

# Controls over native perennial grass exclusion and persistence in California grasslands invaded by annuals

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**Abstract.** Despite obvious impacts of nonnative species in many ecosystems, the long-term outcome of competition between native and exotic species often remains unclear. Demographic models can resolve the outcome of competition between native and exotic species and provide insight into conditions favoring exclusion vs. coexistence. California grasslands are one of the most heavily invaded ecosystems in North America. Although California native perennial bunchgrasses are thought to be restricted to a fraction of their original abundance, the eventual outcome of competition with invasive European annual grasses at a local scale (competitive exclusion, stable persistence, or priority effects) remains unresolved. Here, we used a two-species discrete time population growth model to predict the outcome of competition between exotic annual and native perennial grasses in California, and to determine the demographic traits responsible for the outcome. The model is parameterized with empirical data from several field experiments. We found that, once introduced, annual grasses persist stably with little uncertainty. Although perennial grasses are competitively excluded on average, the most likely range of model predictions also includes stable coexistence with annual grasses. As for many other perennial plants, native bunchgrass population growth is highly sensitive to the survival of adults. Management interventions that improve perennial adult survival are likely to be more effective than those that reduce exotic annual seed production or establishment, reduce competition, or increase perennial seedling establishment. Further empirical data on summer survival of bunchgrass adults and competitive effects of annuals on perennials would most improve model predictions because they contribute most to the uncertainty in the predicted outcome for the perennial grass. This work demonstrates how demographic approaches can clarify the outcome of competition between native and exotic species, identify key targets for future empirical work, and predict the effectiveness of management interventions. Such studies are critical both for understanding the impacts of invasion and for targeting management responses that maximize the benefit to native species.

**Key words:** California grassland; coexistence; competition; European annual grass; exotic species; native species; perennial bunchgrass; *Stipa pulchra*.

## INTRODUCTION

Introduced species are a leading cause and consequence of ecological change (Elton 1958, Williamson 1996, Vitousek et al. 1997, Wilcove et al. 1998, Sax and Gaines 2008). Although invaders may have large impacts on native species, invasive species have only rarely driven native species extinct, and extinction via competition has been even more rare (Sax et al. 2002, 2007, Gurevitch and Padilla 2004). More commonly,

invasive species reduce native populations and leave small remnant native populations intermixed with invasive species or occurring in refugia (Huenneke et al. 1990, Hobbs and Mooney 1998, Seabloom et al. 2003a). Whether native species can stably coexist with invaders on the landscape or are excluded and driven to extinction on long time scales is difficult to observe directly. Priority effects are a third possible outcome, defined here as occurring when either established species can prevent the other from invading. We note that this definition, which focuses on the long-term outcome of competition, differs from other more transient definitions of priority effects used elsewhere (e.g., Corbin and D'Antonio 2004, Wainwright et al. 2012). Disturbances can obscure priority effects when they disrupt native populations and facilitate exotic species invasion (D'Antonio et al. 1999), yet removing the disturbance does not return the system to native dominance (Bartolome and Gemmill 1981, D'Antonio and Vitousek

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1992). As a result, the future of invaded landscapes often remains poorly understood.

Uncertainty about the fate of native species competing with invaders arises in part because few studies have directly addressed the long-term outcome of competition. Because of environmental and demographic stochasticity and slow population dynamics, empirical competition experiments in the field have limited power to distinguish between qualitative outcomes of competition, i.e., stable coexistence, competitive exclusion, or priority effects. Models that describe population growth as a function of demographic processes can help to close this gap by assessing emergent effects of invasions (Thomson 2005). However, previous work on demographic controls over invader spread (e.g., Neubert and Caswell 2000, Parker 2000) and rare species persistence (e.g., Menges 1990, 2000, Schemske et al. 1994) frequently has not examined competition between invasive and native species (but see Everard et al. 2010). This single-species focus masks the fact that most interactions between invaders and native species are bilateral, and that the strength of pairwise intra- and interspecific interactions determines the outcome of competition and ultimately species persistence (Chesson 2000, Snyder and Chesson 2004). Although vital for accurate predictions, the demographic data required to parameterize population growth models in the presence of competitors are often lacking, hampering forecasts of the long-term outcome of competition between native and exotic species.

California grasslands are a widespread habitat that represent one of the most invaded systems in North America (Mack 1989). At the same time, as part of the California Floristic Province, they contain a high diversity of endemic species (Myers et al. 2000). Since the invasion of exotic annual grasses from Eurasia in the 18th century, which coincided with widespread disturbance of California environments, many of the native annual forbs and perennial bunchgrasses typical of "grassland habitat" are restricted to small relict populations. Exotic annual grasses may have increased the probability of extinction for California native annual forbs by reducing habitat area, seed density, and dispersal (Gilbert and Levine 2013). By contrast, less is known about demographic responses of native bunchgrasses, which are sometimes considered the pre-invasion dominants in California grassland ecosystems (Mack 1989, Corbin and D'Antonio 2004, Schiffman 2007, but see Hamilton 1997). While exotic annual grasses are numerically dominant throughout most of the range of California grasslands, native bunchgrass populations remain scattered in some areas, and where present, appear to stably persist even in the presence of annuals at some sites (Hamilton 1997).

Despite numerous hypotheses about factors promoting the spread and rise to dominance of annual grasses (Stromberg and Griffin 1996, Dyer and Rice 1997, Seabloom et al. 2003b, Corbin and D'Antonio 2004, DiVittorio et al. 2007, Everard et al. 2010), the outcome

of competition between exotic annual and native perennial grasses remains unclear. Several possibilities are consistent with the field pattern of widespread exotic grass dominance combined with scattered, but apparently persistent native grass populations: (1) Exotic annuals may eventually competitively exclude native perennials, but exclusion has not yet occurred throughout the region and depends on local grazing and soil conditions; (2) native perennials may coexist stably with exotic annuals, potentially at low density (and especially in untilled soils); and (3) priority effects may occur, whereby established perennial populations can repel invasion by annuals and vice versa, with disturbance mediating the switch between native perennial and exotic annual dominance. Some evidence for the latter is provided by Corbin and D'Antonio (2004). Spatial variation in environmental conditions could affect the distribution of these outcomes across the landscape.

Understanding the outcome of competition, as well as the demographic processes that drive this outcome, is particularly important for designing management responses to promote native population growth. In California grasslands, management strategies may attempt to favor native perennials by reducing the density of annual grasses (through targeted grazing [Stahlheber and D'Antonio 2013], burning [Hatch et al. 1999], or early watering to elicit fatal premature germination [Wainwright et al. 2012]) by promoting perennial grass over-summer survival (through manipulating late-season water availability [Dyer and Rice 1997]) and by increasing the survival of perennial germinants (through removing annual grass thatch buildup [Cox and Allen 2008]). However, a better understanding of how annual and perennial demographic traits drive the outcome of competition will help to pinpoint the management strategies with the greatest positive effect on perennial persistence. Models can further inform empirical work by highlighting how uncertainty in demographic rates affects the outcome of competition, illustrating which empirical work would most improve predictions.

Here, we constructed a two-species population growth model for a native perennial and an exotic annual grass in California. Because existing data are insufficient to fully parameterize the model for individual annual and perennial species, we used empirical data from the literature and from unpublished studies on five exotic annual and six native perennial grass species that commonly occur in California grasslands. We used the models to address the following questions. (1) What is the predicted outcome of competition between exotic annual grasses and native perennial grasses in California? (2) How much uncertainty exists around the predicted outcome? (3) How sensitive is the predicted outcome to various demographic traits, particularly those associated with management activities? (4) Which demographic traits drive the uncertainty in the predicted outcome, and thus are the most important targets for future work? We addressed these questions using

sensitivity and uncertainty analyses, which serve distinct purposes. Sensitivity analyses describe how model predictions change with a fixed percentage of change in the value of each parameter, highlighting the traits for which small perturbations have large impacts on the outcome (e.g., traits for which environmental variation or management activities may have a large impact on population growth). By contrast, uncertainty analyses describe how the estimated range of variation in each trait, due to either variation in field estimates or scarcity of data, contributes to uncertainty in model outcomes, thereby informing the most important traits to target for further empirical study.

## METHODS

### Study system

California grasslands are now largely dominated by Eurasian annual grasses, containing mostly *Avena* and *Bromus* spp., intermixed with remnant patches of the native perennial bunchgrasses *Stipa* spp., *Elymus glaucus*, and others, depending on location relative to coast (Mack 1989, Corbin and D'Antonio 2004). The climate in California grasslands is mediterranean, with cool, wet winters and warm, dry summers. Most seeds germinate after the first substantial (>1 cm) rains in the late fall or early winter, and annuals set seed and senesce in mid to late spring (Chiariello 1989). Perennial bunchgrasses may continue to produce seeds and maintain green tissue throughout the summer or aboveground tissues may die back completely each year.

Despite decades of study on invasions and their impacts in California grasslands, we lack complete demographic data for most individual grass species. We overcame this limitation by assuming that exotic annual grasses and native perennial grasses represent two distinct functional groups: We modeled an “annual species” and a “perennial species” that are broadly representative of these two groups. This approach makes the model more representative of general patterns, but less directly predictive of individual species; previous theoretical and empirical work in this system has made similar assumptions (Seabloom et al. 2003b, Borer et al. 2007). Our annual grass demographic data come from *Avena fatua*, *Avena barbata*, *Bromus diandrus*, *Bromus hordeaceus*, and *Vulpia myuros*, and our perennial grass data come from *Stipa pulchra*, *Elymus glaucus*, *Bromus carinatus*, *Hordeum brachyantherum* ssp. *brachyantherum*, *Melica californica*, *Stipa cermea*, and *Poa secunda* ssp. *secunda*. The data represent a range of coastal and inland California grassland sites in Santa Barbara, Solano, Monterey, Napa, Lake, Marin, San Diego, Santa Clara, and Yolo counties, spanning six degrees of latitude. One set of data on *Avena fatua* seed production came from a plant science research farm in Moscow, Idaho, USA. This geographic breadth makes the model more general, but less predictive of specific outcomes at individual sites, where environmental conditions vary. The publications from which these data were drawn are listed in Appendix A: Table A1.

### Population growth models

We modeled two grass species (a native perennial and an exotic annual) using a discrete-time population growth model that tracks the number of seeds and adults (for the perennial only) at the start of each growing season (late fall). We assume that perennial seeds germinate to become seedlings, which survive their first summer at a density-dependent rate and become reproductive adult bunchgrasses the following year. Perennial seedlings do not produce seeds in their first year. The population growth equations are

$$N_a(t+1) = N_a(t)g_a\lambda_a C_a(N_a(t), N_s(t), N_p(t)) \quad (1)$$

$$N_s(t+1) = N_p(t)\lambda_p C_p(N_a(t), N_s(t), N_p(t)) \quad (2)$$

$$N_p(t+1) = N_s(t)g_s C_s(N_a(t), N_s(t), N_p(t))s_s + N_p(t)s_p \quad (3)$$

where the subscripts a, s, and p represent annual seeds, perennial seeds, and perennial adults, respectively.  $N_a(t)$ ,  $N_s(t)$ , and  $N_p(t)$  are the number of annual grass seeds, perennial grass seeds, and perennial grass adults (at least one year old) at the beginning of the growing season in year  $t$ , respectively. Annual plant population growth depends on the fraction of seeds that germinate and survive to the end of the growing season (hereafter, emergence;  $g_a$ ), the per-plant fecundity in the absence of competition ( $\lambda_a$ ), and the reduction in seed output that annual plants experience due to competition ( $C_a$ ), a function of plant density ( $N_a(t)$ ,  $N_s(t)$ ,  $N_p(t)$ ). Perennial plant population growth depends on the change in both seeds and adults from the start of one growing season to the start of the next. We assume that seeds germinate the first growing season after they are produced, and that perennial seedlings mature into perennial adults if they survive their first summer. Perennial seed production depends on the number of perennial adults ( $N_p(t)$ ), their per capita fecundity in the absence of competition ( $\lambda_p$ ), and the reduction due to competition the perennial adults experience ( $C_p$ ), a function of plant density. The number of perennial adults depends on over-summer survival of adults from the previous year ( $s_p$ ), plus the seeds that germinate and survive the spring (i.e., emergence;  $g_s$ ) and survive the summer ( $s_s$ ), reduced by the competition perennial seedlings experience ( $C_s$ ), a function of plant density. We assume that competition reduces the fecundity, but not the over-summer survival of perennial adults, and that perennial adult mortality only occurs over the summer, following field observations. The competition functions are

$$C_i(t) = \frac{1}{1 + \alpha_{ia}g_a N_a(t) + \alpha_{is}g_s N_s(t) + \alpha_{ip}N_p(t)} \quad (4)$$

where  $i$  is either a, s, or p representing annual seeds, perennial seeds, or perennial adults, respectively, and  $\alpha_{ij}$  represents the competitive effect of species  $j$  on species  $i$ . We used the common Beverton-Holt competition function because it has performed well in other systems (Levine and HilleRisLambers 2009) and preliminary analyses suggested that it provided a good fit to competition data in our system.

The models assume that we can accurately represent perennial population growth by tracking perennial seeds and adults, without regard to age or size differences between adults (at least one year old). Individual variation in the perennial adult fecundity and survival data includes any differences due to age and size, and is represented in the posterior distribution of parameter values (see *Statistical models*). We assume that dormant seed banks are not important for the population growth of either species, i.e., that seeds that do not germinate in their first year die (Bartolome 1979, Chiariello 1989).

#### *Statistical models*

We used Bayesian models to fit demographic model parameters from the raw data from multiple studies. The models combine prior distributions that describe the a priori probability assigned to different parameter values, based on previous information or assumptions, with empirical data. The resulting posterior distributions describe the probability that a parameter takes a particular value given the data, and they provide an estimate of parameter uncertainty. We fit Bayesian models with both “uninformative” priors, which contained minimal information beyond restricting parameters to their biologically meaningful ranges, and “informative” priors, which used our knowledge of the system to place greater prior probability on values deemed more likely a priori. This second set of models allowed us to constrain uncertainty around parameter values based on our knowledge of the system, while still allowing the data to inform the posterior distributions. Because the data strongly informed most parameters, differences between the informative and uninformative prior models are minimal. Appendix B: Figs. B1–B8 show the raw data and fitted parameter distributions for informative and uninformative priors. Results were qualitatively similar between the models, so we present only the results from the informative prior models hereafter. Appendix B: Figs. B9–B11 show the bivariate correlations between parameters that were fitted together:  $\lambda_a$ ,  $\alpha_{aa}$ , and  $\alpha_{ap}$ ;  $\lambda_p$ ,  $\alpha_{pa}$ , and  $\alpha_{pp}$ ; and  $s_s$ ,  $\alpha_{sa}$ ,  $\alpha_{ss}$ , and  $\alpha_{sp}$ . Other parameters were fitted independently from separate data, and were not correlated.

All model parameters and their definitions, Bayesian model structures, posterior means, 95% highest posterior density intervals, and data sources are listed in Appendix A: Table A1. Highest posterior density (HPD) intervals are a type of credible interval that indicate the region of most probable parameter values that together constitute 95% of the posterior probability. We had no

data to inform the competitive effects of perennial seedlings on annuals and perennial adults. Because perennial seedlings are often smaller than annual seedlings (Garnier 1992), we assumed that their competitive effects were less than or equal to the corresponding competitive effect of annuals. To do so, we reparameterized the models by setting  $\alpha_{as} = \phi\alpha_{aa}$  and  $\alpha_{ps} = \phi\alpha_{pa}$ , where  $\phi$  is uniformly distributed from zero to one. Data to parameterize the model came from many published studies (Dyer et al. 1996, Dyer and Rice 1997, Wille et al. 1998, Hamilton et al. 1999, Brown and Rice 2000, Dyer 2003, Corbin and D’Antonio 2004, Malmstrom et al. 2005, Buisson et al. 2008, Seabloom 2011, Wainwright et al. 2012, Stahlheber and D’Antonio 2014), and one unpublished study (N. A. Molinari and C. M. D’Antonio, *unpublished data*). These studies measure plant demographic rates such as seed production, germination, and survival in the field as part of broader ecological experiments. Some studies include both annual and perennial grasses, while others include just one or the other. We fit parameters using the raw data extracted from these studies and the Bayesian models described in Appendix A: Table A1.

We fit all models in R and JAGS using the “rjags” package (Plummer 2003, R Development Core Team 2012). For each parameter or group of parameters, we sampled from the posterior distribution by running two Markov chain Monte Carlo (MCMC) chains, each for a 5000-step burn-in period followed by 5000 additional steps. We thinned the samples and saved a total of 2000 samples from the joint posterior distribution of the parameters (hereafter, parameter samples).

#### *Model analyses*

Growth rates when rare (GRWR), also called invasion growth rates, are a key metric for the outcome of competition that measure the per capita growth rate of a population when it is rare and its competitor is at equilibrium. Coexistence is stable when both species can increase when rare, and when only one species can increase when rare it excludes the other species (Turelli 1978). As defined here, priority effects occur when neither species can invade when rare, but either species can exclude the other when initially more common. We calculated growth rates when rare by simulation, where a growth rate when rare greater than or equal to one permits invasion. To calculate growth rates when rare, we allowed the resident species to equilibrate, then introduced the focal species at a density of  $N_a = 1$  for the annual or  $N_s = N_p = 0.5$  for the perennial, and calculated its per capita growth rate. For the perennial, we calculated the growth rate as the dominant eigenvalue of the matrix of transition rates between the two life stages (Mordecai 2013).

We addressed our first and second questions about the mean and the uncertainty around the outcome of competition by calculating annual and perennial growth rates when rare for each parameter sample. From this



posterior distribution of model outcomes, we calculated a mean and 95% HPD interval.

To address our third question, we performed sensitivity analyses by examining how changes in the individual demographic traits affected the annual and perennial growth rates when rare. For a local sensitivity analysis, we added  $\pm 5\%$  to the mean value of a focal parameter and calculated the percentage of change in growth rates when rare with the remaining parameters fixed at their mean values. We then varied focal parameters across a broader range, across all posterior samples of other parameters, assessing the amount of change required to alter the qualitative outcome of competition. In addition, we manipulated all per capita competition coefficients ( $\alpha$ 's) simultaneously from 0% to 100% of their estimated value to simulate the effect of lowering competition for all populations (e.g., through a management intervention such as spring watering).

Demographic rates may co-vary due to life history trade-offs, individual variation in condition, or other factors. Because the data for various demographic parameters came from different studies, and in some cases from different species, we were unable to estimate the correlations between the parameters (exceptions are the fecundity and seedling summer survival parameters fitted along with competition coefficients; Appendix B: Figs. B9–B11). To address how correlations between parameters would affect the outcome of competition, we resampled from the posterior distribution of parameters in a manner that introduced a correlation of  $\pm 0.5$  to a pair of focal parameters, while keeping the remaining parameters uncorrelated. We calculated growth rates when rare for this new group of 2000 parameter sets. In this analysis, we maintained the existing correlation structure between parameters fitted together. We explored the impact of positive and negative correlations between annual fecundity ( $\lambda_a$ ,  $\alpha_{aa}$ ,  $\alpha_{as}$ ,  $\alpha_{ap}$ ) and germination ( $g_a$ ); perennial fecundity ( $\lambda_p$ ,  $\alpha_{pa}$ ,  $\alpha_{ps}$ ,  $\alpha_{pp}$ ) and germination ( $g_s$ ); perennial fecundity ( $\lambda_p$ ,  $\alpha_{pa}$ ,  $\alpha_{ps}$ ,  $\alpha_{pp}$ ) and adult survival ( $s_p$ ); and perennial germination ( $g_s$ ) and seedling survival ( $s_s$ ,  $\alpha_{sa}$ ,  $\alpha_{ss}$ ,  $\alpha_{sp}$ ).

For the fourth question, we examined how uncertainty in demographic processes contributed to uncertainty in model predictions. To do this, we calculated the width of 95% HPD intervals on growth rates when rare when a single parameter or set of parameters was sampled from its posterior distribution while the other parameters were fixed at their posterior means. This provides an estimate of uncertainty in model predictions due to a particular model parameter. We then calculated the proportion of total model uncertainty explained by a particular parameter by dividing this value by the width of 95% HPD intervals on growth rates when rare when all parameters were sampled from their posterior distributions simultaneously. In this analysis, we sampled all parameters that were fitted from the same data (e.g.,  $\lambda$ 's and  $\alpha$ 's) together to preserve their correlation structure.

## RESULTS

The population growth model predicts that the most likely outcome of annual and perennial grass interac-

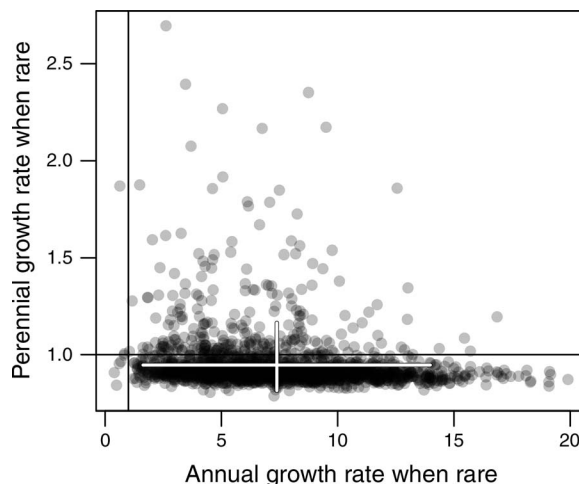


FIG. 1. Outcome of competition for annual (x-axis) and perennial (y-axis) grass species, as measured by growth rates when rare (GRWR). Each species can persist when its GRWR exceeds one (black lines). Points represent GRWR calculated across samples from the posterior distribution of parameters. White crossed lines indicate the 95% highest posterior density (HPD) interval on each species GRWR.

tions is annual dominance, with perennial competitive exclusion occurring for 85% of parameter samples. Coexistence is the next most likely (14%), and priority effects and perennial dominance are both highly unlikely outcomes of competition ( $<1\%$ ), given the distribution of parameter estimates (Fig. 1). On average, the growth rate when rare of the annual grass was 7.42 individuals per individual per year (95% HPD interval: 1.10–13.88), while that of the perennial was 0.95 (95% HPD interval: 0.81–1.17), where a value of at least one indicates stable persistence. The most likely outcome for the annual is stable persistence, but for the perennial the posterior distribution spans both exclusion and persistence.

The local sensitivity analysis pinpointed several parameters that strongly influenced the competitive outcome. Annual grass growth rates when rare were most sensitive to annual fecundity and emergence ( $\lambda_a$  and  $g_a$ ) and perennial adult over-summer survival ( $s_p$ ) (Fig. 2A). The latter effect is indirect, mediated by a larger perennial population imposing larger competitive effects on annuals. Perennial grass growth rates when rare were most sensitive to over-summer survival of adults ( $s_p$ ) and largely insensitive to small perturbations of other parameters (Fig. 2B). Notably, increasing perennial adult over-summer survival had a much larger proportional effect on the annual than on the perennial, because the annual growth rate was more responsive to variation in demographic parameters in general. The effects of subtracting 5% from the parameters were similar in magnitude in the opposite direction.

Varying demographic parameters across broader ranges to reflect possible effects of management or changing

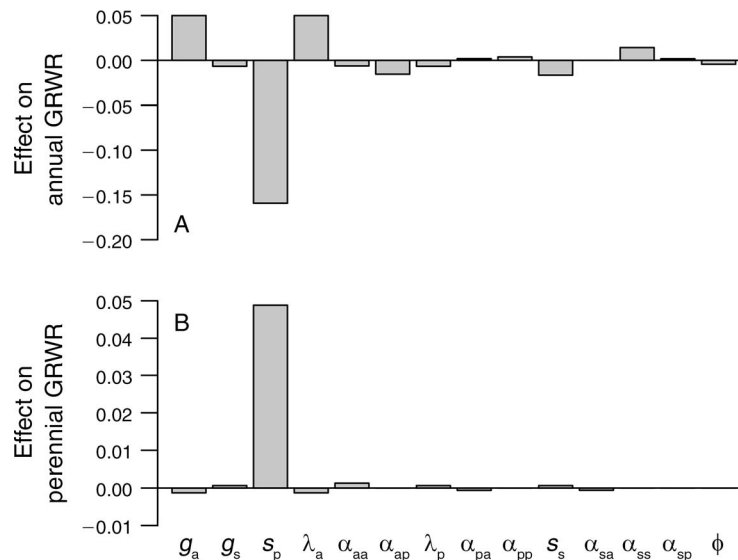


FIG. 2. Analysis of the sensitivity of growth rates when rare (GRWR) to the model parameters. We set all parameters to their posterior mean values, and then calculated the proportional change in GRWR when each parameter individually was increased by 5%, for the (A) annual and (B) perennial grasses. The effect of 5% decreases were similar but opposite in direction (not shown). Parameters are emergence ( $g_a$  and  $g_s$ ), perennial adult survival ( $s_p$ ), fecundity in the absence of competition ( $\lambda_a$  and  $\lambda_p$ ), per capita competitive effects of annuals and perennial adults on annual seed production ( $\alpha_{aa}$  and  $\alpha_{ap}$ ), per capita competitive effects of annuals and perennial adults on perennial seed production ( $\alpha_{pa}$  and  $\alpha_{pp}$ ), perennial seedling survival in the absence of competition ( $s_s$ ), per capita competitive effects of annuals, perennial seedlings, and perennial adults on perennial seedling survival ( $\alpha_{sa}$ ,  $\alpha_{ss}$ , and  $\alpha_{sp}$ ), and the parameter scaling per capita competitive effects of perennial seedlings relative to the competitive effects of annuals ( $\phi$ ), where the subscripts a, s, and p represent annual seeds, perennial seeds, and perennial adults, respectively.

climate also affected competitive outcomes. As expected, the survival of perennial seedlings ( $s_s$ ) and adults ( $s_p$ ) had negative effects on annual growth rate when rare and positive effects on perennial growth rate when rare (Appendix B: Fig. B12). The perennial could stably persist on average when either  $s_s = 0.56$  or  $s_p = 0.93$ , respectively (Appendix B: Fig. B12B, D), whereas the mean estimated values were  $s_s = 0.29$  and  $s_p = 0.88$ . There was no evidence that increasing seedling and adult survival together synergistically affected growth rates when rare. Reducing annual seed production ( $\lambda_a$ ) and emergence ( $g_a$ ) had the same proportional effects: they decreased the annual growth rate when rare and increased that of the perennial (Appendix B: Fig. B13). An 87% reduction in annual seed production or emergence would be required to exclude the annual on average, whereas only a 32% reduction was required to allow perennial grasses to persist on average. Increasing perennial emergence had very little effect on perennial and annual growth rates when rare (Appendix B: Fig. B14). Moreover, a 154% increase in annual intraspecific competition, a 56% and 62% reduction in annual competitive effects on perennial adults and seedlings, respectively, or a 204% increase in perennial fecundity would be required for stable perennial persistence, on average.

Previous work suggests that water limitation is a main source of competition in this system (Hamilton et al. 1999), so we expect that relieving competition by supplementing water supply during the growing season

would decrease all pairwise competition coefficients. When we assumed that watering reduced all competition coefficients proportionally, we found no effect of alleviating competition on species persistence (except when competition was reduced to zero; Appendix B: Fig. B15). This somewhat surprising result arises because increased competitor density offsets the beneficial effects of alleviating per capita competition. By contrast, watering after annuals have senesced would differentially benefit perennial seed production and survival, likely promoting perennial persistence.

Given the lack of empirical data, we tested the sensitivity of model predictions to assumptions about perennial seedling competitive effects on annuals and perennial adults by allowing  $\phi$  to range from zero (no competitive effects) to two (maximum competitive effects twice as large as those of annuals). We found that perennial seedling competitive effects on annuals and perennial adults generally had negligible effects on the outcome of competition. For perennials, this was because an invading species is not affected by intraspecific competition, due to its relative rarity. For annuals, this was because effects of perennial seedling competitors were largely offsetting, by reducing both perennial and annual seed production (Appendix B: Fig. B16). The maximum reduction in annual growth was 19% when  $\phi$  was constrained to be no greater than 1, as we considered in the main model.

Introducing correlations between parameters, which would occur if life history trade-offs or variation in individual condition affected multiple demographic rates simultaneously, had no effect on the outcome of competition on average (Appendix B: Figs. B17 and B18). However, correlations changed annual growth rates when rare by between +86% and –178%, and changed perennial growth rates when rare by between +29% and –25% (95% HPD intervals; Appendix B: Figs. B17 and B18). Although correlated parameters could have large effects on the outcome of competition, their average effect was near zero, suggesting that the lack of correlation between demographic rates is unlikely to systematically bias the results.

As a group, the sensitivity analyses suggest that increasing the survival of adult bunchgrasses would most effectively promote perennial population growth. Although inter- and intraspecific competitive effects of annuals also substantially influenced perennial persistence, it would be difficult to alter these effects in the field without also altering the opposing competitive effects that benefit perennial population growth.

Uncertainty in demographic parameter estimates contributed to the uncertainty in model predictions differently for annuals and perennials. The variation in annual growth rates when rare was driven largely by uncertainty in annual emergence, perennial seedling survival, and annual seed production (Fig. 3A). In turn, perennial seedling survival and annual seed production depend on competition coefficients. By contrast, uncertainty in perennial growth rates was generally half that of annual growth rates (again because the perennial growth rate is less responsive to variation in demographic rates), and perennial adult and seedling over-summer survival and perennial seed production were the largest contributors (Fig. 3B). Again, perennial seedling survival and seed production depend on competition coefficients. Competitive effects of perennial seedlings had very little impact on uncertainty for either species, despite having no empirical data from which to estimate these parameters.

#### DISCUSSION

The model suggests that California native perennial grass populations hover near the boundary between coexistence with exotic annual grasses and competitive exclusion, with exclusion more likely on average (Fig. 1). Once introduced, exotic annual grasses are predicted to stably persist in the long term; it is highly unlikely that perennials could exclude annuals under any realistic parameter values. By contrast, although the perennial bunchgrass is competitively excluded on average, small, biologically reasonable shifts in demographic rates could promote long-term perennial persistence. Such shifts could be found across the wide climatic range of grass-dominated ecosystems in California.

The best targets for future research to improve the accuracy of predictions for perennials are adult over-

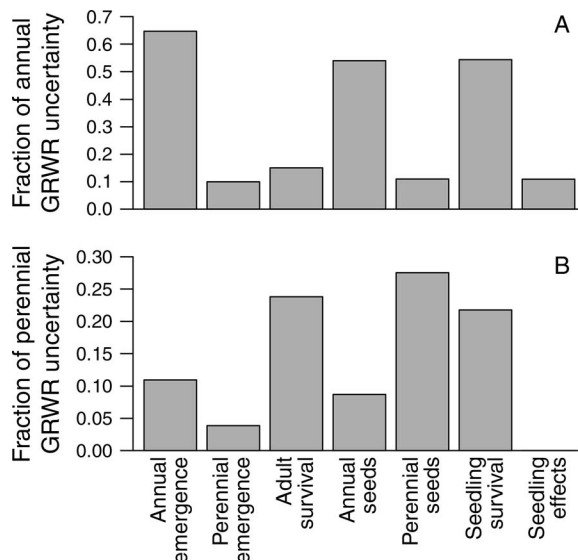


FIG. 3. Analysis of how uncertainty in each parameter or group of parameters contributes to overall model uncertainty. Bars show the width of the 95% HPD interval on growth rates when rare (GRWR) when only the focal parameter varied, divided by the width of the interval when all parameters varied, across posterior parameter samples. Uncertainty analyses are for the GRWR of the (A) annual and (B) perennial grasses. The parameters corresponding to each bar are: annual emergence ( $g_a$ ), perennial emergence ( $g_p$ ), adult survival ( $s_p$ ), annual seeds ( $\lambda_a$ ,  $\alpha_{aa}$ ,  $\alpha_{ap}$ ), perennial seeds ( $\lambda_p$ ,  $\alpha_{pa}$ ,  $\alpha_{pp}$ ), seedling survival ( $s_s$ ,  $\alpha_{sa}$ ,  $\alpha_{ss}$ ,  $\alpha_{sp}$ ), and seedling effects on perennial adult and annual competitors ( $\phi$ ).

summer survival and the competitive effects of annuals on both perennial seedlings and adults (Fig. 3B). Annual persistence is highly likely, but the parameters that most drive the uncertainty in the magnitude of annual grass growth rates are annual emergence and the competitive effects of adult perennials on annual seed production (Fig. 3A). We emphasize that, although many previous studies have measured competition between exotic annual and native perennial grasses in California (particularly the competitive effect of annuals on perennials; Dyer and Rice 1997, Hamilton et al. 1999, Seabloom et al. 2003b, Corbin and D'Antonio 2004), most measure the effect of competition at the population scale, rather than at the per capita scale that demographic approaches such as this model require. For example, both Dyer and Rice (1997) and Hamilton et al. (1999) examined impacts of a monoculture of annual grasses on individual bunchgrass plants (*S. pulchra*) but not vice versa, and inter- vs. intraspecific effects are also rarely evaluated. The data needed to accurately estimate the outcome of competition in models are per capita seed production or survival as a function of competitor density and species, as shown in Appendix B: Figs. B2–B4.

The demographic impact of management actions depends on the sensitivity of population growth to demographic rates. We found that increasing perennial over-summer survival, particularly in the typically long-

lived adult bunchgrass stage, is most likely to promote perennial population growth. This suggests that management actions that selectively promote perennial over-summer survival could be critical for enhancing perennial persistence, since perennial grass individuals in California can live >100 years (Hamilton et al. 2002). Hence, promoting survival through initial stages of adulthood by reducing soil disturbance and potentially adding late-season water could add to population stability for these species. However, such interventions must promote perennial survival in a way that does not concomitantly increase competition with annuals. Likewise, management strategies that remove standing biomass and reduce seed set of annual grasses (targeted fire or seasonal cattle grazing) could selectively favor perennials grasses. Such manipulations must be fairly high intensity to enable perennial persistence (32% reduction), a level consistent with residual dry-matter reductions in experimental and managed grazing areas (Bartolome et al. 2007). Annual grass biomass and seed reduction would have to be even more intense to exclude annuals completely (87% reduction), and long-lived seed banks would impede annual exclusion considerably. In fact, seasonal grazing can enhance the density and cover of native perennial grasses in some settings in California, based on a recent meta-analysis (Stahlheber and D'Antonio 2013).

Notably, actions that reduce per capita competitive effects on conspecific and heterospecific individuals even do not affect the qualitative outcome of competition (coexistence, competitive exclusion, or priority effects), even though they may have dramatic effects on the equilibrium abundance. This is likely to include watering during the growing season, which alleviates both inter-specific and intraspecific competition. This is supported by water-manipulation studies, which have shown that enhanced rainfall during the growing season in California grasslands has little effect on compositional change or perennial grass recruitment or survival (e.g., Seabloom et al. 2003b, Suttle and Thomsen 2007). Conversely, extension of the rainy season (shortening of the summer drought through late-spring water addition) can enhance perennial grass survival with little direct response of the annuals to rainfall (Suttle and Thomsen 2007). In addition to effects of moisture on survival, a previous model of competition for nitrogen and water in a southern California grassland suggested that perennials had greater competitive ability at higher soil moisture levels, allowing them to coexist with annuals when growing season rainfall exceeded 0.74 mm/d (Everard et al. 2010).

In this paper we examine how demographic rates influence the outcome of competition for “characteristic” annual and perennial grass species, using data from multiple species to parameterize the model (Appendix A: Table A1). We do so because current data are insufficient to fully parameterize the model for individual focal species. Ideally, future work would measure the full suite of plant demographic rates in Eq. 1–4 for the

common California native (e.g., *Stipa pulchra*, *Elymus glaucus*, *Poa secunda*) and exotic (e.g., *Avena barbata*, *Avena fatua*, *Bromus hordeaceus*, *Bromus diandrus*) grass species. Moreover, full demographic profiles of individual species would allow the exploration of competition between annual species and between perennial species. This would provide more specific, quantitative predictions of the outcome of competition.

Perennial population growth is sensitive to adult survival in several other systems. In models of established populations of the invasive species *Cytisus scoparius* (Scotch broom), population growth had high elasticity to the survival of large adults (elasticities differed at the invasion front) (Parker 2000). The invasive old-field perennial plant *Dipsacus sylvestris* (teasel) also had high elasticity in the large adult life history transitions, but the Neotropical understory plant *Calathea ovandensis* did not (Neubert and Caswell 2000). A native perennial bunchgrass in exotic annual-invaded grasslands in Utah (USA) showed similar sensitivity to perennial adult survival (Mordecai 2013).

The Utah grassland system shows additional similarities to the focal California system. In both Utah and California grasslands, the confidence intervals on the perennial growth rate when rare were far lower, narrower, and closer to one than those of the annual (Mordecai 2013). This may reflect the trade-off in life history strategy between relatively small, fast-growing annuals and the larger, slower growing perennials, which may differentially invest in productivity under favorable conditions vs. long-term survival (Garnier 1992). In the Utah grassland system, annual and perennial grasses do not compete very strongly, leading to large niche differences that promote coexistence (Mordecai 2013); however, in the California grassland system, the annuals and perennials compete strongly, increasing the likelihood of competitive exclusion.

Priority effects or alternative stable states have been suggested and experimentally supported in California grassland ecosystems because of spatial variation in bunchgrass persistence (Bartolome and Gemmill 1981, Seabloom et al. 2003b, Corbin and D'Antonio 2004). The model suggests that priority effects, in which established populations of both annuals and perennials can each prevent the invasion of the other, are unlikely based on the available empirical data. Note that priority effects have been defined differently in other studies (e.g., Corbin and D'Antonio 2004, Wainwright et al. 2012). Instead, variation in the field may in some cases be indicative of small differences in local conditions, such as climate, soil quality, and disturbance, which shift the outcome between perennial competitive exclusion and coexistence. Studies that document perennial grass persistence (e.g., Stromberg and Griffin 1996, Hamilton et al. 2002, Jackson and Bartolome 2002) and priority effects (Corbin and D'Antonio 2004) are largely in northern or coastal California. In these settings, the length of the summer drought is shorter or is tempered



by summer fog, so adult survival of bunchgrasses is likely greater, consistent with the conditions needed for coexistence that we identify here. Indeed, in these sites exotic perennial grasses are presenting a challenge to native perennial species (Corbin and D'Antonio 2010). Although the model does not explicitly address local environmental variation, it does implicitly incorporate environmental variation by combining data from a range of species and geography to estimate parameters. Nonetheless, additional information from plants growing under differing experimental or natural conditions such as grazing regime, soil type (e.g., serpentine vs. non-serpentine), rainfall regime, and habitat type (e.g., under the oak canopy vs. open grassland) would enable models to further differentiate the impact of spatial and temporal variation in demographic parameters on the outcome of competition.

European annual grass invasion has also occurred in other mediterranean climate regions in South Africa, Chile, and Australia, particularly following cattle grazing (Fox 1990). These invasions can impact community composition and ecosystem function through their effects on water and nutrient uptake, light interception, resource supply, microclimate, and fire cycles (D'Antonio and Vitousek 1992). Because many of the same genera and species of exotic annual grasses in our study have also invaded other mediterranean climate regions, similar dynamics may be at play in these other regions. Thus, adult survival may be critical for the survival of perennial native populations in many different communities and an important target of management activities. In these and other heavily invaded ecosystems, understanding invader impacts on the long-term persistence of native species presents a major challenge. Demographic approaches can help ecologists and managers to understand and mitigate impacts of invasive species on native biodiversity, and to avoid ineffective and counterproductive interventions.

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## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A and B and the Supplement are available online: <http://dx.doi.org/10.1890/14-2023.1.sm>