

Diagnosing restoration trajectories using demographic modeling and modern coexistence theory

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1 Abstract

Restoration success is often measured by comparing target species abundance between re-
stored and reference populations. Abundance may poorly predict long-term success, however,
because seed addition may initially inflate restored population abundances, and reference
population abundances may fluctuate with environmental variation. A demographic ap-
proach, informed by modern coexistence theory, may allow for more accurate diagnosis of
restoration trajectories. We modeled population dynamics of an endangered plant (*Lasthe-*
nia conjugens) in restored vernal pools and compared them to reference populations over 18
years (2000-2017). Model estimates of *L. conjugens* growth rates were better predictors of
long-term trends than observed abundances. Although populations fluctuated in reference
pools, annual rainfall variability acted as a stabilizing factor for *L. conjugens*. In restored
pools however, invasive grasses and associated litter accumulation overrode the benefits of
environmental variability. Our approach improves assessment of restoration outcomes and
indicates when management actions, such as grass removal, will improve future trajectories.

2 Introduction

Understanding what modulates population dynamics after ecological restoration is fundamental for assessing restoration success (Suding, 2011). The goal of many restoration efforts is to achieve long-term persistence of species of conservation concern (Suding, 2011; Schlatter *et al.*, 2016). The population abundances of target species in naturally occurring “reference” communities often serve as a benchmark for restoration success (Ruiz-Jaen & Aide, 2005; Society of Ecological Restoration, 2004). However, comparable abundances between reference and restored populations may not be indicative of ultimate restoration success, because restoration activities (e.g., seed addition, invasive grass removal) can artificially increase the abundance of target species in the first few years (Collinge & Ray, 2009; Collinge *et al.*, 2013). Evaluation is further complicated when environmental conditions and competition among species change over time, making it difficult to discern if differences in abundance between reference and restored populations are transitory or indicative of different long-term trajectories (Perring *et al.*, 2015). An analytical approach that takes environmental variation into account may provide a clearer picture of restoration trajectories and illuminate pathways to improve restoration outcomes.

We propose applying a demographic modeling approach coupled with modern coexistence theory (MCT; Chesson 2000; Ellner *et al.* 2019) to mechanistically understand how desired ecological restoration goals can be achieved in a predictable way. Demographic models have gained traction as a means to forecast population trajectories over time or across environmental gradients (Bischoff *et al.*, 2010; Larios *et al.*, 2017; Mordecai *et al.*, 2015; Thomson, 2005; Thomson *et al.*, 2017; Wainwright *et al.*, 2019). A population’s realized growth rates indicate its ability to increase in an environment (Larios *et al.*, 2017), and can function as early sign-posts for restoration practitioners. For example, equal abundances in restored and reference populations may look promising, but different realized growth

40 rates would signal that these populations will diverge in the future (Shriver *et al.*, 2019).
41 Furthermore, a positive long-term average growth rate when the species is at low densities
42 would suggest that a population is buffered from local extinctions (Chesson, 2000; Barabás
43 *et al.*, 2018) and that restoration of the species was successful.

44 Variable environments pose a particular challenge for assessing restoration efforts, as
45 realized growth rates in a given year may not reflect long-term persistence (Hallett *et al.*,
46 2018; Vaughn & Young, 2010), but this variability may also be key to maintaining coexistence
47 (Chesson, 2000). For example, the storage effect — in which species capitalize on good years
48 while “storing” through bad years, such as in the seed bank — has emerged from MCT as
49 a mechanism of coexistence that is dependent on environmental variability (Chesson, 2018).
50 Comparing reference and restored abundances may be a particularly unreliable indicator of
51 success for species maintained by fluctuation-dependent coexistence, as reference abundances
52 may vary widely even if populations are viable long-term. Quantifying the coexistence
53 mechanisms that shape a target species’ population dynamics, in contrast, may both inform
54 restoration assessment and also indicate when management actions are likely to improve
55 restoration success. While developments in MCT have to date been largely theoretical rather
56 than applied, new quantitative methods can infer coexistence mechanisms from observation
57 data such as restoration monitoring records (Ellner *et al.*, 2019), providing an opportunity
58 to unite MCT with restoration ecology.

59 Management efforts to increase restoration success are regularly tailored to alter com-
60 petitive interactions, in particular between co-occurring exotic and native species (Porensky
61 *et al.*, 2018). For example, mowing or grazing to reduce exotic grasses are common tools
62 to promote native forbs in annual grasslands (Weiss, 1999; Hernandez *et al.*, 2021) and
63 vernal pools (shallow, ephemeral wetlands in the Mediterranean climates) (Marty, 2015).
64 The effectiveness of this practice can be equivocal, sometimes benefiting other exotic species
65 or negatively impacting native species (Stahlheber & D’Antonio, 2013). These variable out-

comes may depend on the target species' intrinsically favorable conditions or the competitive release from the dominant plant species. Modeling the influence of neighboring competitors on target species' population dynamics can improve the outcomes of invasive species management by identifying which invaders to reduce (Wainwright *et al.*, 2019), and which life stages to focus on (Schutzenhofer & Knight, 2007). A strength of MCT is that it decomposes the effects of environments, competitive interactions, and their responses to varying environments (Barabás *et al.*, 2018). Consequently, MCT can indicate periods in which competitor removal is most likely to benefit a target species (Godoy & Levine, 2014), even when these dynamics would be hard to discern from abundance patterns due to competition-environment covariance.

Here, we demonstrate how a demographic modeling approach coupled with MCT can 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 forbs of vernal pool are better adapted to the highly variable ephemeral ponding (Emery *et al.*, 2009; Faist & Collinge, 2015; Tittes *et al.*, 2019), exotic grasses historically are not (Gerhardt & Collinge, 2007). In particular, *L. conjugens* thrives in wet early-season rain years (Gerhardt & Collinge, 2007), while exotic grasses favor wet late-season rain years (Javornik & 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*) the model derived growth rates are more reliable metrics to assess long-term trends than observed abundance in early years; *ii*) *L. conjugens* is buffered from local extinction by environmental variability through time; and *iii*) the persistence of restored populations increases with greater amount of exotic grass removal. To test these hypotheses, we parameterized stochastic population models with monitoring data, analyzed growth rates

and the mechanisms of coexistence with the MCT framework (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.

3 Methods

3.1 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 & 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 & Collinge, 2016). Additional focal species native to vernal pools at this site include *Eryngium vaseyi* (button celery), *Deschampsia danthonioides* (annual hairgrass), *Layia chrysanthemoides* (tidy tips), 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*).

3.2 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 2017, 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.

3.3 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 & 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. The number of seeds in year t of group 1 (i.e. *L. conjugens*) in vernal pool p denoted by $X_{t,k,p}$ is:

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

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

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

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

3.4 The statistical model

The statistical model was designed to estimate the parameters of Eq 1 and Eq 2 to allow us to infer the processes that promote and limit the persistence of *L. conjugens*. Several challenges arose when fitting restoration monitoring data to these models, as experimental tests of MCT typically collect more response data and include fewer competitors than restoration efforts (Ellner *et al.*, 2019). Here, we outline the decisions we made to best adapt monitoring data to model *L. conjugens* using an MCT framework.

The seed bank (the first half of the Eq 1) can maintain annual populations during unfavorable years while enabling them to take advantage of favorable environmental conditions (Faist *et al.*, 2013). It is, however, difficult to measure the seedbank directly, especially when 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 18 years) apart from *L. conjugens*, grouped them in three functional groups, and evaluated whether each species within a functional group followed the same abundance patterns over time. 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.

The data used to parameterize our population model were pools with consecutive years of data during the timeseries. We fitted our model separately for reference (no seed addition) and constructed pools (with seed addition). For reference pools, we used frequency of *L. conjugens*, which we converted to abundance (Figure 1), and frequency of other species from 9 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 & 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.

3.5 Analyses

Restoration trajectory metrics

To test whether growth rates are better metrics for assessing restoration success than abundance, we compared the model-derived mean per capita intrinsic growth rates (λ_t) and low density growth rates (r_t) of *L. conjugens* to observed mean density of *L. conjugens* in reference and constructed pools over time. The low density growth rate at a given time t is defined as $r_t = \ln \frac{X_{t+1}}{X_t}$. We calculated the equilibrium distribution of exotic annual grass group, native annual forb group, and *E. vaseyi* as annual average frequencies in control plots within constructed pools that did not include *L. conjugens*. We then modeled low density growth rates of *L. conjugens* across the entire time series (2000-2017) when a single individual is introduced in the resident community at its steady state each year. We incorporated environmental effects on λ_t and $\alpha_{t,k}$ in reference and constructed pools in these simulations. The average low density growth rate across environmental conditions (\bar{r}) predicts whether *L. conjugens* can persist (\bar{r} is positive) or goes extinct (\bar{r} is negative). 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* without including an invader-resident comparison, allowing us to focus on

single-species persistence rather multi-species coexistence.

Partitioning of persistence mechanisms

To understand what processes 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 in the community in reference and restored pools. Following the decomposition framework from Ellner et al. (2019), we examined the effect of fluctuations in competitive interactions ($\alpha_{t,k}$) and in fecundity (λ_t):

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

Here, the first decomposition term, ϵ_i^0 , is the average growth rate under constant environmental conditions. We set the constant environmental condition to be the weighted mean condition from 2000 to 2017. The second decomposition term, ϵ_i^α , is the main effect of the environmental variation on competition coefficients. This is analogous to relative non-linearity in competition, which means the target species experiences different competitive effects from the neighboring species depending on the year. Similarly, the third decomposition term, ϵ_i^λ , is the main effect of the environmental variation on per capita intrinsic growth rates. This is analogous to relative non-linearity in seed production, which means the target species produces more seeds in favorable years than 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, including the storage effect.

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 2017, 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.

4 Results

4.1 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) and exceeded that of reference pools (103 (se = 57)/m² to 221 (se = 75)/m²) (Figure 1a). However, the mean abundance in both constructed and reference pools started to decline in 2008 (Figure 1a) with an increase in exotic grass cover (Figure 1b). A multi-year drought from 2011 to 2015 (Figure 1c) further reduced the mean abundance, ultimately resulting in a 99.3% decline from 2002 to 2015 in constructed pools; while the reference populations declined by 41.8% during those years. In contrast, the mean per capita intrinsic growth rates in constructed pools was only 2.9% of that in reference pools in 2000, signaling divergence of population trajectories at the start (Figure 2a). The low density growth rate in constructed pools was also lower than that in reference pools for the first five years (Figure 2b). The low density growth rate in constructed and reference pools briefly synchronized between 2005 and 2007 but low density growth rate in constructed pools fell behind reference pools again from 2008 to 2014 (Figure 2b).

4.2 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 (0.278; 95%CI:-2.70 to 2.28) but eventual competitive exclusion in constructed pools (-0.222; 95%CI:-2.89 to 2.63). This difference was primarily driven by strong destabilizing effects of environmental variation on seed production (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 great enough to off-set the negative effects of environmental variation on fecundity (ϵ_i^λ) for *L. conjugens*, allowing persistence in the community (Figure 3a). In constructed pools, the positive effects of relative non-linearity in competition (ϵ_i^α) were less than the negative effects of environmental variation on fecundity (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 fecundity ($\epsilon_i^{\alpha\lambda}$), 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.

4.3 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 -0.220 (95%CI: -2.89 to 2.63) in 0% exotic grass removal scenario, to 0.230 (95%CI: -2.23 to 3.22) in 50% removal scenario, and 0.612 (95%CI: -1.72 to 3.68) in 75% removal scenario (Figure 4b).

5 Discussion

Employing a demographic modeling approach coupled with modern coexistence theory (MCT) provided insight into the population dynamics of target species *L. conjugens* in a fluctuating and invaded environment (Chesson, 2000), enabling us to both quickly diagnose restoration trajectories and identify leverage points that would increase restoration success (Valladares *et al.*, 2015). Model-derived per capita intrinsic growth rates (i.e. density-independent seed production) and low density growth rate (i.e. when accounting for interspecific interactions) were more reliable metrics of long-term trends than stem abundance, particularly in the initial years following restoration. The average low-density growth rate indicated that the restored populations will eventually be competitively excluded, while the reference populations are buffered from local extinction. This difference was explained by the larger negative effect of environmental variability on seed production than the positive effect of varying competitive environments in restored populations compared to reference populations. Furthermore, our experimental simulations predicted that we can leverage the target species' year-to-year response to the competitive release via timing management actions and removal of exotic grass.

Evaluation of 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 seeding treatment in 1999 (Figure 1a). By comparing the per capita intrinsic growth rates over time, however, we found that the restored populations lagged behind the reference populations from the start. In particular, the per capita intrinsic growth rates in constructed pools diverged from those of reference pools as early as the first year (2000; Figure 2a). 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 simply comparing abundances.

The goals of ecological restoration can vary, with some aiming to restore a whole suite of plant species, while others aiming to ensure the persistence of an endangered rare species. For the latter, like in our study, environmental stressors such as drought could make it difficult to evaluate restoration success (Sheley & James, 2014). Accordingly, low density growth rate is a particularly relevant indicator of persistence in fluctuating environments like vernal pools (Ellner *et al.*, 2020; Pande *et al.*, 2020). In practice, comparing the target species' low density growth rates provides more information about the long-term trajectory of populations than abundances. The single-species approach (Shea & Chesson, 2002; Grainger *et al.*, 2019) of examining low density growth rates across environmental conditions lends itself well to restoration of rare species because the focus is on the persistence of target species.

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 favor early-season rains because it can maintain an immature state in inundated pools, giving it a competitive advantage over exotic grasses (Javornik & Collinge, 2016). We observed this stabilizing mechanism in our reference pools: *L. conjugens*'s fecundity was low when exotic

grasses' competitive effect was high in some years (2006, 2008), and *L. conjugens*'s fecundity was high when exotic grasses' competitive effect was low in other years (2005, 2007) (Figure 2a). However, this relationship did not hold when exotic grasses dominated and persisted from 2008 onward (Figure 1b). In fact, the observed abundance of *L. conjugens* declined with increasing exotic grass cover (Supplemental Figure 2). We suspect this is because exotic grasses accumulate a thick layer of litter that inhibits native forb recruitment (Faist & Beals, 2018), but encourages exotic grass recruitment, creating a positive feedback loop in following years. In effect, litter accumulation was a destabilizing mechanism that overrode the existing stabilizing mechanism in this system.

Variable competition with neighboring individuals may also maintain species coexistence. MCT enables us to better understand the mechanisms behind species persistence by mathematically decomposing the low density growth rate of target species (Barabás *et al.*, 2018). We found that the relative non-linearity in competition was the dominate stabilizing mechanism, and stronger in restored populations than in reference populations (Figure 3). This result parallels empirical evidence that relative non-linearity maintains forb species in competition with grass (Hallett *et al.*, 2019). As such, 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 exotic grasses should promote persistence of *L. conjugens*. Our results underscore the importance of partitioning multiple mechanisms of persistence to identify key targets for management interventions.

Restored populations are commonly monitored as part of the adaptive management strategy (Williams, 2011), but a key challenge is knowing how much and when active management is needed given limited time and resources. Calculating the average low density growth rates by treatment is helpful in predicting when management options will likely yield a more desirable restoration outcome. Our results indicated a non-linear effect of exotic grass removal. Specifically, exotic grass removal was more effective when *L. conjugens* populations were

increasing in early years (Figure 4a). This suggests that management action should be taken proactively in target species' favorable years, which is contrary to the common practice of managing in reaction to declining restored populations (Williams, 2011). From a restoration perspective, these data-driven simulations can be helpful to inform adaptive management, and to set expectations for how active management will alter restoration outcomes.

The primary limitation of our approach is the availability of long-term monitoring data of target species, let alone multiple species (Perring *et al.*, 2015). While long-term data is beneficial for assessing fluctuation-dependent persistence, we were able to diagnose divergent trajectories between restored and reference pools using just the first few years of data. This approach works well in cases such as ours, where the focus of restoration is on a single species. The same principles could be applied to other restoration goals, such as removing a key invasive species or restoring a diverse community, although data collection requirements may increase in more specious communities (Saavedra *et al.*, 2017). Furthermore, the starting conditions can presumably determine the fate of restored populations (Weidlich *et al.*, 2020). Future research could use our approach to explore any priority effects possibly caused by seeding mixes on restoration trajectories. We also acknowledge that restoration practitioners may not find the technicalities of MCT to be accessible. Development of accessible and user-friendly web tools (Garcia-Callejas *et al.*, 2020), in which restoration practitioners can input their own data to assess the persistence of target species in restored sites, may overcome this barrier.

The UN Decade on Ecological Restoration - a rallying call from 2021 to 2030 - brings restoration to the forefront of actions needed to protect and revive ecosystems (UNEP, 2019). Restoration in a period of rapid global change faces challenges where the baseline environmental conditions shift and invasive species can drastically disrupt the community's stability (Hobbs & Cramer, 2008). Leveraging long-term monitoring data, we demonstrate that integrating demographic modeling and MCT can diagnose restoration trajectories and

identify effective management actions. This approach is particularly helpful when restoring species in a variable and competitive environment. Broader application of demographic models and MCT in restoration has the potential to inform and update theoretical predictions, explain empirical dynamics, and identify favourable management actions with important implications for ecology and conservation.

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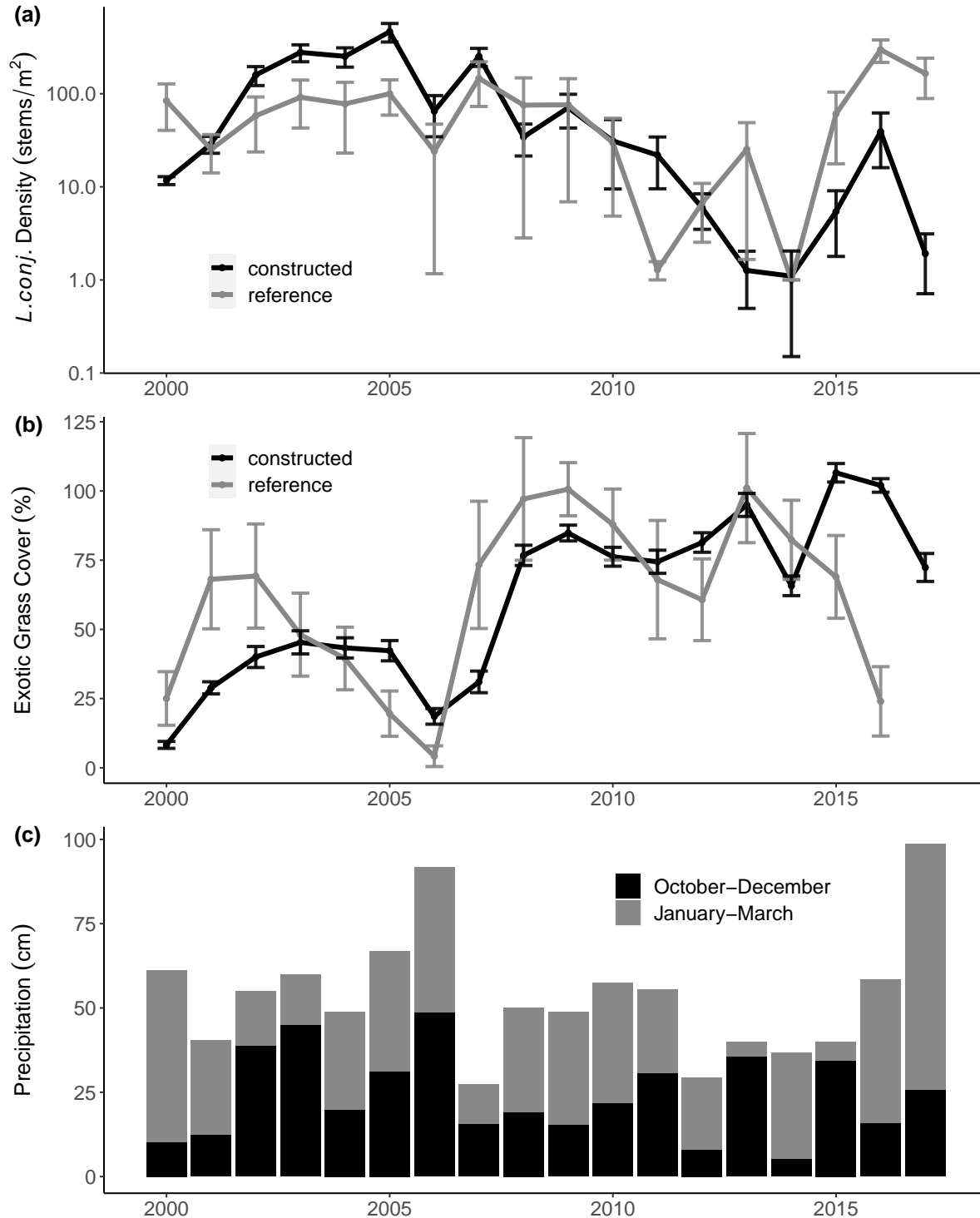


Figure 1: Comparison of *Lasthenia conjugens* density through time in constructed (black) and reference (grey) pools (a; stems/m²; note logarithmic y-axis) compared to key potential drivers of *L. conjugens* dynamics: exotic grass cover (b; (%)) and, (c) growing season precipitation (October - March; cm) in Fairfield, CA. Points are annual means, and error bars are standard errors from means. Mean exotic cover was calculated by summing the cover of three exotic grass species, *Bromus hordeaceus*, *Hordeum marinum*, and *Festuca perennis*, and averaging across pools each year.

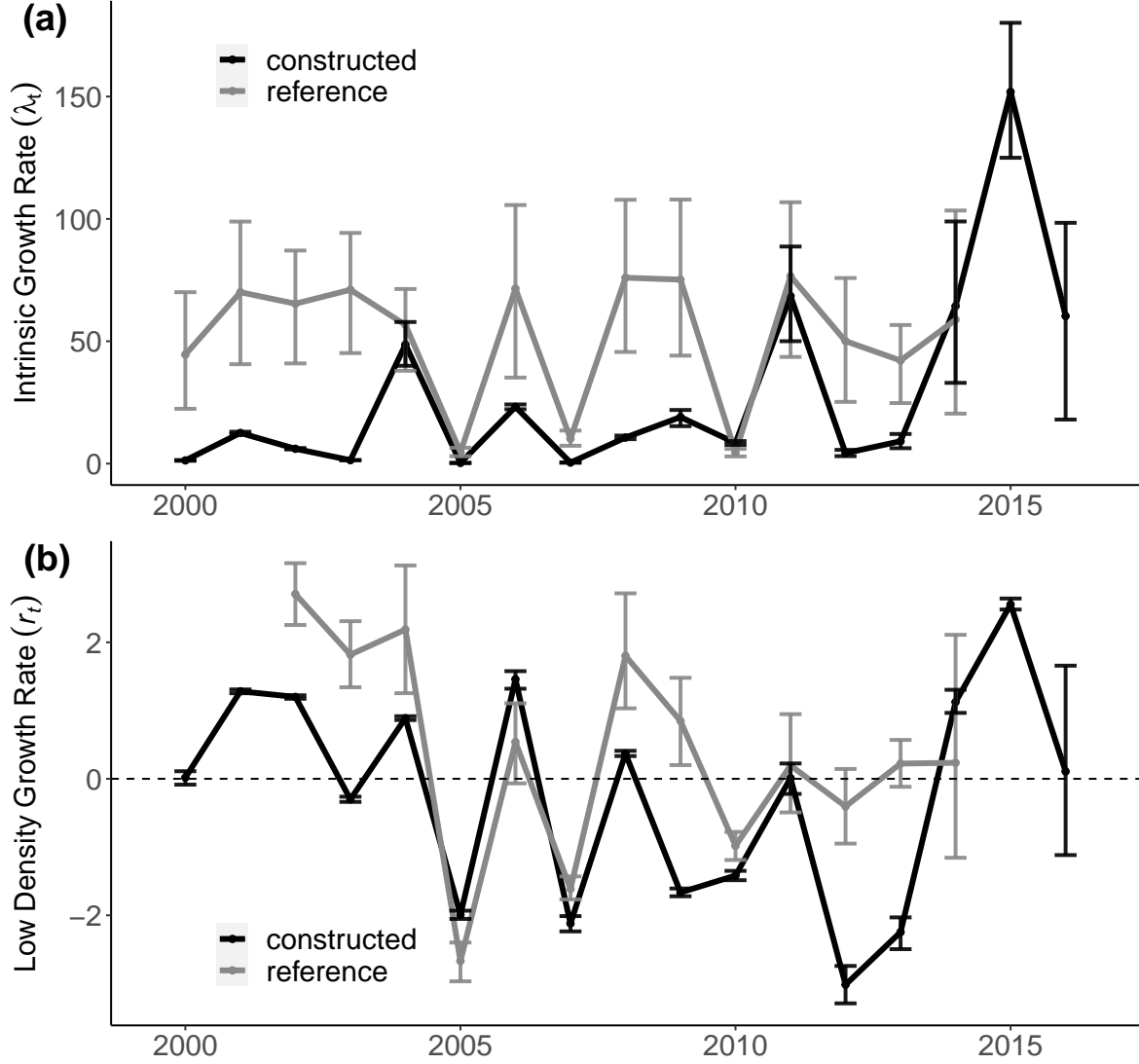


Figure 2: Both the intrinsic growth rate λ_t and low-density growth rate $r_t = \ln(N_{t+1}/N_t)$ of *L. conjugens* trail in the constructed pools versus the reference pools. (a) Posterior estimates of per capita intrinsic growth rate (average number of seeds produced in the absence of competition) and (b) low-density growth rate in constructed (black) and reference (grey) pools from 2000 to 2017. 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.

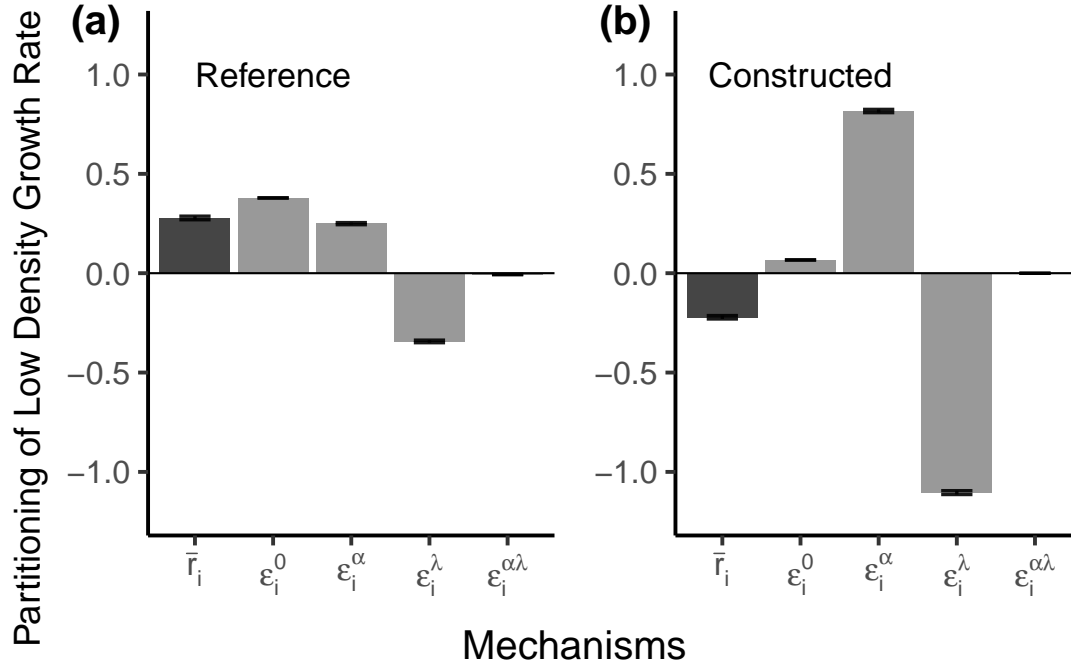


Figure 3: *Lasthenia conjugens* is predicted to persist in reference pools (a), but not in constructed pools (b), due to the effect of variation in λ_t . Partitioning of average low density growth rate (\bar{r} ; dark grey) into contributions from different aspects of the species' environment on competition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

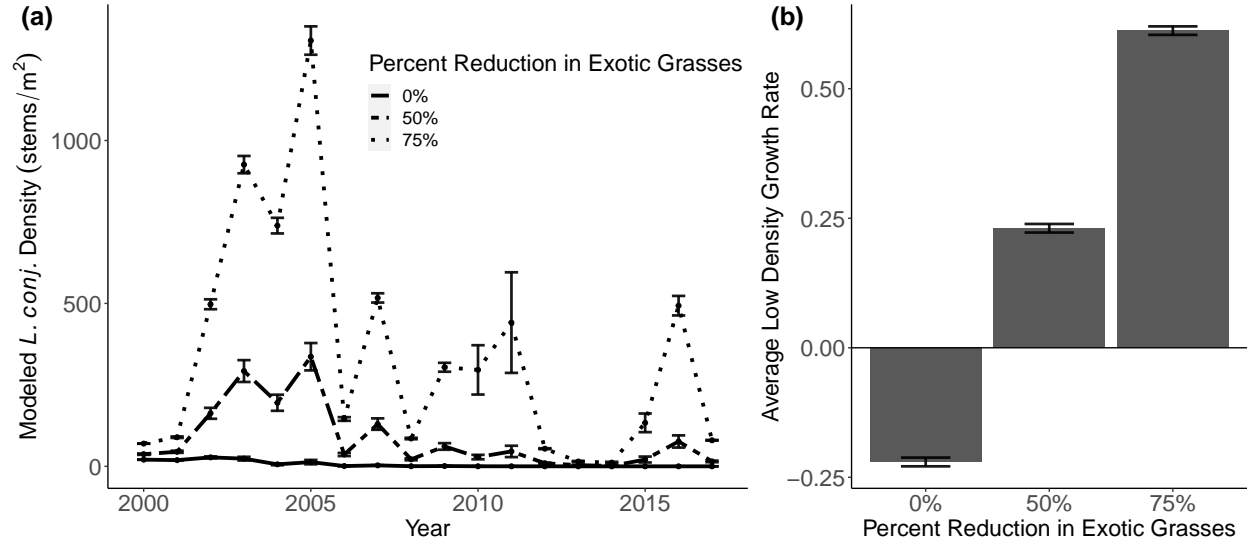
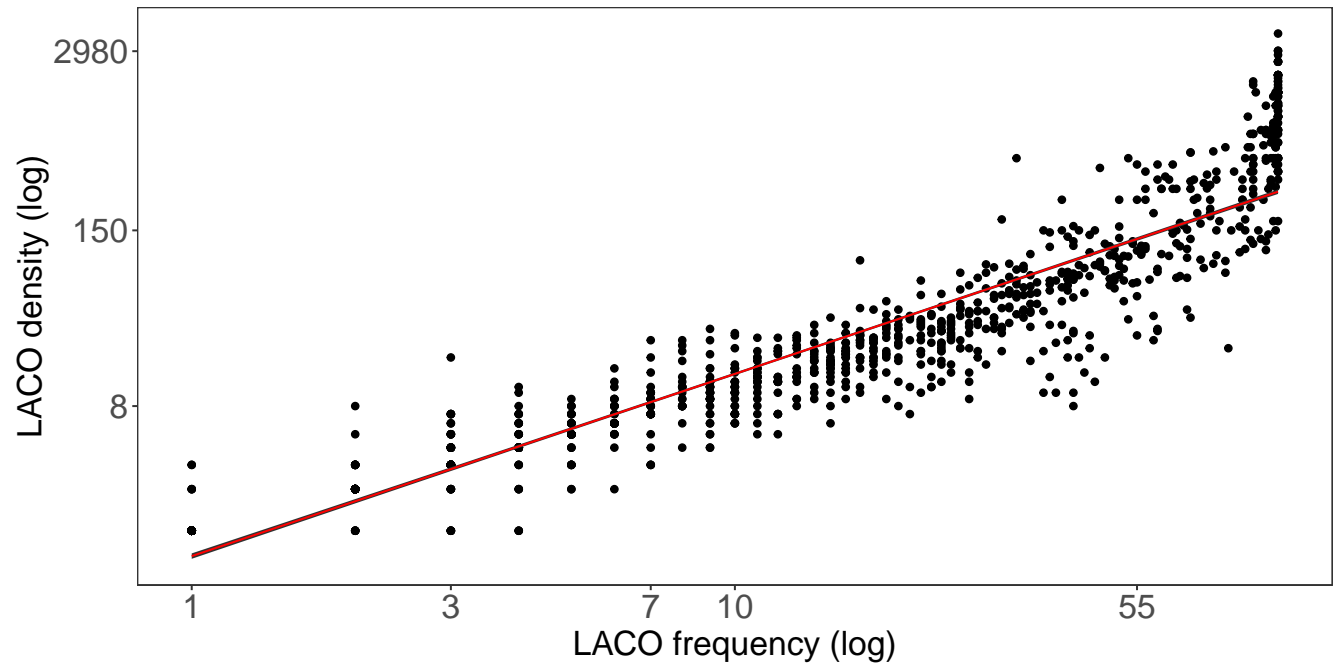
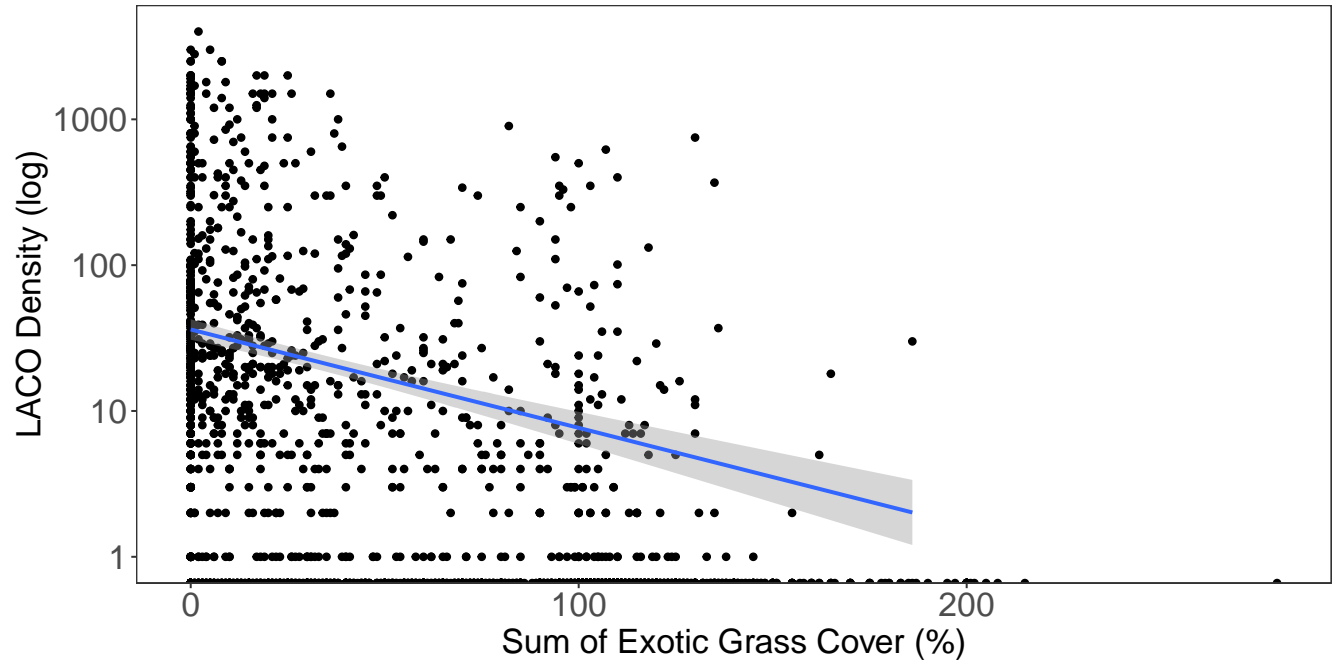


Figure 4: Manual reductions in exotic grass cover are predicted to allow *Lasthenia conjugens* to persist in constructed pools. Simulated effects of exotic grass reduction treatments on (a) mean density (stems/ m^2) through time and (b) its consequent impact on the low density growth rate of *L. conjugens*. Treatment scenarios were 0% grass reduction (solid line), 50% grass reduction (two-dashed line), and 75% grass reduction (dotted line) each year from 2000 to 2017. Error bars represent the standard error around the mean. A positive low-density growth rate predicts long-term persistence of the species while a negative one predicts long-term competitive exclusion.



Supplementary Figure 1: *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 2: Abundance of *Lasthenia conjugens* (LACO; natural log) declined with increase in exotic grass cover (%) in constructed pools from 2000 to 2017. 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
2016	0.533	2.417
2017	1.219	3.329