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Application of modern coexistence theory to rare plant restoration provides early indication of restoration trajectories

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Abstract

Restoration ecology commonly seeks to re-establish species of interest in degraded habitats. Despite a rich understanding of how succession influences re-establishment, there are several outstanding questions that remain unaddressed: are short-term abundances sufficient to determine long-term re-establishment success, and what factors contribute to unpredictable restorations outcomes? In other words, when restoration fails, is it because the restored habitat is substandard, because of strong competition with invasive species, or alternatively due to changing environmental conditions that would

equally impact established populations? Here, we re-purpose tools developed from modern coexistence theory to address these questions, and apply them to an effort to restore the endangered Contra Costa goldfields (*Lasthenia conjugens*) in constructed ("restored") California vernal pools. Using 16 years of data, we construct a population model of *L. conjugens*, a species of conservation concern due primarily to habitat loss and invasion of exotic grasses. We show that initial, short-term appearances of restoration success from population 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 with reference ("natural") pools, coupled with a stronger negative sensitivity to annual fluctuations in abiotic conditions that yield decreased maximum growth rates. Nonetheless, our modeling shows that fluctuations in competition (mainly with exotic grasses) benefit *L. conjugens* through periods of competitive release, especially in constructed pools of intermediate pool depth. We therefore show how reductions in invasives and seed addition in pools of particular depths could change the outcome of restoration for *L. conjugens*. By applying a largely theoretical framework to the urgent goal of ecological restoration, our study provides a blueprint for predicting restoration success, and identifies future actions to reverse species loss.

KEYWORDS
Lasthenia, modern coexistence theory, population dynamics, relative nonlinearity, restoration, storage effect, vernal pools

INTRODUCTION

Ecological restoration is an increasingly important tool to reverse the effects of land degradation, but the success of restoration efforts is often uncertain. Success is often measured by comparing the abundance of target species in the restored community to a natural "reference" community, where similar species abundances between restored and reference are presumed to indicate success (Ruiz-Jaen & Aide, 2005; Society of Ecological Restoration, 2004). This approach is best suited when ecosystems have a monotonic recovery trajectory, which is predicted by the most common ecological theories used to inform restoration, such as succession and community assembly (Wainwright et al., 2017). At the same time, more recent developments in ecological theory, such as modern coexistence theory (MCT), have highlighted the idea that environmental variation and associated fluctuations in species abundances are not only common, but at times essential for maintaining species populations (Adler et al., 2007; Chesson, 2000; HilleRisLambers et al., 2012), complicating efforts to assess success on abundance alone. Applying MCT to ecological restoration

may provide a clearer picture of restoration trajectories and illuminate pathways to improve restoration outcomes, particularly in variable environments.

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

their magnitude of decline under unfavorable conditions (Hallett et al., 2019; Letten et al., 2018).

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; rather, abundance fluctuations can be essential to coexistence (Gravel et al., 2011; Warner & Chesson, 1985). 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 & Wilsey, 2014). Gauging success by annual low-density growth rate rather than abundance may therefore better provide an early indication of restoration trajectories. Furthermore, when restoration projects are monitored over time, average low-density growth rate may indicate whether or not the target species will persist in the long-term, which is critical to restoration success.

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 both altered environmental conditions and novel competitive interactions can 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 (Havrilla et al., 2020; Nilsson et al., 2015), respectively, and mowing or grazing to reduce exotic grasses are common tools to promote native forbs in annual grasslands (Hernandez et al., 2021; Weiss, 1999) 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). Typically, an MCT invasion analysis is applied to understand species coexistence with the resident community (i.e., a pairwise, multispecies approach), but it can also be applied to examine persistence of a single species (Godoy, 2019). Applying this partitioning to restoration monitoring data may help to 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 & 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. Whereas native vernal pool forbs 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), whereas exotic grasses are competitive in 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) model-derived growth rates are more reliable metrics to assess long-term trends than observed abundance in early years; (ii) *L. conjugens* can persist (as indicated by a 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 invasion analysis (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 & 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 to 869.2 mm over the past 50 years; PRISM Climate Group, 2020).

Although 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 (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), *Downingia concolor* (spotted throat downingia), and *Plagiobothrys stipitatus* (popcorn flower; Collinge & 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*, 255 artificial pools were constructed in December 1999 in the vicinity of reference pools as described in Collinge and Ray (2009). Pool sizes were randomly assigned as either small (5 × 5 m), medium (5 × 10 m), or large (5 × 20 m), $n = 85$ each, to reflect the size variation in the reference pools. Constructed pools were also similar to references in maximum depth (0–10 cm), 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 × 0.5 m plots (one plot per pool). Five seed addition treatments were randomly assigned to constructed pools: control (no seeding); LACO 1× (100 *L. conjugens* seeds in 1999); LACO 3× (100 *L. conjugens* seeds in 1999, 2000, and 2001); Group A–Group B (100 seeds of group A species in 1999, 100 seeds of group B species in 2000); Group B–Group A (100 seeds of group B species in 1999, 100 seeds of group A species in 2000). Group A consisted of *L. conjugens*, *Deschampsia danthonioides*, and *E. vaseyi*. Group B consisted of *L. conjugens*, *P. stipitatus*, and *Layia chrysanthemoides*. Plots were initially raked prior to seeding in 1999 but not in 2000 and 2001 to not disturb seeds from previous years.

In April, during approximate peak biomass, each year from 2000 to 2017, plant occurrence was monitored (Collinge & Faist, 2020). A 0.5 × 0.5 m frame divided into 100 subquadrats (5 × 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. At weekly intervals during the wet seasons of 1999–2000, 2001–2002, and 2008–2012, water depths at the center of sampling quadrats in each pool were measured.

Dynamical model

To project the population dynamics of *L. conjugens*, we took into account the effect of environmental conditions, as well as the competition experienced from both conspecific and heterospecific individuals. We used the Beverton–Holt model, which is well suited as an annual plant model (Larios et al., 2017; Levine & HilleRisLambers, 2009). 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 $X_{t,1,p}$ is:

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

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

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

measures the degree of competition experienced by *L. conjugens* stems 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. This model assumes no dispersal among the vernal pools because *L. conjugens* is a self-incompatible annual with gravity-dispersed seeds, and its dispersal range is unknown.

The statistical model

The statistical model was designed to estimate the parameters of Equations (1) and (2) to allow us to infer the
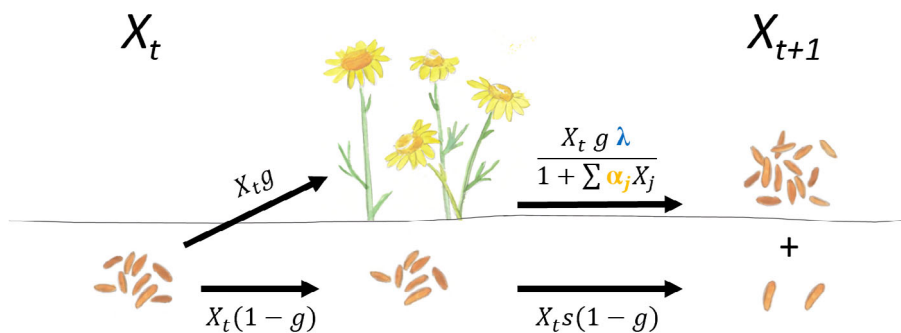
FIGURE 1 Visual representation of the (a) population model, (b) low-density growth rate, and (c) partitioning of persistence mechanisms. (a) The Beverton–Holt equation was used to model the life cycle of the focal species, *Lasthenia conjugens*. The population prior to winter rainfall (X_t) is captured in the number of seeds in a pool. Following sufficient rain, a fraction of the seeds germinate (g), whereas the remainder d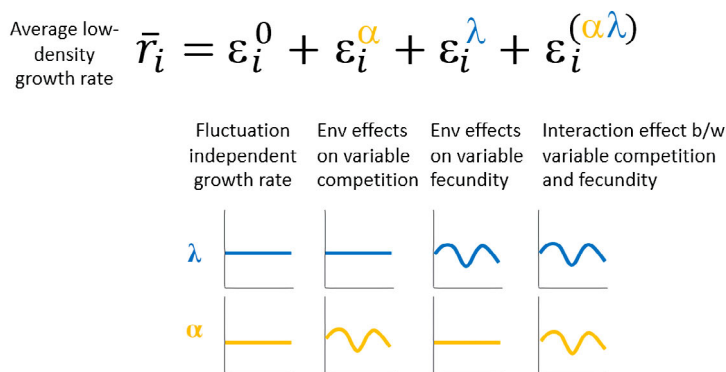o not ($1 - g$). Those seeds that germinate grow to produce new seeds that depend on the maximum fecundity in the environmental conditions encountered that year (λ), which is reduced competition (denominator of the equation at top right, with the sum over all species in the community). The population 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: ($1 - g$) 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. (b) To calculate the low-density growth rate ($r_t = \ln(N_{t+1}/N_t)$), introduction of a single individual into the equilibrium resident community is simulated for each year. The average low-density growth rate across years ($\bar{r}$) predicts persistence ($\bar{r} > 0$) or local extinction ($\bar{r} < 0$) of the focal species. (c) The average low-density growth rate is partitioned into four persistence mechanisms following the decomposition framework from Ellner et al. (2019). Fluctuation-independent growth rate (ε_i^0) is calculated by removing all variability in lambda (density-independent growth rates) and alpha (competition). Environmental effects on variable competition (ε_i^α) is calculated by subtracting ε_i^0 from growth rate with varying alpha but constant lambda. Environmental effects on variable fecundity (ε_i^λ) is calculated by subtracting ε_i^0 from growth rate with varying lambda but constant alpha. The interaction effect ($\varepsilon_i^{\alpha\lambda}$) is calculated by subtracting ε_i^0 from growth rate with varying alpha but constant ε_i^0, ε_i^α, and ε_i^λ from growth rate with varying lambda and alpha.

processes that promoted or limited the persistence of *L. conjugens*. Importantly, model fitting proceeds annually: the data we use to obtain estimates in year $t + 1$ are only those of year t. In other words, whereas long-term monitoring data are necessary to explicitly look at long-term trends, the model can be parameterized for shorter time series. Unlike experimental tests of MCT that typically collect more response data and include fewer competitors than restoration efforts (Ellner et al., 2019), several challenges arose when fitting restoration monitoring data to these models. Here, we outline the decisions we made to best adapt monitoring data to model *L. conjugens* using a MCT framework.

The seed bank (the first half of the Equation 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 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 1 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 3 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: $Y_{t=1,1,p} \sim$ 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 (Equation 2), we selected six species that comprised the majority of the cover (53% of cover across 16 years and plots) apart from *L. conjugens*, and 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 perennial plant, whereas

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), while estimating competition coefficients between *L. conjugens* and all other groups.

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 Equation (1). We checked for model fit of the model by simulating *L. conjugens* population dynamics, and visualizing simulated versus observed stem counts (Appendix S1: Figure S2).

We fitted our model separately for reference (no seed addition) and constructed pools (with seed addition). We only used data from pools with consecutive years of data. Although the data for 2000–2017 were available, the data from 2016 to 2017 were dropped from our analysis because we did not have reference pools with consecutive years of data beyond 2015. For reference pools, we used the frequency of *L. conjugens*, which we converted to abundance (Appendix S1: Figure S3), and frequency of other species from seven pools in 2000–2015 and two additional pools in 2002–2015. For constructed pools, we used stem counts of *L. conjugens* and the frequency of other species from 142 pools in 2000–2015. We compared the following seeding treatments: LACO 1× ($n = 24$), LACO 3× ($n = 24$), Group A–Group B ($n = 43$), and Group B–Group A ($n = 51$). We omitted the control plots because the stem counts of *L. conjugens* in control plots remained zero over time. Pool size classes included small (25 m²; $n = 52$), medium (50 m²; $n = 52$), and large (100 m²; $n = 38$). Pool depth classes were determined by the range of annual maximum pool depth averaged across years: shallow (<3.8 cm; <25th percentile; $n = 29$), intermediate (3.8–8.0 cm; 25–75th percentile; $n = 76$), and deep (>8 cm; >75th percentile; $n = 37$).

We extracted the Bayesian posterior estimates of the seed survival probability s, annual fecundity estimates λ_t, and annual competition coefficient estimates $\alpha_{t,k}$. We assumed that 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. Alternatively, 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 fitted 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), $\lambda_t \sim$ 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, Beta(0.5, 0.5). We generated samples from posterior distributions using the Markov chain Monte Carlo (MCMC) sampling method with four 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), in which we iteratively excluded one pool from the data set and fit the model each time (Appendix S1: Figure S4).

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 with observed abundance, measured as mean density of *L. conjugens*. We directly assessed λ_t at each year between 2000 and 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 $r_t = \ln(X_{t+1}/X_t)$ (Figure 1). 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 with the resident species to test for stable coexistence (Barabás et al., 2018; Chesson, 2000); however, we calculated it solely for *L. conjugens*, allowing us to focus on single-species persistence rather than multispecies coexistence.

Partitioning of persistence mechanisms

To understand how environmentally driven temporal variation in seed production (λ_t) and variation in competition coefficients ($\alpha_{t,k}$) are driving restoration trajectories, we decomposed the average low-density growth rates ($\bar{r}$) of *L. conjugens* into the mechanisms that contributed to its persistence (Figure 1). Following the decomposition

framework from Ellner et al. (2019), the average low-density growth rates ($\bar{r}$) can be decomposed into four mechanisms:

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

where 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 we calculate the growth rate when $\alpha_{t,k}$ varies through time, whereas λ is held at its average value and subtract out the growth rate under averaged conditions (ε_i^0). This is analogous to relative nonlinearity in competition, which means that 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 minus ε_i^0. This mechanism is analogous to relative nonlinearity in seed production, which ecologically equates to favorable years having a stronger positive effect size on seed production than the magnitude of the negative effect in unfavorable years. Finally, the last decomposition term, $\varepsilon_i^{(\alpha\lambda)}$, 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., $\varepsilon_i^{(\alpha\lambda)} = r_i - \left[\varepsilon_i^0 + \varepsilon_i^\alpha + \varepsilon_i^\lambda\right]$). 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 time series of observed annual density 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 that mean density 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 since 2007 in both reference and constructed pools (Appendix S1: Figure S5a), and a multiyear drought hit from 2011 to 2015 (Appendix S1: Figure S5b), *L. conjugens* populations in constructed pools drastically declined from 2007 to 2015, whereas reference populations remained stable (Figure 2a). The mean per capita intrinsic growth rate in the constructed pools was only 2.9% of that in reference pools in 2001, which signaled divergence of population trajectories from the start of the restoration effort (Figure 2b). The low-density growth rate in constructed pools was also lower than that in reference pools throughout the time series (Figure 2c). Overall, the average low-density growth rate ($\bar{r}$) showed long-term persistence of *L. conjugens* in reference pools (0.47; 95% CI: 0.32–0.62), but eventual competitive exclusion in constructed pools (−0.42; 95% CI: −0.46 to −0.39).

Partitioning of persistence mechanisms

To determine whether environmentally driven effects in intrinsic seed production, competitive environments, or their interaction most strongly contribute to differences in persistence between reference and constructed pools, we decomposed the average low-density growth rate of *L. conjugens*. The difference in population trajectories was primarily driven by a strong destabilizing effect 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 nonlinearity in competition (ε_i^α) were large enough to off-set the negative effect 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 effect of

relative nonlinearity in competition (ε_i^α) was less than the negative effect 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 ($\varepsilon_i^{\alpha\lambda}$) 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.

Intermediate pool depth and exotic grass removal improve persistence

None of the seeding treatments improved long-term persistence of *L. conjugens*, even though LACO ×3 seeding treatment initially increased density more than other treatments (Appendix S1: Figure S6). Average low-density growth rate was negative across all seeding treatments: LACO 1× (−0.58; 95% CI: −0.79 to −0.36), LACO 3× (−0.68; 95% CI: −0.84 to −0.52), Group A–Group B (−0.90; 95% CI: −1.07 to −0.76), and Group B–Group A (−0.48; 95% CI: −0.64 to −0.32). Larger constructed pools showed higher average low-density growth rate of *L. conjugens* than smaller pools, but they were all negative (Appendix S1: Figure S7): small (−0.57; 95% CI: −0.68 to −0.45), medium (−0.40; 95% CI: −0.49 to −0.32), and large (−0.20; 95% CI: −0.285 to −0.12). In addition, pool depths improved densities and growth rates of *L. conjugens* (Appendix S1: Figure S8). Specifically, *L. conjugens* in intermediate depth pools persisted – positive average low-density growth rate – (0.84; 95% CI: 0.82–0.87), whereas those in shallow (−0.68; 95% CI: −1.40 to −0.07) and deep (−0.57; 95% CI: −0.69 to −0.44) pools did not (Figure 4a,b).

Exotic grass cover in constructed pools increased over time regardless of the seeding treatment, pool size, or pool depth (Appendix S1: Figure S9). Mean annual exotic grass cover negatively affected the mean annual density of *L. conjugens*, but did not alter the intrinsic growth rate or the low-density growth rate (Appendix S1: Figure S10). Given the stabilizing effect of variation in competition in constructed pools (Figure 3b), we simulated the effects of exotic grass removal on target species, and we found that, on average, 50% exotic grass removal increased predicted mean abundance of *L. conjugens* by 2.1-fold compared with no removal, and 75% exotic grass removal increased mean abundance by 4.4-fold (Figure 4c). 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; Appendix S1: Table S1). Moreover, the threshold at which the average low-density growth rate of *L. conjugens*
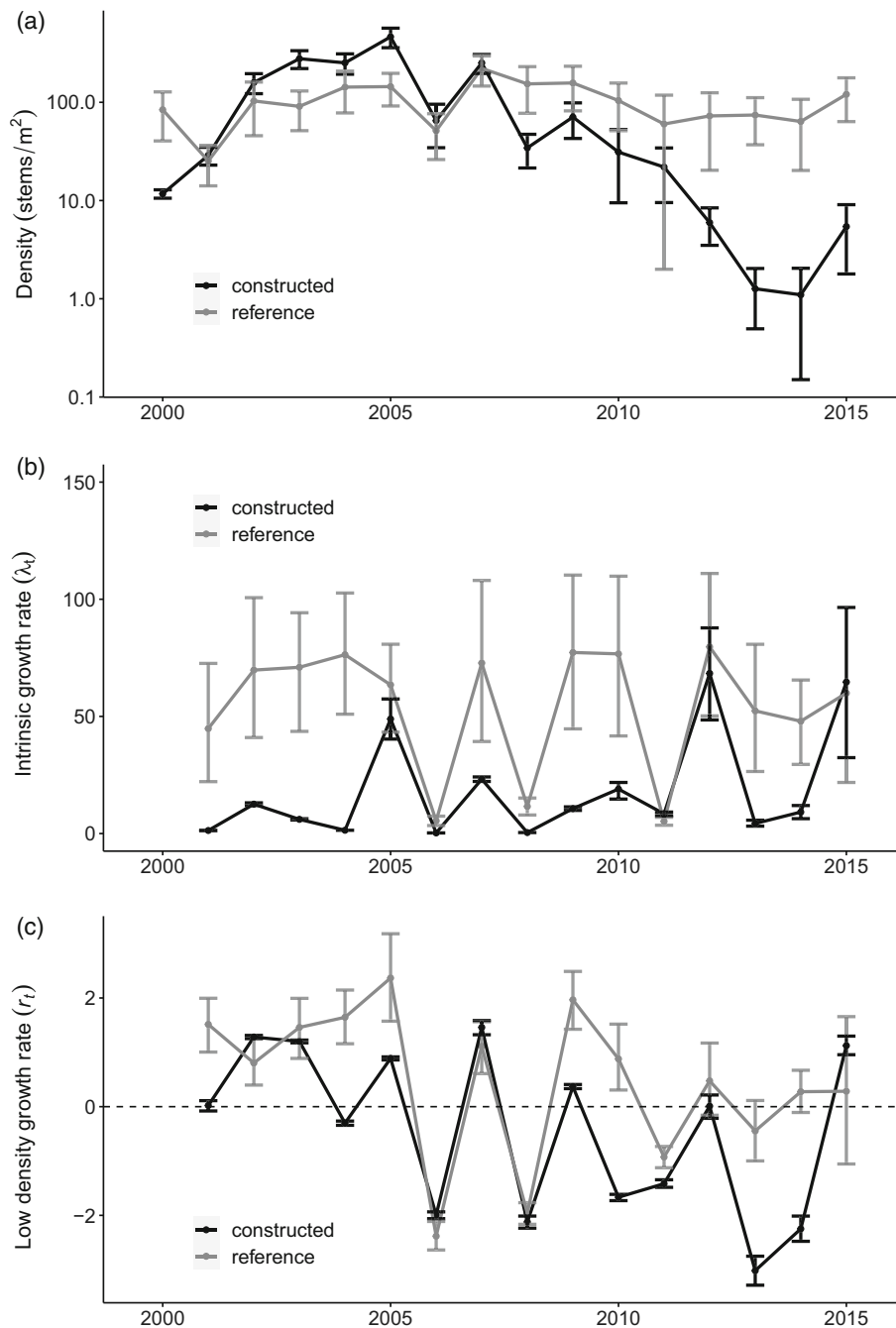
FIGURE 2 Restoration trajectories of *Lasthenia conjugens* are dynamic over time. Restoration success can be assessed by three metrics: (a) *Lasthenia conjugens* density (stems/m^2; note logarithmic *y*-axis), (b) posterior estimates of per capita intrinsic growth rate (λ_t, average number of seeds produced in the absence of competition) and (c) low-density growth rate ($r_t = \ln(N_{t+1}/N_t)$) in constructed (black) and reference (gray) pools. The error bars represent 95% credible intervals. A positive low-density growth rate predicts persistence, whereas a negative one indicates eventual competitive exclusion, and therefore loss from the pools, even though λ_t may be positive. For all three panels, we used data from 142 constructed pools from 2000 to 2015, seven reference pools from 2000 to 2015, and two additional reference pools from 2002 to 2015 to maximize the use of data.

transitions from negative (local extinction) to positive (persistence) was ~50% exotic grass removal: −0.42 (95% CI: −0.46 to −0.39) in the no removal scenario, 0.01 (95% CI: −0.01 to 0.04) in the 50% removal scenario, and 0.38 (95% CI: 0.35–0.41) in the 75% removal scenario (Figure 4d).

DISCUSSION

Here we re-purposed analytical tools from MCT to diagnose restoration trajectories in a highly invaded landscape with large environmental fluctuations. This
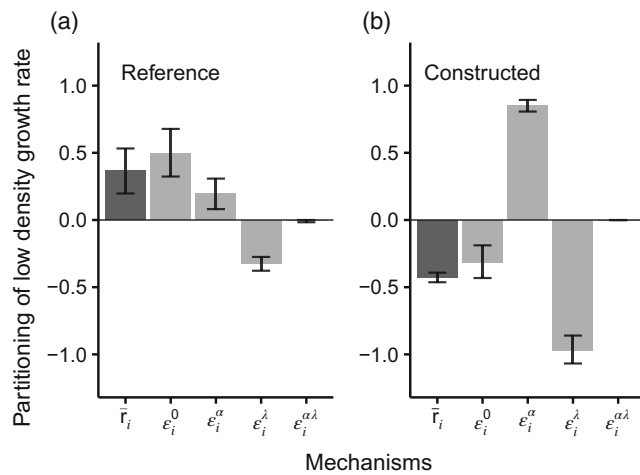
FIGURE 3 *Lasthenia conjugens* is predicted to persist in reference pools (a), but not in constructed pools (b), due to the effect of variation in λ_t. Partitioning of average low-density growth rate ($\bar{r}$; dark gray) into contributions from different aspects of the species' environment on competition (ε_i^α), seed production (ε_i^λ), and their combined interactive effect ($\varepsilon_i^{\alpha\lambda}$) shown in light gray. The error bars represent standard errors from means. The interaction effects are present but are too small to be visible.

approach enabled us to not only detect restoration failure quickly, but to 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 become extinct, whereas 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 with reference populations. Although neither seeding treatment nor pool size changed the restoration trajectories, pool depth, especially intermediate pool depth, supported the long-term persistence of target species. 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, even switching from predicted local extinction to persistence.

Assessing restoration success is complex when restoration activities such as 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 8 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.

Modern coexistence theory has highlighted the importance of environmental variability for 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 & Beals, 2018). This highlights the need to consider redesigning the constructed pools for future vernal pool restoration projects. Specifically, we found that intermediate pool depth (3.8–8.0 cm) is an important feature to support long-term persistence of *L. conjugens*. This is likely to be because shallower pools favored exotic grasses, whereas the deepest pools favored other native forbs. A previous study has also highlighted that the pool depth effect was stronger than the pool size effect, and that there was no strong correlation between pool size and depth, even though that was the intention in the experimental design, due to heterogeneity across the site Javornik and Collinge (2016).

Variable competition with neighboring individuals may, however, maintain species coexistence (Chesson, 2000). We found that relative nonlinearity 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* has a competitive release from the exotic grasses in wet early-season rain years, because it can maintain an immature
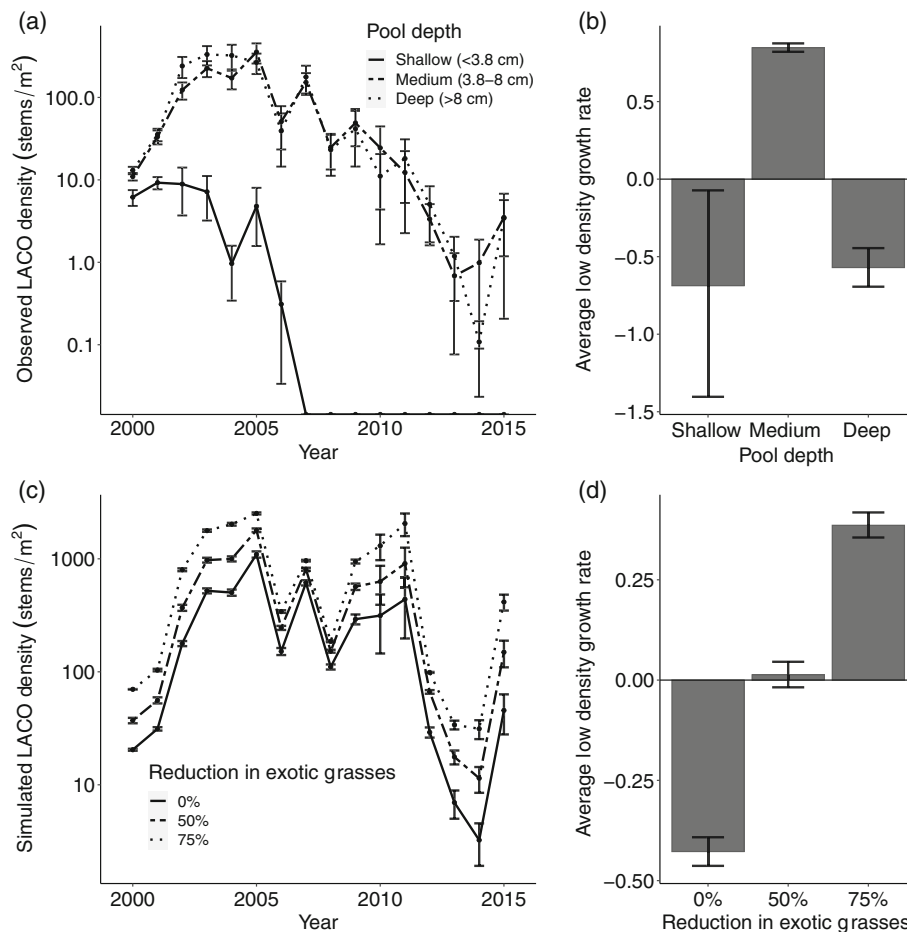
FIGURE 4 Pool depth and exotic grass reduction influence *Lasthenia conjugens*'s persistence in constructed pools. Top two panels are observed effects of pool depth on (a) density and (b) average low-density growth rate. Depth classes are determined by 25th and 75th percentiles of annual maximum pool depth averaged across years: Shallow (<3.8 cm; <25th percentile; dotted line), medium (3.8–8.0 cm; 25–75th percentile; two-dashed line), deep (>8.0 cm; >75th percentile; solid line). The bottom two panels show the simulated effects of exotic grass reduction on (c) density and (d) average low-density growth rate. Simulated treatments include 0% (solid line), 5% (two-dashed line), and 75% (dotted line) exotic grass reduction. Error bars in panels (a) and (c) represent standard error, those in panels (b) and (d) represent 95% credible intervals. The 95% credible interval for shallow pools was large because so few pools had viable populations in 2006 and none since 2007. A positive average low-density growth rate predicts long-term persistence.

state in inundated pools, whereas exotic grasses cannot (Javornik & Collinge, 2016). As 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 competitive neighborhoods. 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). Building on our partitioning of low-density growth rates showing a positive effect of

competitive variability, 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, even if the restored pools were not an optimal depth (Figure 4b). From a restoration perspective, these data-driven simulations can be helpful for informing adaptive management and setting

expectations for how active management will alter restoration outcomes.

Our study takes a novel approach 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. Although long-term data are 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 fitted 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 become more complicated in more specious communities, this should become more feasible as new methods for analyzing multispecies coexistence emerge (Saavedra et al., 2017).

Restoration in a time of rapid global change faces challenges in which the baseline environmental conditions shift and invasive species can drastically disrupt the community's stability (Hobbs & 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.

Sharon K. Collinge designed the experiment and Sharon K. Collinge and Akasha M. Faist collected data. Lina Aoyama developed and implemented the statistical approach with input from Lauren G. Shoemaker, Benjamin Gilbert, and Lauren M. Hallett. Lina Aoyama, Lauren G. Shoemaker, Lauren M. Hallett, BG, Sharon K. Collinge, Akasha M. Faist, Nancy Shackelford, and Vicky M. Temperton wrote the first draft and all authors contributed to manuscript edits.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

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