Predicting Evolutionarily Stable Strategies from Functional Trade-offs of Sonoran Desert Annuals

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Abstract

For many decades, researchers have studied how plants use bet-hedging strategies to insure against unpredictable, unfavorable conditions. We consider how the survival rates of dormant seeds (in a 'seed bank') interact with functional trade-offs to influence optimal germination strategies. Specifically, we explore the functional trade-offs between resource-use capacity and low-resource tolerance, i.e., being able to generate high yield following high rainfall versus maintain performance during a drought. We develop a model that explicitly includes these trade-offs to model fitness as a function of precipitation, and identifies evolutionarily stable strategies (ESS), using data from 10 Sonoran Desert annual plant species. We use our estimated ESS values to predict observed germination fractions. We then explore the relative importance of seed survival and functional trade-offs in driving optimal germination strategies by regressing ESS values and observed germination fractions against these traits. We find survival rates and functional trade-offs to be significant drivers for bet-hedging with survival rates having the strongest influence. Our results offer insight into drivers of bet-hedging strategies in an iconic system, as well as provide the analytical framework to explore how current or future environmental conditions will impact life history evolution.

Keywords:

Bet-hedging, Desert Annuals, Trade-offs, Germination, Water-Use Efficiency

Introduction

For organisms inhabiting variable environments it can be difficult to perfectly time key life history functions, such as emergence or reproduction, with favorable conditions. In such environments, natural selection will favor traits or strategies that buffer against uncertainty, usually by spreading risk over time or space. This risk spreading is often achieved through bet-hedging, in which strategies or traits reduce variance in reproductive success at some cost to mean reproductive success [1–3]. Empirical examples of putative bet hedging strategies include iteroparity [4], variable diapause [5, 6], and variable offspring size [7, 8]. Delayed seed germination in annual plants is the classic example of bet-hedging [9], in which variance in success is reduced by spreading germination over multiple years, which has been clearly demonstrated in annual plants of the Sonoran Desert [10, 11].

Bet-hedging strategies interact with other traits to determine fitness, so the degree of bet-hedging should depend on other traits that may also buffer the organism from risk [10, 12]. For instance, the adaptive value of delaying germination depends on the risk of seed mortality [11, 13], which can depend on seed traits (e.g., varying seed coat thickness). Further, the effect of variable conditions may also be mediated by traits expressed later in the life cycle, such as those that relate to the organism's ability to tolerate stress as well as the ability to capitalize on resource bonanzas.

In desert annual plants, low-resource tolerance (i.e, stress tolerance) and resource-use capacity (i.e., the ability to capitalize on bonanzas) are likely to influence the fitness consequences of germination timing. We expect these functional traits to trade-off, such that the ability to tolerate stress is negatively associated with growth capacity under favorable conditions. Indeed, Sonoran Desert annual plants exhibit among-species trade-offs in functional traits related to stress tolerance, such as water use efficiency, and those related to growth capacity, such as relative growth rate [14–16]. One approach to assess the fitness consequences of such trade-offs is through relating resource availability to two quantities: probability of reproductive success and yield upon reproductive success. The set of intercepts and slopes

from these per-species relations explain performance upon low-resource availability and responsiveness to increased resource availability, respectively. These trade-offs can then be incorporated into models for understanding the adaptive value of germination timing. Of course, abiotic conditions, such as temperature or precipitation, are not the only sources of risk in uncertain environments. The fitness consequences of risk-spreading strategies also depend on biotic conditions, making traits that affect response to competition or other density-dependent processes important as well [17, 18]. Under density dependence, the optimal strategy depends on those employed by other individuals in the population; adaptive dynamics can be used to identify evolutionarily stable strategies (ESSs).

Here, we build upon a density-dependent seed bank model of Gremer & Venable [11] that includes intraspecific competition to estimate long-term stochastic fitness for ten annual plants in the iconic Sonoran Desert winter annual community. Unlike Gremer & Venable [11], we directly model the effect of precipitation on plant yield for this water-limited system. In doing so, we can vary precipitation and see how it relates to the fitness, trait evolution, and bet-hedging strategies of each species. Specifically, we model both the probability of reproductive success and per-capita yield, conditioned on reproductive success, as functions of precipitation and intraspecific density. Correlations among the coefficients of these relationships allow us to determine whether there are trade-offs between low-resource tolerance and resource-use capacity. We incorporate the precipitation-yield relationships into the density-dependent model to estimate ESS values and observe how well they predict germination strategies. To distinguish the relative importance of density, seed survival, and functional trade-offs in driving the evolution of germination strategies, we then build a statistical regression model and use it to explore how well it predicts observed germination strategies.

Model and Methods

To model the seed bank dynamics of annual plants, we adapted a model (Figure 1A) introduced by Gremer & Venable [11] and related their low-density yield to precipitation. Details on the empirical data that we used to parameterise the model can be found in Appendix A3. We parameterise this model in two steps. We first identify how the probability of producing seeds depends on precipitation (Figure 1B). We then determine how yield of reproducing individuals depends on precipitation (Figure 1C). With the parameterised model, we calculate the ESS for germination fraction for each of the 10 species, independently. We then use a regression to estimate the relative importance of several demographic parameters (that reflect species-specific life history traits) in governing both predicted and observed ESS germination fractions. To emphasize, whereas the ESS analysis predicts germination fractions based on a bet-hedging model that adaptively balances trade-offs, the regression model is a curve-fit that does not generate *a priori* predictions, but only assesses the relative importance of different life history traits in explaining observed germination fractions.

Model

Let n_t denote the density of seeds in the seed bank in year t for a focal species. A fraction of g seeds germinate each year. Under low density conditions, germinating seeds contribute K_t seeds to the seed bank in year t; we refer to K_t as the low-density yield in year t. These seeds survive to the next year with probability s_{new}, the survival rate of fresh seeds. Negative density-dependence reduces yield by a factor $1/(1 + agn_t)$, where $a > 0$ is a species-specific competition coefficient for the germinating population. A fraction of $(1 - g)$ seeds remain dormant until the next year, each surviving with probability s_{old}, the survival rate of dormant seeds (Figure 1). Under these assumptions,

$$n_{t+1} = \frac{gK_t s_{new} n_t}{1 + agn_t} + (1 - g)s_{old} n_t. \tag{1}$$

Benaïm & Schreiber ([19]) show that the density of seeds, given by (1), converge to a unique stationary distribution. In particular, if the realized per capita growth rate $r = \mathbb{E}\left[\log(gK_t s_{new} + (1-g)s_{old})\right] < 0$, n_t converges almost surely to 0. If $r > 0$, n_t converges to a unique, positive stationary distribution $\hat{n}(g)$.

Precipitation and Yield

While Gremer & Venable [11] estimated K_t directly from the demographic data, we model how K_t depends on precipitation P_t in each year in order to analyze the effect of precipitation on seed bank dynamics. We used the same 30 years as Gremer & Venable [11] for comparative purposes and obtained each year's observed yield and precipitation values for the ten desert annuals featured in Venable [10]. Following Venable [10], a factor of .5 is added to yield and a factor of 1 is added to precipitation, so that the residuals of the linear regressions between log-yield and log-precipitation were normally distributed. Let $N_t = gn_t$ be the seedlings per m^2 in year t. Then the observed yield Y_t is assumed to be

$$Y_t = \frac{K_t}{1 + aN_t}$$

where a and K_t are the measured competitive coefficient and measured low-density yield for year t, both calculated by Gremer & Venable [11].

To determine a model relating low-density yield to precipitation, we first modeled the probability of reproductive failure or success, $K_t < 1$ or $K_t \geq 1$ respectively (Figure 1B). For the subset of years in which a species experiences reproductive success, we did a linear regression relating low-density yield, $\log(K_t)$, to $\log(P_t)$ (Figure 1C):

$$\log(K_t) = \log(\alpha_2) + \beta_2 \log(P_t),$$

where P_t is the measured precipitation for year t. These two steps result in the following model of K_t as a function of precipitation:

$$K_t = \begin{cases} \alpha_2 P_t^{\beta_2} & \text{with probability } (\pi_t) \\ 0.5 & \text{with probability } (1 - \pi_t) \end{cases}$$

where the probability of reproducing is:

$$\pi_t = \frac{1}{1 + e^{-(\alpha_1 + \beta_1 \log(P_t))}} \, .$$

We call α_1 the reproductive intercept, β_1 the reproductive slope, α_2 the log-yield intercept, and β_2 the log-yield slope. Larger reproductive intercepts and reproductive slopes correspond to higher probabilities of reproductive success on low and high precipitation years, respectively. Upon reproductive success, larger log-yield intercepts and log-yield slopes correspond to higher yield on low and high precipitation years, respectively. For both relationships, higher intercepts represent the ability to reproduce under low resource availability (i.e., tolerance to low water availability) and larger values for slopes represent responsiveness to resources and ability to capitalize on good resource years (i.e., ability to capitalize on wet years for reproduction).

Predicting ESS Values

To identify the ESS for the germination fraction g, consider a "mutant" population at very low density $\tilde{n}$ playing a different germination strategy, $\tilde{g}$. At low densities, this mutant population has a negligible feedback on the resident population and itself, but is influenced by the resident. Hence, its population dynamics are initially approximated by

$$\tilde{n}_{t+1} = \frac{\tilde{g} K_{t+1} s_{new} \tilde{n}_t}{1 + a g n_t} + (1 - \tilde{g}) s_{old} \tilde{n}_t.$$

The success or failure of the invasion of these mutants is determined by their stochastic growth rate,

$$r(g,\tilde{g}) \ = \mathbb{E}\left[\log\left(\frac{\tilde{g}K_1 s_{new}}{1+ag\hat{n}(g)} + (1-\tilde{g})s_{old}\right)\right].$$

If $r(g,\tilde{g}) < 0$, the invasion fails and if $r(g,\tilde{g}) \geq 0$, it succeeds [20]. A germination strategy g is an ESS if $r(g,\tilde{g}) < 0$ for all $\tilde{g} \neq g$, i.e. no other strategy can invade. A necessary condition for an ESS with $0 < g < 1$ is that $h(g) = \frac{\partial r}{\partial \tilde{g}}(g,g) = 0$. Since $\frac{\partial^2 r}{\partial \tilde{g}^2}(g,\tilde{g}) < 0$ for all $\tilde{g}$, if such a g is found, it is unique. Thus to find the ESS, we solve for the root of $h(g)$ strictly between 0 and 1 (see Appendix A1). We then compare ESS values to germination rates.

Results

Survival, Precipitation Response, and Trade-offs

As expected, our analyses reveal trade-offs among functional strategies, as well as variation in seed survival and response to competition (Table 1, Figure 1). In Table 1, we list the relevant parameters and their values for all 10 species, where the ordering is based on survival rates of dormant seeds. An illustrative regression for *Eriophyllum lanosum* (ERLA) is shown in Figure 1B,C. The Pearson correlation between reproductive intercept values and reproductive slope values is $-.68$, between log-yield intercept values and log-yield slope values is $-.85$, and between survival rates of dormant seeds and fresh seeds is .995. The strong negative correlations between intercepts and slopes indicate strong tradeoffs and a gradient of life history strategies where species with high β values (and thus low α values) produce few if any seeds under low precipitation, but are well adapted to take advantage of high rainfall.

Predicting ESS Values

A linear regression on model-estimated ESS values explains 63% of the variance (adjusted R^2) in observed germination fractions but typically overestimate these fractions (Figure 2).

To understand the impact of each trait on determining ESS values and observed germination rates, we also examined how well our model-estimated ESS values and observed germination fractions could be estimated by parameters of Table 1 on the logit scale. The strong correlations between each of the slopes and their corresponding intercepts and between the seed survival rates – along with the non-dimensionalization of equation (1) (see Appendix A2) – allow us to reduce the potential predictors to reproductive slopes, log-yield slopes, and survival rates of dormant seeds. The linear regression

$$L_{ESS} = .86 - .10\hat{\beta}_1 - .29\hat{\beta}_2 - .57\hat{s}_{old}, \tag{2}$$

explains 76% (adjusted R^2) of the variance in the predicted ESS values on the logit scale, where the hatted variables denote the standardized predictor variables. Survival rates of dormant seeds have the most impact on changes in ESS values, log-yield slopes the second most, and reproductive slopes the least. Finally, we analyzed how well these three parameters estimate germination fractions. The linear regression

$$L_{obs} = -.29 - .52\hat{\beta}_1 - .39\hat{\beta}_2 - .70\hat{s}_{old} \tag{3}$$

explains 76% (adjusted R^2) of the variance in the observed germination fractions (Figure 2). The coefficient magnitudes of the L_{obs} values are relatively closer to each other, with seed survival rates having the highest negative effect on the germination fractions. Moreover, reproductive slopes have a much higher negative effect on observed germination rates than they did in the model-predicted ESS values. Both regressions show that germination fractions are lower for species that have higher survival of seeds in the seed bank, and little reproductive success in dry years (low α's), even though they have high yield in wet years (high β's).

Discussion

Our model relating yield to precipitation highlights trade-offs between responsiveness to increased resources and performance when conditions are poor: one trade-off relates the probability of reproductive success to precipitation; the other relates yield to precipitation. Species with larger reproductive slopes will more likely experience reproductive success under high precipitation years but will less likely experience reproductive success under low precipitation years, as reproductive slopes are negatively correlated with reproductive intercepts. That is, species that tend to successfully reproduce on favorable, wet years are less likely to do so in dry years. Similarly species with larger log-yield slopes exhibit higher (conditional) yield with higher precipitation but produce less seeds with lower precipitation.

A linear regression on our estimated ESS values explain approximately 20% more variance in germination fractions than a linear regression on Gremer & Venable's predicted values. However, we consistently overestimate the observed germination fractions, whereas their predictions are a mixture of under- and over-predicted values with smaller summed squared-residuals (Figure 2A) [11]. These over-estimates might stem from all the possible risks or factors that may select for greater bet-hedging, e.g. seed predation, interspecific competition, variable temperature, and disease [21–27], which aren't included in our model. Furthermore, 30 years of precipitation may not fully capture the long-term variation in precipitation that has shaped the evolution of germination timing in these species. If variance was higher than observed in our data, we would expect more bet-hedging through reduced germination.

The statistical model (equation 3) for predicting germination fractions from seed survival and functional trade-offs highlights which coefficients of the model explain the most variance in optimal and observed germination strategies. Our results indicate that that survival rates of dormant seeds account for most of the bet-hedging in the parameter values of the statistical model, followed by reproductive success and conditional yield on high precipitation years. Consistent with classical bet-hedging theory [9, 13], the safer it is to be in the seed bank,

the more beneficial it is to bet-hedge. The same is true with lower reproductive success on dry years; lower reproductive success on dry years (which is correlated with having higher reproductive success in wet years) seems to select for desert annuals to bet-hedge more. Likewise, higher log-yield slopes, i.e. higher rates of seed production on wet years, correspond to lower seed production on dry years, also factor towards more bet-hedging. Log-yield values are also only relevant once an individual has surmounted the obstacle of having reproductive success at all, possibly explaining why those parameters have the lowest impact on explaining observed germination fractions.

The statistical model also highlights what might be driving the difference between the observed germination fractions and the predicted ESS values (Figure 2); specifically, the differences in magnitudes for the intercepts and parameter coefficients between equation (2) and equation (3) highlight what factors are driving the ESS predictions versus long-term observations in the field. The intercepts account for the largest difference in fit between the statistical model and the ESS models' predicted germination fractions. This major difference partially stems from the variance in our predicted yield values generally having lower variance than that of the estimated low density yield values of Gremer & Venable [11]. Other sources of uncertainty, as discussed earlier, may also explain the difference in the intercept values. The second largest difference is that of the coefficient of the β_1 term, or reproductive success. Since reproductive success is determined solely from precipitation as well, the difference in coefficient magnitudes may be highlighting our inability to capture variation in reproductive success from rainfall alone. Consequently, the statistical model suggests that the variance in both yield and reproductive success is not completely explained by the variation in precipitation. Other factors such as temperature may play a role in mediating responses to water availability, particularly in this system [16, 28, 29].

It is worthwhile to note that the statistical model provides an alternate way to estimate germination fractions, using survival rates of dormant seeds, reproductive slopes, and log-yield slopes. However, we mainly use the statistical model to highlight the ESS model's

inability to capture a large amount of the variance within the system, which seemingly stems from the underestimated variance in yield and reproductive success. Although the ESS model can only capture as much variance as we initially input (namely the uncertainty in precipitation), it can be modified to incorporate any of the variable factors mentioned beforehand, such as temperature and predation.

Conclusions

Our approach – which explicitly incorporates an aspect of environmental variation, and trade-offs in functional responses to that variation, into models for understanding the drivers of optimal strategies – provides powerful insight into the drivers of life history evolution in variable environments and is likely to be useful in many other systems. The ESS model predicts germination fractions based on uncertainty in precipitation, whereas the statistical model indicates the relative importance of survival rates, reproductive success, and conditional yield. Our results highlight differences among strategies among species in the desert annual system. Some species have strategies which capitalize on resource bonanzas on wet years, both in terms of reproductive success and in the amount of seed production, but fail to produce enough seeds on dry years and must rely on bet-hedging to mitigate that risk. Others have the opposite strategy in which they have relatively high reproductive success in dry years, and have less bet-hedging. More importantly, those that have a higher chance of surviving in the seed bank benefit most from keeping more seeds dormant in the seed bank.

As a model for displaying the relative importance of survival rates, reproduction rates, and conditional seed production rates, the statistical regression for observed germination fractions captures more sources of uncertainty. The statistical model points to uncertainties in yield and reproductive success which are not being captured by the ESS model. Thus, discerning these biological uncertainties and modeling them will be an important step toward understanding the reasons why desert annuals hedge their bets as much as they do. Finally,

as 30 years of data may not be fully capturing the whole picture in mean and variation in precipitation, it will be equally important to investigate how shifts in mean and variation in precipitation (which will also drive the variability in yield) affect evolutionarily stable strategies in the face of future climate change.

Data Accessibility. All measured quantities for this study can be found at Dr. Lawrence Venable's Desert Annual Archive (http://www.eebweb.arizona.edu/ faculty/venable/LTREB/LTREB%20data.htm).

Authors' Contributions. W.S.C. and S.J.S. conceived of the study and developed the model and analytical methods. All authors gave feedback on the model and methods and were involved in the interpretation of the results. W.S.C. carried out the statistical analysis and model simulations. W.S.C. and J.R.G. wrote the manuscript. All authors contributed to content and editing of the manuscript.

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Appendix

A1 - ESS Calculations

If we let $Z(\tilde{g}) = \left(\frac{\tilde{g}K_1 s_{new}}{1+ag\hat{n}(g)} + (1-\tilde{g})s_{old}\right)$, then

$$\frac{\partial r}{\partial \tilde{g}}(g,g) = \mathbb{E}\left[\frac{\left(\frac{K_1 s_{new}}{1+ag\hat{n}(g)} - s_{old}\right)}{Z(g)}\right] \tag{4}$$

where the expected value is evaluated with respect to $\hat{n}(g)$ and K_1. Letting $h(g) = \frac{\partial r}{\partial \tilde{g}}(g,g)$, it is sufficient to solve for the unique zero of h, if it exists, over the domain $(0,1)$. To accomplish this, we take 2,000 draws from $\hat{n}(g)$, evaluate each of these draws via expression (2) of the main text, and average the corresponding outputs. Using R's uniroot solver, we then solve for when $h(g) = 0$.

A2 - Nondimensionalization

Let $x_t = an_t$, where $a > 0$. Then substituting into (1) of the main text, we obtain

$$x_{t+1} = \frac{gK_{t+1}s_{new}x_t}{1+gx_t} + (1-g)s_{old}x_t. \tag{5}$$

Since a does not appear in (3), solving for the ESS value depends only on whether $a = 0$ or $a > 0$, rather than the specific value of a non-zero competition coefficient. Since all of our a values are positive, we can rule this out as a predictor.

A3 - System Design

Long-term demographic monitoring of the Sonoran Desert winter annual community has been conducted since 1982 at the University of Arizonas Desert Laboratory at Tumamoc Hill in Tucson, AZ ($32°13'$ N, $111°0'$ W), 723 m above sea level. Every year since then, permanently

marked plots along a 250m transect have been visited to record germination of every plant in each plot and then surveyed at roughly monthly intervals to monitor survival. Beginning in the 1989/1990 season, the density of viable, non-germinating seeds were estimated using soil cores collected outside of plots but within the demographic study area. Combined with the demographic surveys, these seed bank estimates were used to calculate annual germination fractions. Details on the demographic and seed bank studies are available, but kept brief here [10, 11, 30, 31]. To be consistent with previous work [10, 11], we analyzed the data for 10 common and abundant species in the winter annual community: *Eriophyllum lanosum A. Gray* (ERLA, Asteraceae), *Erodium cicutarium (L.) L'Hér. ex Aiton* (ERCI, Geraniaceae; naturalized species), *Erodium texanum A. Gray* (ERTE, Geraniaceae), *Evax multicaulis DC* (EVMU, Asteraceae), *Monoptilon bellioides (A. Gray) H.M. Hall* (MOBE, Asteraceae), *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; naturalized species), and *Stylocline micropoides A. Gray* (STMI, Asteraceae). Here we use the nomenclature consistent with previous work on this system; synonymy and currently accepted nomenclature are given in Gremer et al. [31].

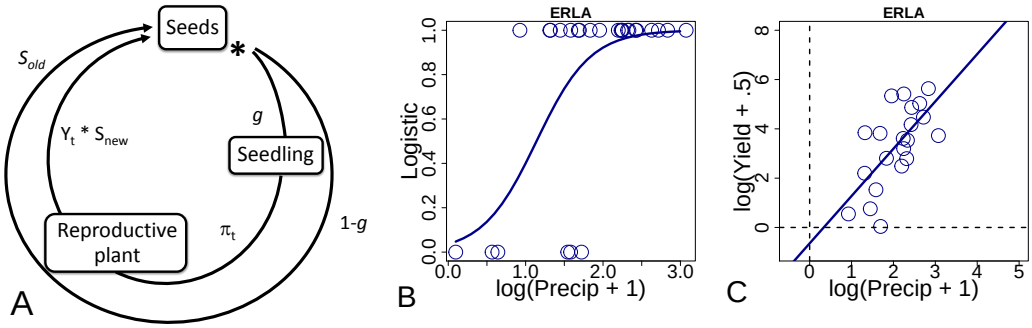

Figure 1: Panel A denotes the life cycle of an individual seed, as described by eqn. (1). An individual seed remains dormant with probability $1 - g$ and survives to the next Fall with probability s_{old} (outer circle). Otherwise, it germinates, becomes a reproductive plant with probability π_t (Panel B), and produces Y_t seeds per square meter (Panel C); a fraction s_{new} of Y_t then contributes to the following Fall (inner circle). Panel B shows the logistic regression for ERLA, where the zeroes and ones denote reproductive failures and successes, plotted against their corresponding precipitation values P_t in year t. Panel C shows the linear regression for ERLA of the low-density yield values K_t attained upon reproductive success against precipitation on a log-log scale.

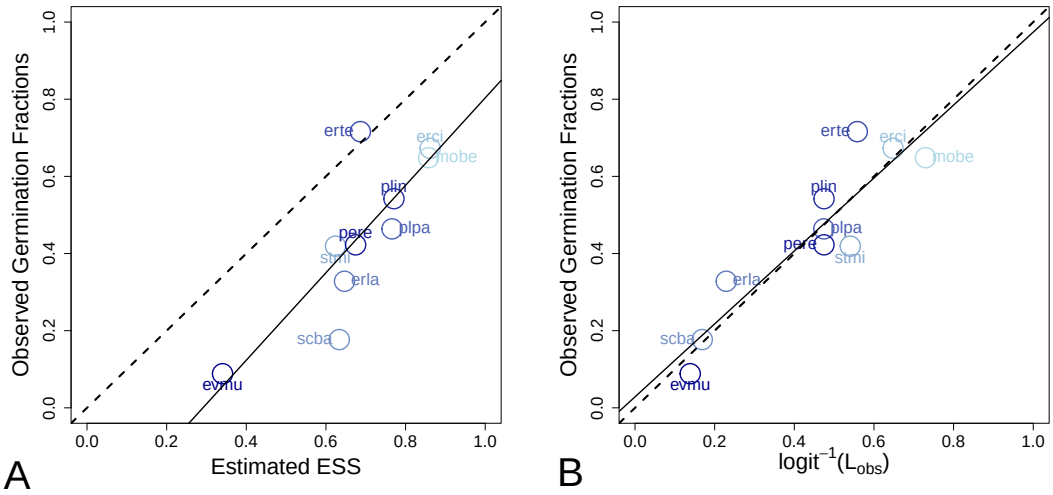

Figure 2: Panel A: the observed germination fractions against model-estimated ESS values for each species. Panel B: germination fractions against germination estimates found by taking the inverse-logit of L_{obs}. The dotted and solid lines represent the one-to-one lines and lines of regression, respectively. Points have been colored from light blue (low seed survival) to dark blue (high seed survival).

Species	s_{old}	s_{new}	α_1	β_1	α_2	β_2	a
Monoptilon belliodes (MOBE)	.273	.102	-3.51$^{\bullet}$	2.79*	1.77	0.78	.0163
Erodium cicutarium (ERCI)	.429	.132	-1.62	1.96*	0.05	1.25*	.0351
Stylocline micropoides (STMI)	.458	.145	-1.97	1.52*	-1.42	2.23***	.0156
Schismus barbatus (SCBA)	.512	.150	-2.02	3.03*	-0.55	2.39***	.0112
Eriophyllum lanosum (ERLA)	.532	.153	-3.28$^{\bullet}$	2.87*	-0.65	1.92**	.0114
Plantago patagonica (PLPA)	.550	.160	-2.25	2.41*	1.54	0.81	.0069
Erodium texanum (ERTE)	.577	.170	-1.41	1.45*	-0.06	1.36**	.0532
Plantago insularis (PLIN)	.596	.168	-1.45	2.11*	1.62$^{\bullet}$	0.86$^{\bullet}$	.0380
Pectocarya recurvata (PERE)	.627	.173	-0.14	1.42	0.70	1.52*	.0167
Evax multicaulis (EVMU)	.828	.214	-3.86*	2.36*	1.58	1.30$^{\bullet}$	.0119

Table 1: p-values for estimated parameters (α's and β's) are denoted as .1$^{\bullet}$, .05*, .01**, and .001***.