worked with should or would be de-listed without the guarantee of perpetual future interventions. Practitioners thought that studying basic biology and natural history, using experiments to determine the best techniques, and repeatedly planting populations were important to project success. However, practitioners also felt they were missing critical resources, including long-term funding for implementation and maintenance, successful and positive relationships between members of the practitioner-agency-scientist-landowner nexus, and assurances/safe harbor agreements for experimental populations. Overall, rare plant reintroductions

are complicated by persistent mismatches in timing and goals, but some individuals have been able to successfully navigate these challenges. Longer duration funding mechanisms for monitoring and maintenance and better data handling, storage, and dissemination would benefit future projects.

Introduction

The Endangered Species Act ('the Act') is one of the strongest pieces of conservation legislation ever to be passed in the United States (Gray 2007; Rohlf 2014). Though the Act has generally been well-supported by the public (Bruskotter et al. 2018), it has been subject to significant scholarly and political criticism both for doing too little to protect species and for overstepping the legal rights of individuals (Bean 2009; Rohlf 2014). The Act, designed in response to concerning declines in the US's biodiversity, was meant to identify species at risk of extinction, halt and reverse their declines, and 'recover' them so that they could be removed from the list. The emphasis, however, has long been on identifying species at risk and managing them in ways to prevent extinction, with fewer resources going towards recovery (Doremus and Pagel 2001; Evans et al. 2016). Indeed, state and federal species protection policies tend to focus on the conditions under which rare and endangered species become protected (e.g., listing) and much less on the viability and recovery of those populations many decades later. Even the much-used habitat conservation plans (HCPs), under Section 10 of the Act, do little to ensure adaptive management for more than a few years after incidental take permits have been granted.

Relatively few species were down- or delisted in the 15 years immediately following the ESA's passage in 1973, resulting in a 1988 amendment requiring the administering agencies (the US Fish and Wildlife Service and US Marine Fisheries Service) to write or update species recovery plans with specific, actionable requirements for delisting. Recovery plans were required to have clear goals, descriptions of necessary management actions, and estimates for the costs and timeline for these criteria to be met. To date, these recovery plans and their implementation have a mixed track record, though they often provide important guidance and support for the conservation of listed species (Foin et al. 1998; Gerber and Hatch 2002; Doak et al. 2015).

For listed plant species with recovery plans, a commonly prescribed recovery action is population introduction (i.e., planting at sites where a species was not historically found) or reintroduction (i.e., planting at a site within its known historical range). For simplicity, we typically use the term "reintroduction" throughout the rest of the paper, though we acknowledge the complex spectrum of activities that exist along the introduction-translocation spectrum that occur in this type of work (Seddon 2010). As more species require human conservation intervention, reintroductions have become increasingly common over the last 30 years, resulting in the advancement of reintroduction science (Seddon et al. 2007; Hölzel et al. 2012). Though species reintroduction should never take precedence over in situ conservation (Maschinski and Haskins 2012), these actions are critical for the protection and persistence of many rare and listed plant species. Over the past few decades, useful

guidelines regarding proper practices have been published, producing a literature documenting the best methods and practices for the planning, implementation and monitoring of rare species reintroductions (Kaye 2008; Maschinski and Albrecht 2017).

To date, several reviews of reintroduction efforts have focused on quantitative measures of project success and population size to identify best practices and techniques (Dalrymple et al. 2011; Godefroid et al. 2011; Guerrant 2013; Albrecht et al. 2019). Overall, these studies have found mixed evidence for the value of plant reintroduction as a conservation tool, with differing criteria of success and plant life history impacting the value of reintroduction as a technique (Guerrant 2013; Albrecht et al. 2019). In combination with other conservation strategies, such as seed-banking, genetic material preservation, or ex situ conservation in gardens and arboreta, reintroduction to historical habitat is one of a palette of techniques that can be used to protect biodiversity. Given the expansion of human enterprise globally, and the many threats faced by plants, it is unlikely that reintroductions will become less necessary or likely in the future. Therefore, it is valuable to understand what factors are perceived to be limiting or enhancing their success.

This study aims to complement past work studying ecological processes governing reintroduction success by examining the perceptions and attitudes of the practitioners involved in plant reintroduction projects in the state of California. We focused on practitioners' definitions of recovery, their assessment regarding the likelihood of recovery, what advice they have for future practitioners of rare plant

reintroductions, and finally, their thoughts on the resources they felt were lacking, but are critical to project success.

Methods

We focused on reintroductions that have occurred in California, U.S.A., since California has stronger protections for listed plant species and has conducted more introductions and reintroductions than other U.S. states. This focus limits our ability to draw conclusions at larger national and international scales, where there is variation in policies protecting and governing the recovery of rare plant species. However, we contend that the challenges facing rare plant conservation efforts are likely to be similar but potentially more problematic outside of California, as these regions may dedicate even fewer resources to rare plant protection and restoration. In California, introduction and/or reintroduction are required or suggested actions for the down- or de-listing of 87 of the 120 listed species with recovery plans in the state of California (72.5%; out of 183 listed plant species total). According to recovery plans and the US Fish and Wildlife Service's Environmental Conservation Online System, introduction or reintroduction plantings have occurred or are underway for between 25 and 38 species, providing a reasonably-sized pool of potential projects and interviewees.

One of us (J.C.L.) conducted semi-structured interviews with individuals who were involved with reintroductions in a variety of ways: as on-the-ground practitioners, scientific advisors, landowners, and/or officials at permitting and

funding agencies. We assured respondents of anonymity, and therefore identify them only as respondents, or by their relationship to a project (“landowner”, “scientific advisor”). Potential interviewees were identified through analysis of published documents and ‘snowball sampling’, in which we asked respondents to identify other potential respondents they felt we should speak with (Goodman 1961). In total, we contacted 32 potential interviewees, of whom 28 responded and 20 consented to being interviewed. These 20 individuals represent projects for 14 species that have undergone reintroduction efforts in California. Some interviewees worked with multiple species or on multiple projects for the same species. We think our respondents are representative of individuals working on rare plant recovery throughout the state, given that respondent’s recommendations for further individuals that we might interview often named those we had already interviewed, or individuals who had declined to be interviewed. Most of the projects were introductions or reintroductions carried out as a part of a recovery plan, though some respondents had also worked with species on mitigation-related introduction and/or reintroduction efforts. For practitioners who provided information about how long they had worked in the field of rare plant reintroductions (16/20), the mean was 15.5 years (range 2-42 years) and the median was 11 years.

Interviews were conducted mostly by phone and a few via email between January and September 2019. Phone interviews lasted 30-120 minutes. J.C.L. took notes on interviews during and directly after interviews. Interviews were structured around the following four sets of questions:

1. Project background: What is your understanding of the species biology/history and project history? How were you involved in the (re)introduction efforts?
2. Defining recovery: How would you define success/recovery for this species or project? Do you (or did you) think the species is likely to recover? How would you describe project outlooks or outcomes? Have your goals for the species or project changed since starting the work?
3. Advice for practice: What key information or knowledge did you learn from this project that you would pass on to future practitioners?
4. Missing resources: What would you change about the project to make it more successful, or what resource do you feel the project could have benefited from most?

To synthesize results, we categorized responses after conducting the interviews, using email text and phone interview notes. Categories were developed based on the responses given. After coding, we calculated the frequency at which topics were noted. We present all responses that were mentioned more than once.

Results and discussion

Defining recovery

Fourteen of the 20 participants provided definitions of species recovery, and six respondents provided definitions for project success (Table S3-1). Interviewee definitions of species recovery aligned with the recommended de- and down-listing criteria presented in USFWS recovery plans and were ecologically sound. We identified five components of species recovery from our interviews.

The most-cited criteria for recovery (86%) was evidence of a self-sustaining population, meaning they reproduced over time, showed “evidence of new plants,” and eventually created “an F3 generation,” meaning that the introduced plants’ offspring successfully produce reproductive offspring. Additional criteria commonly mentioned by respondents were having multiple populations (57%), large populations (50%), land being protected in perpetuity (29%), and spatially distributed populations (14%). The large population sizes and multiple populations criteria for success are supported by ecological theory, as large and multiple populations of rare plants are better buffered against stochastic environmental and demographic events (Menges 2000; Traill et al. 2010). Respondents sometimes provided exact values for what they felt constituted a ‘large population’ (from 50 to 10,000 individuals), but these values varied depending on the species life history. Several respondents felt that having consistently large populations were not valuable recovery criteria, as some species, such as some native annual wildflowers, have notoriously variable population sizes (Eviner 2014) and would need to be compared “over a period of ‘average’ weather

conditions” to obtain an accurate estimate of recovery success, or because they felt that the required population sizes described in recovery plans or other documents were selected arbitrarily.

Outlooks for down- or de-listing

Respondents expressed mixed attitudes towards the likelihood of species delisting, and three preferred not to respond to the question (Table S3-2). The largest proportion (7) of respondents who answered felt that the species they worked with were unlikely to recover to the point of delisting in the near future. Only two out of the 17 respondents who answered the question felt that recovery to the point of delisting was likely in the foreseeable future, though they couched their opinions in warnings about how long it might take to occur: respondents made clear that delisting “wouldn’t be happening anytime soon,” or that at least “ten years of efforts might lead to a sustainable population of the species”. Roughly a third of respondents (6) felt that the species could recover, but only with the guarantee of perpetual intervention from humans, precluding the possibility of delisting. As one respondent explained, their “biggest concern [was] the self-sustaining definition”, as the need to manage invasive species in perpetuity meant they “[didn’t] know if the plant will ever be down-listed or delisted”. Another respondent indicated that they could not reconcile “always need[ing] to manage the occurrence” with the concept of a self-sustaining population.

This conflict between delisting and the need for perpetual management has been discussed in the literature extensively in the past, under the term “conservation-reliant species” (Scott et al. 2005, 2010). These conservation-reliant species are defined as those for which threats cannot be eliminated, but only managed – potentially in perpetuity. For many of the respondents, threat management in perpetuity or stewardship of the species was viewed as the desired outcome, rather than a negative outcome that mitigated success. In other words, respondents indicated that conducting a reintroduction and ‘walking away’ after 3-5 years was rarely the goal of the project.

Finally, two respondents felt that down- and de-listing should not occur, regardless of whether projects resulted in self-sustaining populations and met recovery criteria. Two explanations given for this perspective were concerns over climate change and the value of listed species as ‘umbrella species’ to protect habitat. As one respondent stated, it would be unwise to delist a species that had reached recovery goals, given that “climate change looms large on the horizon.” This uncertainty about how a changing climate will impact currently protected species is supported by model findings that climate change is more likely to negatively affect endangered than common plant species (Bartholomeus et al. 2011). Another respondent felt down- or de-listing species would eliminate the protections for entire habitats and potentially affect swaths of valuable natural spaces that protect substantially more than a single rare species within it. The concept of an umbrella species which protects co-occurring species has been argued to be a potentially

important conservation tool for protecting considerably more than a single species, but most work examining the value of umbrella species in conservation planning and outcomes has focused on animal species (Roberge and Angelstam 2004; Branton and Richardson 2011). Required critical habitat designation does not always occur for listed species, but listed species can provide protection for a variety of high conservation priority habitats in California (Pavlik 2003).

Practitioner Advice

Interviewees provided many pieces of key advice that they would pass onto those conducting future reintroduction projects (Table 3-1). The two most common were for practitioners to study organisms in the field (natural history) and to use experiments as a part of the reintroduction process (Figure 3-1).

Using resources to understand basic biology and natural history

Practitioners who highlighted the need for thorough research prior to starting a project (Table 3-1) lamented the lack of basic information about species ecology: pollination, propagation techniques, seed viability over time, the effects of competitors, and responses to disturbance regimes. While it seems obvious to say that a good understanding of basic biology is necessary for projects to be successful, basic biological and ecological information is missing, scattered, or inaccessible for many rare species, and practitioners find it difficult to gather and access.

Practitioners repeatedly highlighted the importance of conducting natural history studies prior to beginning a project, but also noted the difficulty in balancing limited budgets with the time needed to fill critical information gaps. Some basic biology inventories for rare species (Massey and Whitson 1980; Maschinski and Albrecht 2017) can be partially filled out with valuable information gathered from historical and modern sources (such as USFWS recovery plans, traditional cultural knowledge from indigenous groups and local communities, and peer-reviewed publications when available). Nonetheless, the most consistent recommendation was to spend large quantities of time in the field studying the natural history of a species, especially in different seasons. As one agency scientist with experience permitting rare plant reintroduction projects explained, reintroduction projects based on thorough on-the-ground research are less likely to fail. For another respondent, “spend[ing] enough time with a species to watch the conditions under which it grows” led to crucial insights about the species that improved project outcomes, and yet another described how natural history was important to their process: “I developed a series of research questions based on my years of observation in the field, and then collaborated with different research institutions to conduct the studies... It’s all about learning to ask the right questions. And the right questions come from spending time observing the species in its natural habitat (or a suitable surrogate reference species or population).”

These comments underscore the calls of others for the holistic study of rare plant taxa to better guide management, conservation, and reintroduction strategies

(Silva et al. 2015), and the concerning concurrent decline in support for natural history research, or the observational study of organisms in their habitat, over the past several decades (Tewksbury et al. 2014). Thirty percent of respondents identified information about species ecology as a missing resource that could improve project outcomes, and without support and investment to study the basic biology of listed species, practitioners will be limited in their ability to generate appropriate and successful reintroduction plans.

Using reintroductions as experiments

Numerous authors have called for reintroduction projects to be conducted as scientific experiments with explicit hypotheses to improve our understanding of ecological and evolutionary processes (Sarrazin and Barbault 1996; Guerrant and Kaye 2007; Maschinski and Haskins 2012), and the practitioners we interviewed largely agreed, with nearly half (45%) of respondents listing experimental practice among their advice. Interviewees valued experimentation in reintroductions to provide information about basic species biology and to identify the best techniques for reintroduction. One of the benefits of using experiments as part of population reintroduction is that even if the project itself is not successful, something about the species can be learned regardless, which Pavlik (1996) describes as the differences between project success and biological success. One practitioner referred to their series of experiments as developing a “prescription of how you grow them and how you plant them.” Multiple practitioners told stories of using experiments to compare

techniques, describing their experiments as a “series of learning events” to try to “nail down” which treatment was most successful.

Several interviewees also advocated for using experiments to test the limits of known species niches. One respondent summarized the concept succinctly as “don’t assume that the extant population characteristics are what the species wants.” Another interviewee noted that many listed species are only found in a small number of extant populations but may have been found historically at sites that are “now under shopping malls.” Thus, species could be tolerant of a wider range of biotic and abiotic conditions than is reflected by their extant populations. Greenhouse and field experiments can test these boundaries, potentially providing insight about alternative reintroduction sites. One respondent, lamenting the quality of the distribution and abiotic tolerance information in the recovery plan for their species, declared that future efforts should not “take on faith... the received wisdom of what plants need.”

Planting repeatedly to hedge bets

Planting in multiple years can help practitioners hedge their bets, as published evidence supports the use of repeated plantings to overcome stochastic events like sudden drought, and to improve the chances of catching a good year for plants to establish (Wilson 2015; Stuble et al. 2017). For several interviewees, initial planting efforts during a drought year failed, but the same techniques in later years appeared more successful. One respondent described this technique as “founder cost averaging” (analogous to the financial concept of ‘dollar cost averaging’) in which

repeated plantings would be more likely to lead to long term success: “don’t do it all at one time, do it one year at a time in hopes of catching that one up-year.”

Missing resources

Two resources were identified as likely to improve project outcomes by over half of interviewees: long-term funding and provisions for active management or monitoring (Table 3-2, Figure 3-1).

Fixing mismatches in the scales of funding and timing: monitoring and active management

The most cited resources desired by interviewees were commitments for long-term funding (55%) and long-term monitoring and active management (55%). This is unsurprising, given that most restoration projects are only monitored for short periods (Suding 2011). Moreover, meta-analyses of plant reintroductions have found that monitoring rarely extends more than three years beyond project implementation, and self-sustaining populations are rarely achieved after initial efforts (Godefroid et al. 2011; Guerrant 2013). This short-term funding is a mismatch with practitioner’s perceptions that the species they worked with could recover only with perpetual human intervention or management, reflecting a shift from short-term intervention thinking towards long-term stewardship thinking.

Fixing this mismatch will require alternative funding mechanisms, such as bonds and endowments, to ensure proactive long-term management. Bonds and

endowments are two methods by which large sums of principle funds are used to fund long-term projects using interest or income on the principle investment. Currently, common grants for rare species recovery (such as traditional Section 6 cooperative endangered species conservation fund grants) are limited to a short number of years of funding (1-4 years), which, while valuable for some experimental projects, do not align with the time needed to monitor of a reintroduced population (Figure 3-1). This mismatch in the scale of funding and of ecological processes is well recognized across restoration ecology (Hodge and Adams 2016; Holl 2020). Multiple respondents described piecing grants together from different sources over the years to keep project monitoring afloat, and one succinctly stated, “we want longer funding cycles.” We do not argue for indiscriminate increases in funding, as funds to monitor projects should be put to good use, such as measuring relevant processes and answering specific questions (McDonald-Madden et al. 2010), but rather for funding to be guaranteed over longer periods so that long-term data collection and management can take place as needed.

Enhancing data management to move from individual knowledge to institutional knowledge

Several practitioners identified the need for high quality data collection and management skills in order to improve future project outcomes, reflecting past calls for accessible, distributed networks of knowledge (Godefroid and Vanderborcht 2011), and the troubles that arise when management methodologies go missing, are

trapped in filing cabinets, or never recorded at all (Dickens and Suding 2013). One constraint to high-quality data storage and transmission is the cyclical nature of most organizations, wherein individuals only stay at a single position for a few years. For some organizations, the average tenure of an individual can be quite short (such as masters students at universities and some agency positions), whereas in other cases, individuals may be in a position for decades (such as land owners). Internal turnover can lead to problems if information and data are not stored and shared appropriately. In one case, a respondent was managing several successfully reintroduced populations years after the initial reintroductions had occurred but was missing critical information about what techniques were used and the factors that guided decision-making, as the original efforts had not been recorded in a trackable manner.

With 30% of the respondents describing basic species knowledge as a missing resource and funding for rare plant studies as limited, enhanced database management and results-sharing among different groups are important aspects in overcoming the knowledge deficit. Information about rare plant reintroductions can be difficult or impossible to access unless an individual is working directly with a specific project. Others have called for the creation of accessible online reintroduction information repositories (Godefroid and Vanderborcht 2011), and recently, the Center for Plant Conservation developed the “Rare Plant Academy” web page, which includes resources and a forum for practitioners to discuss seed banking, conservation practices, and reintroduction practices (<https://academy.saveplants.org/>). Though repositories tend to grow slowly at first, they should help fill a gap in rare plant

reintroduction information transfer. Similarly, regional workshops and meetings can facilitate knowledge transfer.

Improving academic-practitioner-agency-landowner communications

The problems preventing rare species conservation and recovery are seldom purely biological (Clark and Clark 1997). As one respondent put it, “the ecology is important, but the policy, the people, and everything else is just as important.”

Despite the rough edges and difficulties that sometimes arise when multiple groups with diverse goals work together, many interviewees recognized that cooperation across organizational and institutional boundaries was critical to achieve project success.

A common stumbling block mentioned by several respondents was obtaining permits to collect rare plant seed, access land, conduct trials, and other tasks, and obtaining those permits depends on relationships with the permit granting agencies. One interviewee explained that while agencies must ensure no harm will come to a listed species, they felt that officials were sometimes so afraid of moving in the wrong direction that they would refuse to take any steps at all to conserve a species, and another described the delays as “permit hand wringing.” Respondents overcame these difficulties by developing strong and trusting relationships with permitting agency officials before and during the process of applying for permits. As one interviewee said, “it’s important to have good working relationships with the agencies” and that it was important for agency staff to “know you, like you, and

respect you” if you hope to conduct successful projects. Most reintroduction best-practices indicate the need to acquire permits well before work is conducted, but few reflect the reality that having a positive, trusting relationship with an agency can make or break a project.

Our interviews also highlighted persistent mismatches between the desires and tenure of research scientists who work with projects and the goals of the project managers. Though they shared the overarching goal of maintaining robust populations of reintroduced rare plants, academic researchers often sought to answer questions that were narrowly focused on the basic ecology of the species, which frequently did not align with specific project goals or inform on-the-ground reintroduction techniques. These responses reflect well-documented gaps in what is published in the conservation and restoration literature, and what is desired by managers (Arlettaz et al. 2010; Dickens and Suding 2013; Matzek et al. 2015). Equally, there is a mismatch in the pace at which scientific journals publish information that could be salient to land managers and when managers may need this information, as peer-review takes a considerable amount of time (Meffe 2001). Interviewees also suggested that even when practitioners and scientists were able to cooperate on a project, project managers sometimes felt burned because academics would move on after several years, either because the results of the initial study were published or because the person who initially worked with the project, such as a graduate student or post-doc, had finished their project or program. This left landowners or agencies without resources to continue monitoring a project, or even

missing entire reports about what had occurred. Bridging this knowledge-action boundary for successful reintroductions will require careful and consistent communication, and can be achieved through several mechanisms, such as boundary organizations or working groups (Cook et al. 2013).

Despite these difficulties, several practitioners described successful cooperation with research scientists, and were able to navigate relationships with research institutions by incorporating researcher interests into specific projects that would produce the natural history knowledge and experiments desired by project managers. By identifying who will be responsible for a project's long-term management before it begins, a project is much more likely to move smoothly from implementation to management. Without preparation for long-term care, projects can end up mismanaged or forgotten, so plans should outline early on who will care for a project and the associated data, potentially in perpetuity.

Providing flexibility and assurance for landowners

Four respondents also brought up the concern of creating perpetual land-use restrictions on a property after successfully reintroducing a listed species. They described rejecting opportunities to gain knowledge about appropriate techniques and management strategies due to fears of highly restrictive regulations that might occur if projects were successful in the long term. As one respondent explained, tensions between landowner desires or mandates (such as the need to maintain public access or

recreation) could be at odds with the need for ‘protection in perpetuity,’ and they wanted to avoid “looking back in the future and wondering ‘what was I thinking?’”

One policy mechanism to solve this problem could be increasing the use of designated experimental populations under the 1982 Section 10(j) amendment of the Endangered Species Act to gain knowledge about techniques and best practices. When a population is designated as experimental, especially as a nonessential population, the regulatory burden associated with take of the species on a property is greatly relaxed. The requirements for experimental designation are that the release has been authorized and that the introduced population is geographically separate from natural populations, so that if ‘take’ occurs, it is clear which population is the experimental one. To date, this designation has never been used on a plant species at the federal level, though a state-level designation has been applied to some populations as part of reintroduction experiments (Holl and Hayes 2006).

Conclusions

Our findings call attention to shortcomings in the ability of the Endangered Species Act to ensure the long-term success of listed species reintroduction efforts, and the ways in which project success could be improved in the future. Though many of the practitioners we interviewed do not perceive de- or down-listing to be likely in the near future, they are dedicated to the long-term stewardship of the rare species they work with. The Act is a valuable piece of legislation for the conservation of flora and fauna in the United States, but for species that require more than a one-time

introduction or reintroduction, or that may depend on human management in perpetuity, the Act itself does relatively little to support the many steps that will be required in the future (Figure 3-1).

Our interviews reinforced prior research indicating that there is a disconnect between scientists and managers, but also revealed a high level of agreement between these groups on the use of well-designed experiments in rare plant reintroductions. We are heartened that the value of experimentation is recognized across groups, and urge continued experimentation to increase project success, and eventually biological success. Increased collaboration on experimental reintroduction projects in the future could go a long way in resolving some of the information gaps that were described in our study, especially if experiments can be designed to improve practitioners understanding of species natural history and specific techniques to improve project success.

Finally, we feel that holistic mechanisms to support projects through the entire recovery and reintroduction process, from natural history study through post-reintroduction monitoring through continued active management, could greatly benefit future project success. This holistic approach mirrors other calls for a diversity of techniques to be using in conserving rare plant species overall (Havens et al. 2006). Likewise, increased communication of findings among practitioners through both formal and informal networks will continue to be necessary in the future. Future policy development with an eye towards improved long-term funding mechanisms such as endowments and bonds that support stewardship and

management, may better protect species than the intervention-style actions currently most supported under the Act. As the science of reintroduction ecology continues to develop, we hope to see the creation of funding and support networks which reduce the pressure on practitioners to string together short-term grants, and provide the stability necessary for long-term data collection, storage, and dissemination.

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Tables and Figures

Table 3-1. Key advice provided by interviewees regarding the reintroduction of rare plant species. Some practitioners provided multiple pieces of advice.

Advice	Number of mentions (n=20)
Study natural history & biology	10 (50%)
Use experiments	9 (45%)
Visit field sites of all extant populations	5 (25%)
Test the edges of the range/niche	5 (25%)
Develop social connections	5 (25%)
Develop high quality data collection and management skills	3 (15%)
Plant repeatedly	3 (15%)
Prepare for long-term investments	2 (10%)

Table 3-2. Key resources interviewees felt were missing and would have improved rare plant reintroduction outcomes. Some practitioners identified multiple missing resources.

Desired resource	Number of mentions (n=20)
More/longer-term funding	11 (55%)
Long-term monitoring/active management	11 (55%)
Better relationships with other groups	7 (35%)
Info on species	6 (30%)
Flexibility/assurance if pop. needs to be moved	4 (20%)
More propagules	4 (20%)

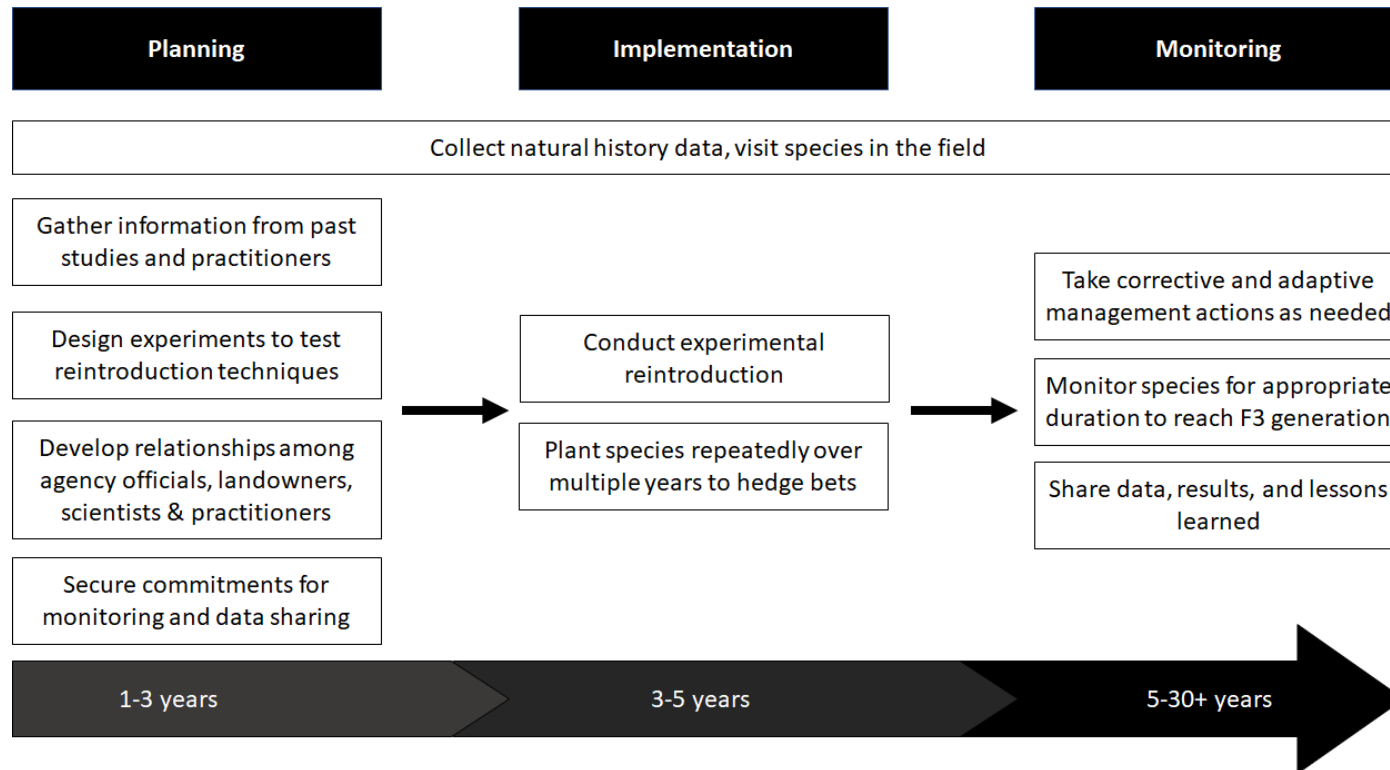


Figure 3-1. A schematic summarizing the most common advice and lessons learned to improve reintroduction project outcomes and when these activities should occur, illustrating the need for longer-term funding and monitoring commitments than are typical.

Supplemental Tables and Figures

Table S3-1. Criteria for defining species recovery according to interviews. Fourteen interviewees provided criteria for species recovery success.

Recovery component	Number of mentions (n=14)
Self-sustaining populations	12 (86%)
Multiple populations	8 (57%)
Large population sizes	7 (5%)
Habitat is protected in perpetuity	4 (29%)
Wide geographic range	2 (14%)

Table S3-2. Respondent opinions on whether species were likely to recover to the point of down- and/or de-listing. Seventeen respondents provided opinions.

Response to whether species can/will recover to the point of down/delisting	Number of mentions (n=17)
Recovery will/can occur	2 (12%)
Recovery could occur with continued or perpetual effort/intervention	6 (35%)
No, recovery to that point is unlikely to ever occur	7 (41%)
Recovery to the point of delisting is possible, but delisting should not happen	2 (12%)

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