

## Bet-hedging strategies of native and exotic annuals promote coexistence in semiarid Chile



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### ABSTRACT

Scientists are increasingly interested in the evolutionary responses of organisms to unpredictable, variable, and extreme climate changes. In semiarid environments, inter-annual variability in the frequency and amount of rainfall affects both the growth and recruitment of plant species, especially annuals. In these inherently variable environments, individual selection should favor demographic responses that spread the risk of mortality over time and enhance long-term reproductive success (i.e., bet-hedging strategies). However, the same processes that allow the persistence and recruitment of native species could facilitate the introduction and establishment of exotics. We assessed whether native and exotic annuals in semiarid Chile displayed similar or contrasting bet-hedging traits, and discuss mechanisms of coexistence of both types of species and their demographic variation under interannual rainfall variability driven by El Niño Southern Oscillation (ENSO). We analyzed a proxy of long-term fitness, i.e., the variability of seed density over 17 years, for the two most common native and two exotic annual plant species present in the study area. We experimentally tested whether the quality of the maternal environment (soil water supply in a given year) had an extended effect (e.g. the next year) on the proportion of seed germination or on the mean and/or variability of seed size and seed dormancy. Results showed that native and exotic species in this annual plant assemblage displayed contrasting bet-hedging strategies as evolutionary responses to variable rainfall. Although rainfall variability promotes the evolution of bet-hedging strategies, the nature of these strategies varies across species, presumably to minimize competitive exclusion. In semiarid Chile, the success of two exotic ephemerals that are components of a diverse community of native annual species seems to reflect bet-hedging germination strategies that complement rather than compete with those expressed in dominant natives.

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## 1. Introduction

Considering that semiarid environments are characterized by unpredictable rainfall inputs over various time scales, species have evolved sets of traits or strategies that spread the risk of mortality

over time, so that establishment failure on one year will not kill the entire progeny (Cohen, 1966; Halley, 1996; Clausen and Venable, 2000; Bell and Collins, 2008; Childs et al., 2010). For example, plant species can experience temporal variation in herbivore density (Hunter, 1992) or water availability (Jiménez et al., 2011) and the average intensity of these factors may fluctuate between years. On the other hand, disturbance events or global climate change can alter plant species environment over longer time scales (Holmgren et al., 2006). Therefore, short- or long-term environmental

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fluctuations lead to intergenerational variation in vital rates (Hairston, 1996) and, by direct implication, fitness. Accordingly, three evolutionary responses have been described that can account for plant species capacity to cope with unpredictable and extreme climate fluctuations: adaptive tracking, phenotypic plasticity, and bet-hedging strategies (Gutschick and BassiriRad, 2003; Chown et al., 2010; Simons, 2011). Since climate change is expected to lead to increasingly variable environments during this century (Karl and Trenberth, 2003), bet-hedging characters may be crucial determinants of altered community dynamics, extinction or invasion risk (Childs et al., 2010), or coexistence too.

The term “bet-hedging” refers to a strategy wherein an individual bypasses opportunities for immediate reproductive gain in favor of long-term reproductive success (Cohen, 1966), considering the trade-off between the expected value of fitness and its variance for a given genotype or life history strategy (Philippi and Seger, 1989). Accordingly, bet-hedging strategies may involve traits that promote the production of fewer and larger offspring (i.e. conservative strategy), or of variable-sized offspring where traits with increased variance spread the risk over the time (i.e. diversified strategy) (Westoby, 1981; McGinley et al., 1987; Simons and Johnston, 1997). Irrespective of the strategy, bet-hedging traits have evolved to minimize fitness variance, and hence the risk of reproductive failure in fluctuating environments (Cohen, 1966; Philippi and Seger, 1989). Such traits are suboptimal under average conditions but reduce the variance in fitness (Gillespie, 1974), thereby maximizing geometric mean fitness across generations (Simons, 2002, 2011; Venable, 2007). For plant ecologists, bet-hedging traits are measurable features that mediate the mean–variance fitness relationship (Childs et al., 2010).

At the community level, differences in bet-hedging strategies among species should contribute to coexistence, because they favor temporal partitioning of environmental resources (Shmida and Ellner, 1984; Chesson, 2003). Since semiarid ecosystems are often highly variable, with punctuated weather patterns in terms of both precipitation and temperature (Huxman et al., 2004; Holmgren et al., 2006; Gutiérrez et al., 2010), recent studies have highlighted the role that bet-hedging strategies play in promoting the coexistence of annual plant species (Clauss and Venable, 2000; Tielbörger and Valleriani, 2005; Venable, 2007), or even among native and exotic species (Jiménez et al., 2011).

Frequently, exotic annual plants may invade the plant assemblage of semiarid ecosystems either because they share similar traits with native species, but are competitively superior (Baker, 1974; Sakai et al., 2001), or alternatively, because invasive species differ from native ones in their bet-hedging strategies (Simons, 2011). A recent analysis of a 17-year annual plant database from a semiarid ecosystem in northern Chile, documented that an extreme drought (i.e. La Niña year 1998) constituted a major disturbance to the annual plant community, facilitating invasion by exotic annual species (Jiménez et al., 2011). This study showed that plant cover of two exotic annuals, *Schismus arabicus* and *Erodium cicutarium*, recorded in the annual plant assemblage since 1989 (i.e. when the long-term study started), increased in 300% after the dry La Niña-year of 1998. Furthermore, the analysis by Jiménez et al. (2011) also showed that the 1998-La Niña represented a window of opportunity that allowed exotics to increase in cover at the expense of the two most dominant native annuals, *Plantago hispidula* and *Bromus berterianus*, which decreased their cover in 83% in subsequent year. However, long-term trends showed that exotic annuals never outcompeted native annuals and that after eight years the community assemblage regained their initial cover values (Jiménez et al., 2011). We therefore hypothesize that these native and exotic annual species should express different bet-hedging traits that allow them to persist in spite of large cover fluctuations and

coexist in a highly variable environment.

For annual plants, bet-hedging traits may include seed dormancy, seed-size distribution, delayed flowering, and delayed fruiting (Simons, 2011). In terms of seed dormancy for instance, seed germination may be strongly restricted to situations that favor seedling establishment and growth (Cohen, 1966; Clauss and Venable, 2000; Mayhew, 2006). These species should have backup mechanisms allowing seed germination to occur when resources are abundant, no matter how unpredictable these situations may be (Philippi, 1993; Clauss and Venable, 2000; Letnic, 2000). In this case, the distribution of seed germination over multiple years decreases the probability that in a bad year all seedlings could die without reproducing (Clauss and Venable, 2000). In relation to seed size one bet-hedging strategy is that shown by mothers that produce a range of offspring sizes, while an alternative strategy is shown by mothers whose seeds are consistently larger than the long-term optimal size (Crean and Marshall, 2009). Here, we will focus on differences in seed size, seed germination and seed production as measures of bet-hedging strategies for exotic and native annuals from semiarid Chile.

## 2. Methods

### 2.1. Study site

Our study was conducted in the semiarid scrublands of Fray Jorge Forest National Park (30° S, 71° 40' W, FJ henceforth), Chile. The local climate has a strong Mediterranean influence (López-Cortes and López, 2004), with extended dry periods of 6–7 months (November–April) and rainfall entirely concentrated (>95%) in the austral winter months (May–August). Annual rainfall measured at the weather station in FJ averages  $125 \pm 18$  mm (mean  $\pm 1$  SE, CV = 73%) over the last 25 years. Years with high annual rainfall are strongly associated with extreme ENSO events. During the period of records, 1991–1992, 1997 and 2002 had annual rainfall between 240 and 360 mm, while 1988 and 1990, were extremely dry, with reported annual rainfall of 11 and 33 mm respectively (Jiménez et al., 2011). Predominant vegetation is a mixed scrubland with presence of evergreen and summer-deciduous shrubs, 1–3 m in height, and a seasonal ground layer of annual herbs. The thorny evergreen shrub *Porlieria chilensis* dominates the overstory layer with 25–35% cover, and coexists with two drought-deciduous species, *Proustia pungens* (10–20% cover) and *Adesmia bedwellii* (3–6% cover), leaving ample open spaces between shrubs where ephemeral plant cover develops from late winter to early spring (Gutiérrez et al., 1993; Meserve et al., 2003).

### 2.2. Data collection

#### 2.2.1. Long-term plant cover and seed bank data

To evaluate differences in long-term reproductive success as a proxy of species fitness we analyzed 17 years of data on seed density and trends in plant cover for the two most dominant native (*P. hispidula* and *B. berterianus*) and exotic (*E. cicutarium* and *S. arabicus*) annual species. These four annuals exhibited contrasting trends in plant cover associated with climatic extremes over the study period (Jiménez et al., 2011). They are henceforth referred to by genus only.

We used plant cover data collected annually in control plots from the large-scale experiment established in 1989 in FJ (Gutiérrez et al., 2010; Gaxiola et al., 2014). Since 1989, cover of ephemeral plants was measured each year at the peak of the growing season (September–October) using the point intercept method. In each of four  $75 \times 75$  m plots, foliage and species intercepting 10 random

1.5 m-long segments subdivided into 30 points (5 cm intervals) along four 75 m permanent transects were recorded. Control plots had low (1-m high) fencing with 2.5 cm mesh, buried ~40 cm, with openings (5 cm diameter) to allow the access of small mammal species, hence representing the complexity of all biotic interactions inherent to the study site. The total number of points per plot was 1200 and we analyzed 52 plot samples overall (4 plots  $\times$  17 years). Plant cover by species was estimated as the proportion of points where the species was recorded.

To obtain annual seed density by species, we analyzed seed bank data for the 17 years since 1989 (Gutiérrez and Meserve, 2003). Soil samples were collected from the same control plots in December each year, as seed densities are maximal in early summer (Gutiérrez and Meserve, 2003). Seeds were extracted from soil by mechanical separation using a fine mesh sieve (0.5–3.35 mm), with the smallest seeds extracted by flotation. All seeds were oven-dried and identified to species under a stereoscopic microscope (NIKON SMZ-10) using a reference seed collection from the study site.

### 2.2.2. Manipulative experiments to test the effects of maternal environment

We performed a field experiment to test whether the quality of the maternal environment under which a plant grows has an extended effect (i.e. following generation) on the mean values and/or variability of seed size and seed germination, both characters related to bet-hedging. For this we considered two experimentally created maternal environments, one where rainfall was equivalent to an ENSO year (i.e. high rainfall), and the other equivalent to a below average, control year. We used synoptic predictions provided by the Climate Prediction Center of the NOAA (NOAA, 2008) to assess whether 2008 was going to be a wet or below average year and thus decided to conduct the experiment during 2008. We then created two maternal environments by setting up five 1 m<sup>2</sup>-plots (control) that received only the rainfall of that year (i.e. in 2008 rainfall was 96 mm) and five irrigated plots where water was added to complete the equivalent of an ENSO year. Irrigated plots received the equivalent of 120 mm plus 96 mm, while control plots received only natural rainfall. We added water to the five irrigated plots during the winter months of 2008 at the same time it was raining. At the end of the growing season (i.e. December), entire plants were harvested and ripe seeds of the two native and exotic annual species studied were collected inside the 1 m<sup>2</sup>-plots.

Seeds collected from this field experiment were used to test the effects of the maternal environment on seed size (i.e. mass) and germination. The number of annuals inside the plots varied between 3 and 10 individuals, and all seeds produced in each plot were collected. Because of the limited plot size (1 m<sup>2</sup>), we had a restricted number of seeds. Nonetheless, we managed to get at least 10 seeds per species per plot, completing 50 seeds per species per environment (100 seeds per species). We first assessed variability in seed size as the coefficient of variation of seed mass of 10 viable seeds per species per treatment. Secondly, we tested for differences in mean seed mass per species per maternal environment. Seed mass was obtained weighing each seed with a Mettler Toledo analytical balance.

Subsequently, we conducted germination assays in the laboratory for the collected seeds using a controlled-environment, growth chamber (12 h light-12 h dark, at constant temperature of 18 °C, following Vidiella and Armesto, 1989). Seeds were individually wrapped in paper towels soaked in tap water, and placed separately in pots (7 cm diameter  $\times$  3 cm depth), covered with aluminum foil, and watered every two days. Five replicate pots per species for each maternal environment were set up containing 10 seeds each. The number of seeds germinated (seedlings emerged) was counted every other day. Seeds were kept separated to assure

that seeds in each pot corresponded to a single 1 m<sup>2</sup>-experimental plot, and “plot” was included as a random variable in the analyses.

### 2.3. Data analyses

#### 2.3.1. Long-term fitness and germination success

We used the ratio of annual seed production by a given species to its annual cover (%) as a proxy of species per capita reproductive success. We then calculated long-term variation (i.e. 17-year data) in reproductive success as the geometric mean and geometric standard deviation (GSD) of per capita reproductive success. It must be noted that per capita reproductive success is based on plant cover measurements of a finite number of plants and hence is measured with uncertainty, thus the geometric SD measurement could be slightly biased by the inclusion of a small sample of the within-year variance. We corrected this by bootstrap resampling of seed density and plant cover for each species with 1000 permutations. The GSD of a species reproductive success was used to estimate species long-term fitness.

To assess whether there was a trade-off between species long-term reproductive success and seed germination as suggested by Venable (2007), we plotted the proportion of seeds germinated in the laboratory trials versus the GSD of long-term species reproductive success (i.e. analysis of long-term data). Taken into consideration that we used seeds that came from plants that grew under two different environmental scenarios, we consider that seed variability represents conditions of two different years and not only one. Finally, to determine the dependency of seed germination on water availability, we used a linear regression analysis to test the relationship between per capita reproductive success and annual precipitation. For this analysis, we used precipitation data from the Fray Jorge weather station, recorded since 1989.

#### 2.3.2. Water manipulation and seed germination

We calculated mean germination success per species and treatment as the proportion of germinated seeds in all pots for both maternal environments (i.e. irrigated and control treatments). Seed germination data were arcsine-square root transformed and differences in the proportion of seed germination between treatments were assessed for each species by a Student's t-test.

#### 2.3.3. Water manipulation and seed size

To analyze variability in seed size (i.e. mass) for both maternal environments we calculated the Coefficient of Variation (CV) of log-transformed seed weight per species and treatment. CV has been previously used to examine offspring variability, because it describes the standard deviation as a percentage of the sample mean, and therefore, higher CVs are less likely to be an artifact of increases in the mean (Crean and Marshall, 2009). We used a nested ANOVA to evaluate differences in seed mass CV between treatments per each species. For this we treated “experimental plots” as a random effect and “maternal environment” (i.e. water treatments) as the fixed effect, given the small sample size of this experiment we analyzed each species separately. Finally, species with CVs of seed mass above 50% were considered diversified bet-hedgers (Crean and Marshall, 2009), producing seeds of different sizes that could germinate under a range of environmental conditions (Simons, 2011).

## 3. Results

### 3.1. Long-term fitness and germination success

In this semiarid community both dominant native annuals had much lower long-term fitness (geometric standard deviation of per

capita seed production = 7.85 and 3.03 for *Bromus* and *Plantago*, respectively; X axis in Fig. 1) than the two most common exotic annuals, *Erodium* and *Schismus* (18.5 and 12.8, respectively; X axis in Fig. 1). Moreover, both native species had higher seed germination success, measured as proportion of germinated seeds in laboratory trials, than the two exotic species, suggesting a trade-off between long-term fitness (low in natives, high in exotics) and their immediate reproductive success (germination success, high in natives, low in exotics), as predicted by bet-hedging (Fig. 1). Only for the exotic *Schismus*, we found a significant relationship between long-term fitness and annual rainfall ( $r^2 = 0.36$ ,  $p = 0.03$ ,  $n = 9$ ); no trend was observed for the native grass *Bromus* ( $r^2 = 0.32$ ,  $p = 0.07$ ;  $n = 11$ ), native *Plantago* ( $r^2 = 0.09$ ,  $p = 0.22$ ,  $n = 13$ ) or the exotic *Erodium* ( $r^2 = 0.0001$ ,  $p = 0.98$ ). Germination success for both exotic species, *Erodium* and *Schismus*, in the lab trials was very low, 0.14 and 0.09 respectively, with low standard deviations of seed germination, 0.13 and 0.11, respectively. In contrast, the native *Bromus* presented the highest seed germination, with a proportion of 0.96 germinated seeds, along with the lowest standard deviation in seed germination ( $\pm 0.08$ ). In turn, the other native species, *Plantago*, had the highest standard deviation of seed germination ( $\pm 0.37$ ), and an intermediate proportion of 0.41 germinated seeds (Fig. 1). *Plantago* presented higher germination success among seeds derived from plants from control plots than plants from watered plots ( $t = 2.42$ ,  $df = 4$ ,  $p = 0.04$ ). For the other three species, there were no differences between treatments (*Bromus*:  $t = 1.63$ ,  $df = 4$ ,  $p = 0.17$ , *Erodium*:  $t = 1.44$ ,  $df = 4$ ,  $p = 0.19$ , and *Schismus*,  $t = 0.76$ ,  $df = 4$ ,  $p = 0.46$ ; Fig. 2).

3.2. Seed size variability

There was no clear differentiation between exotic and native annuals in terms of coefficient of variation of seed size. For the four

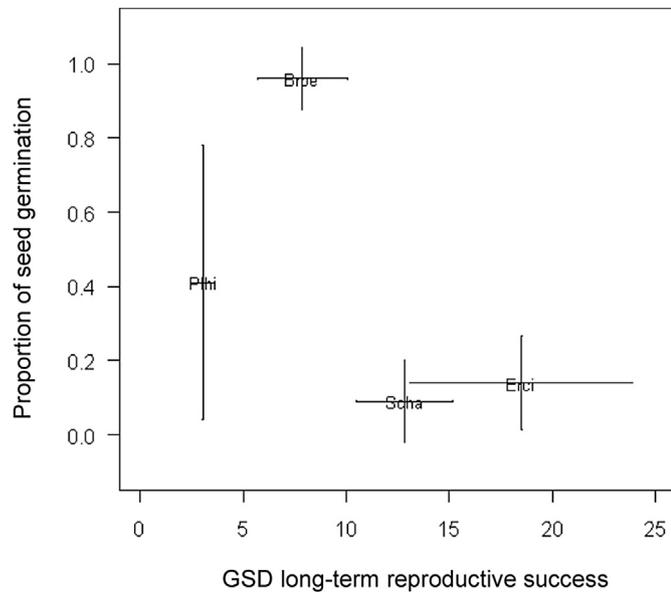


Fig. 1. Differences in mean germination fraction (proportion of germinated seeds in both maternal environments) plotted against the variation in long-term fitness for two native and two exotic annual plants from semiarid Chile. Variation in long-term fitness is estimated as the geometric standard deviation of long-term reproductive success (e.g. GSD of seed density/plant cover, over 17 years). Brbe: *Bromus berterianus*, Erci: *Erodium cicutarium*, Plhi: *Plantago hispidula* and Scha: *Schismus arabicus*. Vertical error bars represent one standard deviation of seed germination and horizontal bars represent one standard deviation of the geometric deviation of long-term fitness obtained from bootstrapping with 1000 permutations.

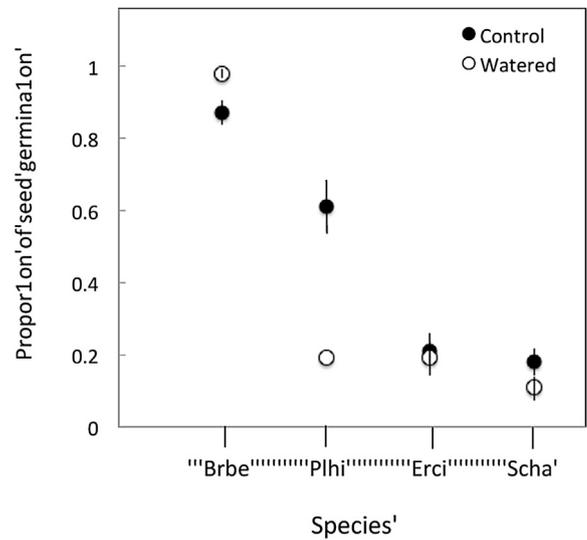


Fig. 2. Germination fraction measured as the proportion of seed germination of seeds derived from plants grown in two contrasting maternal environments (Control: 100% average annual rainfall, Watered: Up to 230% annual rainfall). Species name codes as in Fig. 1. Error bars represent two standard errors.

species there were no effects of “plot” (*Bromus*:  $F_{1,1} = 0.43$ ,  $P = 0.51$ , *Plantago*  $F_{1,1} = 1.34$ ,  $P = 0.24$ , *Erodium*:  $F_{1,1} = 0.51$ ,  $P = 0.47$ , and *Schismus*,  $F_{1,1} = 0.17$ ,  $P = 0.67$ ), hence significant differences in CV were associated with maternal environment. Of the four species the CV of seed size was lowest for *Schismus* (exotic) and CV did not differ between treatments ( $F_{1,1} = 0.12$ ,  $P = 0.72$ ). CV of *Plantago* (native) was also very low and differences in CV between control and watered plots were barely significant ( $F_{1,1} = 3.78$ ,  $P < 0.05$ ; Fig. 3). In *Bromus*, CV was above 25% and we found differences between treatments ( $F_{1,1} = 58$ ,  $P < 0.001$ ; Fig. 3). CV in seed size of the exotic *Erodium* was high in both treatments but we still found differences ( $F_{1,1} = 59.1$ ,  $P < 0.001$ ), and *Erodium* was the only annual plant of this study with a CV of seed size larger than 50% and this was observed in seeds derived from plants grown in watered plots (Fig. 3).

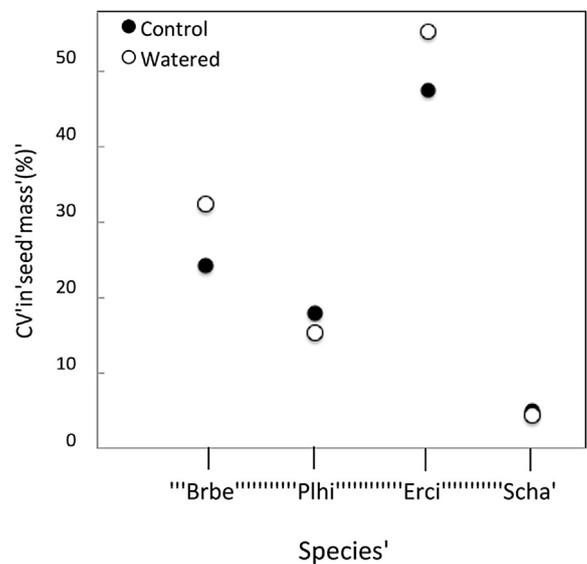


Fig. 3. Coefficient of variation in seed size of native and exotic annual species from semiarid Chile. Seeds were obtained from plants grown in two contrasting maternal environments (Control: 100% average annual rainfall, Watered: Up to 230% annual rainfall). Erci: *Erodium*, Plhi: *Plantago*, Brbe: *Bromus* and Scha: *Schismus*.

#### 4. Discussion

We found differences in bet-hedging strategies among annual plants in terms of seed production, germination, and size, and these differences may contribute to the long-term coexistence of these two groups of plants in semiarid Chile by promoting resource partitioning over space and time under conditions of high resource variability (Chesson et al., 2004; Jiménez et al., 2011). Indeed the four co-existing exotic and native annual species in this study have different bet-hedging strategies revealed by different levels of variability in long-term reproductive success (Fig. 1), seed germination (Figs. 1 and 2), and variability in seed size (Fig. 3). Such different bet-hedging traits and strategies should promote annual plant coexistence in this semiarid ecosystem characterized by strong seasonality and inter-annual variability of rainfall.

Recently Venable (2007) empirically demonstrated the presence of a trade-off between long-term reproductive success (i.e. long-term fitness) and the geometric standard deviation (GSD) of long-term reproductive success. On one end of this trade-off are those species low demographic variation among years (i.e. low GSD of long-term reproductive success) characterized by low variation in the production of seeds per unit plant biomass, and on the other end of the trade-off are those species with high demographic variation among years with a high variability in the production of seeds per unit plant biomass (Venable, 2007). Thus, investing in plant biomass does not guarantee greater reproductive success in exotic species. Indeed, the fact that native annuals had lower variation in long-term reproductive success than exotic annuals (Fig. 1 X axis) suggests that in the last 17 years, seed production per plant cover has been more stable in natives than in exotic species. Accordingly, germination success should have been higher in native annuals than in exotics, since native annuals seem to have lower variation in long-term reproductive success than exotics (Fig. 1), but we did not find a significant correlation for these traits. Nonetheless, considering that very few seeds of both exotics germinated (i.e. a proportion <0.10) and that both species showed had high variability in long-term fitness, it can be inferred that in the last 17-years exotic species had experienced greater demographic variation than native species (Fig. 1). We conclude that during the last 17 years, coexisting exotic and native annuals in this semiarid community have experienced different levels of demographic variation associated with differences in seed germination; the physiological mechanisms behind these differences are yet to be studied.

A high proportion of overall seed germination (Y axis Fig. 1) and differences in percent germination between seeds from the two contrasting maternal environments (e.g. watered vs. control, or normal year; Fig. 2) can reflect a diversified bet-hedging strategy (Tielbörger and Valleriani, 2005). Accordingly, the native *Plantago* could be classified as a diversified bet-hedger as it showed high seed germination (Fig. 2) and germination differed significantly as a result of maternal environment. These two traits illustrate the case of a diversified bet-hedging strategy for *Plantago*. Differential seed germination resulting from differences in the reproductive plant's maternal environment was also reported in a study conducted in the Negev Desert (Tielbörger and Valleriani, 2005). In accordance with our results, Tielbörger and Petru (2010) found lower seed germination in seeds from plants grown under favorable maternal environments (see *Plantago* in Fig. 2) (2010). An explanation for these counterintuitive results is that seeds coming from mothers that experienced a good year (e.g. wet year) may have different germination thresholds in terms of rain pulses than seeds coming from mothers that experienced a bad (e.g. dry year). Therefore species can reduce the risk of false germination (*sensu* Timson, 1965) if conditions become less favorable in the following year. On the other native annual *Bromus* does seem not have a bet-

hedging strategy as it showed the highest proportion of germinated seeds irrespective of long-term fitness (Fig. 1) and germination was not affected by maternal environments. In contrast, both exotics showed very low germination irrespective of maternal environment (Fig. 2), hence exotics are conservative bet-hedgers for this trait.

The low CV of seed mass observed in *Plantago* and *Schismus* (Fig. 3), regardless of the maternal environment, indicates that seed size remains nearly constant despite environmental variation, which reflects a conservative bet-hedging strategy for this seed trait. In contrast, *Bromus* seems to have a diversified strategy regarding seed size variability, as we found that CV of seed size differed between maternal environments (Fig. 3). At the same time, seed germination was very high in *Bromus* (Fig. 1) irrespective of environmental conditions (i.e. low variability in long-term fitness). Consequently, plant traits associated with high quality seeds in the case of *Bromus* may be playing a key role in the demographic success of this species in this strongly variable semiarid environment.

The widespread exotic *Erodium* is characterized by a diversified bet-hedging strategy, based on the results showing low seed germination percentage (Y axis Figs. 1 and 2) and high CV in seed size (Fig. 3). Previous studies have shown that *Erodium* seeds have physiological dormancy (Figueroa et al., 2004), a condition that may prevent false germination in bad years but may hamper germination in favorable years. When *Erodium* seeds are scarified, by breaking the seed coat, the proportion of seeds that germination increases from 0.18 to 0.75 (M. Jiménez et al., unpublished data). In the present study, there were no differences between seeds from the two maternal environments (watered and control, Fig. 2) in the proportion of seeds germinated. Therefore, *Erodium* may compensate for its low germination by producing seeds that start to germinate early in the season, and early germination could be an advantage by pre-empting space during years of high precipitation. Jiménez et al. (2011) found that *Erodium* and *Schismus* were the only two annual species that increased their relative plant cover (%) in FJ after the extreme dry event of 1998, presumably because the dormant seed bank of these species emerged in the following rainy years of 2000, 2001 and 2002 (Jiménez et al., 2011).

Our results suggest that the exotic annual grass *Schismus* displayed a conservative bet-hedging strategy based on the low proportion of seeds that germinated (Fig. 2) and the low CV of seed size for irrigation and control treatments (Fig. 3). From our perspective these results show that irrespective of annual rainfall (e.g. our two water treatments) variability in seed size is relatively constant and seed germination is on average very low for this species. Similar results had been previously reported by Gutterman (1996), who considered that *Schismus* had an "opportunistic" strategy of partial germination whereby few seeds germinate even after very small rainfall pulses (i.e. 5–10 mm) but also very few individuals die if those small pulses were not followed by more rain. This strategy may explain the increased cover of *Schismus* in Fray Jorge following the extreme drought event of 1998, which negatively impacted native annuals such as *Bromus* and *Plantago* (Jiménez et al., 2011), but temporarily promoted *Schismus*.

We have shown that annual species in this semiarid plant community exhibit different bet-hedging traits, but neither natives nor exotics can be grouped in relation to these strategies. In terms of long-term fitness (i.e. geometric standard deviation of long-term reproductive success), both natives *Plantago* and *Bromus* were conservative, whereas the exotics, *Erodium* and *Schismus*, did not show a clear strategy (Fig. 1). For the rest of the bet-hedging traits evaluated here (seed germination, variability in seed size), we did not find a clear separation between native and exotic annual species. We must conclude that annual species coexist in this

semiarid community despite sharing their major life history trait (i.e. ephemerality), because they possess distinct fitness-related reproductive traits (Baker, 1974; Sakai et al., 2001), or what Simons and Johnston (1997) called multiple strategies. Our results on long-term reproductive success provide a partial explanation for the trends shown by Jiménez et al. (2011), where the native annuals *Plantago* and *Bromus* managed to recover from the negative effects of the 1998-extreme drought that promoted an increase in cover of *Erodium* and *Schismus* over both natives. Therefore, evaluating species adaptations that promote coexistence in temporally variable environments (i.e. bet-hedging strategies) is essential for understanding long-term plant community dynamics and assessing the risks of invasion.

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