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Effects of Temporal Variability on Rare Plant Persistence in Annual Systems

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ABSTRACT: Traditional conservation biology regards environmental fluctuations as detrimental to persistence, reducing long-term average growth rates and increasing the probability of extinction. By contrast, coexistence models from community ecology suggest that for species with dormancy, environmental fluctuations may be essential for persistence in competitive communities. We used models based on California grasslands to examine the influence of interannual fluctuations in the environment on the persistence of rare forbs competing with exotic grasses. Despite grasses and forbs independently possessing high fecundity in the same types of years, interspecific differences in germination biology and dormancy caused the rare forb to benefit from variation in the environment. Owing to the buildup of grass competitors, consecutive favorable years proved highly detrimental to forb persistence. Consequently, negative temporal autocorrelation, a low probability of a favorable year, and high variation in year quality all benefited the forb. In addition, the litter produced by grasses in a previously favorable year benefited forb persistence by inhibiting its germination into highly competitive grass environments. We conclude that contrary to conventional predictions of conservation and population biology, yearly fluctuations in climate may be essential for the persistence of rare species in invaded habitats.

Keywords: environmental fluctuations, rarity, exotic invasion, grasslands.

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Growing concerns over the persistence of threatened and endangered species have rekindled interest in one of the classic problems in ecology: how rare species persist (Griggs 1940; Roughgarden 1975; Harper 1981; Leigh 1981; Grubb 1986). Motivating interest in this problem is the expectation that rare species, with their small populations, are vulnerable to extinction from the natural variability ubiquitous in ecological systems. A large literature in conservation biology examines how environmental stochasticity threatens rare species persistence (Leigh 1981; Lande 1988; Boyce 1992; Menges 2000). Because of the geometric nature of population growth, variation in demographic parameters reduces long-term average growth rates and increases the probability of extinction (Tuljapurkar 1990; Boyce 1992; Menges 1998, 2000).

In contrast to this well-accepted principle in conservation biology, a very different prediction concerning the effects of environmental variability emerges from theory in community ecology (Higgins et al. 2000). In what are often called "storage effect" models (Chesson 1982, 1990, 1994; Ellner 1984, 1987; Chesson and Huntly 1989; Rees and Long 1992), temporal variation in the environment is essential to the coexistence of species. In these models, different species benefit from different types of years and have some mechanism for storing the benefits of favorable years, such as seed banks or long-lived adults. Coexistence is determined using invasibility conditions, meaning all species increase when rare in stochastic environments with their competitors at equilibrium. Thus, model predictions directly concern rare species persistence (Higgins et al. 2000) and are contradictory to predictions from more simple population viability models.

Several differences between the conservation biology and community ecology approaches to the effects of environmental fluctuations could explain the disparate results. Among the most obvious is the shift from a single species to a more complex multispecies dynamical system. In this context, storage effect models do not dispute the mathematical arguments underlying negative effects of stochasticity on geometric population growth (Efford 2001). Rather, they suggest that in more complex systems, where

there are species-specific responses to variation in the environment and competition, environmental stochasticity may favor persistence. This is a significant realization because the importance of incorporating the dynamics of the surrounding community in population viability analyses remains unclear. Although some studies have argued that building multispecies models may be important for understanding the viability of strongly interacting populations (Boyce 1992), few have done so. This is not to say that current approaches ignore species interactions, because single species models parameterized in the field may implicitly include processes such as competition. For example, without competition from the surrounding community, vital rates measured in the field would otherwise be greater. However, storage effect models suggest that when the focal species and the surrounding community respond differently to variation in the environment and when this is explicitly modeled, very different predictions concerning the effects of environmental fluctuations on persistence may emerge.

One major life-history process causing plant species to differ in their response to the environment is their seed dormancy and germination biology (Ellner 1984, 1987; Chesson 1990; Rees and Long 1992). Species possess wide variation in germination rates, germination cues, and seed longevity (Rees and Long 1992; Baskin and Baskin 2001). Thus, dormancy and germination biology are almost certain to strongly influence whether temporal variability favors or inhibits persistence. Unfortunately, seed vital rates can be difficult to measure (Pavlik et al. 1993; Doak et al. 2002), and our understanding of how seed banks influence rare plant population dynamics is just developing (Doak et al. 2002). With limited empirical evidence, models provide an excellent opportunity to explore how seed banks modulate the effects of variability on persistence in multispecies systems. In addition, despite the large literature on coexistence achieved through differences in germination (Ellner 1984, 1987; Chesson 1990), this work has yet to be applied to the persistence of rare plant populations (Higgins et al. 2000).

In this article, we explore models based on annual plant–dominated grasslands of California to ask how temporal variation in the environment influences rare plant persistence in competitive systems. We first summarize existing knowledge about plant life histories in the study system and then use models to show that temporal variability should positively affect the persistence of rare annuals with seedbanks in these grasslands. This prediction is analogous to those from storage effect models but arises from the basic biology of the system. Importantly, rather than species specializing in different types of years as is typical in storage effect models, we demonstrate a novel mechanism for persistence, where specialization occurs on different sequences of year types. We use these results to explore the systems in which population viability models must incorporate the dynamics of the surrounding community to accurately assess the effects of environmental variability.

Study System

California grasslands provide ideal systems for examining the research question because they contain a diversity of rare annual plants persisting in a climatically variable habitat dominated by exotic annual grasses (Heady et al. 1977). The annual nature of the system facilitates the development of mathematical models that reasonably approximate population dynamics (Levine and Rees 2002). In addition, a large body of empirical work examines the processes important for the structure of these systems, providing reasonable parameters for our models.

California's Mediterranean climate is characterized by a cool rainy season from winter through spring, followed by a summer drought through early fall. The timing and quantity of rainfall varies tremendously from year to year (Heady et al. 1977). Most regions experience four- to five-fold variation in total annual precipitation over a period of several decades (Schonher and Nicholson 1989; Haston and Michaelsen 1997). Years also differ markedly in the timing of rainfall, and midseason droughts, for example, can cause high seedling mortality (Young et al. 1981).

Parallel to these climatic fluctuations is large interannual variation in the abundance of California grassland annuals (Talbot et al. 1939; Heady 1958). Most species germinate with the first major rains in fall or winter and senesce after the rains end in late spring. Water is the dominant limiting resource in these systems, and numerous studies have correlated variation in grassland composition and production with variability in precipitation (Murphy 1970; Duncan and Woodmansee 1975; Pitt and Heady 1978; Young et al. 1981). In large part, the temporal variability of these grasslands and their sensitivity to climatic fluctuations relate to the annual life history of the common grasses, nearly all of which are exotic. European annual grasses in the genera *Bromus*, *Avena*, and *Hordeum* now dominate a habitat once covered by native bunchgrasses and to a lesser extent shrubs. Numerous studies have documented the ability of the exotic grasses to uptake water at shallow depths in the soil and shade their competitors (Holmes and Rice 1996; Dyer and Rice 1997; Brown and Rice 2000; Carlsen et al. 2000). In fact, their invasion is thought to have driven a large decline in native annuals (Heady et al. 1977; Dyer and Rice 1997).

Existing within this fluctuating habitat are a wide diversity of annual forbs (nonleguminous dicots), many of which are listed as rare and endangered by the California

Native Plant Society. Among the factors believed to threaten these species, the most prominent include the surrounding community of exotic annual grasses and interannual variation in rainfall (Hobbs and Huenneke 1992; Pavlik et al. 1993; Carlsen et al. 2000; Parsons and Whelchel 2000; Seabloom et al. 2003). Nonetheless, even with a potentially reduced range and population size, many native annuals have persisted with exotic grasses since their invasion in the mid-1800s. The effect of interannual fluctuations in the environment on this persistence remains poorly understood.

One of the major advantages the rare annual forbs might have in their battle for persistence with exotic grasses is that the forbs often have well-developed seed banks while the grasses do not. Dormancy is a common feature of winter annual dicots in general and documented specifically for several California forbs (Rice 1985; Pavlik et al. 1993; Vivrette 1999). It is particularly well represented in the genera that dominate the California native annual forb flora (Pavlik et al. 1993; Bertiller 1998; Vivrette 1999; Baskin and Baskin 2001; Cavieres and Arroyo 2001; N. Huntly and P. Chesson, unpublished manuscript) and is further suggested by population dynamic observations where species virtually disappear in some years, only to return to large numbers in subsequent years (K. McEachern, unpublished data). In contrast to the forbs, the exotic grasses, like grasses in general, have little between-year dormancy. The most common species have flexible germination requirements and germinate nearly all their seeds each growing season (Marshall and Jain 1970; Bartolome 1979; Wu and Jain 1979; Roberts 1981; Young et al. 1981; Jain 1982; Ewing and Menke 1983; Pavlik et al. 1993).

Annual Plant Population Models

To model the population dynamics of a rare annual forb with a seed bank, we begin with the population model developed by Watkinson (1980), Pacala (1986), and Rees and Long (1992):

$$F_{t+1} = (1 - g)(1 - d)F_t + \frac{\lambda g F_t}{c + g F_t}, \qquad (1)$$

where F_t is the number of seeds in an annual forb population at the beginning of the growing season of year t prior to germination, g is the fraction of seeds that germinate, d is the death rate of ungerminated seeds in the soil, and λ is the number of seeds produced per individual in the absence of intraspecific competition that survive to the start of the growing season; c is a constant influencing the rate at which seed production changes with density and is usually set equal to 1 (Watkinson 1980; Pacala 1986; Ellner 1987; Chesson 1990; Levine and Rees 2002). The

first part of the sum is the number of seeds that carry over in the seed bank—those that do not germinate or die. The second part is the number of seeds added through germination and then reproduction divided by intraspecific competition (the competition coefficient = 1). In contrast to the age-structured matrix model approach of Kalisz and McPeek (1993), this model makes the simplifying assumption of constant seed mortality rates but has the added complexity of density-dependent seed production.

A two-species competition model including a forb (F_t) and a grass (G_t) follows from model (1) (Ellner 1984; Pacala 1986; Chesson 1990; Venable et al. 1993; Rees and Westoby 1997; all examine similar models):

$$F_{t+1} = (1 - g_F)(1 - d_F)F_t + \frac{\lambda_F g_F F_t}{c + g_F F_t + \alpha_{FG} g_G G_t}, \qquad (2)$$

$$G_{t+1} = (1 - g_G)(1 - d_G)G_t + \frac{\lambda_G g_G G_t}{c + g_G G_t + \alpha_{GF} g_F F_t}, \qquad (3)$$

where α_{FG} and α_{GF} are the competition coefficients for grass effects on the forb and forb effects on the grass, and the F and G subscripts denote the forb and grass-specific demographic rates. More complex than in model (1), competition in this model includes both intra- and interspecific effects. This model forms the basis on which our simulations and analyses are developed.

Persistence in Variable Environments

We examine the persistence of the forb in the most basic variable environment, one with simply favorable and unfavorable years (Ellner 1984; Chesson 1990; Venable et al. 1993). With respect to California grassland systems, favorable years might correspond to years of high rainfall and unfavorable years to drought years. The specific rainfall pattern that makes for favorable and unfavorable years in California grasslands can be quite complex (Talbot et al. 1939; Heady 1958; Pitt and Heady 1978), but our model merely requires variability in year quality and does not specify its cause. Year quality influences dynamics via its effects on germination and fecundity. Thus, in an environment varying between years that are favorable ($+$) and unfavorable ($-$) for these species, germination and fecundity vary between g_+ and λ_+ and g_- and λ_-.

The existing literature on California grasslands permits us to explore model simulations with parameters that are generally reasonable for grasses and forbs in these systems. Nonetheless, the different forbs and grasses that make up these communities encompass a diversity of demographic rates that cannot be represented by a single set of parameter combinations. Moreover, some parameters, such as those involving the seed bank, are necessarily speculative.

Thus, our approach is to use simulations to introduce the effects of variability on forb persistence in the California grassland environment and then use analytical solutions to explore the wider behavior of the model. All simulations were conducted in R version 1.8 (R Development Core Team 2003), and the code is available in the appendix in the online edition of the *American Naturalist.*

Simulations

Our model focuses specifically on those forbs with long-lived seeds, and thus we assign their annual seed mortality in the soil, $d_F = 0.1$. We assign the competition coefficient for grass effects on the forb, $\alpha_{FG} = 2$, and following an assumption of reciprocal competition, $\alpha_{GF} = 0.5$. With these values, the per capita grass effect on the forb is four times as great as the reverse effect, giving the grass a significant competitive advantage, as documented in the literature (Talbot et al. 1939; Heady et al. 1977; Holmes and Rice 1996; Carlsen et al. 2000). Following demographic data collected for several California rare annual forbs and exotic grasses in years of differing rainfall (Bartolome 1979; Young et al. 1981; L. Fox, unpublished data; K. McEachern, unpublished data), we assume that both the grass and the forb produce six times the seed in favorable years as compared with unfavorable years ($\lambda_+ = 30$, $\lambda_- = 5$).

Our model applies to forbs that germinate most seeds in favorable (wet) years ($g_{F+} = 0.7$) and few seeds in unfavorable (dry) years ($g_{F-} = 0.1$). By contrast, we assume that the grass competitor germinates 90% of its seed in all years ($g_{G+} = g_{G-} = 0.9$; Marshall and Jain 1970; Bartolome 1979; Wu and Jain 1979; Roberts 1981; Young et al. 1981; Pavlik et al. 1993). Grass seed mortality in the soil is assumed to be much greater than that of the forb ($d_G = 0.7$), resulting in little interannual grass carryover of seed, as demonstrated by numerous authors (Bartolome 1979; Roberts 1981; Young et al. 1981; Ewing and Menke 1983; Pavlik et al. 1993).

Simulating the model in equations (2) and (3) with the above parameters shows that the forb persists with the exotic grass in the simplest variable environment, one in which favorable and unfavorable years occur independently at random with an equal probability (fig. 1*A*). The grass, however, dominates. Grass density (mean ± 1 SD of density over 500,000 years = 13.41 ± 9.51) is more than twice as great as that of the forb (6.29 ± 5.08). Moreover, if we look specifically at the germinated fraction of both species (fig. 1*B*) or what we would measure in vegetation sampling, aboveground grass density (12.07 ± 8.56) is almost five times greater than that of the forb (2.52 ± 3.17). This is consistent in a general sense with field observations of California grasslands where forbs are sparse within the grass matrix (Dyer and Rice 1997). Den-

sity can be regarded as being measured over a 10 × 10-cm plot, roughly the area occupied by a single individual in the absence of competition.

By comparing the variable environment results in figure 1*A* to those in constant environments (fig. 1*C*–1*E*), it is apparent that environmental fluctuations are key to forb persistence. The forb quickly drops to a density near 0 in a constantly favorable (fig. 1*C*), constantly unfavorable (fig. 1*D*), or constantly intermediate environment (fig. 1*E*). These positive effects of temporal variability are not the inevitable outcome of examining a two-competitor model in a stochastic environment. Chesson and Huntly (1989) and Chesson (1994) explain that depending on the covariance between the environment and competition, variability can have a positive, negative, or zero effect on coexistence in models like the one examined here. Thus, it is the specific traits of the forb and grass and their response to the environment that underlie our results.

The simulation results also provide clues as to why annual climate fluctuations favor forb persistence. During unfavorable years, as seen from years 19–25 in figure 1*A*, the forb germinates only a small fraction of its seeds and thus declines gradually. If this continues for many years, as seen in the constantly unfavorable environment (fig. 1*D*), the forb goes extinct. More severe declines are observed during consecutive favorable years, as seen in years 37–42. This is because favorable years allow grass populations to build (fig. 1*A*, years 37–42). Thus, in consecutive favorable years, the forb is germinating most of its seed into highly competitive grass environments. This intense grass competition prevents the forb from persisting in constantly favorable (fig. 1*C*) or intermediate (fig. 1*E*) environments.

In contrast, the forb increases in the first favorable year after an unfavorable year. Poor grass seed production in the previous unfavorable year, coupled with little seed bank, keeps grass density low in the current year, even if favorable. This gives forbs the opportunity to exploit the favorable conditions with relatively little grass competition. Thus, forb populations build when the environment fluctuates between favorable and unfavorable years, as can be seen in years 83–90 and to a lesser extent in years 2–7 in figure 1*A*. In sum, though the forb goes extinct in a constantly favorable or unfavorable environment, it persists in an environment that fluctuates between these states by exploiting favorable years after unfavorable years.

Invasion Condition

The simulations suggest that environmental fluctuations may benefit the persistence of a rare forb with a seed bank in this grassland system. To examine how different demographic parameters and variable environments influ-
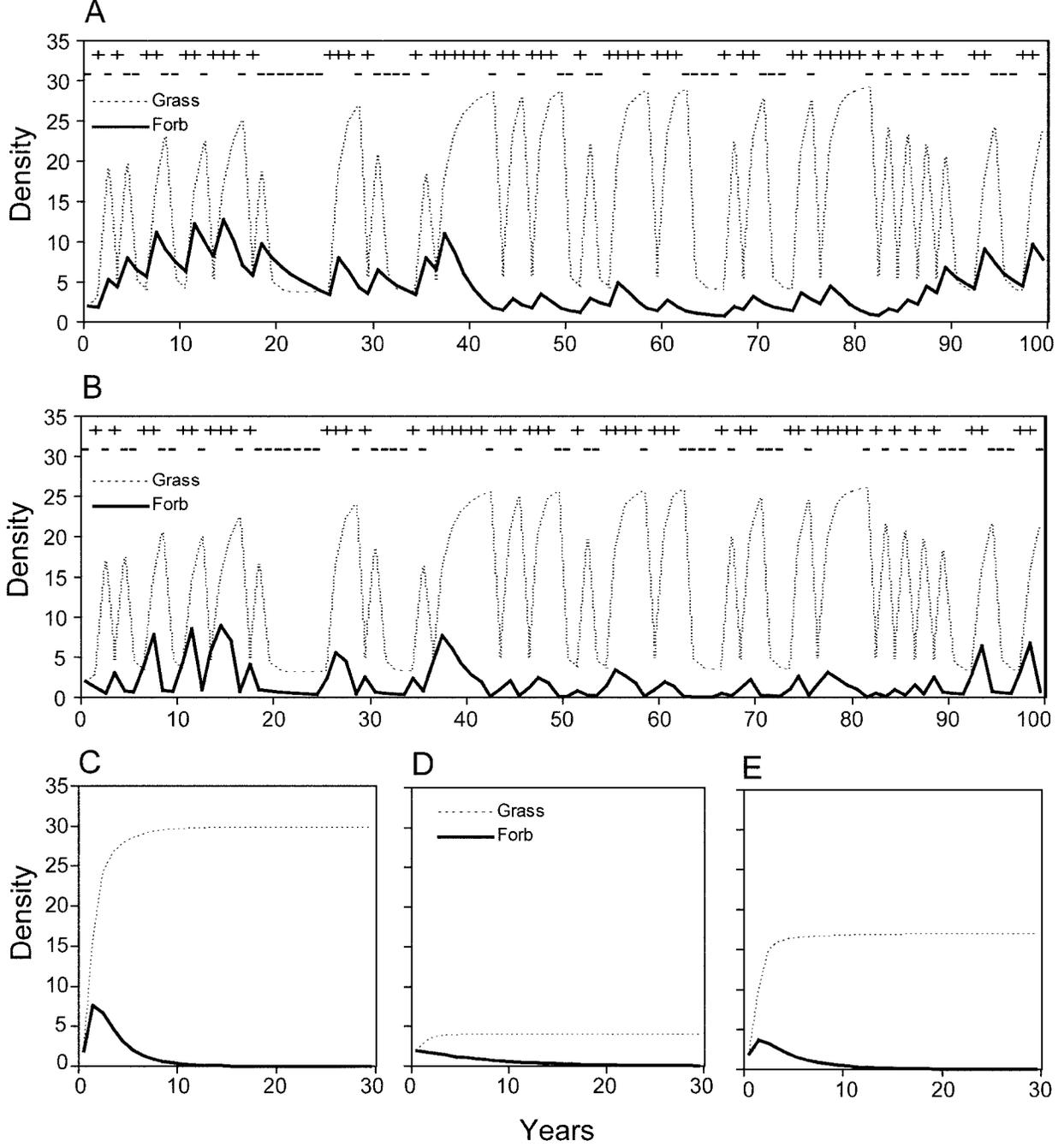
Figure 1: Simulations of a forb and grass competition model (eqq. [2], [3]) based on California grasslands. *A*, Density (germinated and ungerminated seed) in a variable environment with an equal probability of favorable and unfavorable years and no temporal autocorrelation. *B*, Same simulation as in *A*, except only the germinated fraction of the populations are shown. By contrast to persistence in *A* and *B*, the forb declines toward 0 in constantly favorable (*C*) and unfavorable (*D*) environments. In all these simulations, both the grass and the forb produce six times the seed in favorable years as compared with unfavorable years ($\lambda_+ = 30$, $\lambda_- = 5$). Species differ in that the forb has a long-lived seed bank ($d_F = 0.1$) and germinates most of its seed in favorable years ($g_{F+} = 0.7$) and little in unfavorable years ($g_{F-} = 0.1$). In contrast, the grass germinates nearly all its seed in all years ($g_{G+} = g_{G-} = 0.9$) and has low seed longevity ($d_G = 0.7$). The grass, however, has the advantage of being a superior competitor ($\alpha_{FG} = 2$, $\alpha_{GF} = 0.5$). We assume that $c = 1$. See text for parameter justification. In *E*, species are simulated in a constantly intermediate environment ($\lambda_+ = \lambda_- = 17.5$ for both species, $g_F = 0.7$). All simulations begin with two individuals of each species.

ence forb persistence and more rigorously examine the underlying mechanisms, we turn to analytical solutions. We examine the special case where the germination biology is simplified so that the grass has no seed bank ($g_{G+} = g_{G-} = 1$), and the forb germinates all its seeds in favorable years and none in unfavorable years ($g_{F+} = 1$, $g_{F-} = 0$). In addition, following empirical work examining seed production as a function of density in annual plants (Harper 1977), we will assume $c = 0$. As in Ellner (1987), this makes analytical solutions to this model possible. The results also approximate systems where c is not 0, as long as $\lambda_- \gg c$. Although these germination and competition parameters represent a simplified version of the biology outlined in the previous section, we will show through simulation that the qualitative behavior of the model is not changed when the parameters are returned to the values used in figure 1*A*.

With $c = 0$ and complete germination of the grass, equations (2) and (3) can be simplified to

$$F_{t+1} = (1 - g_t)(1 - d)F_t + \frac{\lambda_{F,t} g_t F_t}{g_t F_t + \alpha_{FG} G_t}, \qquad (4)$$

$$G_{t+1} = \frac{\lambda_{G,t} G_t}{G_t + \alpha_{GF} g_t F_t}. \qquad (5)$$

Without a grass seed bank, we drop the *F* and *G* subscripts attached to *g* and *d*, because only the forb possesses these parameters. We add a subscript *t* to fecundity and germination (λ and *g*) to indicate their time dependence. As in the simulations, $\lambda_{F,t} = \lambda_{G,t}$, and both vary between λ_+ and λ_- through time.

From equation (4), the forb's rate of increase when rare ($F_t \ll 1$) is

$$\frac{F_{t+1}}{F_t} = (1 - g_t)(1 - d) + \frac{\lambda_{F,t} g_t}{\alpha_{FG} G_t}, \qquad (6)$$

where germination, fecundity, and grass competition all vary with time. This can be used to calculate the condition for forb persistence in a variable environment following Chesson (1982) and Chesson and Ellner (1989):

$$\left\langle \ln\left(\frac{F_{t+1}}{F_t}\right) \right\rangle_t > 0, \qquad (7)$$

where $\langle \rangle_t$ is the temporal average. This means that on average the forb population tends to increase when rare. This formulation assumes that demographic stochasticity is not important.

Equation (7) can also be regarded as the temporal average of forb population growth rates when rare in all possible environments, weighted by the probability of each environment. With the forb germinating no seed in unfavorable years ($g_- = 0$), its rate of increase when rare (eq. [6]) in an unfavorable year reduces to

$$\frac{F_{t+1}}{F_t} = (1 - d). \qquad (8)$$

By contrast, in a favorable year ($g_+ = 1$), it reduces to

$$\frac{F_{t+1}}{F_t} = \frac{\lambda_+}{\alpha_{FG} G_t}. \qquad (9)$$

Grass density, G_t, is equivalent to its fecundity in the previous year (eq. [5] becomes $G_{t+1} = \lambda_{G,t}$, with no interspecific competition owing to the rarity of the forb [$F_t = 0$]). Thus, in a favorable year preceded by an unfavorable year ($G_t = \lambda_-$), the forb rate of increase when rare (eq. [9]) becomes

$$\frac{F_{t+1}}{F_t} = \frac{\lambda_+}{\alpha_{FG}\lambda_-}, \qquad (10)$$

and in a favorable year preceded by a favorable year ($G_t = \lambda_+$), it becomes

$$\frac{F_{t+1}}{F_t} = \frac{\lambda_+}{\alpha_{FG}\lambda_+} = \frac{1}{\alpha_{FG}}. \qquad (11)$$

Thus, in our simplified model, the forb can exhibit one of three growth rates when rare, given by equations (8), (10), and (11). These equations support our interpretation of forb dynamics in the simulations (fig. 1). As long as the forb suffers any mortality in the seed bank ($d > 0$), it declines in unfavorable years, albeit slowly (eq. [8]). Moreover, as long as it is an inferior competitor to the grass ($\alpha_{FG} > 1$), it declines in favorable years after favorable years (eq. [11]). Its only opportunity for positive growth is in favorable years after unfavorable years (eq. [10]).

Given the probability of unfavorable years, favorable years after unfavorable years, and favorable years after favorable years, we can calculate the condition for forb persistence as a function of environmental and demographic parameters. We assume changes in the environment can be modeled by a two-state Markov chain. The properties of this model can be characterized in terms of the stationary distribution where *P* is the probability of a favorable year and ρ is the temporal autocorrelation. The stationary probability of a favorable year preceded by an unfavorable year is $(1 - P)[P(1 - \rho)]$, and the probability of a favorable year preceded by a favorable year is $P[P(1 - \rho) + \rho]$ (see Caswell 2001, p. 379, for a detailed description of this model). The invasion criteria for the
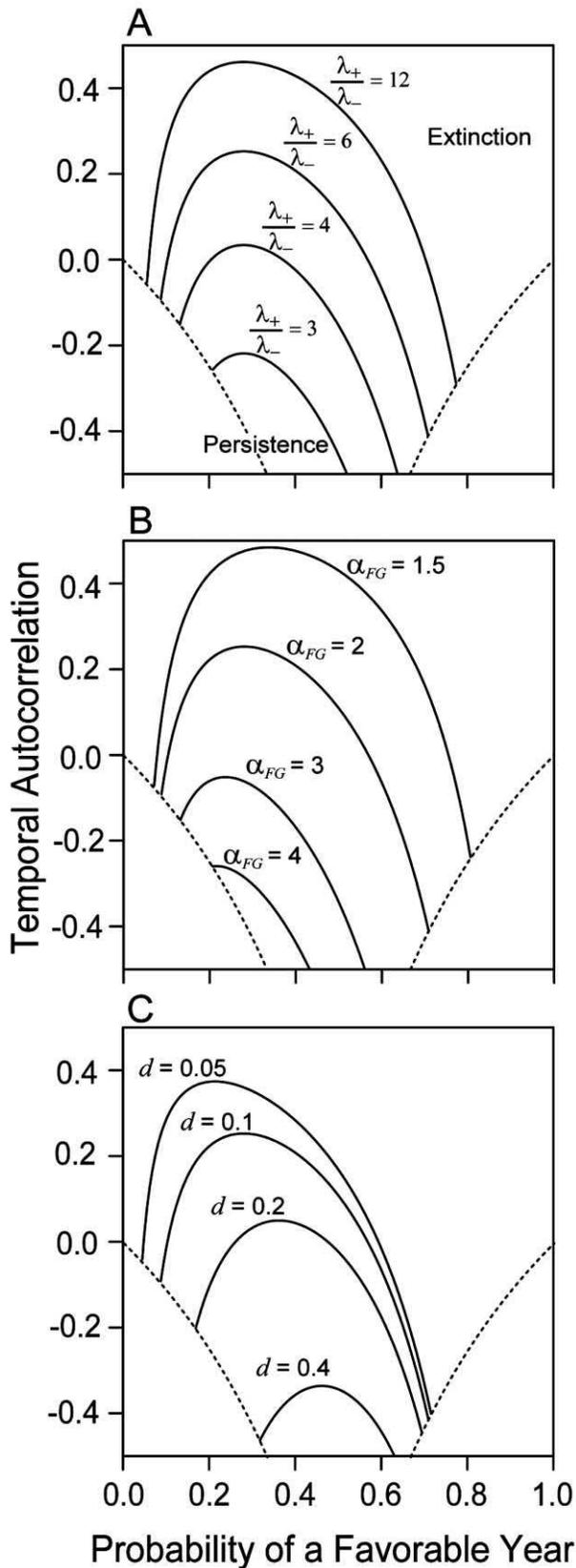
forb (eq. [7]) can now be expressed as the average of the forb growth rates when rare in unfavorable years, favorable years preceded by unfavorable years, and favorable years preceded by favorable years, all weighted by the probability of each year type:

$$(1 - P) \ln (1 - d) + P(1 - P)(1 - \rho) \ln \left(\frac{\lambda_+}{\alpha_{FG} \lambda_-} \right)$$

$$+ P[P(1 - \rho) + \rho] \ln \left(\frac{1}{\alpha_{FG}} \right) > 0.$$

$$(12)$$

This can be simplified to

$$\left(\frac{\lambda_+}{\lambda_-} \right)^{1-\rho} (1 - d)^{1/P} > \alpha_{FG}^{1/(1-P)}. \qquad (13)$$

Thus, for the forb to have a positive growth rate when rare, the variability in fecundity from favorable to unfavorable years times survivorship in the seed bank must exceed grass competitive effects (with all these terms differentially weighted by the environment). These same conclusions also emerge in models with years that are favorable to the forb but unfavorable to the grasses and vice versa, though the effects of environmental parameters (P and ρ) are very different (J. Levine and M. Rees, unpublished data).

Shown graphically (fig. 2), equation (13) reveals complex effects of the environment on forb persistence. Consistent with the result that forb persistence is maintained by seed production in favorable years preceded by unfavorable years, negative temporal autocorrelation in year quality favors forb persistence (fig. 2). Moreover, because consecutive favorable years are so detrimental to the forb, owing to intense grass competition, its persistence is maximized in environments with a relatively low probability of a favorable year, around 0.3. In environments with a high probability of a favorable year and/or strongly positive temporal autocorrelation, the forb frequently faces con-

Figure 2: Zero-growth isoclines bounding the region of forb persistence as a function of the probability of a favorable year and the temporal autocorrelation (eq. [13]). The forb persists in the region below the isocline. *A* shows the effect of changing the ratio of fecundity in favorable to unfavorable years, with $d = 0.1$, $\alpha_{FG} = 2$. *B* shows the effect of changing the competitive effect of the grass on the forb, with $d = 0.1$ and $\lambda_+/\lambda_- = 6$. *C* shows the effect of changing the death rate of forb seeds in the soil, with $\alpha_{FG} = 2$ and $\lambda_+/\lambda_- = 6$. Combinations of negative temporal autocorrelation and the probability of a favorable year below the dashed lines are impossible.

secutive favorable years, with strong negative effects on its persistence. At the other extreme, in environments with too low a probability of a favorable year, the forb does not have the opportunity to replenish losses in the seed bank.

Widely varying environments that produce large variation in fecundity also favor forb persistence. In figure 2*A*, the region of persistence increases with an increasing ratio of fecundity in favorable to unfavorable years. This is because in a favorable year after an unfavorable year, forb maximal fecundity is given by λ_+ but is reduced by grass density, λ_- (eq. [10]).

Other model parameters have predictable effects on persistence. Increasing the per capita effects of grasses on the forb from $\alpha_{FG} = 1.5$ to $\alpha_{FG} = 4$ (fig. 2*B*) reduces the range of environments in which the forb can persist. Increasing mortality rates in the seed bank also strongly reduces forb persistence (fig. 2*C*). Thus, an important caveat to our predictions is that they are only relevant to forbs with long-lived seeds. Nonetheless, our solutions show that as long as the forb and grass are intrinsically favored by the same types of years and the forb possesses long-lived seeds while the grass does not, our results concerning beneficial effects of negative temporal autocorrelation, a low probability of a favorable year, and high variation in fecundity are robust to variation in other model parameters. Therefore, the type of result seen in figure 1*A* should also apply to systems where the competition, fecundity, and environmental parameters are somewhat different from those we examined.

The Effects of Litter

One important feature of California grasslands not included in our model is the inhibitory effects of the grass litter. Dead grass individuals from the previous year fail to fully decompose, creating a thatch layer in the subsequent year (Talbot et al. 1939; Heady 1956, 1958; Heady et al. 1977; Bartolome et al. 1980). One would then expect that the litter has negative effects on forb persistence. However, because grass biomass is maximized during favorable years, litter inhibition of forb germination will be strongest in the year after a favorable year. This could benefit forbs in the long run by reducing their germination in favorable years after favorable years. To explore this, we incorporated litter into our model.

We assume that litter in the current year is entirely produced by grass in the previous year, a simple approximation for California annual grasslands (Heady 1956; Bartolome et al. 1980). Thus the reduction in forb germination due to litter is a function of the previous years' growing conditions only. We assign l_+ and l_- to be the fractional reduction in forb germination caused by litter

produced in a previously favorable and unfavorable year, respectively. Thus, in a favorable year preceded by an unfavorable year, the forb growth rate when rare changes from the expression in equation (10) to

$$\frac{F_{t+1}}{F_t} = l_-(1-d) + \frac{(1-l_-)\lambda_+}{\alpha_{FG}\lambda_-}. \qquad (14)$$

In a favorable year preceded by a favorable year, the growth rate changes from equation (11) to

$$\frac{F_{t+1}}{F_t} = l_+(1-d) + \frac{1-l_+}{\alpha_{FG}}. \qquad (15)$$

Note that litter causes the forb to now retain a fraction (l_- in eq. [14] and l_+ in eq. [15]) of its seeds in the seed bank (the first part of the sum) in favorable years. We assume that litter produced in a favorable year better inhibits forb germination than that produced in an unfavorable year ($l_+ \geq l_-$), and following empirical results (Heady 1956; Bartolome et al. 1980), litter does not inhibit grass germination or fecundity. Litter has no effect in an unfavorable year because forb germination is already 0 in such years.

Replacing the growth rates in equation (12) with the litter-modified growth rates (eqq. [14], [15]) and then simplifying yields

$$\left[l_-(1-d) + \frac{(1-l_-)\lambda_+}{\alpha_{FG}\lambda_-}\right]^{1-\rho}\left[l_+(1-d) + \frac{1-l_+}{\alpha_{FG}}\right]^{[P/(1-P)]+\rho}$$

$$> \left(\frac{1}{1-d}\right)^{(1/P)}.$$

$$(16)$$

Shown graphically (fig. 3), this result illustrates how litter tends to benefit forb persistence in environments where consecutive favorable years are otherwise detrimental. With litter reducing germination 25% after unfavorable years, increasing litter effects on germination after favorable years from 25% to 100% significantly increases the range of environments in which forb persistence is possible. The benefits of not germinating in the second of consecutive favorable years and avoiding the intense grass competition in those years outweigh the costs of litter effects in favorable years after unfavorable years. For this reason, litter effects allow the forb to persist in environments with a greater probability of a favorable year, expanding the region of persistence in figure 3 to the right. In sum, litter, which at first seems detrimental to persis-
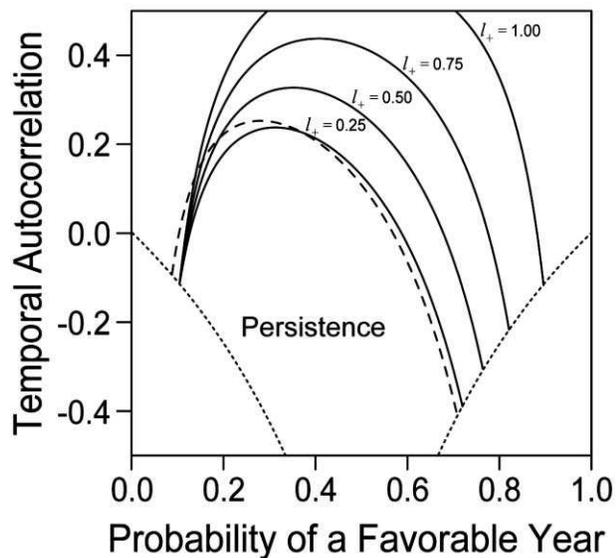
Figure 3: Effect of increasing litter inhibition of forb germination after a favorable year (eq. [16]; $d_F = 0.1$, $\lambda_+/\lambda_- = 6$, $\alpha_{FG} = 2$). Litter reduces germination 25% after an unfavorable year. The dashed line shows the region of persistence with no inhibition of forb germination after favorable or unfavorable years. Combinations of negative temporal autocorrelation and the probability of a favorable year below the two dotted lines are impossible.

tence, may ultimately favor persistence by preventing germination at times when grass competition is most severe.

Relevance to More Complex Germination Biologies

The solutions to the invasion condition presented in figures 2 and 3 were made possible by simplifying the germination of the forb ($g_+ = 1$, $g_- = 0$) and grass ($g_+ = g_- = 1$) and also assuming $c = 0$. We now use simulations to show that the analytical results also characterize the qualitative behavior of the model with the more complex germination and competition assumed in our simulations of equations (2) and (3) in figure 1A.

For a given combination of P and ρ, we simulated the environment for 50,000 years. Following the grass demographic parameters in figure 1A (justified in the text), we simulated grass dynamics alone ($F_t = 0$), yielding for each time step, year quality and grass density. We then calculated the forb growth rate when rare at each time step (eq. [6] with $c = 1$, not 0 as presented) and calculated the temporal average (eq. [7]). By repeating this calculation of forb growth rates for a range of environments (all possible combinations of 26 values of P from 0 to 1 and 26 values of ρ from -0.5 to 0.5), we could then produce a zero-growth isocline as a function of the environmental

parameters (fig. 4). These isoclines are analogous to those analytically solved in figure 2.

Results show that even with more subtle germination differences between the grass and forb, a small grass seed bank, and competition with $c = 1$, persistence is maximized in environments with an intermediate probability of favorable year and negative temporal autocorrelation. Thus, the behavior of the model under simplified parameters (figs. 2, 3) is qualitatively similar to the more complex model (fig. 4). Also similar are the effects of changing forb and grass demographic parameters. For example, in both the simple (fig. 2A) and more complex model (fig. 4), increasing fecundity in favorable years relative to unfavorable years increases forb persistence. Simulations also show that the effects of litter on persistence are similar to those shown in figure 3 (J. Levine and M. Rees, unpublished data).

This same approach can also be used to assess the conditions under which the better competing grass can invade a system with the forb at its stochastic equilibrium. Using this technique, we found that the grass can invade the entire parameter space of figure 4 (and with all variabilities in fecundity). Thus, regions of forb persistence in figure 4 are also regions of coexistence.
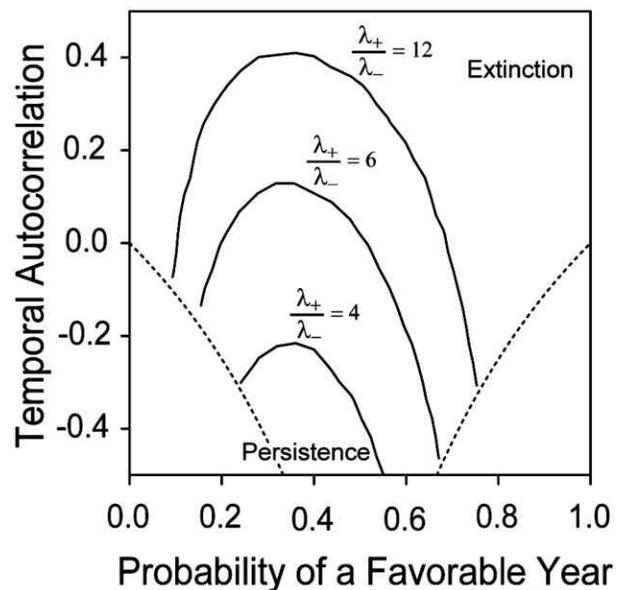

Figure 4: Simulated region of forb persistence based on the full model (eqq. [2], [3]) incorporating the more realistic germination and competition parameters of the figure 1 simulations (see text for methods). Combinations of negative temporal autocorrelation and the probability of a favorable year below the dashed lines are impossible.

Discussion

Our results modeled on a California grassland system demonstrate that in contrast to prevailing notions in population and conservation biology, annual fluctuations in the environment may benefit the persistence of rare plants. More precisely, the results of our model and those of classic population biology are not directly contradictory, because it is not environmental variability per se that benefits rare forb persistence in our framework. Rather, as demonstrated in community ecology models by Chesson and Ellner, temporal variability gives the forb the opportunity to avoid competition from the otherwise dominant exotic grass. Our results thus support the application of storage effect models to understanding the persistence of rare species existing in competitive environments. Moreover, given the tendency of environmental fluctuations to promote coexistence in these models, we suggest that positive effects of temporal variability may be underappreciated.

Also underappreciated are the benefits of seemingly unfavorable years. In consecutive favorable years, years that would presumably enhance rare forb persistence in our model, forb populations decline severely owing to the buildup of grass competitors. Thus, unfavorable years benefit persistence by strongly reducing grass density while the forb lies in the seed bank. When applied to California grasslands, this result suggests that drought years may be essential for forb persistence, a prediction running completely counter to the prevailing management ideas for these plants (Parsons and Whelchel 2000; Thomas 2000).

In favorable years occurring immediately after unfavorable years, rare forbs benefit from the environment while suffering relatively little grass competition. This result bears on how we evaluate the influence of natural variability in the California climate on persistence. Because of the periodicity inherent in the dominant controls over the region's precipitation, consecutive favorable (high rainfall) years occur with low probability. El Niño Southern Oscillation events, the largest control over interannual variability in California rainfall, coincide with nearly all high rainfall years (Schonher and Nicholson 1989). Although many forbs show large population sizes during El Niño years (Parsons and Whelchel 2000; L. Fox, unpublished data; K. McEachern, unpublished data), our model suggests that these benefits arise not just because of the favorable rainfall regime but also because El Niños have a periodicity of 3–8 years and thus rarely occur in consecutive years (Schonher and Nicholson 1989). If they did, forb populations might suffer due to the buildup of grass.

Another counterintuitive prediction of our model is that inhibition of forb germination by grass litter could benefit forb persistence. By strongly inhibiting germination in the second of consecutive favorable years, litter allows the forb to avoid the intense grass competition characteristic of those years. Importantly, this assumes that litter effects on germination occur primarily in the year after the litter is produced. Where litter decomposes much more slowly, it would reduce germination in years that would otherwise be beneficial, countering its positive effects.

Relation to the Storage Effect and Other Models

Model results showing potential benefits to persistence of climate variability, unfavorable years, negative temporal autocorrelation, and litter emphasize the importance of considering the dynamics of the surrounding community when attempting to understand the persistence of rare plants in competitive environments. Each of these results would be obscured or even missed in a single-species analysis. However, population viability analyses are often limited by available data (Morris and Doak 2002; Reed et al. 2002), and information on the surrounding community is unlikely to be readily available. Considering the resources required to collect these data, it is important to understand when we should expect multispecies models to yield markedly different predictions than their single species counterparts. Understanding how our results fit into the larger storage effect framework (Chesson 1990, 1994) sheds light on this problem.

Species differences in their response to the environment are essential for positive effects of variability on coexistence in storage effect models. Such differences temporally separate species and emerge in our model because of differences in germination biology between the forb and grass. Even though both species have high fecundity in the same years, the lack of a seed bank means that grass density in the current year is entirely determined by the previous year's conditions, enabling some favorable years for the forb to coincide with little grass competition. Had the grass also possessed a reasonable seed bank, its density would be much greater in favorable years after unfavorable years, driving a more positive correlation between grass competition and year quality for the forb. As Chesson and Huntly (1989) note for storage effect models in general, a positive correlation between environmental favorability and interspecific competition lessens beneficial effects of temporal variability on coexistence. Thus, including the dynamics of the surrounding community in plant population viability models will only change the effects of variability if the interacting species respond differently to the environment. If species respond similarly, then single-species models incorporating vital rates obtained in the presence of the surrounding community should reasonably describe dynamics, even though the individual effects of the environment and competition are not separable.

Our model also suggests new ways in which temporal

autocorrelation can influence persistence. In traditional storage effect models, species specialize on different annual environments, and temporal autocorrelation is unimportant because the intensity of competition is largely a function of conditions in the current year (Chesson 1990, 1994). In contrast, in our model, grass competition depends on conditions in the previous year, causing the forb to specialize not on individual years but rather on particular sequences of years. This gives temporal autocorrelation a major influence on our results.

More generally, when competition is a function of the environment in the previous year, temporal autocorrelation can be incorporated into the storage effect framework by treating it as a control over the covariance between the environment and competition. In our model, in an environment alternating perfectly between favorable and unfavorable years (extreme negative autocorrelation), favorable years for the forb always correspond to years of weak grass competition, while grass competition is intense in unfavorable years. Thus, the negative temporal autocorrelation generates strong negative covariance between environmental favorability and grass competition. Because the forb avoids the unfavorable years with high grass competition while it lies in the seed bank, this covariance strongly benefits its persistence. Any lessening of the negative temporal autocorrelation weakens this covariance, inhibiting beneficial storage effects. Alternatively, if competition is largely a function of the environment in the current year, but species prefer different year sequences due to innate physiological requirements, then the temporal autocorrelation simply controls the balance between year sequences that are favorable to one species versus the other.

In addition to the work of Chesson and of Chesson and Huntly, our results also follow general models by Ellner (1984, 1987) and specific models by Kalisz and McPeek (1993). Ellner (1987) showed how a species germinating a constantly low fraction of its seeds can coexist with a competitor germinating a higher fraction. Our model differs somewhat because of the inclusion of variable germination and a competitor with no seed bank, but our result can be regarded as an application of Ellner's ideas to rare forb persistence in California grasslands. In a more empirical study, Kalisz and McPeek (1993) explored the effects of a fluctuating environment on the seed bank–producing annual *Collinsia verna*. In a single-species model, they showed benefits of negative temporal autocorrelation achieved because long runs of bad years increase the probability of extinction. Although true in other models, including ours, it was long runs of favorable years that more severely inhibited persistence in the system studied here.

Support from California Grasslands

Unfortunately, seed bank data for rare plants are difficult to obtain in both the field and the literature (Doak et al. 2002). Probably the most important germination biology assumption made in our model is that forbs germinate a high fraction of seeds in years that will ultimately be favorable for their reproduction. This assumption of "intelligent germination" or directed dispersal in time has been supported in a different California grassland context by Rice (1985) but requires further evaluation.

Although poor availability of seed bank demographics precludes us from testing our model, seedling data for a *Bromus* (exotic grass)-dominated grassland through periods of El Niño rains and droughts (1974–1978) support our predictions concerning the dependence of grass density on rainfall in the previous year. Young et al. (1981) found the lowest grass seedling densities in the year after a drought year even when the current year was wet. Moreover, they found the highest seedling densities after wet years even when the current year was dry. Even after dry years, however, grass density was exceedingly high in an absolute sense (2,000 per m^2), a potential explanation for why forbs did not exploit these periods (Young et al. 1981).

The lagged grass competition in our model also involves several other important assumptions about how competition works. We are assuming that the per capita competitive effects of the grasses are the same during favorable and unfavorable years. Thus, the tendency for plants to grow larger in favorable years does not compensate for the reduced grass density after unfavorable years. The reasonableness of this assumption depends on the mechanism of competition. If species compete for water (Pavlik et al. 1993; Holmes and Rice 1996; Carlsen et al. 2000), then the increased plant size in wet years will not increase the competition coefficient because water is abundant. In fact, the competition coefficient may be reduced in favorable years under this scenario. In contrast, if increased grass biomass shifts competition from water to light, then a temporally variable coefficient would be required.

Experiments to Test Model Predictions

Our model predicts that rare annual forbs with variable germination and dormancy may benefit from annual fluctuations in the environment when competing with species that lack seed dormancy. However, even with a long time series of population dynamics and year quality, testing this prediction can be difficult because so much of the forb population dynamics occur in the seed bank. Note that while the total forb population increases markedly in the fluctuating series of years in figure 1*A* (years 83–90), if we look specifically at the germinated fraction of the pop-

ulation (years 83–90, fig. 1*B*), these increases are more difficult to discern. A more direct approach involves experimentally imposing different sequences of year quality. One unique prediction of our model is that consecutive favorable years are ultimately detrimental to persistence. Thus, for California grasslands, a watering experiment simulating a favorable rainfall regime for three consecutive years should cause an initial increase in the forb population, followed by a steep decline associated with a buildup of its grass competitor. By contrast, forb populations should be larger at experiment's end in a treatment where favorable rainfall is imposed only in the first and third year of the experiment, with an unfavorable year imposed in year two.

Testing multispecies persistence models like the one developed here may be critical for understanding the complex processes underlying persistence in interactive communities. We have shown that incorporating the dynamics of exotic grasses surrounding rare annual plants can yield counterintuitive effects of environmental fluctuations, unfavorable years, and grass litter on rare plant persistence. Given that exotic invaders now threaten half the imperiled species in the United States (Wilcove et al. 1998), multispecies approaches to modeling rare plant dynamics may become increasingly necessary for preserving native diversity in exotic-dominated habitats.

Acknowledgments

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