



## 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

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