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Assessing seed and microsite limitation on population dynamics of a gypsophyte through experimental soil crust disturbance and seed addition

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Abstract Understanding the factors limiting population growth is crucial for species management and conservation. We assessed the effects of seed and microsite limitation, along with climate variables, on *Helianthemum squamatum,* a gypsum soil specialist, in two sites in central Spain. We evaluated the effects of experimental seed addition and soil crust disturbance on *H. squamatum* vital rates (survival, growth and reproduction) across four years. We used this information to build integral projection models (IPMs) for each combination of management (seed addition or soil disturbance), site and year. We examined differences in population growth rate (λ) due to management using life table response experiments. Soil crust disturbance increased survival of mid to large size individuals and germination. Contributions to λ of positive individual growth (progression) and negative individual growth (retrogression) due to managements varied among years and sites. Soil crust disturbance increased λ in the site with the highest plant density, and seed addition had a moderate positive effect on λ in the site with lowest plant density. Population growth rate (λ) decreased by half in the driest year. Differences in management effects between sites may represent a shift from seed to microsite limitation at increasing densities. This shift underscores the importance of considering what factors limit population growth when selecting a management strategy.

Keywords Density-dependent germination · *Helianthemum squamatum* · Integral projection models · Microsite limitation · Seed limitation · Soil crust disturbance

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Introduction

The availability of propagules (e.g. seed abundance) and the conditions affecting their recruitment (microsite availability, precipitation, etc.) have been identified as limiting factors for population growth (Harper et al. 1965). While these constraints are present across many plant populations, their relative importance has been shown to vary with species level factors such as plant density (Eriksson and Ehrlén 1992) and seed dispersal (Clark et al. 2007). Abiotic and biotic factors such as fire (Setterfield 2002), and grazing (Eskelinen and Virtanen 2005) have also been shown to interact with the effects of both seed and microsite limitations.

In arid habitats, water availability is a particularly important limiting factor of plant recruitment. Plants living in these environments often cope with drought either by strong recruitment from a seed bank and high seed production in non-drought years [e.g. annuals; (Pake and Venable 1996; Luzuriaga et al. 2012)], heavy investment in vegetative tissue to increase survival during drought periods [e.g. long-lived perennials (Wiegand et al. 1995, 2004)], or some combination of the two [e.g. short-lived perennials (Aragón et al. 2009)]. If water availability is limited, species reliant on a seed bank could fail to establish and reproduce (Aronson et al. 1992) and those reliant on adult survival could fail to survive their first stressful period (Sánchez and Peco 2007). In both cases, seed availability and seedling establishment are critical for persistence in arid environments.

Helianthemum squamatum (L.) Dum. Cours. is a short-lived perennial which specializes on gypsum soils. This species inhabits semi-arid gypsum environments in Mediterranean Spain (Olano et al. 2011) and maintains high reproductive effort under different environmental conditions (Aragón et al. 2007, 2008), even at the cost of future survival (Aragón et al. 2009). Recruitment increases with seed density and is controlled by microhabitat availability for germination and establishment (Escudero et al. 1999). Seedling recruitment is associated with perturbation, such as trampling by sheep, that reduces plant competition and creates openings in hard soil crusts (Escudero et al. 2000; De la Cruz et al. 2008; Quintana-Ascencio et al. 2009; Martínez-Duro et al. 2010). *Helianthemum squamatum* seeds enter the soil seed bank where they can remain dormant for several years, but most seeds are short-lived due to high seed predation and occasional massive emergence during favourable years (Olano et al. 2012a). Consequently, *H. squamatum* may have a strong dependence on frequent seed production for persistence.

We carried out field experiments in which soil crust perturbation and seed bank density were manipulated over three years. We combined the resulting data, as well as climatic data, in a demographic modelling framework based on Integral Projection Models (IPMs) (Easterling et al. 2000). We hypothesized that (i) soil crust disturbance mimicking, one of the effects of trampling by grazing sheep, would have a positive effect on *H. squamatum* population dynamics by increasing safe sites for germination and establishment, thus reducing microsite limitation; (ii) seed addition would have a strong positive effect due to its direct effect on seedling recruitment (Clark et al. 2007); (iii) the relative importance of seed and microsite limitation would vary depending on local conditions and (iv) the positive effects of decreasing seed and microsite limitation would be reduced or nullified by stronger limitations in water availability during drought years.

Methods

Natural history and study area

Helianthemum squamatum (Cistaceae) is a small perennial shrub that occurs in the eastern half of the Iberian Peninsula. It is a specialist of gypsum soils, where it is a dominant species (Palacio et al. 2007). Its life span ranges from 4 to 6 yrs. (Olano et al. 2011), and reproduction usually occurs during late spring and summer, from May to August, beginning a year after seedling establishment (Aragón et al. 2007; Quintana-Ascencio et al. 2009). Flowers are hermaphroditic and arranged in dense inflorescences. Fruits are small capsules (3 mm diameter) generally bearing 1–7 seeds, with an average of 1.7 viable seeds per fruit (Aragón et al. 2007). *Helianthemum squamatum* fecundity is associated with climate conditions (Aragón et al. 2008), and its age structure is determined by fine-scale climate variation, with sporadic summer rainfalls being especially critical (Olano et al. 2011).

Our study was conducted at Aranjuez/Sotomayor Experimental Station located 50 km south of Madrid, in central Spain (40°4′31.94″N, 3°36′4.29″W, 600 m a.s.l.). The climate is Mediterranean and semi-arid with an average temperature of 15.8 °C and mean annual precipitation of 350 mm (data from Aranjuez Meteorological Station www.aemet.es). Gypsum soils are prevalent, and vegetation is dominated by gypsum plant specialists. Perennial plant cover rarely surpasses 40% and is dominated by tussocks such as *Stipa tenacissima* L. and shrubby gypsophytes such as *H. squamatum* and *Lepidium subulatum* L. Locally abundant plants include *Centaurea hyssopifolia* Vahl. and *Thymus lacaitae* Pau. Bare ground areas are covered by well-developed biological soil crusts (Martínez et al. 2006), which shelter a diverse community of cryptogams and annuals.

Experimental design

We collected plant demographic data in 15 permanent plots during 2008–2011. Each plot was 1 m wide and long enough to include at least 100 adult individuals. Focal plant density was quite heterogeneous so plot lengths ranged between 2 and 7.5 m (online resources Table 1). Plots were distributed in two different hills (hereafter Site 1 and Site 2) located 400 m apart but similar in terms of total plant cover, slope and orientation (i.e. south-oriented and perennial cover below 20%). Plots within sites (9 plots in site 1 and 6 plots in site 2) were randomly assigned to one of three treatments: soil crust disturbance; seed addition and control. Three of five plots per treatment were in Site 1 and two in Site 2. We sampled a total of 2617 established plants across all years (1537 in Site 1 and 1080 in Site 2). *Helianthemum squamatum* individual density in the plots was consistently higher in site 1 than in site 2 independently of year or treatment (20.9 ± 5.3 [mean ± s.e] plants/m^2 vs 14.0 ± 3.1 plants/m^2 and 218.4 ± 50.6 seedlings/m^2 vs 126.4 ± 43.7 seedlings/m^2 for site 1 and 2 pooled by treatment and year, respectively across plots, $n = 9$; Table 1 in online resources).

We disturbed the soil at the end of each July by thoroughly destroying the biological soil crust with a hammer without damaging existing plants. This treatment was intended to create favourable conditions for seed germination but may have affected soil attributes relevant for established plants (e.g. water availability, soil aeration, etc.). Concerning the seed addition treatment, in 2008, total seed production of plants in each plot was calculated, and an equivalent number of seeds was added. The number of seeds added ranged between 1200 and 9500 seeds/m^2 according with each plot's seed production. No seeds were produced in 2009, so we added a constant amount of seeds, 2000 seeds/m^2, to the five seed addition plots. Finally, in 2010, we added 900 seeds/m^2 in each of these plots, as we did not collect enough seeds to reach previous year's seed addition level. Seeds were added in late autumn, prior to field seed germination and after cessation of the activity of granivorous ants, mainly *Messor* sp. (Sánchez et al. 2006). Seeds were homogeneously distributed on the ground surface after watering plots to increase attachment of their mucilage to the ground. Added seeds were collected from wild plants in the previous year at Aranjuez Biological Station. Capsules were air dried and manually processed to obtain their seeds. Seeds were stored in paper bags under lab conditions before use.

In May of each year, we counted seedlings in the plots. Adult sampling was performed annually in late July, well after fruit ripening. For each plant, we recorded its status (alive/dead) together with its two main crown diameters and number of infrutescences. Fifty infrutescences from randomly selected plants located outside plots at both sites in 2008, 2010 and 2011 were collected. We used these infrutescences to estimate the number of fruits per infrutescence and seeds per fruit.

Integral projection model construction

We used generalized linear models (GLMs) to evaluate the effect of different biotic and environmental factors on vital rates (survival, growth, probability of reproduction and per-capita fecundity) of *H. squamatum*. Growth and per-capita fecundity were assessed using Gaussian distributions and identity link, while survival and probability of reproduction were modelled with binomial distributions and logit link. In all cases, our primary predictor variable was size, measured as the natural log of average crown diameter (cm). We considered four additional potential predictors: experimental management treatment (control, soil crust disturbance and seed addition), sampling location (sites), summer temperature (average monthly temperature from June to September) and winter–spring precipitation (total precipitation from January to May). Both climatic predictors are surrogates of main climatic constraints for the plant: summer drought stress and water availability during the growing season (Aragón et al. 2007). Observed climatic values during the study period were representative of the gradient of precipitation and temperature recorded between 1977 and 2012 (see Online resource Figs. 1, 2).

We evaluated a set of 20 models for each vital rate (survival, probability of reproduction and per-capita fecundity; *see* Online resource Table 2). For growth, we used the same set of covariates as for survival (Morris and Doak 2002). All of the most informative models included plant size plus different combinations of predictive variables. The most plausible model for each vital rate was selected with corrected Akaike Information Criterion (AICc; Burnham and Anderson 2002).

GLMs results were used to build an integral projection model (IPM). We used modified code from version 1.5 of *IPMPack* (Metcalf et al. 2013) in R (2.15.2, R Development Core Team 2012) to allow for the incorporation of continuous covariates. Our IPM was organized into a single continuous stage that incorporated all extant non-seed plants and a single stage for the seed bank. The continuous stage was calculated using a standard IPM kernel function (Easterling et al. 2000):

$$n(y,t+1)=\int_{T}^{U}[s(x,y)g(x,y)+f(x,y)]n(x,t)\mathrm{d}x,$$

where the probability function of individuals at time t + 1 ($n(y,\ t+1)$) is equal to the integration of survival ($s(x,y)$), growth ($g(x,y)$) and reproduction ($f(x,y)$) across the possible range of sizes.

Reproduction was calculated as the product of probability of reproduction and per-capita fecundity. We calculated the number of individuals in the seed bank as the sum of seeds entering into the seed bank and seeds remaining from the previous year's seed bank (as in Ramula et al. 2009). New seedlings enter the continuous stage (i.e. individuals with aboveground biomass) with size frequencies matching an estimated normal distribution for offspring diameter (1.52 ± 0.44 cm). New produced seeds were split into individuals entering next year's soil seed bank (0.281) and individuals germinating next spring (0.138). Seedlings were assumed to survive at a rate of 0.160. These parameters were obtained from previously collected data on this species (Caballero et al. 2008a, b; Olano et al. 2012a, b; Quintana-Ascencio et al. 2009).

We built site-specific population models (IPMs) that represented conditions with different levels of soil crust disturbance and seed addition under different winter–spring precipitation and summer temperature regimes. We compared and characterized variation of these estimated population growth rates across environments calculating confidence intervals using bootstrapping within years and sites with 999 iterations per treatment combination.

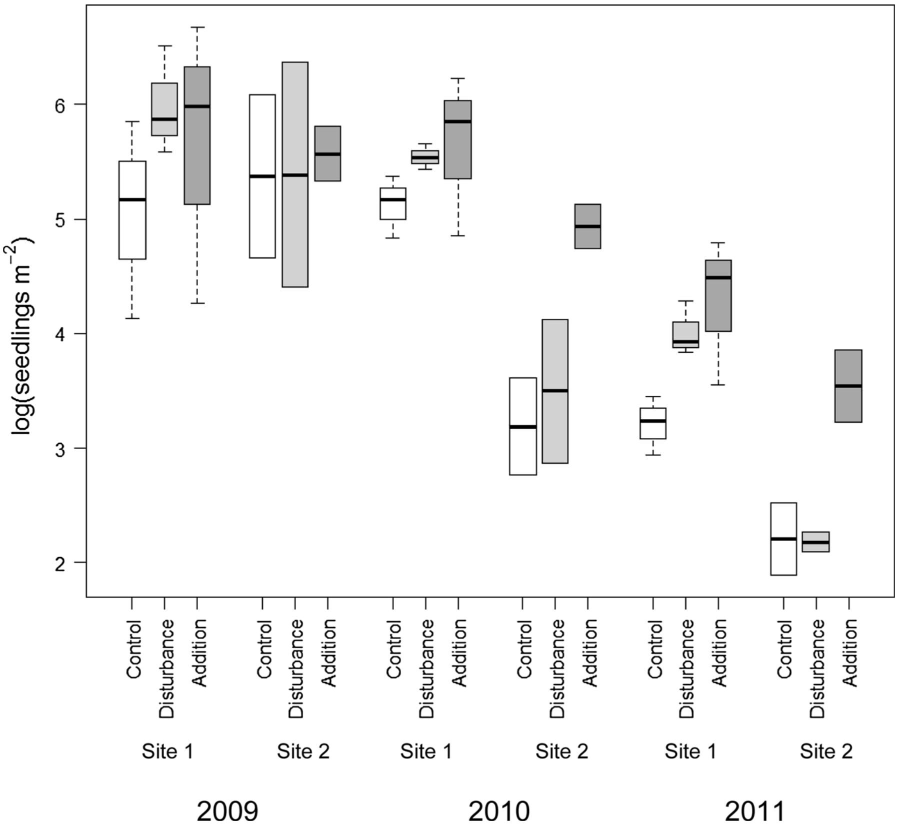
We carried out Life Table Response Experiments (LTREs; Caswell 2001) to assess effects of experimental treatments on each part of the life cycle of *H. squamatum* onto the resulting deterministic population growth rates. After IPMs were discretized into 200 × 200 matrices, we assessed cell-by-cell differences between each treatment and the control for each annual transition. The resulting matrix was then multiplied by the sensitivity of the control matrix. We summed the columns of each resulting matrix to determine how plant size contributed to population growth rate (λ) variation through differences in survival, growth and fecundity. For each column, we also calculated individual growth contribution as summed contributions higher than equivalent row size. Similarly, we calculated individual retrogression contributions as summed contributions of IPM elements lower than or equal to column size. We additionally assessed the relative contributions of the seed bank to λ.

Results

Vital rates and their GLM models

Number of seedlings recruited m^{-2} varied significantly as a function of treatment, site and year (Fig. 1; online material Table 3, data logarithmic transformed for analysis). Overall, there were on average 119 ± 130 (SE) seedlings m^{-2} in the control plots. Seed addition plots had more seedlings than controls (226 ± 214). There was marginal evidence of more seedlings in plots with soil disturbance compared with the controls (199 ± 209). There were more seedlings in Site 1 than in Site 2 (218 ± 199 vs 126 ± 165) and

Fig. 1 Boxplot of number of seedlings m^{-2} as a function of treatment (control, soil crust disturbance and seed addition), site and year. There were significant differences due to year, site and treatment (in online material Table 3)



more in 2009 than in 2010 or 2011 (326 ± 225, 179 ± 134 and 40 ± 33, respectively).

Plant survival varied as a quadratic function of plant diameter. The most plausible set of covariates for survival was the interaction between treatment and site as well as temperature and precipitation as additive effects (Table 2 in online material). Treatment effects on survival depended on site. In site 1, the one with the highest plant density, highest survival was reached under the soil crust disturbance treatment, while survival was lowest in the control. Survival in seed addition plots was intermediate across all observed climate conditions (Fig. 2). In site 2, survival after soil crust disturbance and seed addition treatments were similar to each other and higher than in the control. Survival was higher during years with intermediate (209 mm; 2010) and high (273 mm; 2008) winter–spring precipitation, and moderate (22.7 °C; 2008 and 22.8 °C; 2010) summer temperatures (Fig. 2 and in online material Figs. 1, 2).

In site 1, plants in the control plots grew faster than in experimental plots, while in site 2, all treatments had nearly identical growth (Fig. 3). Variation in predicted individual growth rates between years was minimal, indicating non-significant decreases in plant growth rate due to drought. The set of covariates associated with probability of reproduction was again the interaction between treatment and site as well as temperature and precipitation as additive effects (Online resource Table 2). The probability of reproduction increased with plant size and precipitation. In the hottest and driest year (2009), no plants reproduced. In the year of intermediate rainfall and temperature (2010), almost all individuals reproduced. Treatment effects on reproduction differed depending on site. At site 1, probability of reproduction was higher for control treatment followed by soil crust disturbance and seed addition (Fig. 4), whereas at site 2, plants in seed addition treatment had the highest probability of reproduction, followed by control and soil crust disturbance treatments.

The most informative model for seed production was the same as the one identified for probability of reproduction (Online resource Table 2). Seed

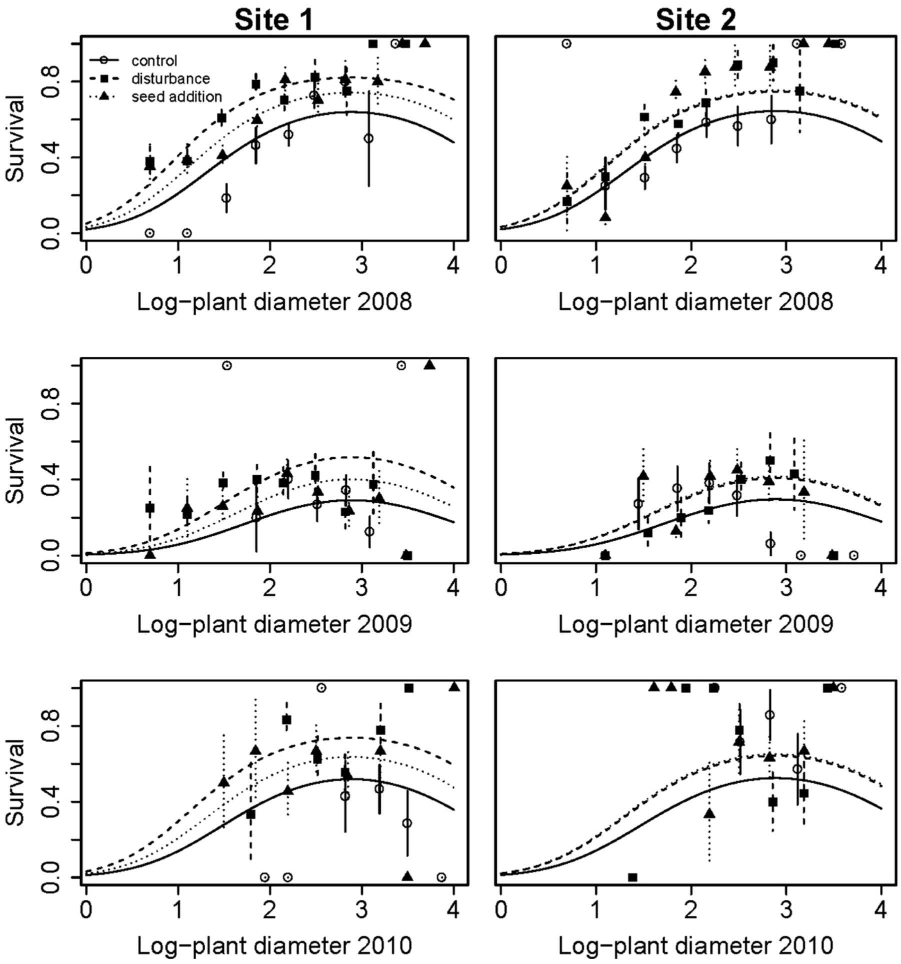


Fig. 2 Survival for plants as a function of treatment year and site. Model variation among years reflects the effect of summer temperature and winter–spring precipitation on survival (2008 = low temperature, high rainfall; 2009 = high temperature, low rainfall; 2010 = intermediate temperature and rainfall). *Dots* are observed proportions (±SE) with bins optimized by sample size and provided as a heuristic reference

production increased with plant size and was higher in site 1 than in site 2 (Fig. 5). Seed production was higher in the control than in addition and soil crust disturbance treatments at site 1, whereas in site 2, seed production was higher in the addition treatment. Reproduction was higher in the year with moderate rainfall (2010) compared to the year with highest rainfall (2008; Fig. 5).

Integral projection models

We calculated λ for each treatment, site and year combination (Fig. 6). Population growth rate was lower in 2009 as compared to the other two years for all combinations of treatment and site (non-overlapping 95% CI). In site 1, soil crust disturbance treatment showed higher population growth rate than the control (non-overlapping bootstrap 95% CI in all three years). Mean lambda was consistently higher with soil crust disturbance than with seed addition in site 1, but partial overlap between their 95% CI made this contrast inconclusive. In site 2, population growth was similar under the three treatments across all three years.

Life table response experiments

In site 1, during annual transitions 2008–2009 and 2010–2011, both treatments had large positive contributions of survival and growth to variation in λ among individuals of intermediate diameter (Fig. 7). The largest negative contributions came from seeds entering and persisting in the seed bank (Fig. 8). In contrast, in site 1 in 2009–2010, the largest positive contributions of treatments came from the largest individuals (Fig. 7; notice the bootstrap CI). The largest negative

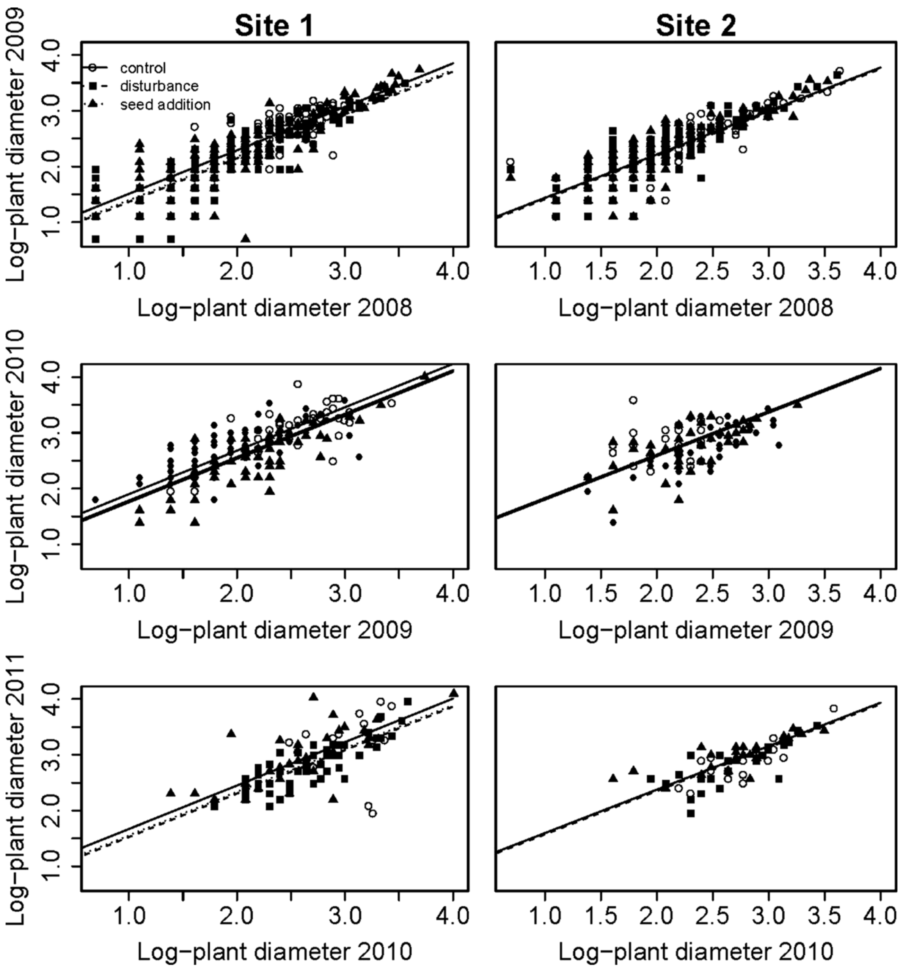


Fig. 3 Annual change in size (log of plant diameter) for plants as a function of treatment, year and site. Model variation among years reflects the effect of summer temperature and winter–spring precipitation on growth (2008 = low temperature, high rainfall; 2009 = high temperature, low rainfall; 2010 = intermediate temperature and rainfall)

contribution during 2009–2010 was from individuals entering the seed bank (Fig. 8). In site 1, both treatments had more retrogression than growth in the year with intermediate rainfall, but less retrogression than growth for the wet year. Contributions of both components were lower in the dry year 2009 (Fig. 9). The contribution of growth was higher for smaller individuals and negative or low for larger individuals. The contribution of retrogression was higher for larger individuals and negative or low for smaller individuals. Site 2 showed similar trends, but with several exceptions. The largest positive contributions in wet and moderately wet years (2008 and 2010) occurred at intermediate plant sizes. Positive contributions of seed addition to λ were higher than those of soil crust disturbance in all studied years (Fig. 7). In site 2, growth had higher contributions to variation in λ than retrogression in wet and moderate years (Fig. 9). Seed addition in site 2 was the only condition having a positive contribution of seed bank to λ compared to the control (Fig. 8).

Discussion

Evaluation of cumulative effects of both biotic and abiotic factors is critical to forecast population persistence (Salguero-Gómez and De Kroon 2010). Our results demonstrated positive effects of soil crust disturbance on *H. squamatum* population dynamics. We observed a minor positive effect of seed addition, particularly in the site with low densities of conspecifics. We documented a strong demographic effect of precipitation that varied among years.

Soil perturbation increased population growth in one of our sites. Positive association of *H. squamatum*

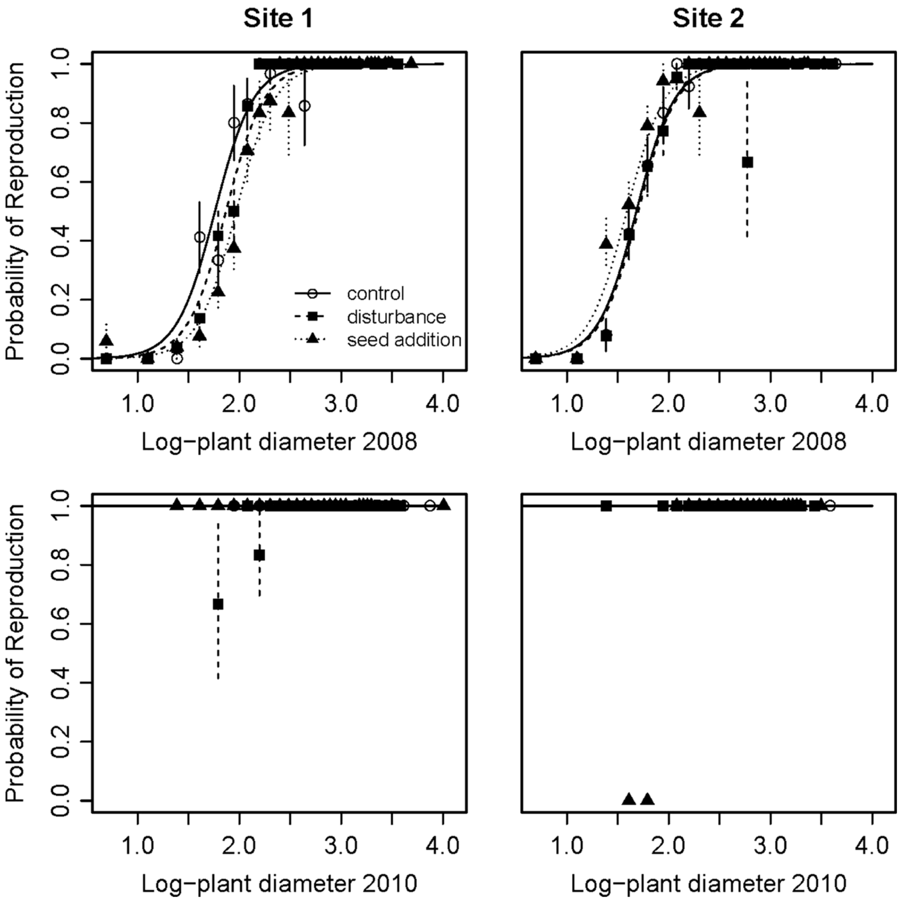


Fig. 4 Probability of reproduction as a function of size for plants in treated and control plots across three yearly transitions for both sites. Model variation among years reflects the effect of summer temperature and winter–spring precipitation on probability of reproduction (2008 = low temperature, high rainfall; 2010 = intermediate temperature and rainfall). There were no fruits in the driest year (2009). *Dots* are observed proportions (±SE) with bins optimized by sample size and provided as a heuristic reference

establishment with bare soil crust surfaces has been related to decreases in competition (Escudero et al. 2000; De la Cruz et al. 2008). Previous data indicate that seedling survival and growth of *H. squamatum* are dependent on the existence of clearings and negatively affected by the presence of perennials and annuals (Escudero et al. 1999). Trampling creates fissures through the hard physical crusts facilitating better anchoring and recruitment (Romao and Escudero 2005), as in these environments seeds of many species possess adhesive mechanisms helping seed attachment to soil (Gutterman and Shem-Tov 1997).

Herbivores are key species responsible for maintaining open spaces in grassland and shrublands by direct consumption and trampling (Moret-Fernández et al. 2011). Short-lived gypsophytes can be favoured by herbivory, not only by reducing annual plants due to direct consumption, but also by maintaining clearings and increasing the amount of favourable microsites for establishment. The net effect of this interaction will depend on the relative effects of direct consumption on the short-lived gypsophytes.

Both soil crust disturbance and seed addition showed differences in efficacy between sites. Less competition might explain the positive response to seed addition in the site with lower plant density. Thus, the effect of seed addition seems to be density dependent (Waser et al. 2010). Additionally, soil crust disturbance may be more effective at the higher density site by opening up more suitable microsites. These results suggest that there may be a shift from seed limitation to microsite limitation as plant and seed density increases (Eriksson and Ehrlén 1992). However, we recognize that there could be possible confounding factors due to location since we did not study replicated sites with variable densities.

Helianthemum squamatum seems to rely on high fecundity for persistence even at the cost of survival (Aragón et al. 2009). More specifically, it depends on

Fig. 5 Number of inflorescences as a function of size for plants in treated and control plots across three yearly transitions for both sites. Model variation among years reflects the effect of summer temperature and winter–spring precipitation on number of inflorescences (2008 = low temperature, high rainfall; 2010 = intermediate temperature and rainfall). There were no fruits in the driest year (2009)

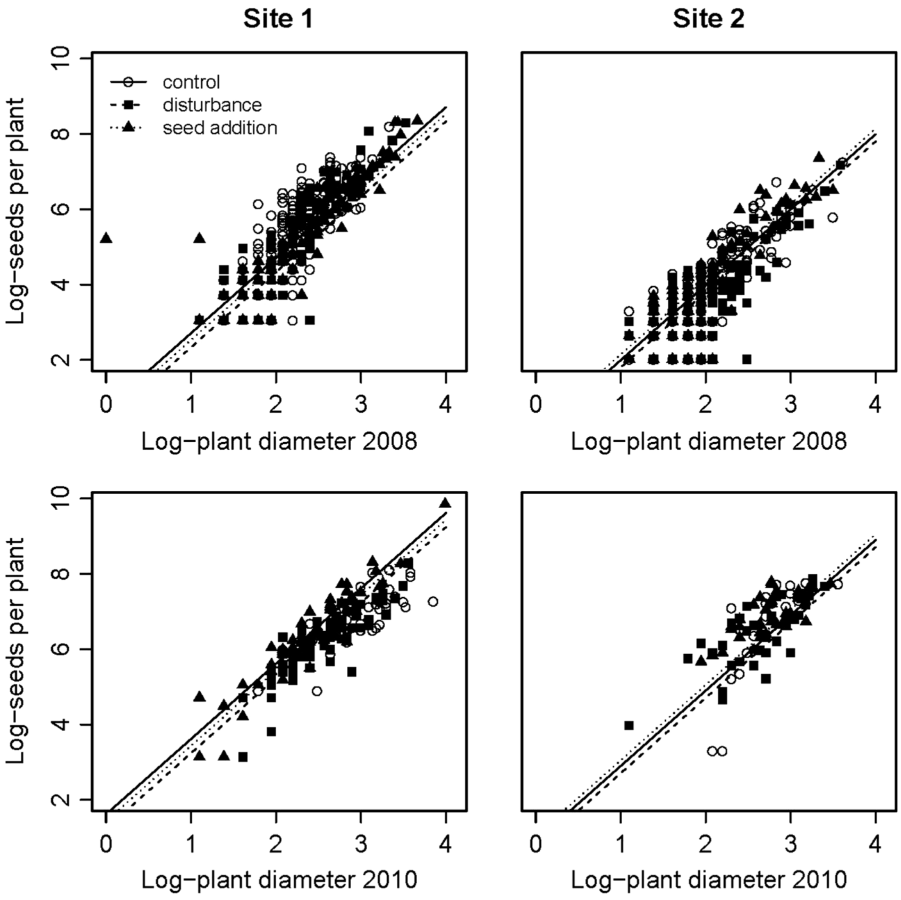
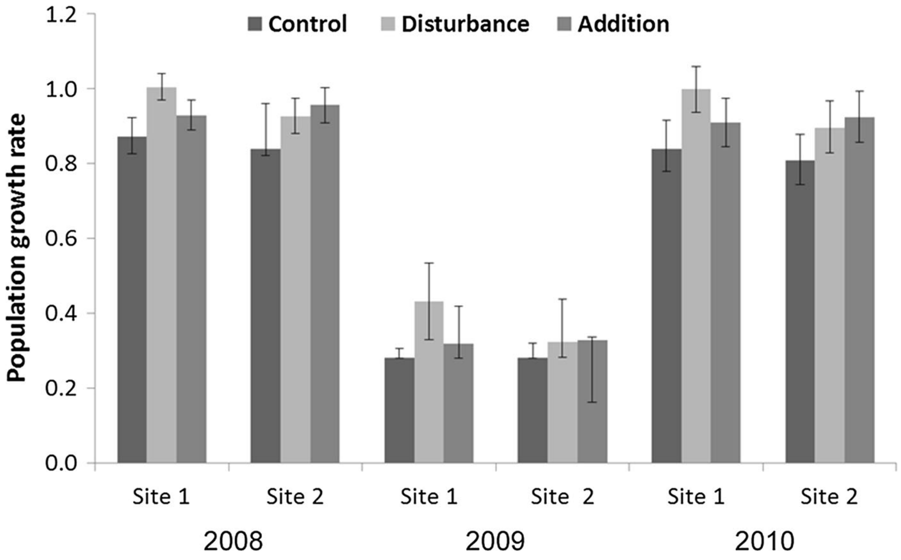
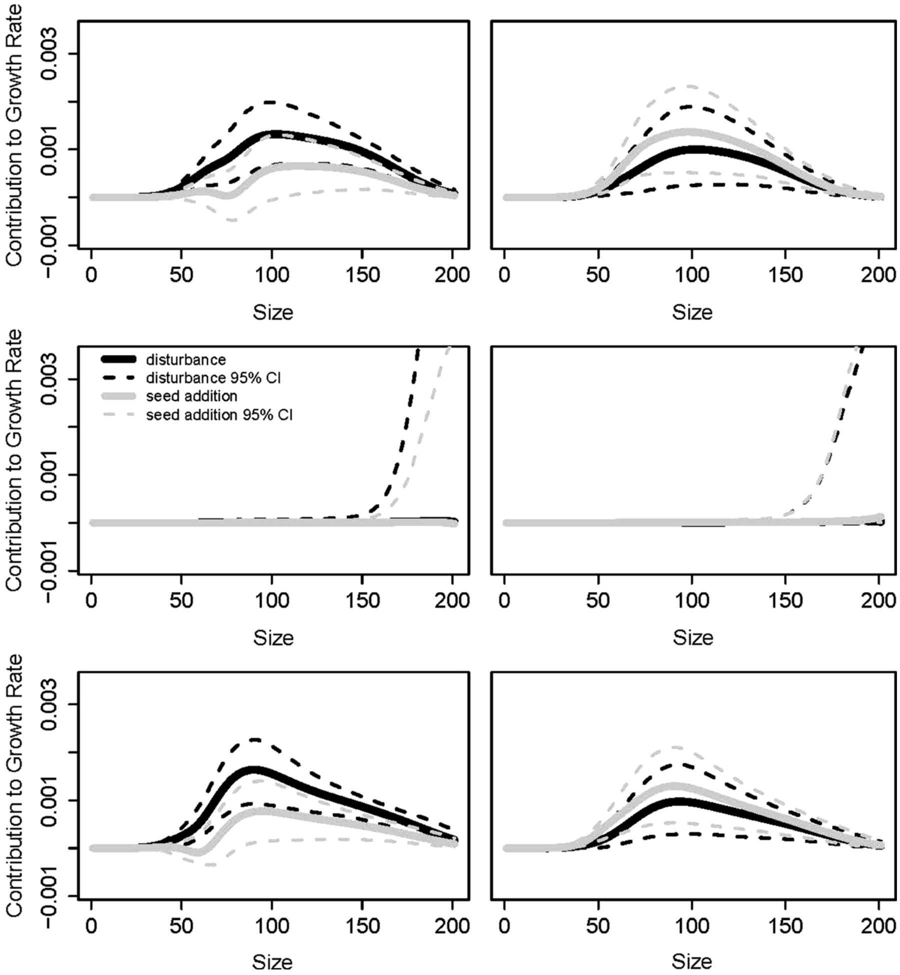


Fig. 6 Deterministic population growth rates (λ) for each combination of treatment, site and year. Among years, 2008 showed highest rainfall and 2010 showed moderate rainfall while 2009 was a drought year. *Error bars* correspond to 95% confidence intervals calculated from bootstrapping (999 iterations)



seed availability and seedling establishment, which are particularly relevant to overall population dynamics of this species. This strategy appears to be efficient under harsh and unstable conditions when perturbation is frequent and intense (Escudero et al. 2000). This plant life strategy is similar to annual plants in the

Fig. 7 LTRE analysis showing changes in summed contribution by column (plant size) to population growth rate for seed addition (*thick grey line*) and soil crust disturbance (*thick black line*) treatments as compared to control. *Dotted lines* represent 95% confidence intervals calculated from bootstrapping (999 iterations). *Plots* in rows designate differing years (Top row = 2008, Middle Row = 2009, Bottom row = 2010)



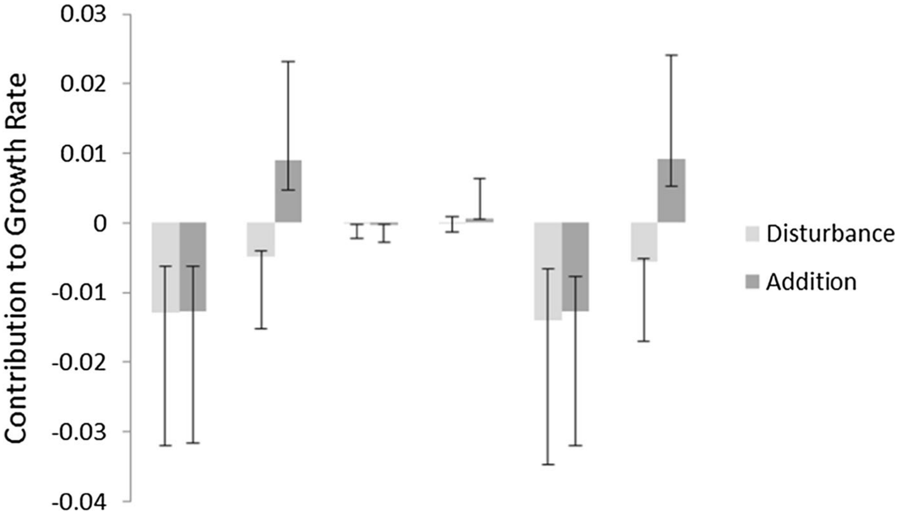
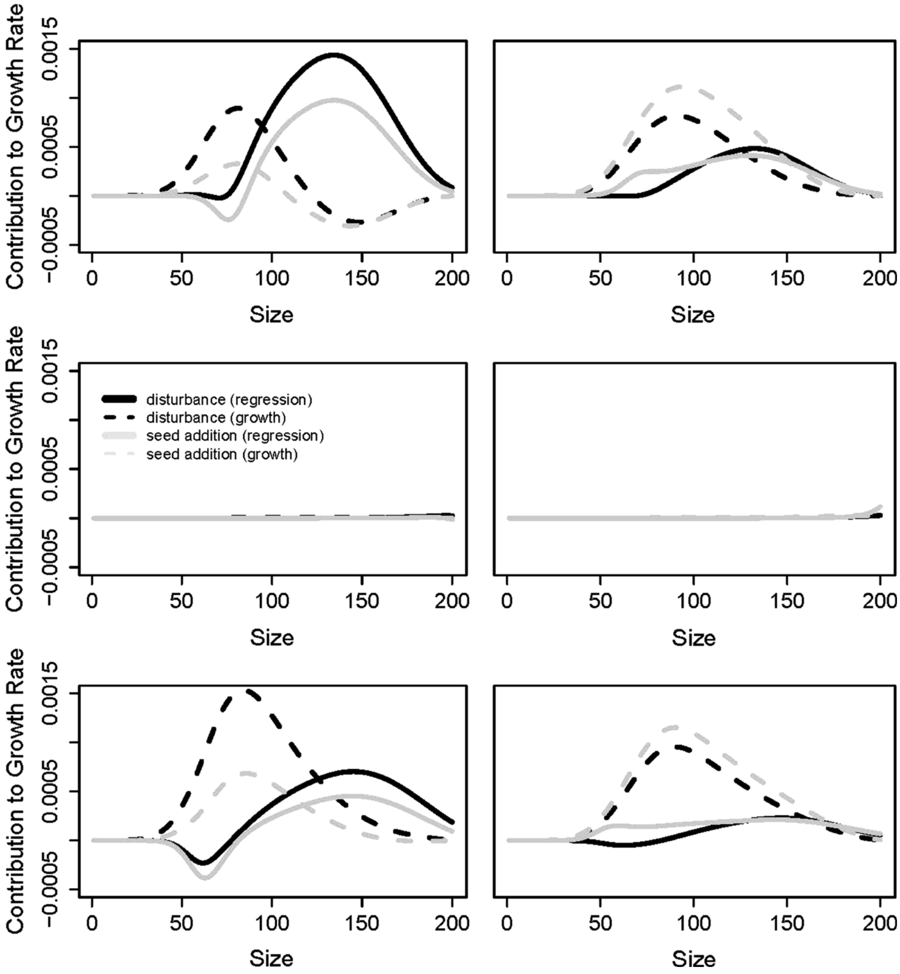


Fig. 8 Seed bank contributions to population growth rate in comparison to the control calculated from LTRE. *Error bars* represent 95% confidence intervals calculated from bootstrapping (999 iterations)

Fig. 9 Changes in summed contributions calculated from LTRE analysis by vital rate components, growth (*dashed lines*) and regression and stasis (*solid lines*), to lambda for soil crust disturbance (*black*) and seed addition (*grey*) treatments. *Plots* in rows designate differing years (Top = 2008–2009, Middle = 2009–2010, Bottom = 2010–2011)



production of abundant seed crops under a wide range of climate conditions, which maximizes the probability of seedling establishment whenever microhabitat structure provides enough safe sites for germination and establishment. As shrubby perennials, these species can maintain an aboveground population able to increase chances of massive seed production independently of recruitment year.

Our results suggest a strong negative effect of low water availability on both survival and reproduction and on the overall population dynamics of *H. squamatum*. This effect is markedly higher than those of factors affecting seed dynamics. It is well known that plants in dry lands are particularly limited by water availably (Crawley and Ross 1990). The lack of reproduction in the driest year of the study also suggests that there may be conditions that are too harsh for species to maintain any reproductive effort.

From a conservation and management perspective, our models emphasize that conservation of these populations and associated endangered habitats requires a certain level of perturbation to minimize encroachment and competitive exclusion. This concurs with the idea that in open habitats with a long tradition of livestock grazing, moderate grazing pressure preserves rangeland productivity and biodiversity (Moret-Fernández et al. 2011). Additionally, land abandonment, a critical driver of landscape level changes in developed countries, may push open habitats to the verge of extinction due to encroachment and forest expansion (Gimeno et al. 2012; Olano et al. 2012b). The critical role of livestock in these Mediterranean regions is higher because they can act as seed dispersal agents that reduce isolation between vegetation remnants in fragmented landscapes (Sánchez and Peco 2002; Pueyo et al. 2008).

Linking environmental effects to differences in vital rates provides a way to unravel mechanisms governing population dynamics (Dahlgren and Ehrlén 2009). Integral projection models constitute an excellent approach for tackling basic and applied ecological questions (e.g. Coulson 2012; Dahlgren and Ehrlén 2009). Combining experimental and modelling approaches provides a link between causal mechanisms and population dynamics (Dahlgren and Ehrlén 2011; Kolb 2012; Shefferson and Roach, 2012).

This study highlights the importance of opportunistic demographic behaviour displayed by a short-lived specialist, which requires openings by disturbance and, under some conditions, can become seed limited. We document positive effects of soil crust disturbance under an array of environmental conditions. Seed addition may be effective only when the effect of seed limitation exceeds the effect of microsite limitation. It is thus critical for land managers to identify the primary limiting factors to population growth in order to select appropriate treatments.

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