

Diagnosing restoration trajectories using modern coexistence theory

Running Head: Assessing restoration with coexistence theory

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Abstract

Restoration ecology often seeks to reestablish species of interest in degraded habitats. Despite a rich understanding of how succession influences reestablishment, there are several outstanding questions that remain unaddressed for many restoration efforts: are short-term abundances sufficient to determine reestablishment success, or do year to year fluctuations require more elaborate quantification of population trends? When restoration fails, is it because the restored habitat is substandard, because of proliferation of invasive species, or due to changing environmental conditions that would equally impact established populations? Here, we re-purpose tools developed for Modern Coexistence Theory to address these questions, and apply them to an effort to restore *Lasthenia conjugens* in constructed ('restored') vernal pools. Using 16 years of data, we construct a population model of *L. conjugens*, a species of conservation concern. We show that the initial restoration success of this species gleaned from short-term abundances is misleading, as year-to-year fluctuations cause long-term population growth rates to fall below zero. The failure of constructed pools is driven by lower maximum growth rates compared to reference ('natural') pools, coupled with a greater (negative) sensitivity to annual fluctuations. Nonetheless, our modeling shows that fluctuations in competitors (mainly exotic grasses) benefit *L. conjugens* through competitive release, and we explore how reductions in invasives could change the outcome of restoration for this species. By applying a largely theoretical framework to the urgent goal of ecological restoration, our study provides a blueprint for in-depth understanding of restoration success and failure, and identifies future actions to reverse species loss.

Keywords: *Lasthenia*, modern coexistence theory, population dynamics, relative nonlinearity, storage effect, restoration, vernal pools

24 Introduction

25 Ecological restoration is an increasingly important tool to reverse the effects of land degra-
26 dation, but the success of restoration efforts is often uncertain. Success is often measured by
27 comparing the abundance of target species in the restored community to a natural “refer-
28 ence” community, with similar species abundances between restored and reference presumed
29 to indicate success (Ruiz-Jaen and Aide, 2005; Society of Ecological Restoration, 2004).
30 This approach is best suited when ecosystems have a monotonic recovery trajectory, which
31 is predicted by the most common ecological theories used to inform restoration, such as
32 succession and community assembly (Wainwright et al., 2017). At the same time, more
33 recent developments in ecological theory, such as Modern Coexistence Theory (MCT), have
34 highlighted that environmental variation and associated fluctuations in species abundances
35 are not only common, but at times essential for maintaining species populations (Chesson,
36 2000; Adler et al., 2007; HilleRisLambers et al., 2012), complicating efforts to assess suc-
37 cess on abundance alone. Applying MCT to ecological restoration may provide a clearer
38 picture of restoration trajectories and illuminate pathways to improve restoration outcomes,
39 particularly in variable environments.

40 Modern coexistence theory has gained prominence as a tool to understand how the envi-
41 ronment and species interactions jointly structure species diversity (HilleRisLambers et al.,
42 2012; Letten et al., 2018; Grainger et al., 2019). A cornerstone of MCT is that species can
43 coexist if they can increase when rare (Barabás et al., 2018). Critically, the ability to in-
44 crease when rare is assessed by average low-density growth rates; many persistent species
45 still experience periods of negative growth and low abundance (Letten et al., 2018; Hallett
46 et al., 2019). Moreover, this variability can in fact be key to maintaining coexistence among
47 species (Chesson, 2000). For example, the storage effect - in which species capitalize on good
48 years while “storing” through bad years, such as in the seed bank - is a classic fluctuation-
49 dependent mechanism of coexistence (Chesson, 2018). While the storage effect is based on

species-specific responses to the environment, relative nonlinearity in species' responses to the environment or competition can also enhance coexistence if species experience a greater magnitude of benefit under favorable conditions compared to their magnitude of decline under unfavorable conditions (Letten et al., 2018; Hallett et al., 2019).

Integrating methods from MCT into restoration ecology may improve our ability to diagnose restoration trajectories. A key lesson from fluctuation-dependent coexistence is that a low abundance of target species may not necessarily indicate failure; abundance fluctuations can be essential to coexistence (Warner and Chesson, 1985; Gravel et al., 2011). Conversely, high abundances of target species may not indicate success, because restoration activities such as seed addition may yield abundances that belie an overall negative low-density growth rate (Martin and Wilsey, 2014). Gauging success by low-density growth rate rather than abundance may therefore better provide an early indication of restoration trajectories. When restoration projects are monitored over time, average low-density growth rate may ultimately provide a more robust assessment of success than possible from abundance patterns alone.

Assessing restoration outcomes through the lens of MCT may also improve our ability to identify the factors governing success or failure, ultimately improving the adaptive management process. Classic models of ecological restoration (e.g. ecological filters framework) have highlighted that altered environmental conditions and novel competitive interactions can both act as barriers to restoration success (Temperton et al., 2004). Management efforts in restoration regularly tailor both barriers. For example, land-moving to reshape hydrology or amendments to alter soil conditions are common tools in riparian and grassland restoration (Nilsson et al., 2015; Havrilla et al., 2020), respectively, and mowing or grazing to reduce exotic grasses are common tools to promote native forbs in annual grasslands (Weiss, 1999; Hernandez et al., 2021) and vernal pools (shallow, ephemeral wetlands in the Mediterranean climates) (Marty, 2015). A strength of MCT is that it decomposes the effects of the environment, competitive interactions, and their responses to varying environments on species

growth rates (Barabás et al., 2018). Applying this partitioning to restoration monitoring data may help isolate the effect of the restoration actions on abiotic versus biotic barriers. For example, a strong negative effect of environmental variability on species’ intrinsic growth rate would indicate that an intervention is needed to ameliorate the abiotic environment. Similarly, MCT can indicate periods in which competitor removal is most likely to benefit a target species (Godoy and Levine, 2014), even when these dynamics would be hard to discern from abundance patterns due to covariance of competition and environment.

Here, we demonstrate how principles and methods of MCT can be used to improve the assessment of restoration trajectories and guide restoration actions. We leverage long-term monitoring data of an endangered annual forb species, *Lasthenia conjugens* Greene (Contra Costa goldfields, Asteraceae: Heliantheae), from a restoration project in California vernal pools. Vernal pools are critical habitats for rare plant diversity. While native vernal pool forbs are better adapted to the highly variable ephemeral ponding (Emery et al., 2009; Faist and Collinge, 2015; Tittes et al., 2019), exotic grasses historically are not (Gerhardt and Collinge, 2007). In particular, *L. conjugens* thrives in wet early-season rain years (Gerhardt and Collinge, 2007), while exotic grasses are competitive in wet late-season rain years (Javornik and Collinge, 2016). Because of these environmental fluctuations, determining restoration success solely from the abundance of *L. conjugens* is difficult (Collinge et al., 2013; Schlatter et al., 2016). We hypothesized that *i*) model-derived growth rates are more reliable metrics to assess long-term trends than observed abundance in early years; *ii*) *L. conjugens* can persist (positive average low-density growth rate) because environmental variability has a positive effect on the intrinsic growth rate and relative nonlinearity in competition; and *iii*) the average low-density growth rate of *L. conjugens* increases with greater amount of exotic grass removal. To test these hypotheses, we parameterized stochastic population models with monitoring data, partitioned growth rates with MCT (Ellner et al., 2019), and experimentally simulated the effects of active management on restored populations. This approach

has a wide application potential for restoration of rare species and species of conservation concern.

Methods

Study site: We conducted this study in a vernal pool system at Travis Air Force Base (AFB) near Fairfield, California, USA (38°15'00" N, 122°00'00" W, 6 m elevation). Approximately 100 naturally occurring vernal pools exist in the 15-ha study area. The site experiences cool, wet winters and hot, dry summers. The pools fill with water and the growing season begins with winter rains, usually starting in October. The pools dry out and the growing season ends in April or May, when the rain stops and temperature increases (Keeley and Zedler, 1998). The amount of water in the pools varies each year due to high seasonal and annual rainfall variability [growing season rainfall averages 455.4 mm but has ranged from 159.8 mm to 869.2 mm over the past 50 years (PRISM Climate Group, 2020)].

While the pools support a diverse native plant community, restoration efforts often center on the annual forb *L. conjugens*, because it is a protected endangered species (Federal Register, 1997). Previous work has shown that *L. conjugens* populations are weakly positively correlated with higher early-season rainfall in October to December, deeper pools, and longer inundation (Javornik and Collinge, 2016). Additional focal species native to vernal pools at this site include *Eryngium vaseyi* (button celery), *Downingia concolor* (spotted throat downingia), and *Plagiobothrys stipitatus* (popcorn flower) (Collinge and Ray 2009). Exotic annual grasses dominant in this system are *Bromus hordeaceus*, *Hordeum marinum*, and *Festuca perennis* (previously called *Lolium multiflorum*).

Restoration design: To restore *L. conjugens*, SKC constructed 256 artificial pools in December 1999 in the vicinity of reference pools as described in Collinge and Ray (2009). Pool sizes were randomly assigned as either large (5 x 20 m), medium (5 x 10 m), or small

(5 x 5 m), to reflect the size variation in the reference pools. Constructed pools were also similar to references in elevation, topography (0-2% slopes), and soil type (Antioch San Ysidro complex and San Ysidro sandy loam). To establish populations of *L. conjugens* (LACO) in constructed pools, SKC collected seeds from reference pools during May and June of 1999, 2000, and 2001. In early December of 1999, 2000, and 2001, constructed pools were sown with seeds within permanently marked 0.5 x 0.5 m plots (one plot per pool). Three seed addition treatments were randomly assigned to constructed pools: control (no seeding); LACO 1x (100 *L. conjugens* seeds in 1999); LACO 3x (100 *L. conjugens* seeds in 1999, 2000, and 2001). Other native species were at times included in the mix for other focal studies, and they are accounted for in our statistical model that incorporates competition. Plots were initially raked prior to seeding in 1999 but not in 2000 and 2001 because raking may disturb seeds from previous years.

In April, during approximate peak biomass, each year from 2000 to 2015, plant occurrence was monitored. A 0.5 x 0.5 m frame divided into 100 subquadrats (5 x 5 cm) was placed in a permanently marked plot in each pool, and stem counts of five focal species and frequency (number of subquadrats out of 100 in which the species occurred) of all species present were measured within each plot.

The dynamical model: To project the population dynamics of *L. conjugens*, we took into account the effect of environmental conditions as well as the competition it experiences from both conspecific and heterospecific individuals. We used the Beverton-Holt model, which is well-suited as an annual plant model (Levine and HilleRisLambers, 2009; Larios et al., 2017). This model tracks the number of seeds (X) at the end of each year, as the entire population of the annual plant is captured in its seeds just prior to germination cues (Figure 1). The number of seeds in year t of group 1 (i.e. *L. conjugens*) in vernal pool p denoted by $X_{t,k,p}$

150 is:

$$X_{t+1,1,p} = s(1 - g_t)X_{t,1,p} + \frac{\lambda_t}{C_{t,p}}g_tX_{t,1,p} \quad (1)$$

151 where s is the (time- and pool-independent) annual survival probability of each *L. conjugens*
 152 seed, and g_t is its germination rate in year t . The term $s(1 - g_t)X_{t,1,p}$ describes the carryover
 153 of seeds in the seed bank that contribute to future years' *L. conjugens* population size. In
 154 turn, λ_t is the maximum, density independent number of *L. conjugens* seeds produced in
 155 year t by a single plant, and

$$C_{t,p} = 1 + \sum_{k=1}^4 \alpha_{t,k}Y_{t,k,p} \quad (2)$$

156 measures the degree of competition experienced by *L. conjugens* in year t and vernal pool p ,
 157 translating into reductions in the maximum annual fecundity λ_t . Here $\alpha_{t,k}$ is the competition
 158 experienced by *L. conjugens* from individuals of group k in year t , and $Y_{t,k,p}$ is the number
 159 of stems of group k in year t and pool p .

160 **The statistical model:** The statistical model was designed to estimate the parameters
 161 of Eq 1 and Eq 2 to allow us to infer the processes that promote and limit the persistence
 162 of *L. conjugens*. Importantly, model fitting proceeds annually: the data we use to obtain
 163 estimates in year $t + 1$ are only those of year t . This said, while long-term monitoring data is
 164 necessary to explicitly look at long-term trends, such extended time series are not actually
 165 required for parameterizing the demographic model. Unlike experimental tests of MCT that
 166 typically collect more response data and include fewer competitors than restoration efforts
 167 (Ellner et al., 2019), several challenges arose when fitting restoration monitoring data to
 168 these models. Here, we outline the decisions we made to best adapt monitoring data to
 169 model *L. conjugens* using a MCT framework.

170 The seed bank (the first half of the Eq 1) can maintain annual populations during unfa-
 171 vorable years while enabling them to take advantage of favorable environmental conditions

(Faist et al., 2013). It is, however, difficult to measure the seed bank directly, especially when destructive soil disturbance would threaten the success of restoration projects. In such cases, as with our data, only stems ($Y_{t,1,p}$) were measured, and we needed to estimate the total number of seeds ($X_{t,1,p}$). We did this by using the expected number of seeds given the number of stems: $X_{t,1,p} = Y_{t,1,p}/g_t$. Although stem number was our best estimate of population size, there were some pools that recorded zero stems in one year, followed by stems present in the subsequent year. To account for the possibility of observing zero stems when seeds are present but at low abundance, we used a different estimate of population number for the first year in which stems were absent from a pool. Specifically, in the first year with no stems recorded for *L. conjugens* ($Y_{t,1,p} = 0$), we used the population estimate of the prior year and adjusted seed survivability, so that $X_{t+1,1,p} = s^2 X_{t-1,1,p}$.

To account for manual seed addition in the first three years, we modeled stem counts of *L. conjugens* in constructed pools as follows. For the initial year, we drew the individuals from a binomial distribution: $Y_{t=1,1,p} \sim \text{Binomial}(X_{1,1,p}, g_1)$, where $X_{1,1,p}$ is a matrix of seeds added at time $t = 1$ in pool p , and g_1 is the germination rate of *L. conjugens*. For the second and third years, we added the number of seeds manually added via the experimental treatment to our modeled population $X_{t,1,p}$.

The California vernal pool system is species-rich, but most species occur at low abundance. To reduce the dimensionality of this competitive environment and minimize the number of parameter estimates (Eq 2), we selected six species that comprised the majority of the cover (highest sum of cover across 16 years and plots) apart from *L. conjugens*, grouped them in three functional groups based on similar temporal fluctuations (Appendix S1: Figure S1). Specifically, we grouped *B. hordeaceus*, *H. marinum*, and *F. perennis* as an exotic grass group; and *P. stipitatus*, *D. concolor* as a native annual forb group. We kept *E. vaseyi* separate from the native forb group because it is a biennial plant, while other native forbs are annual plants. We labeled these aggregated groups as group 1 (*L. conjugens*),

group 2 (exotic annual grass), group 3 (native annual forb), and group 4 (*E. vaseyi*). Of the four groups, we only created an explicit model for the population dynamics of our focal species *L. conjugens* (group 1).

To include demographic stochasticity, which can increase extinction risk at small population sizes (Lande, 1993; Shoemaker et al., 2020), we drew the number of individuals at a given time and pool from a Poisson distribution with a mean given by the right-hand side of Eq 1.

We fitted our model separately for reference (no seed addition) and constructed pools (with seed addition). We only used pools with consecutive years of data. For reference pools, we used frequency of *L. conjugens*, which we converted to abundance (Appendix S1: Figure S2), and frequency of other species from 7 pools in 2000-2015 and 2 additional pools in 2002-2015. For constructed pools, we used stem counts of *L. conjugens* and frequency of other species from 142 pools in 2000-2015. We omitted data from control plots in the constructed pools because they did not receive any seed addition and the stem counts of *L. conjugens* remained zero over time. We checked for model-fit of these two models (reference and constructed pools) by simulating *L. conjugens* population dynamics, fitting simulated data in each model, and regressing simulated vs. predicted stem counts.

We extracted the Bayesian posterior estimates of the annual seed survival probability s , the fecundity λ_t , and the competition coefficients $\alpha_{t,k}$. We assumed germination rates of *L. conjugens* were lower in years with a thick litter layer (Faist and Beals, 2018). As such, we set g_t to 0.2 when previous year’s total exotic grass cover was 100% or greater. Otherwise, the germination rate was set to 0.7 based on a seed germination trial of a related species, *L. californica* DC. ex Lindley (Gulmon, 1992). All models were fit using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter et al., 2017), using the **rstan** package in R (R Core Team, 2013). We specified that λ_t has a partially informed prior (probability distribution of uncertainty based on a known range), $\lambda_t \sim \text{Normal}(60, 20)$, with a lower bound

of 0 (Faist et al., 2015). Prior distributions on competition coefficients were half-normal distributions centered on 0 with standard deviations of 1. For survival, we used an uninformed Jeffreys prior, $\text{Beta}(0.5, 0.5)$. We generated samples from posterior distributions using the Markov chain Monte Carlo (MCMC) sampling method with 4 chains and 1000 iterations. We checked for convergence using the Gelman-Rubin diagnostic (Rhat), and precision of parameter estimates using the effective sample size. We validated the models using a subsampling approach (i.e., leave-one-out sensitivity analysis); we iteratively excluded one pool from the dataset and fit the model each time (Appendix S1: Figure S3).

Analyses:

Restoration trajectory metrics: We tested whether model-derived mean per capita intrinsic growth rates (λ_t) or low-density growth rates (r_t) of *L. conjugens* in reference and constructed pools were better metrics for assessing restoration success compared to observed abundance, measured as mean density of *L. conjugens*. We directly assessed λ_t at each year between 2000-2015 from our Bayesian model output. The low-density growth rate was measured as *L. conjugens*' growth rate from rarity into the rest of the community at equilibrium (Chesson, 2000). To do so, we first calculated the equilibrium distribution of the exotic annual grass group, native annual forb group, and *E. vaseyi* as average annual frequencies in control plots within constructed pools that did not include *L. conjugens*. We then modeled low-density growth rates of *L. conjugens*, introducing a single individual into the equilibrium resident community for each year (2000-2015), calculating $r_t = \ln(X_{t+1}/X_t)$. The average low-density growth rate across environmental conditions (\bar{r}) predicts whether *L. conjugens* can persist ($\bar{r} > 0$) or goes locally extinct ($\bar{r} < 0$). The average low-density growth rate of the invader is usually compared to the resident species to test for stable coexistence (Chesson, 2000; Barabás et al., 2018); however, we calculated it solely for *L. conjugens*, allowing us to focus on single-species persistence rather than multi-species coexistence.

Partitioning of persistence mechanisms: To understand how environmentally-driven temporal variation in seed production (λ_t) and interannual variation in competition ($\alpha_{t,k}$) are driving restoration trajectories, we decomposed the average low-density growth rates (\bar{r}) of *L. conjugens* into the mechanisms that contribute to its persistence. Following the decomposition framework from Ellner et al. (2019), the average low-density growth rates (\bar{r}) can be decomposed into four mechanisms:

$$\bar{r}_i = \epsilon_i^0 + \epsilon_i^\alpha + \epsilon_i^\lambda + \epsilon_i^{(\alpha\lambda)} \quad (3)$$

Here, the first decomposition term, ϵ_i^0 , is the growth rate under constant, averaged environmental conditions, where we use the weighted mean condition from 2000 to 2015. In other words, we set λ and α_k terms to their average values, rather than letting them vary through time; we calculate the low-density growth rate given these averaged parameter values. The second decomposition term, ϵ_i^α , is the main effect of the environmental variation on competition coefficients, where $\alpha_{t,k}$ varies through time while λ is held at its average value. This is analogous to relative non-linearity in competition, which means the target species experiences different competitive effects from the neighboring species through time. Similarly, the third decomposition term, ϵ_i^λ , is the main effect of the environmental variation on seed production (per capita intrinsic growth rates). This is calculated as the low-density growth rate of *L. conjugens* when λ_t varies through time according to our statistical model output, but α_k are held at their averaged value. This mechanism is analogous to relative non-linearity in seed production, which ecologically equates to favorable years having a strong positive effect size on seed production than the magnitude of the negative effect in unfavorable years. Finally, the last decomposition term, $\epsilon_i^{(\alpha\lambda)}$, is the interaction effect between variability in α and λ and accounts for environmental fluctuations simultaneously affecting competition and fecundity that are not accounted for by each main effect (i.e. $\epsilon_i^{(\alpha\lambda)} = r_i - [\epsilon_i^0 + \epsilon_i^\alpha + \epsilon_i^\lambda]$).

We calculate the above decomposition separately in the reference versus constructed pools to compare how average conditions versus temporally-dependent mechanisms alter the low density growth rate of *L. conjugens* in each pool type.

Simulation of exotic grass removal: To test the effects of exotic grass removal on *L. conjugens*, we simulated an experimental manipulation of the percentage of exotic grass cover on a yearly basis. We simulated the population dynamics of *L. conjugens* with 0, 50, and 75% reduction of exotic grass cover each year from 2001 to 2015, using frequency and abundance data and parameter estimates from above, and estimated the expected abundances of *L. conjugens*. We then calculated the average low density growth rate of *L. conjugens* for each treatment given the simulated management reduction in exotic grasses.

Results

Diagnosing population trajectories with growth rates: We compared the timeseries of observed annual abundance to model-derived mean per capita intrinsic growth rate (λ_t) and low density growth rate (r_t) of *L. conjugens* to assess restoration trajectories. The observed mean abundance in constructed pools increased from 2002 to 2007 (158 (se = 36)/m² to 251 (se = 55)/m²), exceeding that of reference pools (103 (se = 57)/m² to 221 (se = 75)/m²) (Figure 2a). However, as exotic grass cover increased in both reference and constructed pools (Appendix S1: Figure S4a) in 2007 and a multi-year drought hit from 2011 to 2015 (Appendix S1: Figure S4b), *L. conjugens* populations in constructed pools drastically declined from 2007 to 2015, while reference populations remained stable (Figure 2a). The mean per capita intrinsic growth rate in constructed pools was only 2.9% of that in reference pools in 2001, which signaled divergence of population trajectories at the start (Figure 2b). The low-density growth rate in constructed pools was also lower than that in reference pools throughout the timeseries (Figure 2c).

Partitioning of persistence mechanisms: We decomposed the average low density growth rate (\bar{r}) of *L. conjugens* due to environmental variation and its effect on intrinsic growth rates, competition, and their interaction. Overall, the average low-density growth rate showed long-term persistence of *L. conjugens* in reference pools (0.47; 95% CI: 0.32 to 0.62) but eventual competitive exclusion in constructed pools (-0.42; 95% CI: -0.46 to -0.39). This difference was primarily driven by strong destabilizing effects of environmental variation on intrinsic growth rate (ϵ_i^λ) in constructed pools. In reference pools, the positive effects of fluctuation-independent mechanisms (e.g., average fitness differences; ϵ_i^0) and relative non-linearity in competition (ϵ_i^α) were large enough to off-set the negative effects of environmental variation on intrinsic growth rate (ϵ_i^λ) for *L. conjugens*, allowing persistence in the community (Figure 3a). In constructed pools, the positive effects of relative nonlinearity in competition (ϵ_i^α) were less than the negative effects of environmental variation on intrinsic growth rate (ϵ_i^λ), such that *L. conjugens* was excluded from the community in the simulations (Figure 3b). The interactive effect of the environment on competition and intrinsic growth rate ($\epsilon_i^{\alpha\lambda}$), was negligible in both reference and constructed pools. More generally, these results highlight how the response of *L. conjugens* to temporal environmental variation is altered in constructed pools versus their reference counterparts.

Exotic grass removal improves persistence: We simulated the effects of exotic grass removal on target species in constructed pools, and we found that both 50 and 75% exotic grass removal increased mean density of *L. conjugens* (Figure 4a). On average, 50% exotic grass removal increased predicted mean abundance by 2.1 fold compared to no removal, and 75% exotic grass removal increased mean abundance by 4.4 fold. The effect of exotic grass removal was non-linear and diminishing over time; the effect sizes were higher in the first 5 years since the first seeding treatment in 1999 than in later years (after 2004) (Table S1). Across the timeseries, the average low density growth rate of *L. conjugens* increased from -0.42 (95% CI: -0.46 to -0.39) in the 0% exotic grass removal scenario, to 0.01 (95% CI: -0.01

to 0.04) in the 50% removal scenario, and 0.38 (95% CI: 0.35 to 0.41) in the 75% removal scenario (Figure 4b).

Discussion

Here we re-purposed analytical tools from modern coexistence theory (MCT) to diagnose restoration trajectories in a fluctuating and invaded environment. This approach enabled us to not only detect restoration failure quickly, but understand why the target species did not persist and identify interventions that would increase restoration success. Model-derived per capita intrinsic growth rates (i.e. density-independent seed production) and low-density growth rates (i.e. when accounting for interspecific interactions) were more reliable metrics of long-term trends than stem abundance, particularly in the initial years following seed addition. The average low-density growth rates indicated that the restored populations will eventually go extinct, while the reference populations will persist. The difference was explained by a stronger negative effect of environmental variability on per capita intrinsic growth rates than a positive effect of varying competitive environments in restored populations compared to reference populations. Furthermore, our experimental simulations showed that the effect of exotic grass removal is variable over time but can increase the average low-density growth rate of restored populations.

Assessing restoration success is complex when restoration activities like seed addition can overcome dispersal limitation and artificially increase the abundance of target species. In our study, we used the reference populations of *L. conjugens* to set expectations for restored populations. At a glance, restoration looked successful because the mean abundance in constructed pools was higher than that in reference pools in the first eight years since the seed addition in 1999 (Figure 2a). However, by using annual per capita intrinsic growth rates and annual low density growth rates as indicators we found that restored populations lagged behind reference populations from the start. In particular, the annual per capita intrinsic

growth rates in constructed pools diverged from those of reference pools as early as the first year (2000; Figure 2b). In other words, the initial surge in mean abundance in constructed pools was a temporary seed addition effect. As such, incorporating demographic growth rates as additional metrics of restoration success may aid in detecting problems much earlier than relying on abundances.

MCT has highlighted the importance of environmental variability to niche partitioning, which promotes species coexistence (Bimler et al., 2018; Matías et al., 2018). In California annual grassland systems, temporal rainfall variability is particularly important to maintain forb species (Hallett et al., 2019). In our study, we expected *L. conjugens* to intrinsically favor environmental variability because it has adapted to fluctuating water levels of vernal pools already. However, by partitioning the contribution of environmental variability to average low density growth rates, we found that environmental variation had a negative effect on per capita intrinsic growth rate of *L. conjugens*. In other words, the bad years were worse than the good years were good for *L. conjugens*, and the abiotic environment of constructed pools was not as suitable as the reference pools (Faist and Beals, 2018). This highlights the need to consider redesigning the constructed pools for future vernal pool restoration projects.

Variable competition with neighboring individuals may also maintain species coexistence (Chesson, 2000). We found that relative non-linearity in competition was the dominant stabilizing mechanism, and it was stronger in constructed pools than in reference pools (Figure 3). This result parallels empirical evidence that *L. conjugens* can maintain an immature state in inundated pools, while exotic grasses cannot, thus resulting in a competitive release from the exotic grasses in years with high early-season rainfall (Javornik and Collinge, 2016). Since the biological reason for *L. conjugens* persistence is a competitive release under some environmental conditions as opposed to intrinsically favoring those conditions, reducing the competitive effect from competitors should promote persistence of *L. conjugens*. In practice, we may not be able to change the pools once they are constructed, but we can manipulate

the vegetation. Our results underscore the importance of partitioning multiple mechanisms of persistence to identify key targets for management interventions.

In adaptive management of restoration sites, one of the challenges is knowing how much and when active management is needed given limited time and resources (Williams, 2011). Our experimental simulation results showed a non-linear effect of exotic grass removal. Specifically, exotic grass removal was more effective when *L. conjugens* populations were increasing in early years than later years (Figure 4a). This suggests that management action should be taken proactively in the target species' favorable years to further reduce the competition they experience, which is contrary to the common practice of managing in reaction to declining restored populations (Williams, 2011). More importantly, positive average low density growth rates with exotic grasses removal indicated that the long-term persistence of restored populations is possible (Figure 4b). From a restoration perspective, these data-driven simulations can be helpful to inform adaptive management and set expectations for how active management will alter restoration outcomes.

Our study is the first to integrate methods from MCT and long-term monitoring data from a restoration project to assess restoration success. By leveraging the long-term data set, we were able to determine whether the focal species can persist over time and why. While long-term data is beneficial for assessing long-term persistence, it is not critical for discerning initial trajectories. The parameterization of the demographic model can proceed one time step at a time (in our case, the model was fit each year); this does not require a long-term data set. Even with few years of monitoring data, it is possible to fit the demographic model and assess initial restoration trajectories using annual low density growth rates. Moreover, lessons learned from this approach can be applied to other restoration goals across ecosystems. For instance, we focus here on conservation of a single species, but some restoration efforts may focus on removing a key invasive species or restoring a diverse community with multiple focal species (Perring et al., 2015). Although data collection requirements may increase

and the demographic models may get more complicated in more specious communities, this should become more feasible as new methods for analyzing multi-species coexistence emerge (Saavedra et al., 2017; Stump, 2017).

Restoration in a time of rapid global change faces challenges where the baseline environmental conditions shift and invasive species can drastically disrupt the community’s stability (Hobbs and Cramer, 2008). Using the framework of MCT in diagnosing restoration trajectories is particularly helpful when restoring species in a variable and competitive environment because we can understand what mechanisms are driving species persistence, which can point us to what we can do to change the restoration trajectories. Broader application of MCT in ecological restoration has the potential to inform and update theoretical predictions, explain empirical dynamics, and identify management actions for desirable restoration outcomes.

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Figure 1: Visual representation of the Beverton-Holt equation used to model the life-cycle of the focal species, *Lasthenia conjugens*. The population prior to winter rainfall (X_t) is captured in the number of seeds in a pool. Following sufficient rain, a fraction of the seeds germinate (g) while the remainder do not ($1-g$). Those seeds that germinate grow to produce new seeds that depend on the maximum fecundity in the environmental conditions encountered that year (λ), which is reduced competition (denominator of the equation at top right, with the sum over all species in the community). The population at the outset of the next year (X_{t+1}) is the sum of the new seeds produced ($X_t g \lambda / (1 + \sum(\alpha_j X_j))$) plus the ungerminated seeds that survive ($X_t s(1 - g)$). Although the total population at time t is given by the total number of seeds prior to germination, population size is estimated from the aboveground community (germinated plants). When germination rates are known, the ungerminated number of seeds is calculated as: $(1-g)\text{plants}/g$, where plants is the observed number of stems in a vernal pool. This calculation follows from our estimate of the population size (plants/g), and is necessary because ungerminated seeds cannot be sampled directly without disturbing the vernal pools.

Figure 2: Restoration trajectories of *Lasthenia conjugens* are dynamic over time. Restoration success can be assessed by three metrics: (a) *Lasthenia conjugens* density (stems/m²; note logarithmic y-axis), (b) posterior estimates of per capita intrinsic growth rate (λ_t , average number of seeds produced in the absence of competition) and (c) low-density growth rate ($r_t = \ln(N_{t+1}/N_t)$) in constructed (black) and reference (grey) pools. The error bars represent 95% credible intervals. A positive low-density growth rate predicts persistence, while a negative one indicates eventual competitive exclusion, and thus loss from the pools, even though λ_t may be positive. For all three panels, we used data from 142 constructed pools from 2000-2015, 7 reference pools from 2000-2015, and 2 additional reference pools from 2002-2015 to maximize the use of data.

575 **Figure 3:** *Lasthenia conjugens* is predicted to persist in reference pools (a), but not in con-
576 structed pools (b), due to the effect of variation in λ_t . Partitioning of average low density
577 growth rate (\bar{r} ; dark grey) into contributions from different aspects of the species' environ-
578 ment on competition (ϵ_i^α), seed production (ϵ_i^λ), and their combined interactive effect ($\epsilon_i^{\alpha\lambda}$)
579 shown in light grey. The error bars represent standard errors from means. The interaction
580 effects are present but too small to be visible.

581 **Figure 4:** Manual reductions in exotic grass cover are predicted to allow *Lasthenia conju-*
582 *gens* to persist in constructed pools. Simulated effects of exotic grass reduction treatments
583 on (a) mean density (stems/ m^2) through time and (b) its consequent impact on the low den-
584 sity growth rate of *L. conjugens*. Treatments include 0% (solid line), 50% (two-dashed line),
585 and 75% grass reduction (dotted line) each year from 2000 to 2015. Error bars represent
586 standard error. A positive low-density growth rate predicts long-term persistence.

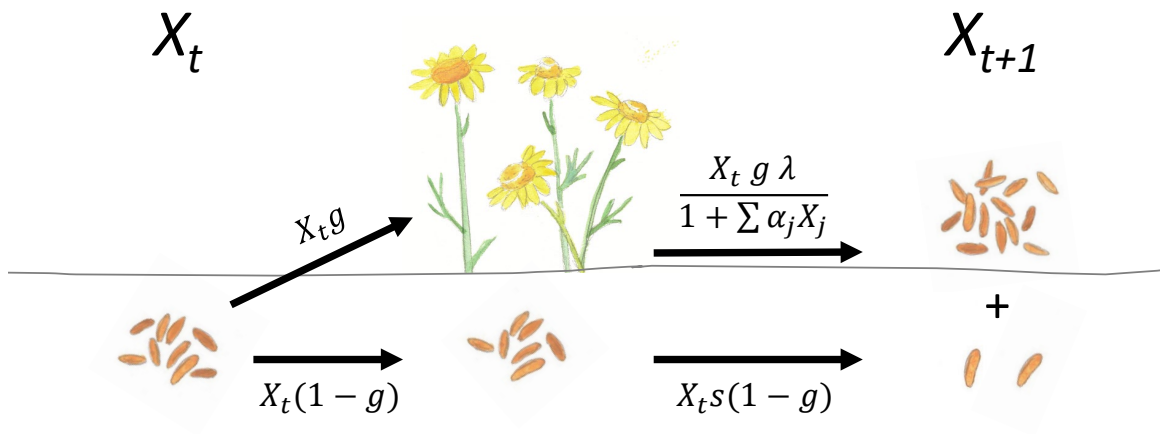


Figure 1:

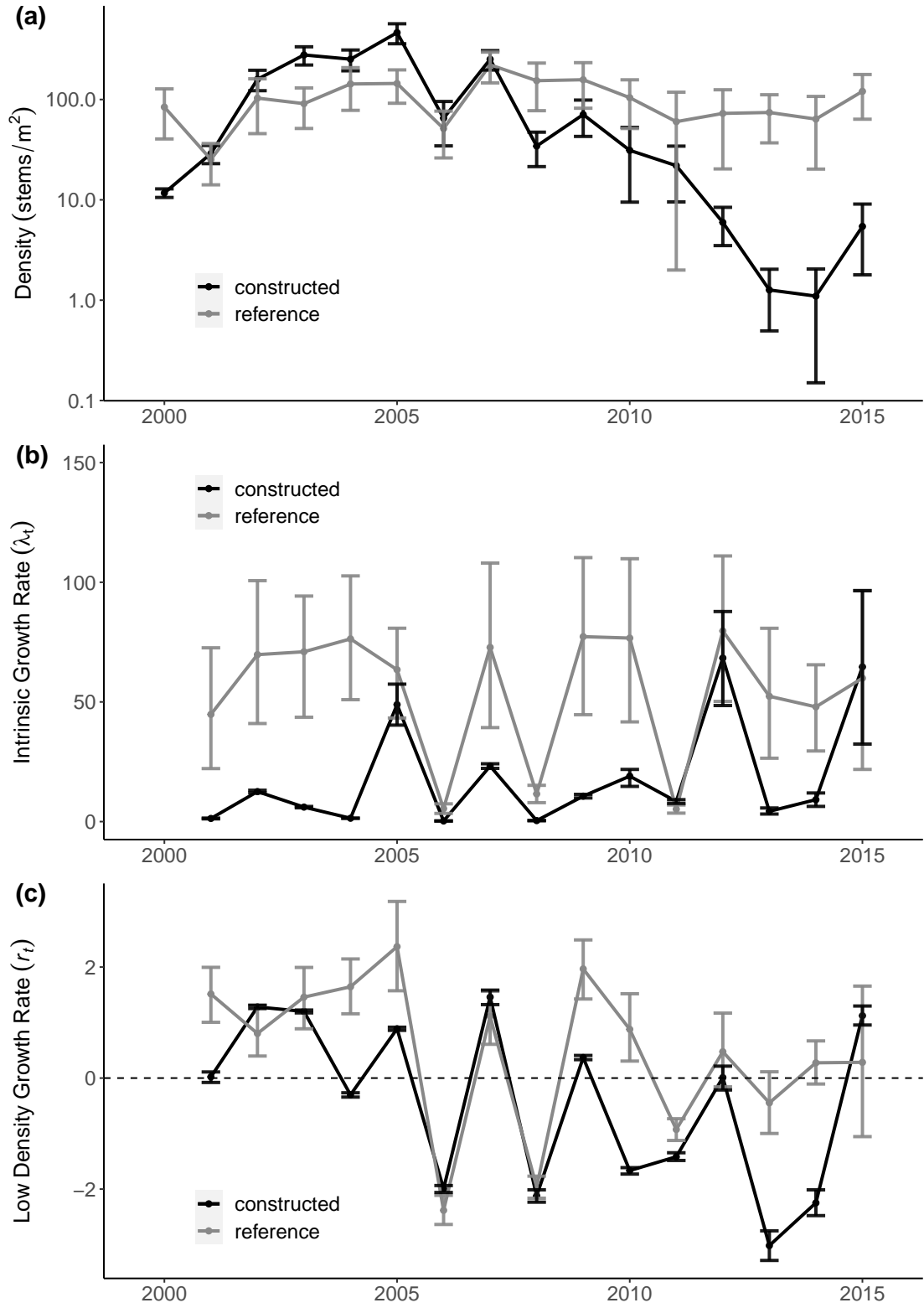
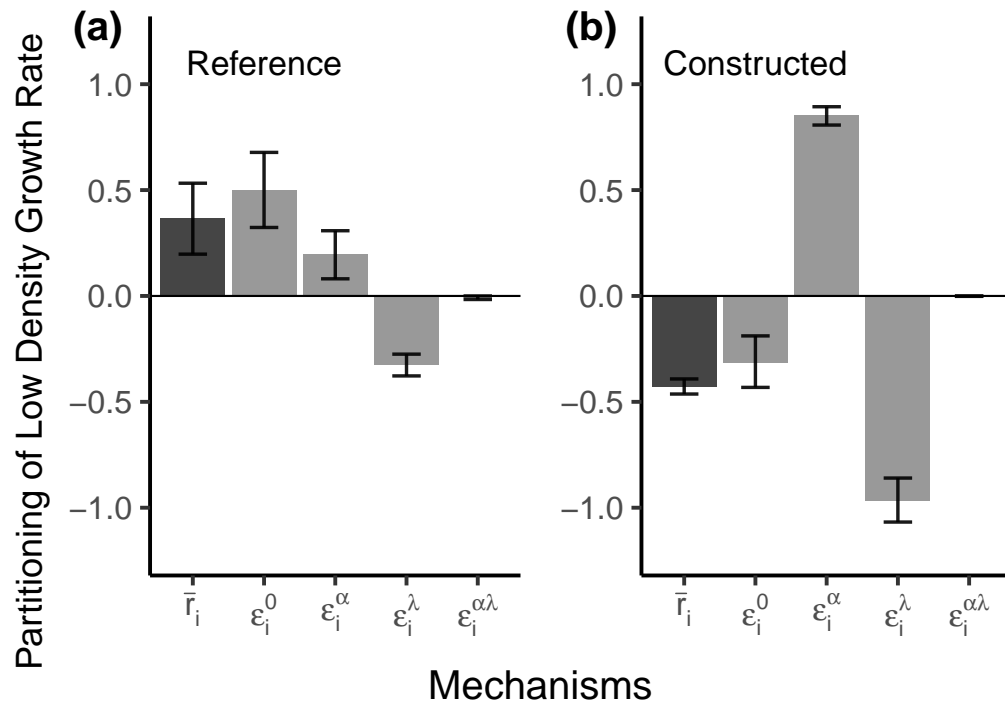


Figure 2:



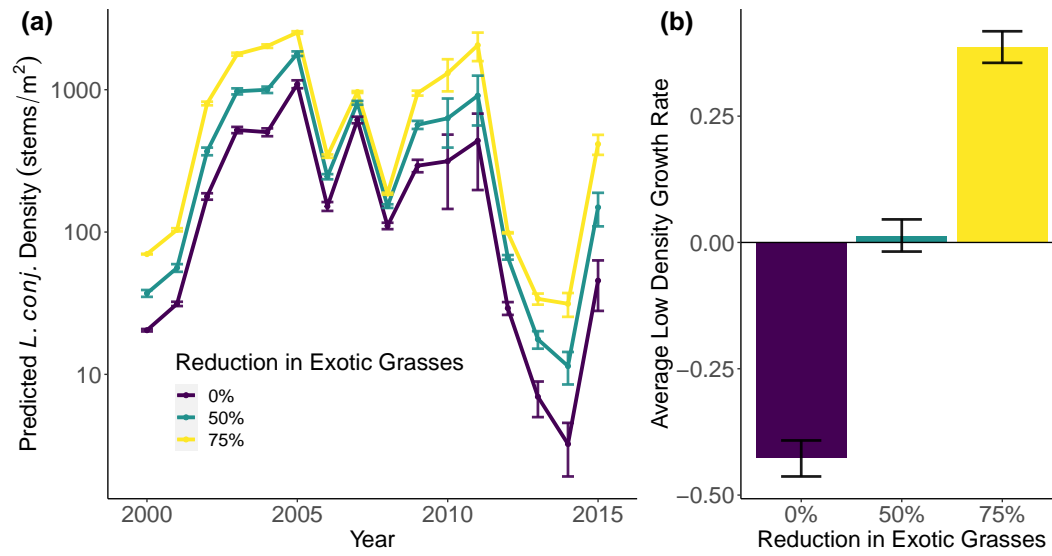
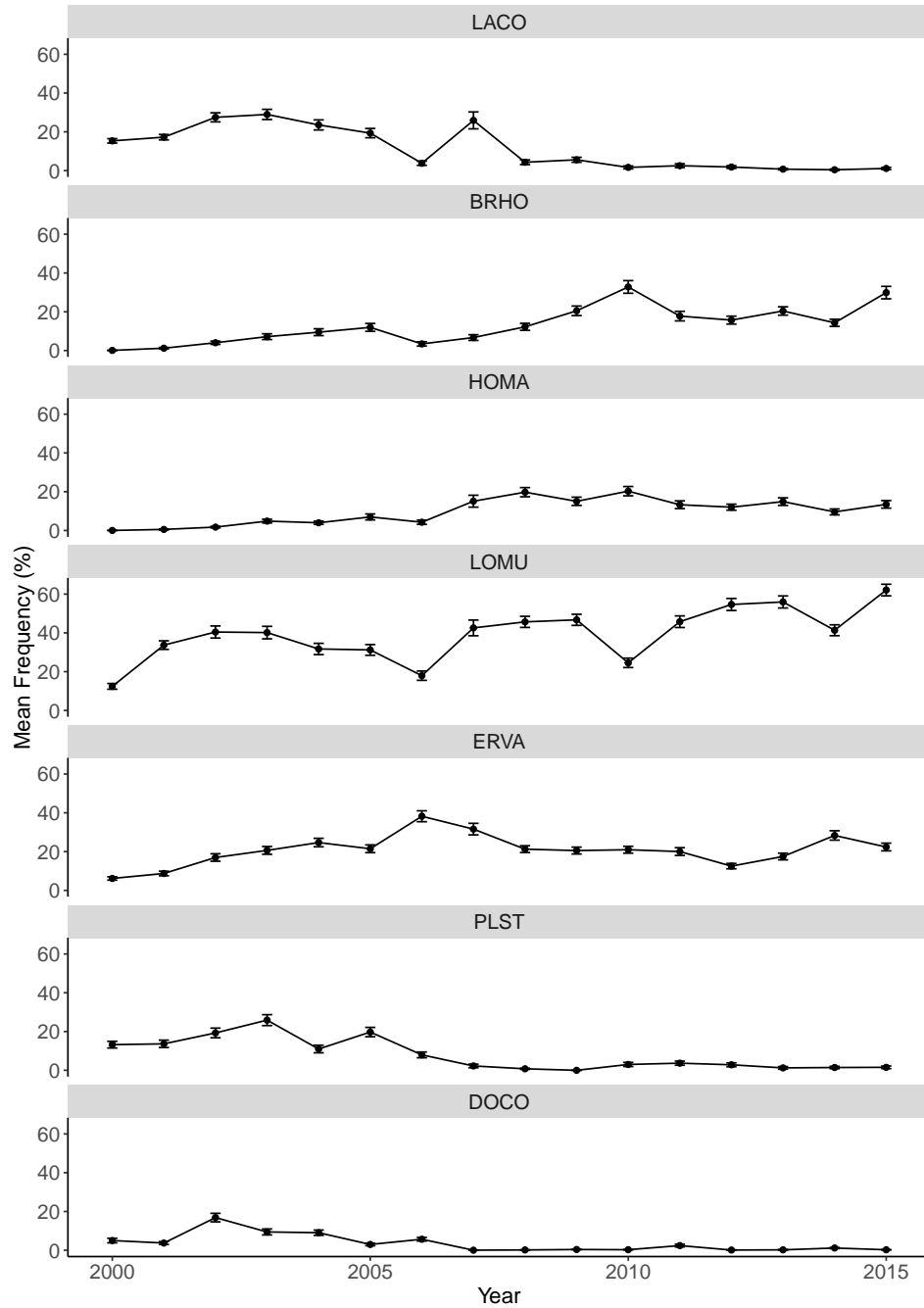
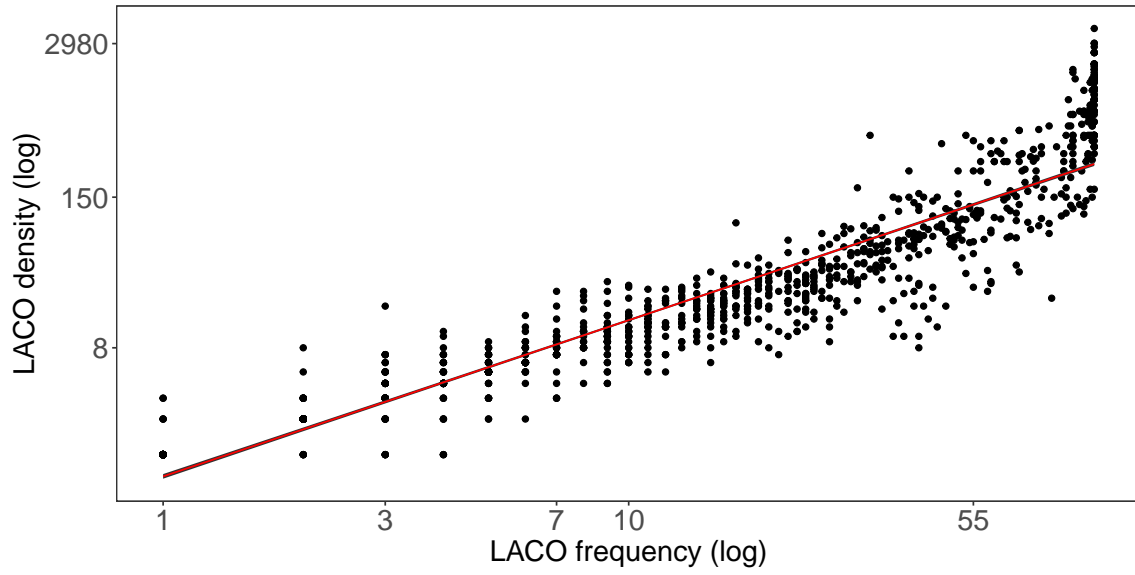


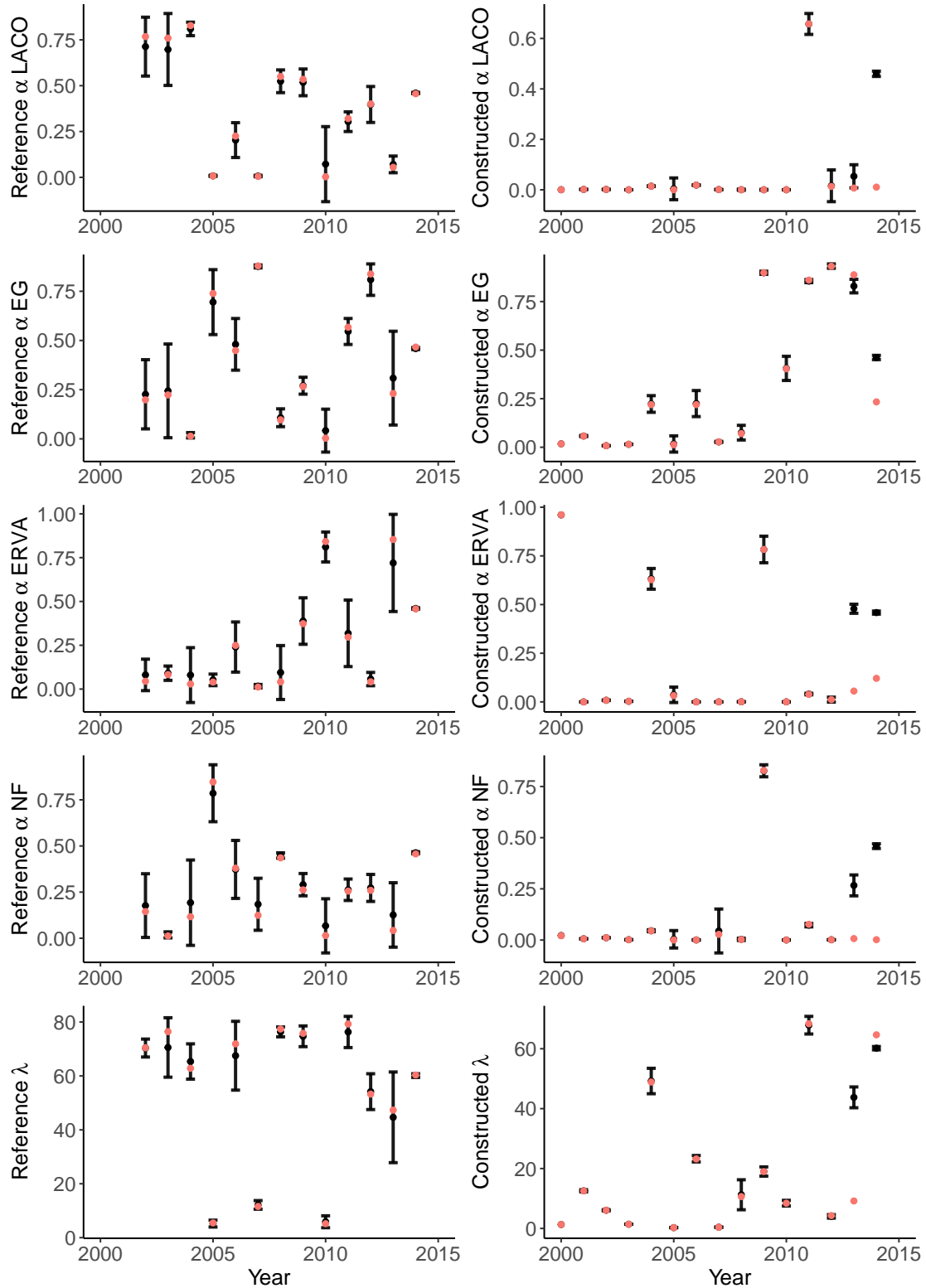
Figure 4:



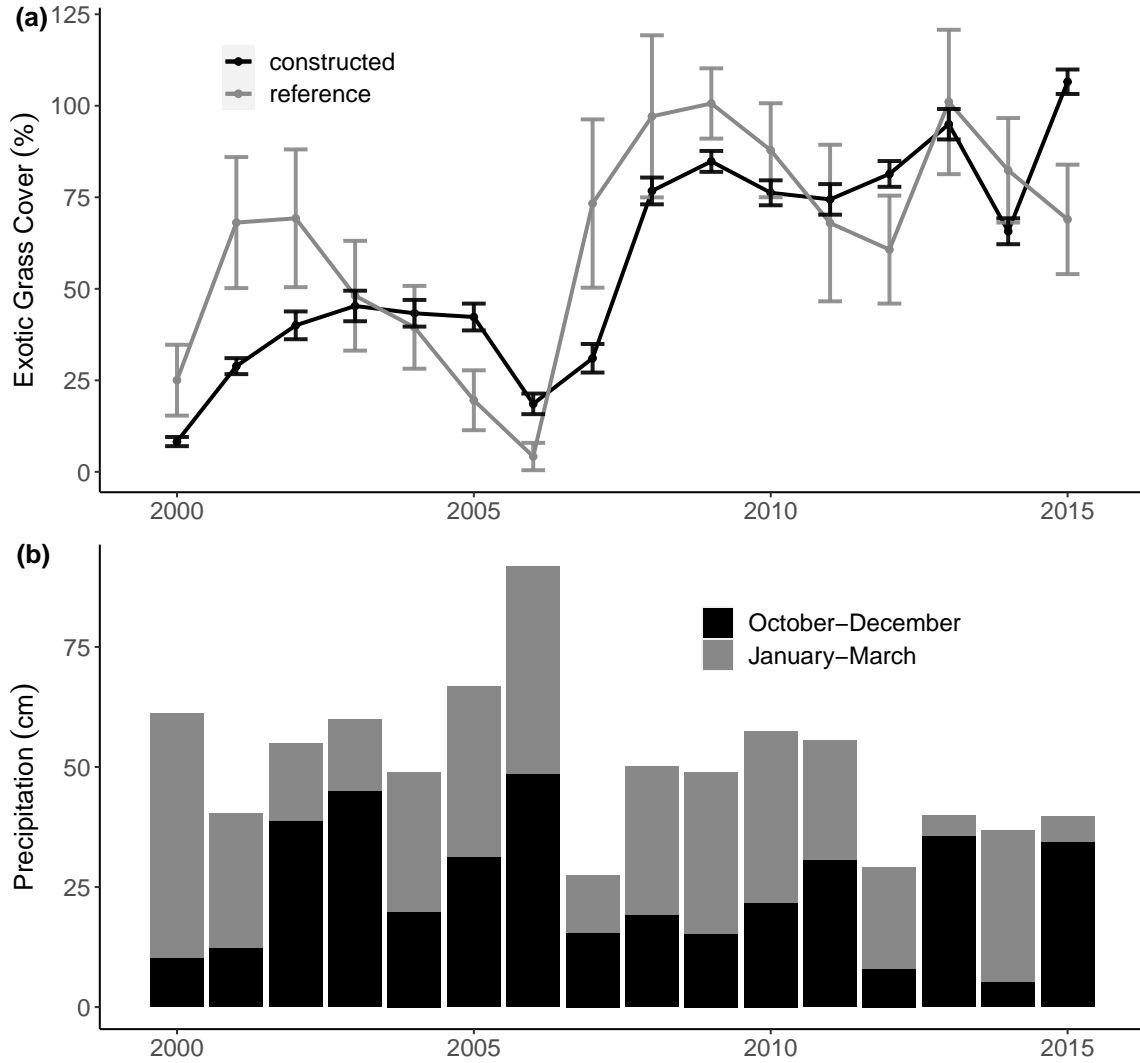
Supplementary Figure 1: Trajectories of species in the constructed pools. Species included in the population models: *Lasthenia conjugens* (LACO; focal species); *Bromus hordeaceus* (BRHO), *Hordeum marinum* (HOMA), and *Festuca perennis* (previously called *Lolium multiflorum* (LOMU), exotic annual grasses); *Eryngium vaseyi* (ERVA; native biannual forb); *Plagiobothrys stipitatus* var. *micranthus* (PLST) and *Downingia concolor* (DOCO; native annual forb). Points and error bars represent mean and standard error of frequency (%).



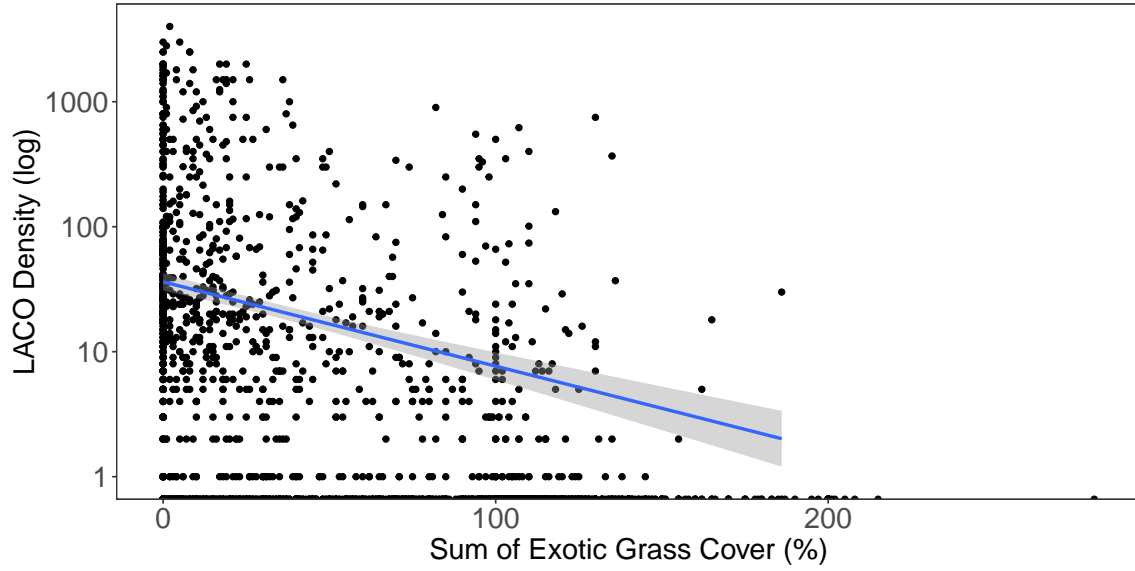
Supplementary Figure 2: *Lasthenia conjugens*'s (LACO) density (natural log) and frequency (natural log) are correlated linearly. The points represent a pool in a given year where both density and frequency were measured.



Supplementary Figure 3: Timeseries of parameter estimates from the leave-one-out sensitivity analysis of constructed and reference pool models. Parameters estimated were the following: alpha of *Lasthenia conjugens*, alpha of exotic annual grasses, alpha of *Eryngium vaseyi*, alpha of native forbs, and lambda of *L. conjugens*. Red points represent the mean posterior estimates from the full dataset (141 pools in the constructed pool model and 9 pools in the reference pool model). Black points and error bars represent the mean and standard deviation of mean posterior estimates from models run on subset of the dataset by leaving out one pool each analysis.



Supplementary Figure 4: Timeseries of observed exotic grass frequency and precipitation. (a) Mean exotic grass frequency (%) increased over time in both reference (grey lines) and constructed pools (black lines). Mean exotic frequency was calculated by summing the frequency of three exotic grass species, *Bromus hordeaceus*, *Hordeum marinum*, and *Festuca perennis*, and averaging across pools each year. Points and error bars represent annual means and standard errors from means, respectively. (b) Growing season precipitation (cm) in Fairfield, CA varied across years. Black bars represent total rainfall in October to December of the previous year, and grey bars represent total rainfall in January to March of that year.



Supplementary Figure 5: Abundance of *Lasthenia conjugens* (LACO; natural log) declined with increase in exotic grass cover (%) in constructed pools from 2000 to 2015. The points represent a pool in a given year and all years are represented. Exotic grass cover is the sum of annual percent cover for *Bromus hordeaceus*, *Hordeum marinum*, and *Festuca perennis* in each pool.

Table S1: Effect sizes of simulated exotic grass removal on *Lasthenia conjugens* abundance by year. Two treatments include 50% grass removal and 75% grass removal. The effect sizes are calculated as the difference between mean *L. conjugens* abundance with and without treatment divided by the standard error of mean *L. conjugens* abundance without treatment.

Year	50% removal	75% removal
2000	2.970	8.469
2001	1.970	5.539
2002	1.925	6.016
2003	1.483	4.399
2004	1.194	3.985
2005	0.700	1.909
2006	0.665	1.761
2007	0.558	1.261
2008	0.797	1.633
2009	0.939	2.535
2010	0.392	1.222
2011	0.395	1.191
2012	0.686	2.185
2013	0.309	1.296
2014	0.574	2.785
2015	0.390	1.797