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LETTER

Bet hedging in desert winter annual plants: optimal germination strategies in a variable environment

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Abstract

In bet hedging, organisms sacrifice short-term success to reduce the long-term variance in success. Delayed germination is the classic example of bet hedging, in which a fraction of seeds remain dormant as a hedge against the risk of complete reproductive failure. Here, we investigate the adaptive nature of delayed germination as a bet hedging strategy using long-term demographic data on Sonoran Desert winter annual plants. Using stochastic population models, we estimate fitness as a function of delayed germination and identify evolutionarily stable strategies for 12 abundant species in the community. Results indicate that delayed germination meets the criteria as a bet hedging strategy for all species. Density-dependent models, but not density-independent ones, predicted optimal germination strategies that correspond remarkably well with observed patterns. By incorporating naturally occurring variation in seed and seedling dynamics, our results present a rigorous test of bet hedging theory within the relevant environmental context.

Keywords

Bet hedging, delayed germination, density dependence, desert annuals, evolutionarily stable strategies, population dynamic models, seed bank.

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INTRODUCTION

Organisms in variable environments may respond by adjusting phenotypes to maximise performance as the environment changes through rapid evolution or adaptive plasticity, or they may respond by adopting conservative strategies to avoid risk through bet hedging (Seger & Brockmann 1987; Philippi & Seger 1989; Simons 2011). With bet hedging, average fitness is sacrificed to reduce variance in fitness, thus maximising long-term stochastic growth rate (Seger & Brockmann 1987). The classic example of bet hedging is delayed germination in desert annual plants, first modelled by Cohen (1966). Since annual plants have a single season to grow and produce offspring, the environment during that season can determine failure or success. Therefore, in a variable environment, spreading germination over multiple seasons can reduce the risk of complete reproductive failure from conditions in any one year. While delayed germination as a bet hedging strategy has received much theoretical development, strong empirical tests are much less common (Evans & Dennehy 2005; Childs *et al.* 2010; Simons 2011). On a community level, variation in germination strategies among species in a community may contribute to coexistence, because it can allow for temporal partitioning of environmental resources as well as provide a buffer against extinction (Ellner 1987a; Chesson 2000). Thus, understanding bet hedging strategies has implications for trait evolution as well as population and community dynamics. Here, we used a long-term demographic dataset on Sonoran Desert winter annual plants to parameterise the relationship between delayed germination and fitness in a variable environment. We then identified optimal germination strategies for multiple species and compared predicted germination strategies with those observed in the field. By doing so, we aimed to achieve a comprehensive understanding of delayed germination as a bet hedging strategy in a system where the environmental drivers are well-understood.

Cohen's (1966) classic model of delayed germination in annual plants predicted that the amount of germination delay should directly match the probability of reproductive failure. In other words, germination fractions should reflect the probability of favourable environmental conditions such as high precipitation and moderate temperatures. However, abiotic conditions are not the only factor to influence the fitness of annual plants. Ellner (1985a,b) demonstrated that competition significantly influenced the adaptive value of delayed germination. With density dependence, optimal germination fractions are more sensitive to variance in fitness than to probability of reproductive failure and delaying germination provides the possibility of germinating when conditions are favourable *and* density is low (Ellner 1985a,b, 1987b). Therefore, delayed germination can act to avoid risk due to the combination of unpredictable abiotic conditions and variable density (Westoby 1981; Ellner 1985a,b, 1987b; Tielborger & Valleriani 2005). To date, very few studies have assessed the role of both environmental stochasticity and density dependence in the evolution of germination strategies for multiple species in a community (Tielborger & Valleriani 2005).

The adaptive value of delayed germination relies on the relative risk of death in the seed bank vs. poor survival and reproduction after germination. Generally, seeds are assumed to be less vulnerable to environmental hazards than germinants, but seed predation, disease and damage can reduce the benefits of delayed germination (Ellner 1985a,b; Donohue *et al.* 2010; Dalling *et al.* 2011). So all else being equal, species with lower seed survival rates are predicted to have higher germination fractions since the benefits of remaining in the persistent seed bank are lower. Therefore, a full understanding of the adaptive significance of delayed germination requires quantifying the seed mortality risk associated with delay. Observing mortality patterns of seeds in the soil is logistically difficult and spatial and temporal heterogeneity further complicate accurate estimates of seed survival (Thompson *et al.* 1993; Saatkamp *et al.* 2009). One solution to these complexities is to combine detailed studies of seed bank dynamics with demographic monitoring of germinants. The latter provides information on the flow of seeds into and out of the seed bank (via reproduction and germination), and the former provides a measure of species abundance in the seed bank over time.

The Sonoran Desert exhibits highly variable, unpredictable and punctuated weather patterns, in terms of both precipitation and temperature (Davidowitz 2002). Sonoran Desert winter annual plants form a mature, persistent community, and their short life cycles make observing entire life spans and multiple generations relatively easy. Therefore, this system is ideal for understanding life history responses to environmental stochasticity. In this community, we have combined long-term observation of both seed bank and germinant demography, as well as short-term observation and experimentation to identify traits that relate to population and community dynamics over time (reviewed in Huxman *et al.* 2013; Venable & Kimball 2013). These studies have highlighted the critical role of germination in driving variation in demographic patterns and species coexistence. A previous study in this system demonstrated that species with greater variance in per capita reproductive success tend to have lower long-term average germination fractions (Venable 2007). While this was interpreted as evidence for bet hedging, a better test would explicitly incorporate demographic rates for the entire life cycle into estimates of fitness, including survival in the seed bank and the effects of competition on germinant survival and reproduction (Childs *et al.* 2010; Simons 2011). Such an approach can predict evolutionarily stable strategies which can be compared to observed patterns (Simons 2011).

Here, we combine long-term demographic data on seed bank dynamics and germinant performance for 12 species of desert winter annual plants to predict evolutionarily stable strategies (ESS) for delayed germination and compare them to observed germination fractions. We also (1) test whether delayed germination meets the criteria for bet hedging and (2) assess the role of competition in driving the evolution of delayed germination. We use long-term stochastic growth rate (λ_s) as our measure of fitness in a variable environment. We parameterise density-independent and density-dependent models with field data to estimate fitness in relation to germination strategies. We then use stochastic simulations to predict ESS germination strategies for each species, and compare long-term average germination fractions to model predictions. We predict that species with higher seed survival should have lower observed germination fractions. For delayed germination to act as an adaptive bet hedging strategy, predicted germination fractions should be less than one and should reduce arithmetic mean fitness and lower variance in fitness. If competition significantly alters the adaptive value of delayed germination, density-dependent models should provide a better fit to germination behaviour observed in the field. Our long-term data on vital rates in a natural field environment together with the comparison of predicted to observed germination strategies for multiple species make this an unusually thorough investigation of bet hedging and delayed germination.

METHODS

Study system and demographic data

Detailed demographic data on Sonoran Desert winter annuals have been collected since 1982 at the University of Arizona's Desert Laboratory at the base of Tumamoc Hill in Tucson, AZ (32°13′ N, 111°01′ W), a nature preserve and field station which has been protected from grazing since 1906 (Venable & Pake 1999; Venable 2007; Venable & Kimball 2013). Sonoran Desert winter annuals germinate at this site with the onset of autumn and early winter rains, usually between October and January of each year. Flowering occurs in spring, and plants complete their life cycle before the onset of the arid fore-summer (May to June; Venable & Pake 1999; Clauss & Venable 2000). Permanently marked plots were established along a 250-m transect through a gently sloping alluvial plain dominated by creosote shrubs (*Larrea tridentata*; $n = 72$, 24 plots are 0.05 m^2, the rest are 0.10 m^2). These plots, located both in the open and under creosote shrubs, were visited within 10 days following every autumn and winter rain event to record germination. Plots were then visited at roughly monthly intervals to monitor survival or following additional rain events to document any further germination. Individual plants were mapped upon germination and followed until death to quantify lifetime survival and reproduction. This research has resulted in detailed demographic data for each species in the community for the past 30 years including *per capita* survival from germination to reproduction (l), average seeds produced by plants that survived to reproduction (b), and lifetime fecundity per germinant (lb, the product of the previous two).

Every year starting with the 1989/1990 season, the density of viable non-germinating seeds was estimated from one hundred and eighty 23-cm^2 soil cores collected in the open and under shrubs ($n = 90$ in each habitat) following a stratified random sampling scheme covering the demographic census area (Pake & Venable 1996; Venable & Pake 1999; Venable 2007). Soil cores (5.4 cm diameter) sampled approximately the top 2 cm of soil, since very few seeds get buried below that depth in this system (Pake & Venable 1996). These annual samples were collected after all germination had occurred, usually in February, but before new seeds fell in March or April. Seed counts were obtained by separating seeds from the soil and poking them to test for viability (dead seeds in the desert are usually dry or moulded; see Pake & Venable (1996) for more details on seed recovery and viability testing). The fraction of seeds that germinate in a particular year, $G(t)$, was determined from the density of seeds that germinated in the long-term plots, $E(t)$, and the density of seeds that did not germinate from the seed bank samples, $D(t)$. Specifically, the germination fraction was calculated as $G(t) = E(t)/(E(t) + D(t))$.

For this study, we focused on 12 usually abundant species in the winter annual community for which we have good demographic data across the sampling period: *Eriophyllum* *lanosum* A. Gray (ERLA, Asteraceae), *Erodium cicutarium* (L.) L'Hér. ex Aiton (ERCI, Geraniaceae; naturalised species), *Erodium texanum* A. Gray (ERTE, Geraniaceae), *Evax multicaulis* DC (EVMU, Asteraceae), *Monoptilon bellioides* (A. Gray) H.M. Hall (MOBE, Asteraceae), *Pectocarya heterocarpa* I. M. Johnst.(PEHE, Boraginaceae), *Pectocarya recurvata* I. M. Johnst. (PERE, Boraginaceae), *Plantago patagonica* Jacq. (PLPA, Plantaginaceae), *Plantago insularis* Forssk. (PLIN, Plantaginaceae), *Schismus barbatus* (Loefl. ex L.) Thell. (SCBA, Poaceae; naturalised species), *Stylocline micropoides* A. Gray (STMI, Asteraceae) and *Vulpia octoflora* (Walter) Rydb. (VUOC, Poaceae). Here, we use the nomenclature consistent with previous work on this system, but synonymy and currently accepted nomenclature are given in Kimball *et al.* (2011).

Density-independent model for optimal germination fraction

To investigate whether delayed germination acts as a bet hedging strategy, and to understand the adaptive significance of germination strategies in winter annuals, we estimated fitness across a range of values for germination fractions. We used λ (finite rate of increase) to measure yearly growth rate, calculated from the following density-independent growth equation corresponding to the life cycle in Fig. 1:

$$\frac{n(t+1)}{n(t)} = \lambda = GY(t)S + (1-G)WS \tag{1}$$

where $n(t)$ is the density of seeds just prior to germination in year t, G is the proportion of seeds that germinate and $(1\text{-}G)$ is the proportion of seeds remaining dormant between years (assumed to be constant across years), S represents the survival of seeds through the summer from the time of seed production until the next germination season, and W is the survival of non-germinating seeds from the fall germination season until the next reproductive season in the spring (Venable 1989). $Y(t)$ is per capita yield and is calculated as $Y(t) = l(t)b(t)$, where l is the survival to reproduction of germinating seeds and b is the average seeds produced by individuals that survived to reproduce. Environmental variation was incorporated by allowing $Y(t)$ to vary randomly among years. We used the long-term demographic data to parameterise these temporally varying per capita yield values.

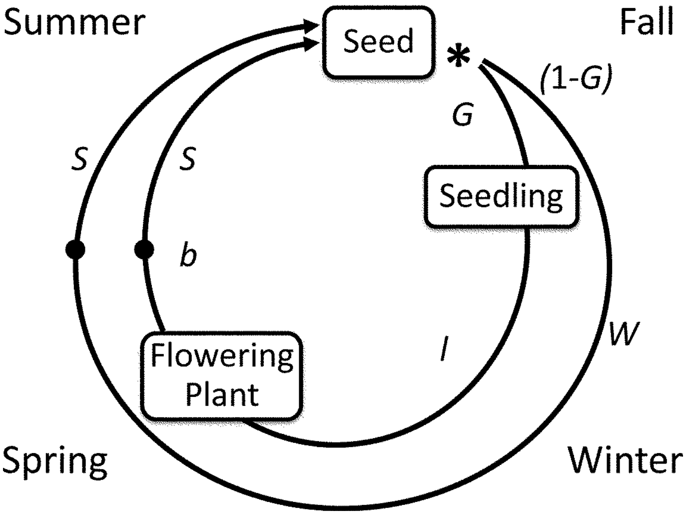

Figure 1 Diagram of the life cycle for Sonoran Desert winter annual plants. The asterisk is the time of seed germination, which begins the life cycle in our models. Arrows represent pathways through the life cycle. Variables represent vital rates seen in eqn. 1, dots represent the time of seed production. The outer loop describes seeds that do not germinate (1-*G*) that may survive through the winter growing season (*W*) and the subsequent summer (*S*) to make it to the next growing season. The inner loop represents seeds that germinate (*G*) to become seedlings that may survive to reproduction (*l*) and produce seeds (*b*). These seeds may survive during their first summer (*S*) to make it to the next growing season.

Seed survival rates (S and W), were estimated using the long-term seed bank study. To estimate seed bank survival, we determined how much seed mortality was necessary to balance year-to-year seed bank population numbers (see Appendix S1). We then tested for differences in survival between older seeds and freshly produced seeds (new seeds). Since new seeds typically had lower summer survival than old seeds, we then calculated summer survival separately for new (S_n) and old seeds (S_o, see Appendix S1). Allowing for the observed differences in the survival of new and old seed, eqn. 1 becomes

$$\frac{n(t+1)}{n(t)} = \lambda = GY(t)S_n + (1-G)WS_o \tag{2}$$

This growth equation was used to estimate long-term stochastic growth rate (λ_s) across a range of fixed germination fractions (G's) for each species using stochastic simulations with time-varying $Y(t)$. In the stochastic simulations, growth rate was projected for 1000 years at each value of G with values for $Y(t)$ chosen at random each year from the 30 year historical values. For each species a simulation was conducted for 101 values of G between 0 and 1 (incrementing G by 0.01 for each new simulation) using the same random sequence of $Y(t)$ values. Temporal autocorrelation in vital rates, such as $Y(t)$ may reduce the adaptive value of life history delays (Metcalf & Koons 2007; Childs *et al.* 2010), potentially affecting the relationship between G and fitness. Therefore, we tested for temporal autocorrelation in $Y(t)$ by estimating the autocorrelation function (function acf in R, R Foundation for Statistical Computing 2009). Only one significant relationship was revealed (*Vulpia octiflora*: significant lag 4 autocorrelation), which is no greater than we would expect by chance, so we did not include temporal autocorrelation in our final analyses.

To compare fitness among the possible germination fractions for each species, we calculated the arithmetic mean, geometric mean and variance of λ. The set of 101 simulations for each species was repeated 50 times, with the sequence of $Y(t)$ values being resampled for each repetition. We then determined which value of G maximised geometric mean fitness for each species at each repetition and calculated the mean and variance of these optimal germination fractions. To test Cohen's (1966) prediction that germination fraction should mainly respond to the probability of a good year, we examined the relationship between predicted germination optima and the probability of a 'good year' (successful germination and reproduction). We calculated the probability of a good year as one minus the probability of a 'bad year' defined as the number of years in which germination occurred and reproduction completely failed [e.g., mean $l(t)b(t)$ across all plots was zero], divided by the total number of years in which germination occurred. We then tested for correlations between the probability of a good year and observed germination fractions, and compared observed mean germination fractions to predicted germination optima from the density-independent model.

Density-dependent model for optimal germination fraction

To determine how competition may affect the adaptive value of delayed germination, we modified eqn. 2 to allow germinated plants to compete using a standard saturating yield model (cf. Ellner 1987b). In a density-dependent model, consequences of a germination strategy for an individual's fitness depend on the strategies being used by other individuals in the population. Therefore, we used an adaptive dynamics approach to find the ESS. We simulated fitness as a function of germination fraction for a resident and a mutant strategy (eqns. 3–5) as follows:

$$\text{Resident}: n_r(t+1) = n_r(t)G_rY(t)S_n + n_r(t)(1-G_r)WS_o \qquad (3)$$

$$\text{Mutant}: n_m(t+1) = n_m(t)G_mY(t)S_n + n_m(t)(1-G_m)WS_o \qquad (4)$$

$$\text{where } Y(t) = \frac{K(t)}{1 + aG_rn_r(t)} \qquad (5)$$

Subscripts r and m refer to resident and mutant strategies. K is low-density fecundity (i.e., lb at low density) and a is the competition parameter. Because we assume the mutant strategy is at low density ($n_m(t) \rightarrow 0$), all competition is due to germinating residents (G_rn_r(t)). We used natural variation in density among plots in our long-term field data to estimate K and a for each species in each year of the study (see Appendix S2 for details). In some years, we were not able to obtain estimates of K for some species. For those species/years, we used average $l(t)b(t)$ for $K(t)$. In our stochastic simulations, $K(t)$ was allowed to vary randomly, as described for the yields in the density-independent models. We used an average value of a as the competition parameter for each species. Growth was projected for 1000 years and the geometric mean growth rate of the mutant strategy was compared to the resident strategy to test for the potential of the mutant to invade. Using a simple search algorithm, we then identified the resident strategy (i.e., germination fraction) that is resistant to invasion by any mutant strategy (the ESS) for each species. This entire approach was replicated 50 times and the mean ESS of those replicates was determined. This process was repeated across a range of start values for G without significant effects on the ESS values. The germination ESS's from this model that was parameterised with 30 years of field data were then compared to probabilities of a good year, the variance in low-density yield (K, natural log-transformed) and observed mean germination fractions.

RESULTS

Seed survival

To test whether increased risk of mortality in the seed bank influences the degree of germination delay, we analysed the relationship between seed survival rates and observed germination fractions. As expected, species with higher seed survival rates tended to have lower germination fractions (Fig. 2, Table 1; Pearson's correlation coefficient, $r = -0.564$, $P = 0.056$), though this trend is slightly above the $\alpha = 0.05$ level.

Density-independent germination optima

Optimal germination fractions from the density-independent model were always less than 1 (Fig. 3, Fig. S3-1), indicating that delayed germination increased geometric mean fitness for all species. In addition, arithmetic mean λ and variation in λ both increased with increasing germination fraction (Figs S3-2 and S3-3). Therefore, delayed germination meets the criteria for bet hedging. As expected from Cohen's (1966) density-

Table 1 Seed survival estimates for 12 species of desert winter annuals, including means and standard errors (*SE*, see *Methods* and *Appendix S1* for details)

			Fall survival		Winter survival		Summer survival, new seeds		Summer survival, old seeds	
Species	Family	Abbrev.	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Erodium cicutarium	Geraniaceae	ERCI	0.731	0.06	0.766	0.05	0.132	0.02	0.560	0.09
Eriophyllum lanosum	Asteraceae	ERLA	0.795	0.04	0.823	0.04	0.153	0.02	0.646	0.07
Erodium texanum	Geraniaceae	ERTE	0.777	0.09	0.799	0.08	0.170	0.04	0.722	0.15
Evax multicaulis	Asteraceae	EVMU	0.907	0.07	0.916	0.06	0.214	0.03	0.904	0.15
Monoptilon belliodes	Asteraceae	MOBE	0.593	0.09	0.635	0.08	0.102	0.03	0.430	0.12
Pectocarya heterocarpa	Boraginaceae	PEHE	0.753	0.06	0.785	0.05	0.142	0.03	0.600	0.11
Pectocarya recurvata	Boraginaceae	PERE	0.836	0.05	0.858	0.04	0.173	0.02	0.731	0.09
Plantago insularis	Plantaginaceae	PLIN	0.813	0.06	0.836	0.05	0.168	0.03	0.713	0.11
Plantago patagonica	Plantaginaceae	PLPA	0.788	0.06	0.814	0.05	0.160	0.03	0.676	0.11
Schismus barbatus	Poaceae	SCBA	0.778	0.05	0.807	0.04	0.150	0.02	0.635	0.09
Stylocline micropoides	Asteraceae	STMI	0.715	0.09	0.743	0.08	0.145	0.03	0.616	0.15
Vulpia octoflora	Poaceae	VUOC	0.873	0.08	0.886	0.07	0.200	0.04	0.849	0.18

Species four-letter abbreviations (Abbrev.) listed here. Values were estimated using demographic data and seed bank samples from 1990 to 2012 (see Appendix S1 for details).

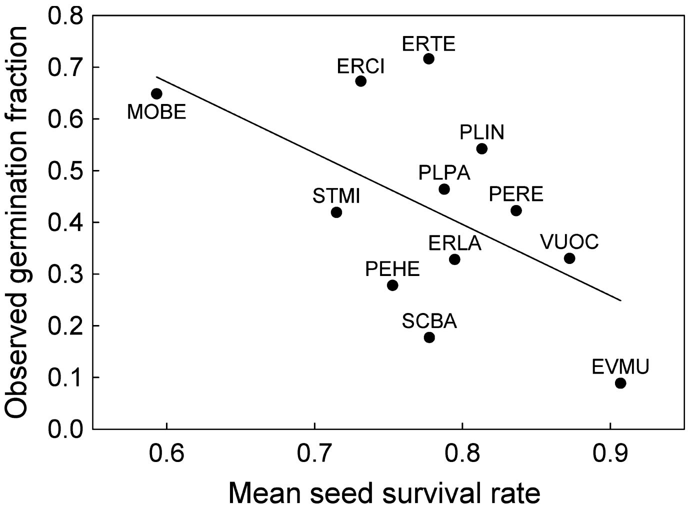

Figure 2 Mean seed survival rates (Q; see Appendix S1 for details) vs. mean observed germination fraction for 12 species of desert annual plants. Each point is the mean value for each species (see Table 1 for abbreviations).

independent model, probability of a good year was strongly associated with the predicted germination fractions ($r = 0.648$, $P = 0.023$). However, the probability of a good year did not correlate with observed germination fractions (Fig 3a; $r = 0.168$, $P = 0.602$). Consequently, predicted germination fractions from the density-independent model did not correspond well with observed germination fractions (Fig. 3b; $r = 0.178$, $P = 0.578$), and the model usually predicted higher germination fractions than were observed in the long-term data set.

Density-dependent germination optima

Incorporating density dependence significantly affected predicted germination optima. Specifically, the ESS germination fractions from the density-dependent model are significantly lower than those from the density-independent model ($t = 5.097$, d.f. = 11, $P < 0.001$). Compared to the density-independent model, the density-dependent predictions did not respond as strongly to the probability of a good year ($r = 0.446$, $P = 0.146$). As predicted by Ellner (1985a,b), ESS germination strategies were negatively correlated with variation in yield, calculated as the standard deviation of ln-transformed K ($r = -0.762$, $P = 0.004$). Observed germination strategies were also negatively related to the standard deviation of low-density yield (ln-transformed K, Fig. 4a; $r = -0.823$, $P = 0.001$). The predicted ESS germination fractions were significantly positively correlated to the mean historically observed germination fractions (Fig. 4b; $r = 0.686$, $P = 0.014$).

DISCUSSION

It is generally accepted that the empirical evidence for bet hedging involves 'more smoke than fire' since most examples are anecdotal, with strong empirical tests being the exception (Simons 2011). Here, we used long-term data on 12 species of co-occurring annual plants to parameterise population dynamic models to test if delayed germination acts as a bet hedging strategy. In this highly variable desert environment, differences in precipitation and temperature translate into variation in per capita survival and reproduction (Venable 2007; Kimball *et al.* 2012). In addition to this environmentally driven variation in vital rates, the risks of seed mortality and competition are likely to affect the adaptive value of delayed germination. Our results for all 12 species of desert winter annual plants indicated that both arithmetic mean fitness and variance in fitness increased with germination fraction, satisfying the first two criteria for bet hedging (Appendix S3). Geometric mean fitness was optimised at germination fractions below one for all species, in both density-independent and dependent models, meeting the final requirement for delayed germination to act as an adaptive bet hedging strategy. Optimal germination strategies predicted by

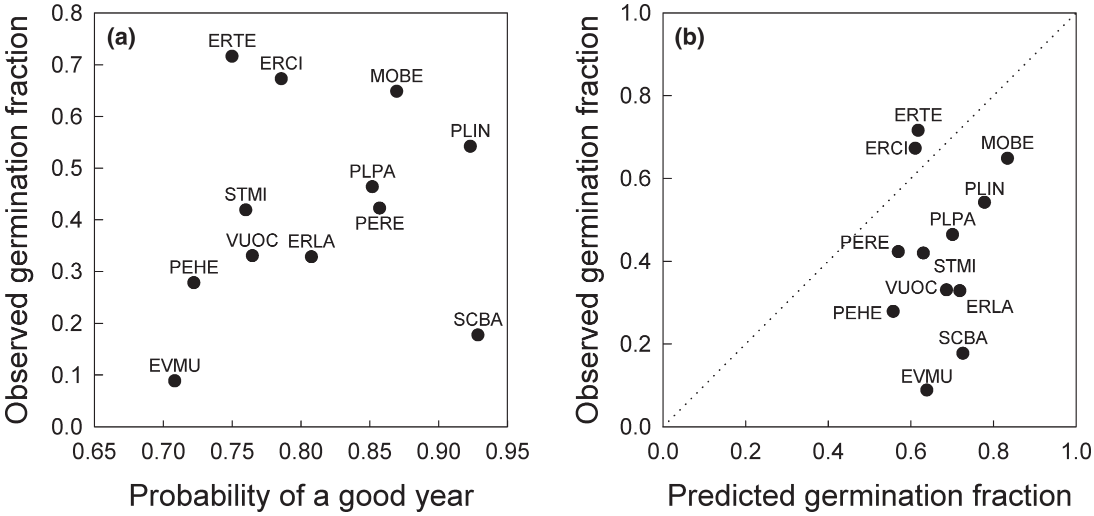

Figure 3 Observed germination fractions in relation to the observed probability of a good year (a) and optimal germination fractions predicted by the density-independent model (b). See Table 1 for species abbreviations. Probability of a good year is the likelihood of germinating and surviving to produce offspring; values are means from 1982 to 2012. Observed germination fractions values are means from 1990 to 2012. The dotted line in (b) provides a 1 : 1 line for reference; values below the line indicate that model predicted optimal fractions are higher than observed.

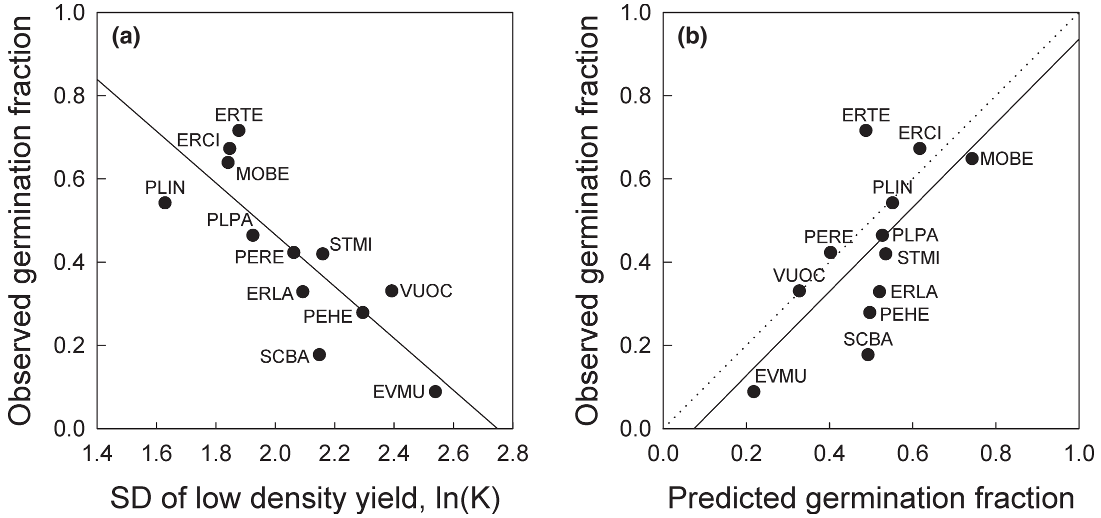

Figure 4 Observed germination fractions in relation to (a) variation in reproductive success and (b) optimal germination fractions predicted by the density-dependent model. See Table 1 for species abbreviations. Variation in reproductive success is measured as the standard deviation of low-density yield (*K*, natural-log transformed). Observed germination fractions values are means from 1990 to 2012. Dashed line in (b) indicates 1 : 1 line for reference.

the density-dependent model showed better correspondence with observed germination fractions than strategies predicted by the density-independent model, suggesting that competition mediates the fitness advantage of germination delay. Together, these results constitute the strongest form of evidence for bet hedging suggested by Simons (2011).

Fluctuations in fitness can be due to both abiotic conditions as well as variation in the competitive environment, and competition can magnify the effect of even small abiotic environmental fluctuations (Ellner 1987b). If so, then competition can increase the need for bet hedging strategies. Therefore, germination strategies should evolve to bet hedge against variation caused by both abiotic weather conditions and by the effects of crowding. In this study, incorporating density dependence decreased predicted values for optimal germination strategies and provided a better fit to observed germination strategies, suggesting that competition increases the value of germination delay in our system. Adding density dependence to the model had a stronger effect on the ESS germination fractions for some species, especially those with high variance in per germinant fecundity such as *Evax multicaulis* (EVMU) and *Vulpia octoflora* (VUOC). These species also had the highest seed survival rates (Fig. 1). These patterns are consistent with theory and demonstrate that integrating performance throughout the life cycle and including the effects of competition are critical for understanding the forces driving the evolution of bet hedging strategies.

The adaptive value of delayed germination depends on both pre- and post-germination risks. Remaining in the seed bank is often considered to be safer than germinating, but seeds that delay germination are also subject to mortality factors (Venable & Lawlor 1980; Brown & Venable 1991). In our system, species with lower seed survival have higher germination fractions and *vice versa*, consistent with predictions of life history models (Cohen 1968). Further, newly produced seeds had lower survival rates than those that had remained in the seed bank for one or more seasons. Lower seed survival for new seeds may simply be a result of their vulnerability to predators and pathogens at the soil surface before burial or dispersal. In the Sonoran Desert, seed predation from a variety of rodents, birds, and ants is expected to be a significant source of mortality (Brown *et al.* 1979). Rodents are likely to be important seed predators and they are more active from late spring to fall (Reichman & Van de Graaf 1973; Horst 2011) which may be a time when new seeds are easier to locate by predators. These costs of early seed mortality for new seeds can reduce the benefit of germinating and producing new seed, and increase the adaptive value of delayed germination. A recent study in this system suggests that seed predation is frequency-dependent, indicating that predators are more likely to preferentially consume seeds that are common relative to those that are rare (Horst 2011). This could reduce the variance in reproductive success by limiting high yield in favourable years and thus potentially reduce selection for delayed germination. While studying seed mortality in the field is logistically difficult, studies in this system suggest that understanding survival in the seed bank provides important insight into the factors driving germination strategies.

Several aspects of seed biology were not included in our model. For instance, predictive germination can allow seeds to germinate more readily in response to environmental cues that may signal favourable conditions for subsequent growth and reproduction (Cohen 1967; Venable & Lawlor 1980; Venable 1989; Baskin & Baskin 1998). If conditions at germination are predictive of future survival and reproduction, then the value of bet hedging decreases (Cohen 1967; Clauss & Venable 2000). Additionally, while we have assumed that germination and seed mortality of old seeds are independent of seed age, this may not be true. Unfortunately determining age-dependent germination and mortality for old seeds requires careful long-term experimentation and is not easily incorporated in a long-term observational study like ours. Other traits, such as seed size, dispersal, and seasonal germination timing may affect the adaptive value of delayed germination (Templeton & Levin 1979; Venable & Lawlor 1980; Brown & Venable 1986; Venable & Brown 1988; Donohue *et al.* 2010; Snyder 2006; Volis & Bohrer 2013). Whatever effects seed size and seasonal patterns of germination timing have on fitness and the evolution of delayed germination, they should already be reflected in our long-term data. However, we did not model the consequences of seed dispersal. It has been suggested that seed dispersal may substitute for delayed germination by spreading risk over space instead of time, or that the two traits may co-evolve depending on ecological conditions (Venable & Lawlor 1980; Snyder 2006; Volis & Bohrer 2013). In our Sonoran Desert community, dispersal distances are quite short relative to the scale of spatial heterogeneity (Venable *et al.* 2008). Therefore, in our system, delayed germination seems to be more important as a risk-spreading strategy than dispersal. This may not be the case in some other systems, but as with bet hedging, empirical studies that incorporate the effects of delayed germination, dispersal, and seed size on fitness are lacking. Understanding how these traits interact to affect fitness in the field is an important area for future study.

In a variable world, organisms may evolve behaviours or life history strategies to optimise fitness as environmental conditions change. Since climate change is expected to bring an increase in environmental variability, understanding the role of bet hedging is critical for predicting responses to change (IPCC 2007; Childs *et al.* 2010; Simons 2011). If bet hedging strategies are sufficient to buffer the effects of increased environmental variability, species with delayed germination may be more resistant to change (Childs *et al.* 2010; Simons 2011). Such patterns not only buffer population dynamics of individual species, but can dampen the effects of change on community dynamics and structure. Indeed, as the Sonoran Desert has been warming and drying over the last 30 years, patterns of diversity have remained fairly stable (Kimball *et al.* 2010; Venable & Kimball 2013). This stability arises from the buffering capacity of the seed bank, since patterns of seedling diversity have been more sensitive to short- and long-term weather patterns than seed bank diversity (Kimball *et al.* 2012; Venable & Kimball 2013). However, over the long term, the effects of climate change may overwhelm the ability of seed banks to buffer dynamics (Ooi 2012). Therefore, a comprehensive understanding of the role of risk-reducing mechanisms, as well as their potential for evolutionary response, is necessary to understand the ecological and evolutionary implications of change. Our current study provides an important step in that direction, by incorporating the effects of species-specific variation in demographic performance, seed-bank dynamics and density dependence into the understanding the adaptive significance of delayed germination.

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JRG performed analyses of DLV's long-term monitoring data; DLV provided valuable guidance on analyses. JRG wrote the manuscript and DLV contributed substantially to content and revisions.

REFERENCES

Baskin, C.C. & Baskin, J.M. (1998). *Seeds. Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego.

Brown, J.S. & Venable, D.L. (1986). Evolutionary ecology of seed-bank annuals in temporally varying environments. *Am. Nat.*, 127, 31–47.

Brown, J.S. & Venable, D.L. (1991). Life-history evolution of seed-bank annuals in response to seed predation. *Evol. Ecol.*, 5, 12–29.

Brown, J.H., Davidson, D.W. & Reichman, O.J. (1979). An experimental study of competition between seed-eating desert rodents and ants. *Am. Zool.*, 19, 1129–1143.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.

Childs, D.Z., Metcalf, C.J.E. & Rees, M. (2010). Evolutionary bet hedging in the real world: empirical evidence and challenges revealed by plants. *Proc. Biol. Sci.*, 277, 3055–3064.

Clauss, M.J. & Venable, D.L. (2000). Seed germination in desert annuals: an empirical test of adaptive bet hedging. *Am. Nat.*, 155, 168–186.

Cohen, D. (1966). A general model of optimal reproduction in a randomly varying environment. *J. Ecol.*, 56, 219–228.

Cohen, D. (1967). Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. *J. Theor. Biol.*, 16, 1–14.

Cohen, D. (1968). A general model of optimal reproduction in a randomly varying environment. *J. Ecol.*, 56, 219–228.

Dalling, J.W., Davis, A.S., Schutte, B.J. & Arnold, A.E. (2011). Seed survival in soil: interacting effects of predation, dormancy and the soil microbial community. *J. Ecol.*, 99, 89–95.

Davidowitz, G. (2002). Does precipitation variability increase from mesic to xeric biomes? *Glob. Ecol. Biogeogr.*, 11, 143–154.

Donohue, K., de Casas, R.R., Burghardt, L., Kovach, K. & Willis, C.G. (2010). Germination, postgermination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics*, 41, 293–319.

Ellner, S. (1985a). ESS germination strategies in randomly varying environments 2. Reciprocal yield-law models. *Theor. Popul. Biol.s*, 28, 80–116.

Ellner, S. (1985b). ESS germination strategies in randomly varying environments. 1. Logistic-type models. *Theor. Popul. Biol.*, 28, 50–79.

Ellner, S. (1987a). Alternate plant life-history strategies and coexistence in randomly varying environments. *Vegetatio*, 69, 199–208.

Ellner, S. (1987b). Competition and dormancy - a reanalysis and review. *Am. Nat.*, 130, 798–803.

Evans, M.E.K. & Dennehy, J.J. (2005). Germ banking: bet hedging and variable release from egg and seed dormancy. *Q. Rev. Biol.*, 80, 431–451.

Horst, J.L. (2011). Frequency dependent predation on winter annual seeds by granivorous rodents. Masters Thesis. Dept. of Ecology and Evolutionary Biology, University of Arizona Tucson, AZ.

Huxman, T.E., Kimball, S., Angert, A.L., Gremer, J.R., Barron-Gafford, G.A. & Venable, D.L. (2013). Understanding past, contemporary, and future dynamics of plants, populations, and communities using Sonoran Desert winter annuals. *Am. J. Bot.*, 100, 1369–1380.

Intergovernmental Panel on Climate Change, IPCC. (2007). Fourth Assessment Report of the Intergovernmental Panel on Climate Change.

Kimball, S., Angert, A.L., Huxman, T.E. & Venable, D.L. (2010). Contemporary climate change in the Sonoran Desert favors cold-adapted species. *Glob. Change Biol.*, 16, 1555–1565.

Kimball, S., Angert, A.L., Huxman, T.E. & Venable, D.L. (2011). Differences in the timing of germination and reproduction relate to growth physiology and population dynamics of Sonoran Desert winter annuals. *Am. J. Bot.*, 98, 1773–1781.

Kimball, S., Gremer, J.R., Angert, A.L., Huxman, T.E. & Venable, D.L. (2012). Fitness and physiology in a variable environment. *Oecologia*, 169, 319–329.

Metcalf, C.J.E. & Koons, D.N. (2007). Environmental uncertainty, autocorrelation and the evolution of survival. *Proc. Biol. Sci.*, 274, 2153–2160.

Ooi, M.K.J. (2012). Seed bank persistence and climate change. *Seed Sci. Res.*, 22, S53–S60.

Pake, C.E. & Venable, D.L. (1996). Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology*, 77, 1427–1435.

Philippi, T. & Seger, J. (1989). Hedging ones evolutionary bets, revisited. *Trends Ecol. Evol.*, 4, 41–44.

Reichman, O.J. & Van de Graaf, K.M. (1973). Seasonal activity and reproductive patterns of 5 species of Sonoran Desert rodents. *Am. Midl. Nat.*, 90, 118–126.

Saatkamp, A., Affre, L., Dutoit, T. & Poschlod, P. (2009). The seed bank longevity index revisited: limited reliability evident from a burial experiment and database analyses. *Ann. Bot.*, 104, 715–724.

Seger, J. & Brockmann, H.J. (1987). What is bet hedging? In: *Oxford Surveys in Evolutionary Biology* (eds Harvey, P.H. & Partridge, L.) Oxford University Press, Oxford, pp. 182–211.

Simons, A.M. (2011). Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proc. Biol. Sci.*, 278, 1601–1609.

Snyder, R.E. (2006). Multiple risk reduction mechanisms: can dormancy substitute for dispersal? *Ecol. Lett.*, 9, 1106–1114.

Templeton, A.R. & Levin, D.A. (1979). Evolutionary consequences of seed pools. *Am. Nat.*, 114, 232–249.

Thompson, K., Band, S.R. & Hodgson, J.G. (1993). Seed size and shape predict persistence in soil. *Funct. Ecol.*, 7, 236–241.

Tielborger, K. & Valleriani, A. (2005). Can seeds predict their future? Germination strategies of density-regulated desert annuals. *Oikos*, 111, 235–244.

Venable, D.L. (1989). Modeling the evolutionary ecology of seed banks. In: *The Ecology of Soil Seed Banks* (eds Leck, M.A., Parker, V.T. & Simpson, R.L.). Academic Press, San Diego, pp. 67–87.

Venable, D.L. (2007). Bet hedging in a guild of desert annuals. *Ecology*, 88, 1086–1090.

Venable, D.L. & Brown, J.S. (1988). The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.*, 131, 360–384.

Venable, D.L. & Kimball, S. (2013). Population and community dynamics of Sonoran Desert winter annuals. In: *Temporal Dynamics and Ecological Process* (ed. Kelly, C.K., Bowler, M.G. & Fox, G.A.). Cambridge University Press, Cambridge, pp. 140–164.

Venable, D.L. & Lawlor, L. (1980). Delayed germination and dispersal in desert annuals - escape in space and time. *Oecologia*, 46, 272–282.

Venable, D.L. & Pake, C.E. (1999). Population Ecology of Sonoran Desert Annual Plants. In *Ecology of Sonoran Desert Plants and Communities*. (ed Robichaux, R.H.). The University of Arizona Press Tucson, Arizona, USA, pp. 115–142.

Venable, D.L., Flores-Martinez, A., Muller-Landau, H.C., Barron-Gafford, G. & Becerra, J.X. (2008). Seed dispersal of desert annuals. *Ecology*, 89, 2218–2227.

Volis, S. & Bohrer, G. (2013). Joint evolution of seed traits along an aridity gradient: seed size and dormancy are not two substitutable evolutionary traits in temporally heterogeneous environment. *New Phytol.*, 197, 655–667.

Westoby, M. (1981). How diversified seed-germination behavior is selected. *Am. Nat.*, 118, 882–885.

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