








RESEARCH ARTICLE

Natural selection favours drought escape and an acquisitive resource-use strategy in semi-arid Mediterranean shrubs

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Abstract

1. Natural selection is the major force driving adaptive evolution in natural populations, varying in strength, direction, and form through space and time, especially in highly variable environments such as Mediterranean ecosystems. Although a conservative resource-use strategy has been hypothesized to be adaptive in Mediterranean taxa, patterns of selection at the intraspecific level, that is, the suite of traits determining individual fitness, are largely unknown.
2. Using a phenotypic selection experiment in natural semi-arid conditions, we measured direct and indirect selection acting through two different fitness components (survival and reproduction), to assess the adaptive value of 20 eco-physiological traits on individuals of two gypsum endemic species, *Centaurea hyssoipifolia* and *Helianthemum squamatum*, dwelling in environments with contrasting abiotic conditions (south- and north-facing slopes) during two climatically contrasting years (dry and mesic). This allowed quantifying the magnitude and direction of natural selection at different spatiotemporal scales.
3. Our results revealed that different abiotic conditions did not alter selection patterns, being the magnitude of selection more strongly affected by temporal environmental variation. Selection through reproduction indicated consistent selection for early phenology, low water use efficiency, high specific leaf area, low leaf dry matter content, and high leaf N across slopes and years in both species. In contrast, phenotypic trait variation was not linked to survival in either species. Furthermore, while individual reproductive output was higher or similar in environments with higher abiotic stress in both species and years, survival was similar across environmental conditions, and it was neither affected by plant size nor reproductive output.
4. Contrary to our expectations, natural selection via reproductive fitness consistently favoured a drought-escape, acquisitive resource-use strategy in Mediterranean semi-arid plants, rather than a conservative resource-use strategy, even under conditions of higher abiotic stress (i.e. south slopes and dry

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year). Such acquisitive strategy could allow rapid development by maximizing resource assimilation and reproduction before the most limiting climatic conditions of mid-late summer. Our results shed light on adaptive functional strategies of Mediterranean taxa at the intraspecific level, providing insight on future responses to environmental change, and highlight remarkable differences in selection acting through different fitness components.

KEYWORDS

acquisitive strategy, gypsum specialists, individual fitness, Mediterranean, natural selection, phenotypic selection, selection differential, stress escape

1 | INTRODUCTION

Natural selection is the main process underlying adaptive evolution. Pioneer studies on phenotypic selection analyses indicated that variability in functional traits is a strong driver of fitness variation (Kingsolver et al., 2001; Lande & Arnold, 1983; Phillips & Arnold, 1989). Furthermore, environmental variation may affect both the phenotypic expression of individuals and the patterns of selection, because natural selection is a dynamic force that can vary in magnitude, direction, and form through space and time (see Kingsolver et al., 2001; Siepielski et al., 2009), especially in highly variable environments. Therefore, identifying adaptive traits is key to unveil successful plant strategies in contrasting environments, which may, in turn, provide insight on evolutionary responses to further environmental change (Hoffmann & Sgró, 2011).

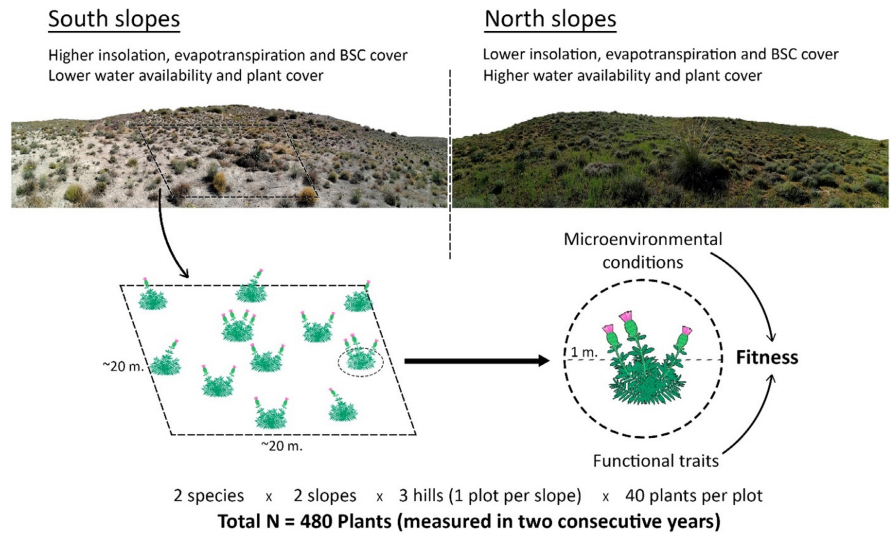
Mediterranean ecosystems show large spatiotemporal environmental heterogeneity, with high climatic seasonality, marked summer drought, low resource availability and the occurrence of simultaneous and fluctuating abiotic stresses (Blondel et al., 2010). Plants in the Mediterranean region have evolved functional adaptations to cope with abiotic stress (Blondel et al., 2010; Matesanz & Valladares, 2014), many of which are drought related and occur along a continuum of adaptive strategies: tolerance, escape and avoidance (Volaire, 2018). Tolerant plants often have slow growth rates and a conservative resource-use strategy characterized by low specific leaf area (SLA), high leaf dry matter content (LDMC), high water use efficiency (WUE), low photosynthetic rates, leaf nutrient concentrations, etc. In contrast, plants with an escape strategy reproduce early to avoid the most stressful conditions of the growing season. This requires higher rates of resource acquisition and growth, which is often achieved through high SLA, low LDMC, low WUE, high leaf nutrient concentrations, photosynthetic rates, etc. (Kooyers, 2015; Pérez-Ramos et al., 2013; Volaire, 2018; Welles & Funk, 2021). Finally, plants with an avoidance strategy minimize the risk of hydraulic failure during the most stressful part of the growth season by reducing transpiration and/or tapping onto more reliable water sources (McKay et al., 2003; Pérez-Ramos et al., 2013). Therefore, specific trait values are usually associated with contrasting resource acquisition rates and physiological strategies (Adler et al., 2014; Kooyers, 2015; Pérez-Ramos et al., 2013). Specifically,

in stressful Mediterranean ecosystems, plants have often been catalogued as tolerant taxa (Matesanz & Valladares, 2014), but stress-escape strategies have also been reported (e.g. Franks, 2011; McKay et al., 2003). While these categories have proved useful to predict patterns of interspecific trait variation across resource gradients (e.g. Reich, 2014), how individuals of the same species differ in traits related to resource use and stress response and, importantly, how such among-individual variation is related to fitness is unknown for most Mediterranean plants (Bolnick et al., 2003; Welles & Funk, 2021).

A particular example within the Mediterranean are gypsum habitats, characterized by high soil gypsum content, semi-arid climate and remarkable spatiotemporal heterogeneity (Escudero et al., 2015; Palacio et al., 2007). Temporal heterogeneity is linked to high seasonal and interannual climatic variability (Escudero et al., 2015), while landscape-scale spatial heterogeneity is mostly associated with strong environmental differences between slope aspects (Figure 1). In the northern hemisphere, south-facing slopes receive greater insolation, resulting in higher evapotranspiration and lower water availability, leading in turn to profound differences in the biotic structure, which altogether may impose different selection pressures. Given the adaptive value of conservative water and resource use often reported in water-limited Mediterranean environments (Blondel et al., 2010; Matesanz & Valladares, 2014) and their frequent late flowering phenology, gypsum endemics (gypsophiles) are predicted to be stress tolerant (Escudero et al., 2015; Palacio et al., 2007). However, although several studies assessed adaptive traits in the wild in different habitats (Kingsolver et al., 2001, 2012), there is virtually no information on the suite of traits that determine the success of Mediterranean gypsophiles at the intraspecific level, whether adaptive traits fit the predicted stress-response strategy, and how selection patterns vary across spatiotemporal scales.

In this study, we evaluated the patterns of phenotypic selection on natural conditions on two dominant Mediterranean gypsum species, *Centaurea hyssopifolia* and *Helianthemum squamatum*. We measured a wide suite of functional traits related to resource-use and response to abiotic stress, and considered two different fitness components, survival and reproductive output, while accounting for the spatiotemporal variation inherent to these systems. Using phenotypic selection analyses (Lande & Arnold, 1983; Phillips & Arnold, 1989), we assessed which traits were under selection and

FIGURE 1 Diagram of the phenotypic selection study. Plots were established in south-facing and north-facing slopes in the study site. Three hills were randomly selected and one 20×20 m plot was established at each slope and hill for each species (12 plots total). In all, 40 reproductive individuals per species and plot were selected ($N = 480$ individuals). Phenotypic traits and fitness were measured at each plant in two consecutive years, and microenvironmental conditions surrounding each individual were characterized.



how the direction and magnitude of selection for those traits varied in environments with contrasting abiotic conditions (south- and north-facing slopes; a priori higher and lower abiotic stress, respectively), during a dry and a mesic year. We addressed the following questions: (a) What functional traits determine reproductive fitness and survival in Mediterranean gypsum habitats? that is, what traits are under selection?; (b) Are adaptive traits consistent with a stress tolerance, avoidance or escape strategy?; (c) Are patterns of selection affected by spatiotemporal differences between slopes and years, and do they vary between species?; (d) Is selection acting through reproductive fitness consistent with selection acting through survival? Based on functional and life-history traits of these species, we predict that a conservative resource-use and stress-tolerant strategy characterized by more sclerophyllous leaves, higher WUE and lower leaf nutrient concentrations would be adaptive in scenarios where water availability is lower (i.e. south-facing slopes and dry year), whereas more mesophyllous leaves (higher SLA and nutrient concentrations), with lower WUE would be beneficial for fitness under more mesic conditions (i.e. north slopes and mesic year).

2 | MATERIALS AND METHODS

2.1 | Study site and species description

Our study was carried out in Belinchón, Spain (40°04'N, 3°04'W; ~700m a.s.l.). The area has a Mediterranean semi-arid climate, with pronounced summer drought, high interannual variation (mean annual precipitation 419.2mm; 192–504mm) and mean annual temperature of 14.6°C (35-year climatic data, CHELSA; Karger et al., 2017). Massive gypsum outcrops in the form of gypsum hills harbour gypsophile populations from hundreds to thousands of individuals (Figure 1). North-facing and south-facing slopes in gypsum hills at mid-latitudes strongly differ in environmental conditions. While north-facing slopes show higher plant cover, south-facing slopes are characterized by a patchy shrub community dominated

by endemic gypsum plants and higher cover of biological soil crusts (BSC hereafter).

Centaurea hyssopifolia Vahl. (Asteraceae) and *Helianthemum squamatum* (L.) Dum. Cours. (Cistaceae) are small chamaephytes (20–60cm height) endemic to gypsum outcrops of the Iberian Peninsula (IP). *Helianthemum squamatum* is a widely distributed species, while *C. hyssopifolia* is a narrow endemism mostly found on central IP (Palacio et al., 2007). Both species are dominant in central Iberian gypsum habitats (Matesanz et al., 2018), accounting for 46% and 35%, respectively, of the total perennial cover in our study site. The reproductive period of *C. hyssopifolia* lasts from May to July, while *H. squamatum* shows delayed phenology, from late May to early-mid August (Matesanz et al., 2018). The studied species differ in their longevity, with *H. squamatum* showing a shorter life span (Supporting Information 1).

2.2 | Experimental design

In both species, we quantified phenotypic selection on two environmentally contrasting slope aspects (south- and north-facing), and two climatically contrasting years (dry and mesic), accounting for the effect of the microenvironment on each plant (Figure 1). We randomly selected three different hills and established 20×20m plots at the north and south slopes of each hill for each species (3 hills×2 slopes×2 species = 12 plots). In each plot, we randomly tagged 40 reproductive individuals that encompassed the size range of the species in the plot, for a total of 480 plants (Figure 1). All plots were established within an area of ~1 km², to minimize climatic differences among them. The study was carried out over 2017 and 2018 (2017 was warmer and drier than 2018; Supporting Information 2). Indeed, 2017 had the highest number of heat waves in the IP, the second warmest summer temperature, and was the second year with an early heat wave (mid-June) recorded in a 46-year time series (Spanish meteorology agency; Supporting Information 2). Data were collected from late April to mid-August each year, ending when

both the vegetative and reproductive seasons were completed for both species. Several plants died between the first and the second study years, likely due to the harsh climatic conditions during 2017. Therefore, we replaced 15 *C. hyssopifolia* (6.25%) and 109 *H. squamatum* plants (45.42%) in 2018. Note that new-tagged individuals were similar in size, reproductive output, phenotypic traits and microenvironmental conditions compared to surviving individuals ($p > 0.05$ in all cases).

2.3 | Collection of phenotypic and fitness traits

Our field study did not need permission for fieldwork and all traits were measured in all individuals in both study years. We measured height and maximum diameter before the onset of reproduction (end of April) and calculated plant volume (Supporting Information 1). At the reproductive peak of each species, we collected one primary branch per plant, wrapped it in moist paper in a zipper plastic bag and stored in a portable cooler box, guaranteeing transportation to the laboratory in cool, water-saturated conditions (Pérez-Harguindeguy et al., 2013). Then, we followed Garnier et al. (2001) to ensure complete leaf rehydration (see Supporting Information 1). The next morning, five undamaged, non-senescent and fully expanded leaves per plant were haphazardly selected. First, we weighed the fresh mass of all leaves using a microbalance (1 µg precision; Mettler Toledo). Second, we measured leaf thickness on three leaves (two measurements per leaf, one at each side of the leaf midrib) using a dial thickness gauge (Mitutoyo Corporation). Third, the five leaves were scanned, oven-dried at 60°C for 48 hr and weighed. Specific leaf area (SLA) was calculated as the one-side area of the leaves divided by their oven-dry mass. Leaf dry matter content (LDMC) was calculated as dry mass divided by water-saturated fresh mass.

We monitored reproductive phenology and leaf senescence every 12–14 days during 2017 (7 censuses), and every 6–8 days during 2018 (14 censuses). At each census, we visually estimated the percentage of closed inflorescences, inflorescences with open flowers, fully developed fruits, dispersed inflorescences, and the percentage of senescent and green leaves. From these data, we calculated the onset, duration and peak of flowering, fruiting and dispersion, and plant senescence (see Supporting Information 1).

We measured midday maximum photochemical efficiency of photosystem II (F_v/F_m) with a portable fluorometer Handy PEA+ (Hansatech, UK) at the reproductive peak of each species. To test whether early-season ecophysiological status affected plant fitness, F_v/F_m was also measured before the onset of reproduction in 2018 (Supporting Information 1). Leaf chlorophyll content was measured twice in 2018 (early-season and flowering peak) in three leaves per plant, using a SPAD 502 chlorophyll meter (Konica Minolta). Leaf carbon and nitrogen content (leaf C and N hereafter), and carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were also determined, using leaves from the same branch collected for morphological traits (Supporting Information 1).

We randomly collected five closed and mature inflorescences per plant before seed dispersion and stored them separately. Inflorescences were dissected individually to separate viable seeds from those aborted/predated. Then, we calculated the mean number of viable seeds per inflorescence. Finally, five viable seeds per plant were randomly selected and individually weighed to obtain mean seed mass per plant. At the end of the reproductive season (end of July) of each year, we counted the number of viable inflorescences (not predated/aborted). From this, we calculated two plant-level reproductive fitness traits for each plant: (a) total seed number, the product of the number of viable inflorescences and the number of viable seeds per inflorescence and (b) total seed mass, the product of the total seed number and the mean seed mass. Since an important proportion of *H. squamatum* individuals died between the first year and second year, we also assessed survival at the beginning of 2018 in this species as an additional fitness trait.

2.4 | Microenvironmental and environmental conditions

We measured local biotic and abiotic microenvironmental conditions around each plant. In early April 2017, we established a circle of 1 m in diameter centred around each plant, and we visually estimated the percentage of perennial, annual and total cover, bare ground cover, BSC cover and litter cover. Cover estimations were always performed by the same observer. As a proxy of intraspecific competition, we counted the number of conspecifics within the circle and measured the distance of the closest conspecific to each tagged plant.

Soil water content was monitored in 2017 at the peak of flowering of each species, and twice in 2018, before the onset of reproduction and at the peak of flowering of each species. At each sampling point, four measurements were recorded around each plant ($N = 1,920$ measurements in 2017 and 3,840 in 2018), using an HH2 Moisture Meter (Delta-T devices). Insolation was estimated through the Gandullo's method (Gandullo, 1974) based on the latitude, orientation and micro-slope around each plant (see Supporting Information 1).

2.5 | Statistical analyses

All analyses were performed in R (R Core Team, 2018; see a detailed description of models' specification in Supporting Information 3). We arranged the functional traits and fitness data into different datasets according to our research questions (see details in Supporting Information 1). Phenotypic selection analyses provide information on (a) the magnitude of phenotypic selection, that is, the strength of the relationship between traits and fitness; (b) direction, whether positive or negative trait values are associated with higher fitness and (c) form, the shape (linear or quadratic) of the relationship between traits and fitness.

To assess directional selection, we calculated for each species, year and slope: (a) linear selection differentials ($S' = \text{Cov}[w, z]$), the covariance between relative fitness and a given standardized trait, which quantify direct and indirect selection, and (b) linear selection gradients ($\beta' = P^{-1}S'$), the vector of partial regressions of multiple traits included in the same regression model, which estimate direct selection. To assess stabilizing or disruptive selection, we calculated (a) quadratic selection differentials ($C' = \text{Cov}[w, (z - \bar{z}) (z - \bar{z})^T]$) and (b) quadratic selection gradients ($\gamma' = P^{-1}C'P^{-1}$), where w is the vector of relative fitness, z is the vector of standardized phenotypic values and P is the phenotypic variance–covariance matrix (Lande & Arnold, 1983; Phillips & Arnold, 1989). Nonlinear selection was considered only when both significant quadratic estimators (C' and γ') and an intermediate maximum or minimum in the fitness function were observed (see Ramírez-Valiente et al., 2021). For each species, traits were standardized and reproductive fitness was relativized (see Supporting Information 1 for details).

Selection differentials and gradients were calculated using generalized linear mixed models (GLMMs) with function *glmer* (package `LME4`; Bates et al., 2015). Relative reproductive fitness (and survival in *H. squamatum*) was included as the dependent variable, and the standardized trait (in selection differentials) or traits (in selection gradients) were included as fixed factors. Total seed mass integrated the information of total seed number, and both reproductive fitness traits showed very similar selection patterns, so we present results using total seed mass (see Supporting Informations 4 and 5 for results using total seed number, and Supporting Information 6 for results of *H. squamatum* using survival). Plant volume and microenvironmental data (see below) were also included in the models as covariates, and plot was included as a random factor (Supporting Information 3). As reproductive fitness did not follow a gaussian distribution, models were performed using family = 'Gamma' and link = 'log' (family = 'binomial' and link = 'logit' in the models using survival). To avoid potential multicollinearity issues, we computed both variance inflation factors (VIFs) and pairwise correlations for each trait in all datasets before performing selection analyses (see Supporting Informations 1 and 7). To account for the consequences of multiple testing, results from selection models were corrected using false discovery rate (FDR) for each species, year and slope (Benjamini & Hochberg, 1995) using *p.adjust* function.

Microenvironmental data from each plant was summarized using principal component analyses (PCA) using function *prcomp* (R Core Team, 2018) for each slope, year, and species (see Supporting Information 1). We selected the three first principal components of each PCA, which explained ~75% of the microenvironmental variance (Supporting Information 8). The eigenvectors of the three first principal component of each PCA were consistently associated with different microenvironmental variables: PC1 was in general related to total and perennial cover; PC2 to the number of conspecifics, the distance of the closest conspecific and BSC cover; and PC3 to soil water content, annual and litter cover (Supporting Informations 8 and 9). Eigenvalues for each plant were included in the models to

account for the microenvironmental conditions experienced by each plant.

We tested whether the relationship between a trait and reproductive fitness differed between slopes and/or years, that is, variation in the magnitude and direction of selection for a given trait, by quantifying the interactions trait-by-year and trait-by-slope, respectively, using GLMMs. Plant volume and microenvironmental data (nested in slope or year) were included as covariates and plot as a random factor. Significance levels were corrected using FDR. Significant trait \times slope and trait \times year indicates that the magnitude and/or the direction of selection for a given trait varied among slopes and years, respectively. Furthermore, to test the relative effect of environmental variation across space (slopes) and time (years) on selection patterns, we assessed whether selection was more similar between slopes in the same year or between years in the same slope. First, we performed pairwise correlations between selection differentials (and gradients) from each slope and year. Then, we evaluated the percentage of variation of the selection differentials and gradients explained by slope and year through commonality analysis (see Supporting Informations 1, 10 and 11).

Finally, we tested whether functional traits, fitness (reproductive output and survival) and environmental conditions varied across space (between slopes) and time (years) for each species, and the relationship between both fitness components. First, we performed GLMMs to test the effect of slope, year and their interaction on fitness and phenotypic traits, including plant volume as covariate. Then, we tested the differences between slopes in the same year with GLMMs.

3 | RESULTS

There were large differences in the environmental conditions between slopes and years (Figure 2). Despite great biotic and abiotic differences between slopes, both the identity of the traits under selection and the direction of selection acting through reproductive fitness were consistent across slopes in both species, particularly for *H. squamatum* (Figure 3; Supporting Information 12). Furthermore, plot explained less than 10% of the variance of the selection models in most of the cases (~80%; Supporting Information 9). Similarly, the direction of selection on adaptive traits based on the sign of selection differentials was similar in both years (Figure 3; Supporting Information 12). However, the magnitude of selection differed between slopes mainly in *H. squamatum*, and between years mainly in *C. hyssopifolia* (Table 1). In contrast, we did not detect any trait under selection through survival in *H. squamatum*. Overall, selection was stronger on *H. squamatum* than in *C. hyssopifolia*, especially in the south slopes and in 2018.

3.1 | Spatiotemporal heterogeneity between slopes and years

North and south slopes differed in their environmental conditions in both years (Figure 2). While total, perennial and bare soil cover

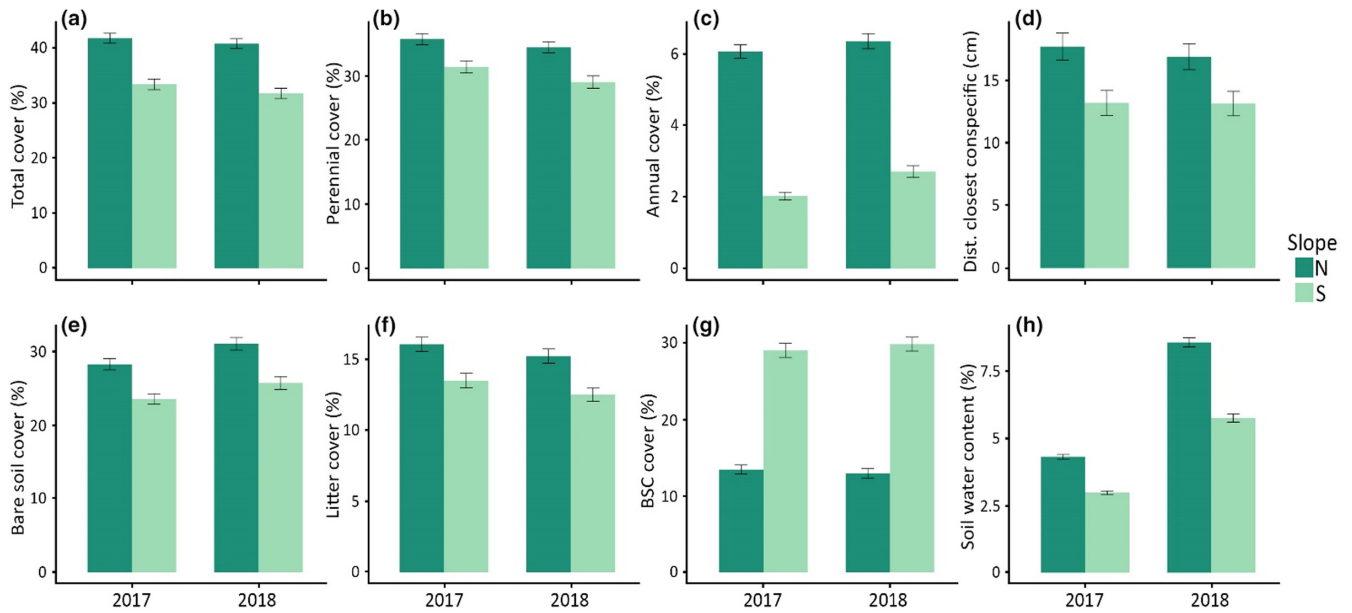


FIGURE 2 Differences in environmental conditions between slopes and years. Means and standard errors of (a) total cover (%); (b) perennial cover (%); (c) annual cover (%); (d) distance to the closest conspecific individual (cm); (e) bare soil cover (%); (f) litter cover (%); (g) BSC cover (%) and (h) SWC (%) are shown. Data from both species were grouped in these analyses. All variables were significantly different ($p < 0.05$) between slopes but not between years within slopes, except for SWC (see text).

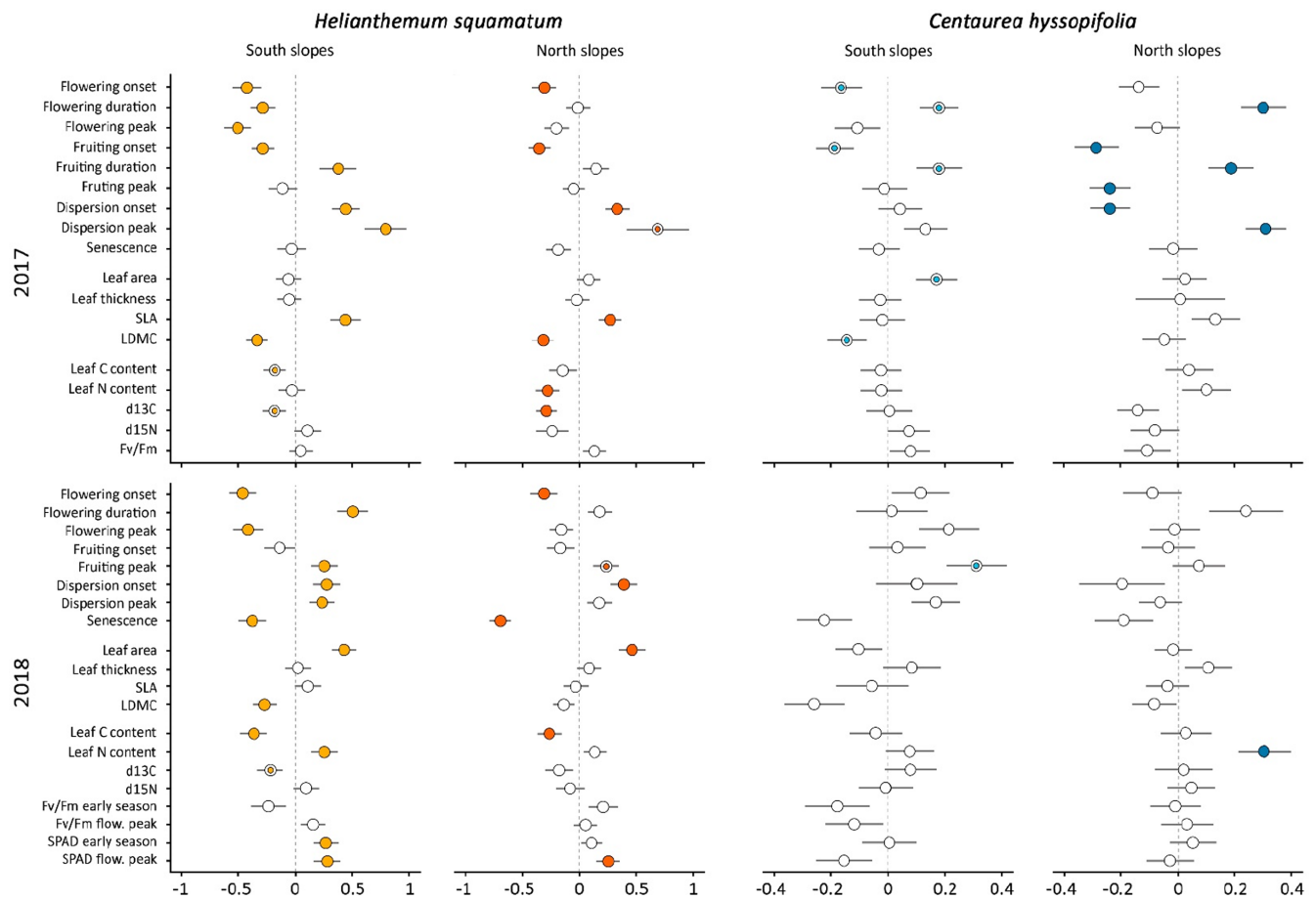


FIGURE 3 Directional selection differentials (S') and their standard error for *Helianthemum squamatum* and *Centaurea hyssopifolia* in both slopes and years using total seed mass as fitness variable. Significance levels after FDR corrections: Coloured circle = $p < 0.05$; small coloured dot inside circle = $0.05 < p < 0.1$; white = n.s. ($p > 0.05$) selection differentials.

TABLE 1 Results from the GLMMs testing differences in the magnitude and/or the direction of selection between slopes and years, using total seed mass fitness variable. χ^2 -statistic and significance (in brackets) of each model are shown. A significant ($p < 0.05$) value after FDR correction (trait:slope or trait:year columns) indicates that the magnitude and/or the direction of selection varied between slopes or years (significant trait:slope or trait:year interaction). Significant terms are shown in bold. In columns 2017 (S vs. N) and 2018 (S vs. N), the magnitude and the direction of selection is compared between slopes within the same year. In columns south slope (2017 vs. 2018) and north slope (2017 vs. 2018), the magnitude and the direction of selection is compared between years within the same slope. Significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

	<i>H. squamatum</i>						<i>C. hysopifolia</i>									
	2017 S vs. N		2018 S vs. N		South slope 2017 vs. 2018		North slope 2017 vs. 2018		2017 S vs. N		2018 S vs. N		South slope 2017 vs. 2018		North slope 2017 vs. 2018	
	trait:slope		trait:slope		trait:year		trait:year		trait:slope		trait:slope		trait:year		trait:year	
Leaf area	1.018		32.407***		17.049***		14.761**		4.637		2.186		7.104		0.303	
Leaf thickness	1.174		0.580		0.531		1.037		0.107		2.049		0.826		5.820	
SLA	17.746***		1.117		12.337**		6.531		2.258		0.073		0.455		4.072	
LDMC	20.992***		10.754*		21.777***		11.858**		5.305		9.001		12.600*		2.607	
Flowering onset	23.399***		20.014***		18.908***		15.988**		9.592*		2.966		6.829		6.938	
Flowering duration	8.547*		17.732***		18.435***		3.586		22.133***		4.098		5.256		15.708**	
Flowering peak	24.878***		10.233*		17.832***		7.050*		2.505		5.077		6.596		1.943	
Fruiting onset	12.840**		3.818		1.495		15.771**		20.457***		0.541		6.530		12.535*	
Fruiting duration	8.507*		NA		3.795		5.855		9.454*		NA		4.825		7.471	
Fruiting peak	2.774		10.320*		5.951		4.991		10.177*		8.359		11.634*		11.505*	
Dispersion onset	23.302***		13.708**		19.893***		12.219**		10.516*		3.186		1.316		16.548**	
Dispersion peak	22.586***		8.106*		14.428**		8.481*		22.675***		4.827		7.877		11.347*	
Senescence	3.324		55.285***		10.920**		52.495***		0.187		9.034		6.721		4.669	
Leaf carbon content	5.610		16.581**		10.465**		9.348*		0.444		0.458		0.489		1.201	
Leaf nitrogen content	8.274*		6.721		4.142		8.998*		1.431		6.492		0.777		11.724*	
Leaf $\delta^{13}C$	14.374**		5.673		8.628*		12.443**		4.015		0.570		0.786		2.280	
Leaf $\delta^{15}N$	7.442*		1.651		1.007		7.523*		2.396		0.109		0.741		0.087	
F_v/F_m	4.293		2.903		2.662		3.658		2.853		0.647		3.517		3.346	

was ~20% higher, and annual cover ~1.5 times higher in the north slopes (Figure 2; $p < 0.01$ in all cases), BSC cover was ~50% higher in the south slopes (Figure 2; $p < 0.001$). Biotic conditions within the same slope did not vary between years. Soil water content (SWC) varied between slopes and also between years. North slopes had higher SWC than south slopes in both years (Figure 2; $p < 0.001$). Furthermore, the higher rainfall in 2018 resulted in higher overall SWC in both slopes. In fact, SWC in the south slopes of 2018 was higher than those found in the north slopes of 2017 (Figure 2; $p < 0.001$).

3.2 | Linear and quadratic selection differentials and gradients

For *H. squamatum*, selection differentials showed that most phenological traits had a significant association with the reproductive output of individuals in both years and slopes (Figures 3 and 4; Supporting Information 12). Specifically, individuals that flowered earlier showed a shorter flowering period (only in the south slopes), an advanced and longer fruiting period and a delayed onset of seed dispersion showed higher reproduction in 2017 in both

slopes. Similarly, in 2018, early flowering, delayed fruiting peak and delayed dispersion onset were also under selection in both north- and south-facing slopes, although, in contrast to 2017, long rather than short flowering periods were adaptive in the south slopes. Other morphological and ecophysiological functional traits were also under directional selection in this species. In 2017, SLA and LDMC had a positive and negative association with reproduction in both slopes, respectively, and both leaf N and $\delta^{13}\text{C}$ (a proxy of WUE) were negatively linked to fitness in the north slopes. In 2018, individuals with larger leaves and higher leaf chlorophyll content at the peak of flowering showed higher reproduction in both slopes. Early-season leaf chlorophyll content and LDMC had a positive and negative impact on fitness in the south slopes, respectively (Figure 3; Supporting Information 12). Selection gradients showed that the duration of flowering and leaf N were under negative direct selection in the south and north slopes, respectively, in 2017. In 2018, leaf senescence was under negative direct selection only in the north slopes (Supporting Information 12). In contrast, the results performed using survival as fitness did not show any trait under selection in *H. squamatum*, except for leaf senescence, which was negatively linked to survival in the north slopes (Supporting Information 6).

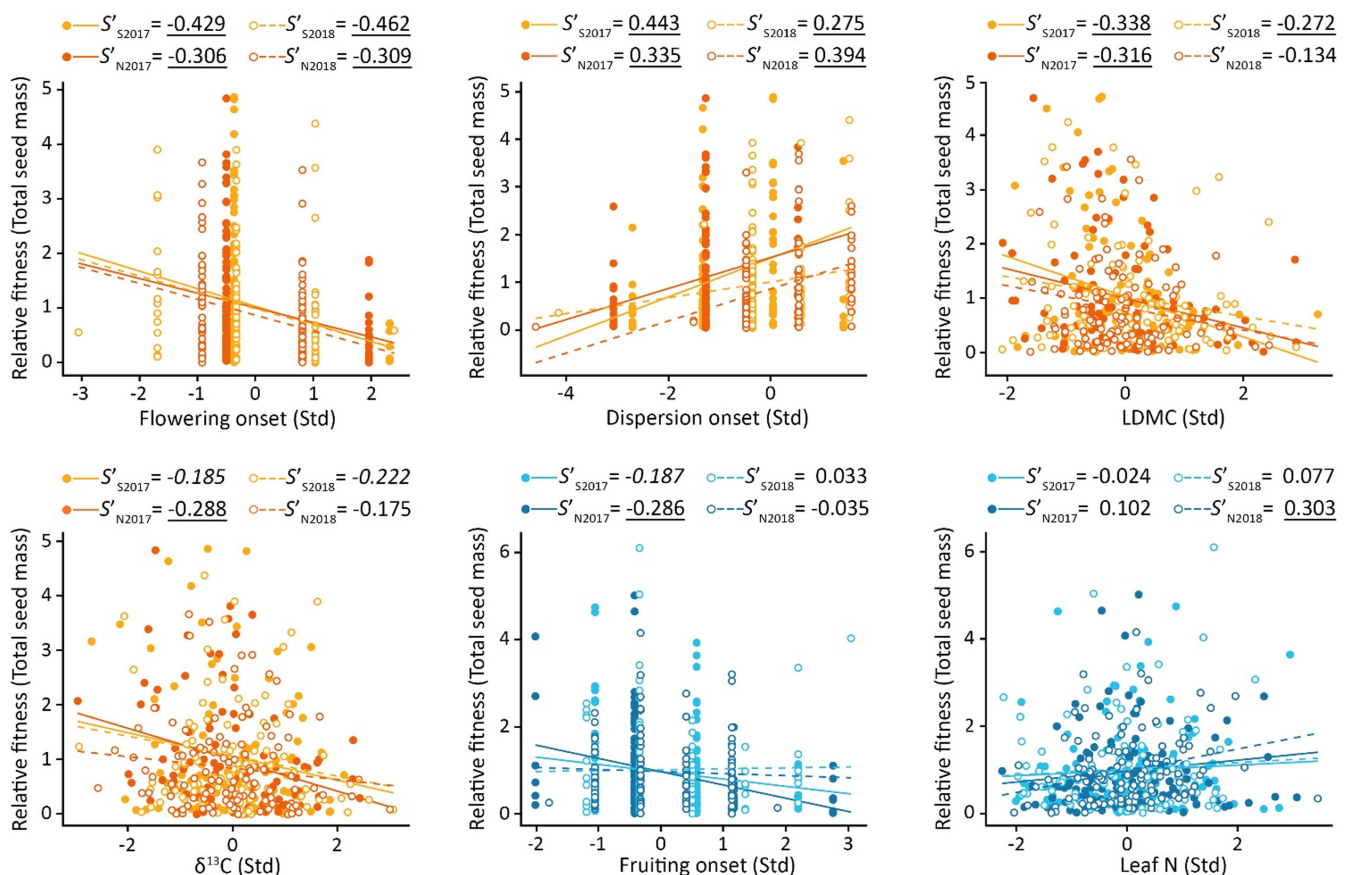


FIGURE 4 Relationship between relative reproductive fitness (total seed mass) and functional traits in both species, slopes and years, with orange shades for *Helianthemum squamatum* and blue shades for *Centaurea hyssopifolia*. Estimated values of linear selection differentials (S') are shown in each plot. Subscripts indicate the slope and year. Significant ($p < 0.05$) and marginally significant ($0.05 < p < 0.1$) selection differentials are underlined and italicized, respectively.

For *C. hyssopifolia*, significant selection differentials for phenological traits were also found, but mostly in the north slopes in 2017. Individuals with longer flowering and earlier and longer fruiting and dispersal periods showed higher reproduction. There were virtually no functional traits under selection in the south slopes in 2017 and in either slope type in 2018 (Figure 3; Figure 4; Supporting Information 12). Selection gradients showed that lower WUE in 2017 and higher duration of flowering in 2018 were under direct selection in north slopes (Supporting Information 12).

Quadratic selection was less frequent than directional selection (Supporting Informations 5, 13 and 14). Significant and marginally significant quadratic selection differentials and gradients were observed only in 2018, in both slopes and species.

3.3 | Differences in selection between years and slopes

Phenotypic selection analyses and GLMMs revealed that selection acting through reproductive fitness varied between years and slopes depending on the species, mainly as a result of differences in magnitude rather than direction. For *H. squamatum*, selection was stronger in the south slopes for all the traits under selection in 2017, except for leaf N, $\delta^{13}\text{C}$ and fruiting onset (Table 1), as shown by the significant trait-by-slope interaction, and the larger selection differentials in the south (Figure 3; Supporting Information 12). In 2018, selection was also stronger in the south slopes, except for leaf area, dispersion onset and leaf senescence. Between years, the magnitude of selection was stronger for certain traits in 2017 than in 2018 within the same slope, and vice versa. For instance, late phenological phases were under selection more intensely in 2017, while there was stronger selection for flowering traits in 2018 in the south slopes. For *C. hyssopifolia*, the magnitude of selection was clearly stronger in the north slopes in 2017 (Table 1; Figure 3; Supporting Information 12). Both correlation and commonality analyses showed more similar patterns of selection between slopes in the same year than for the same slope between years, especially in *H. squamatum* (Supporting Informations 10 and 11).

3.4 | Microenvironment effect on individual fitness

We found significant effects of the microenvironmental conditions experienced by each individual on reproduction, evidenced by significant effects of PCA components in the selection models (Supporting Information 9). For *H. squamatum*, reproduction in 2017 was negatively associated with total, perennial and BSC cover (significant PC1 and PC2; Supporting Information 9), and positively associated with the number of conspecific individuals and SWC in the north slopes (significant PC2; Supporting Information 9). In 2018, reproduction was negatively associated with total and perennial cover in the north slopes (significant PC1; Supporting Information 9).

For *C. hyssopifolia*, reproduction in 2017 was negatively associated with BSC cover in the north slopes (significant PC3; Supporting Information 9). In 2018, reproduction was marginally positively correlated to litter cover and SWC in the south slopes (PC3; Supporting Information 9).

In contrast, individual survival was not related to the microenvironmental conditions surrounding each plant in both slopes and study species (not significant effects of PC1, PC2 and/or PC3 on survival; Supporting Information 15).

3.5 | Differences in fitness and mean trait values between slopes and years

Overall, reproduction was higher, or similar, in the south slopes compared to the north slopes in both species (Figure 5). There were also significant interannual differences in fitness, which were larger in *H. squamatum* than in *C. hyssopifolia* (Figure 5). For *H. squamatum*, reproduction in 2018 was approximately one order of magnitude higher than in 2017, due to the higher number of viable seeds per inflorescence (10-fold difference) in 2018. Fitness was also higher in the south compared to the north slopes in both years in this species (Figure 5). For *C. hyssopifolia*, there were differences between slopes in reproduction in 2017, with higher fitness in south slopes. There were also differences between years in total seed mass, due to the higher mass of seeds in 2018 (Figure 5).

In contrast, we found no differences in survival across slopes in both study species ($p > 0.05$; Supporting Information 15). Furthermore, survival was not associated with either plant size (a proxy for plant age) or the reproductive output of individuals, that is, there was no apparent trade-off between survival and reproduction ($p > 0.05$ in both cases; Supporting Information 15).

Mean values of most functional traits varied significantly between years and slopes in both species. While phenology was delayed in 2018 with respect to 2017 for both species, leaf morphological and chemical composition traits varied in a species-specific manner (see Supporting Informations 16 and 17 for details).

4 | DISCUSSION

Our results showed significant linear selection acting through reproduction in both species, years and slopes. The adaptive value of traits related to reproductive phenology showed similar selection patterns across slopes and years, particularly in *H. squamatum*. Contrary to our hypotheses, and despite the contrasting environmental conditions found between north and south slopes, neither the direction of selection nor the identity of the traits under selection through reproduction varied between slopes within years in either study species, that is, we generally observed a consistent adaptive strategy in both species across slopes. Indeed, selection was more similar between slopes within years than within slopes between years, suggesting that the climatic differences between

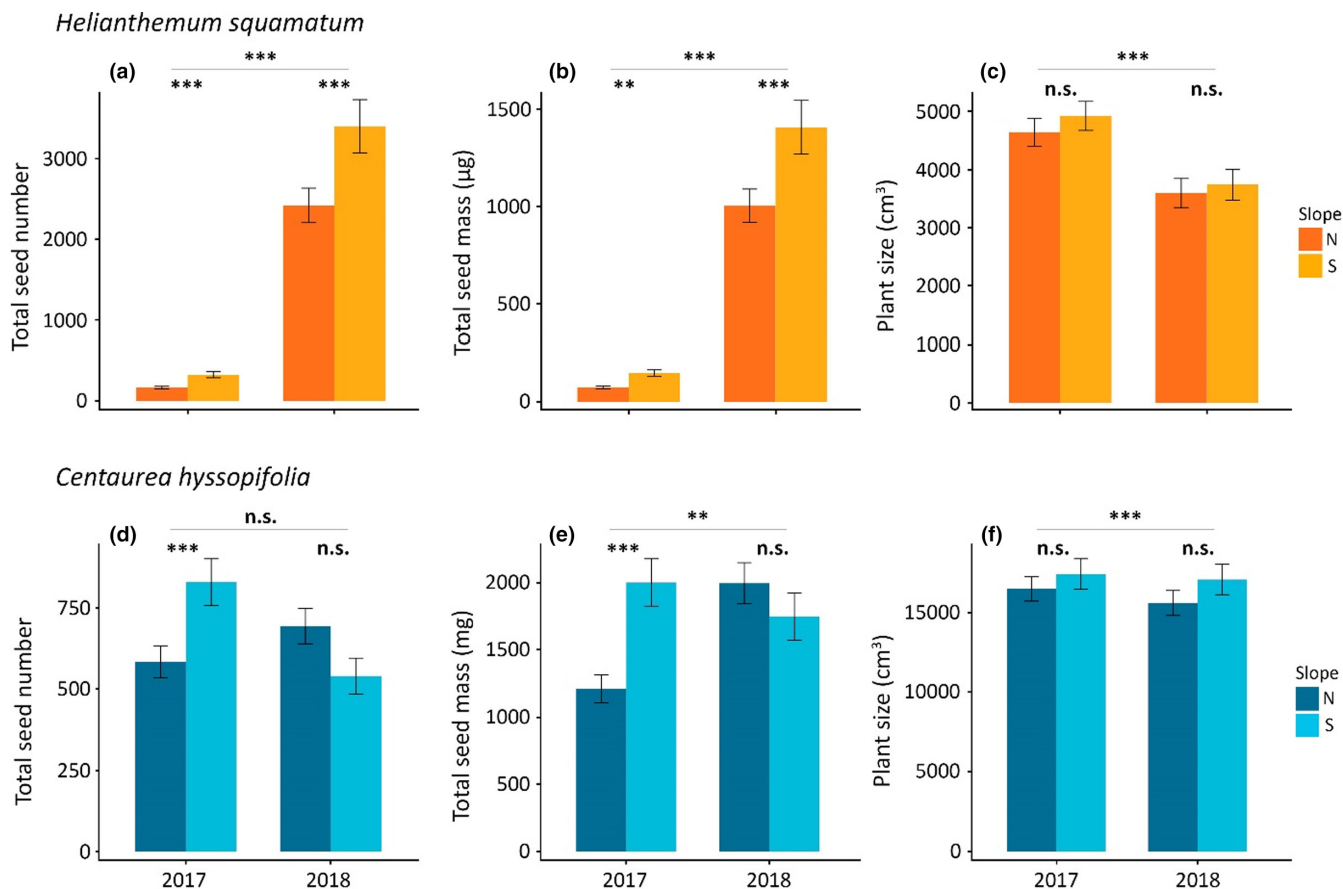


FIGURE 5 Means and standard errors for each slope and year of: (a) total seed number in *H. squamatum*; (b) total seed mass in *H. squamatum*; (c) plant size (plant volume) in *H. squamatum*; (d) total seed number in *C. hyssopifolia*; (e) total seed mass in *C. hyssopifolia* and (f) plant size (plant volume) in *C. hyssopifolia*. Significance levels: n.s. = not significant; ** $p < 0.01$; *** $p < 0.001$.

years had a stronger effect on selection than the environmental differences found between slopes. Contrastingly, selection through survival was negligible. Interestingly, our results assessing selection through reproduction showed that, rather than the expected conservative use of resources, a drought-escape, acquisitive strategy was adaptive in Mediterranean gypsum plants, even in the most restrictive conditions.

4.1 | The adaptive value of an acquisitive resource-use strategy in Mediterranean gypsum plants

We found that early phenology, lower WUE, higher SLA, lower LDMC, and, to a lower extent, higher leaf N, were associated with higher individual reproductive output (Figure 3), consistent with a resource-acquisitive strategy. The phenological traits under selection and the direction of selection for those traits were highly consistent in both north- and south-facing slopes and years, particularly in *H. squamatum*. Specifically, an advanced phenology, where plants that reproduced earlier had higher reproductive output, was generally adaptive in *H. squamatum*. A similar pattern was found in *C. hyssopifolia* in the harsher year, although selection for early reproduction was weaker in the south

slopes. Our results concur with a meta-analysis on 87 different species showing that selection consistently favours early flowering (Munguía-Rosas et al., 2011) across biomes. Several factors have been discussed to explain selection on advanced phenology. First, early flowering may minimize water loss later in the season, when the negative effects of abiotic stress are more severe (Franks, 2011; Herrera, 1992; Sherrard & Maherali, 2006). Indeed, an advanced phenology is usually related to drought-escape rather than to a drought-tolerance strategy (Franks, 2011; Volaire, 2018; Welles & Funk, 2021). Second, early flowering individuals could avoid competition for pollination (Herrera, 1992; Munguía-Rosas et al., 2011), and finally, an advanced flowering phenology may allow longer fruiting periods before seed dispersal, maximizing fruit maturation (Kudo, 2006). This could explain the adaptive value of earlier but longer fruiting periods and delayed dispersion found in our study. Although we cannot pinpoint the exact mechanism underlying selection on early phenology, our results clearly show that an advanced and extended reproductive phenology is adaptive in semi-arid gypsum plants, even in the less environmentally restrictive conditions (milder year and north slopes).

Other leaf morphological, physiological and chemical composition traits significantly impacted reproduction in both years and species, although again, we found stronger selection in *H. squamatum*.

In this species, lower LDMC, higher SLA and leaf area (larger and less sclerophyllous leaves) were under selection in both slopes and years, consistent with an acquisitive strategy. This matches the pattern often observed at the species level, with high resource-use species showing large, high SLA leaves to maximize light capture, photosynthesis and resource assimilation (Pérez-Ramos et al., 2013; Reich, 2014). Although plant species living in special substrates usually present morphological adaptations to minimize water loss (Damschen et al., 2012; Escudero et al., 2015), at the intraspecific level, selection favoured trait values associated with an acquisitive strategy, contrary to our expectations.

We also detected a negative relationship between WUE, estimated from leaf $\delta^{13}\text{C}$ isotopic composition, and reproduction in both species (Figure 3 and significant selection gradients in *C. hyssopifolia*; Supporting Information 12). Individuals with lower WUE, that is, more negative $\delta^{13}\text{C}$, had higher reproductive output. Several selection studies have reported the adaptive value of high WUE under water stress, often associated with a tolerance strategy (e.g. Dudley, 1996; Heschel et al., 2002). However, our results showed that water conservation was not advantageous for either species, suggesting that stomatal regulation is optimized to maintain C gain. Furthermore, the adaptive value of WUE can vary depending on the timing of water stress throughout the growing season. For instance, Heschel and Riginos (2005) showed that lower WUE and earlier phenology were favoured when water stress occurred early in the season because it allowed rapid individual development through high water use (see also Agrawal et al., 2008). The climatic anomalies that occurred in 2017, for example, heat waves and extremely high temperatures, could explain the observed adaptive value of lower WUE during the harsher year. However, our study also showed the adaptive value of lower WUE in the milder year. Selection on lower WUE has also been reported when water stress occurs late in the season in Mediterranean environments, which, again, has been interpreted as a drought-escape strategy (Franks, 2011).

Overall, patterns of selection for early reproduction and traits related to high resource acquisition observed in our study are consistent with a stress-escape strategy, where high C gain at the expense of fast water spending would allow rapid development and reproduction before water becomes critically limiting (e.g. Franks, 2011; Heschel & Riginos, 2005; Welles & Funk, 2021). Selection for drought escape and fast resource use has been similarly reported in other Mediterranean and semi-arid ecosystems, favouring, for instance, early reproductive phenology in highly seasonal environments (Sherrard & Maherali, 2006; Stanton et al., 2000) and low WUE in plants living under Mediterranean and arid/semi-arid climatic conditions (Donovan et al., 2007; Heschel & Riginos, 2005). Indeed, some studies have reported a positive association between early-flowering and lower WUE, as evidence of a drought-escape strategy (Franks, 2011; McKay et al., 2003; but see Sherrard & Maherali, 2006). The acquisitive strategy observed in our species could be favoured due to other unmeasured morphological traits, including those below-ground, related to resource assimilation and

nutrient uptake. For instance, several studies revealed a surprisingly diverse mycorrhizal community associated with gypsophiles, including *H. squamatum* (Palacio et al., 2012). Therefore, our study provides evidence of a mismatch between the tolerant strategy predicted for semi-arid Mediterranean taxa and the acquisitive strategy observed at the intraspecific level.

Quadratic selection was consistently less frequent than directional selection in both slopes, years and species. However, the results from nonlinear selection should be interpreted cautiously due to relatively low sample size. Further analyses with larger sample sizes may provide a more robust test of the occurrence and relative importance of nonlinear selection in these species (see Kingsolver et al., 2001, 2012).

In contrast with the results obtained for reproductive fitness, individual survival in *H. squamatum* was not associated with functional trait variation in either slope, indicating that the same selection pressures may act differently on the phenotype depending on the fitness component. Furthermore, we found no evidence of a trade-off between survival and reproductive fitness, which could have accounted for opposing selection patterns via different fitness components. Differences in selection among fitness components match previous studies reporting weaker estimates of linear selection via survival than those via reproduction (Kingsolver et al., 2012 and references therein). These results highlight that the phenotype expressed in the growing season prior to plant death was not a reliable predictor of individual survival in gypsum ecosystems.

4.2 | Environmental effects on fitness components

Although traits under selection were generally consistent across slopes and years, we observed differences in reproduction between slopes and years (Figure 5). Individual reproductive output was higher (or similar) in the south slopes compared to the north slopes for both species. This result indicates that, despite the lower SWC and the higher insolation, south slopes were not more stressful than north slopes for our study species. Differences in reproduction could be partly explained by the differential effect of the microenvironmental conditions at the plant level in north and south slopes. In the harsher year, BSC cover had a negative effect on reproduction in *C. hyssopifolia* in north slopes, and both total and perennial cover negatively influenced reproduction in *H. squamatum* in north slopes (Supporting Information 9). Similarly, in 2018, total and perennial cover had, again, a negative effect on reproduction in the north slopes in *H. squamatum*, and litter and soil moisture had a positive effect in the south slopes in *C. hyssopifolia*. These results suggest that although abiotic environmental conditions are harsher in the south slopes, higher competition—based on the negative effect of total and perennial cover—in the north slopes could have a larger negative effect on individual reproductive output than the abiotic conditions. Gypsophiles and other edaphic endemics growing on serpentines have been described as competition avoiders (Anacker

et al., 2011; Harrison et al., 2009; Mota et al., 2011), which could explain the negative effect of total and perennial cover on fitness. Conversely, survival was not influenced either by the environmental differences between slopes, individual size or the microenvironmental conditions experienced by each individual (Supporting Information 15).

Reproduction in the milder year, 2018, was higher than in the harsher year, but interannual differences varied between species. While *H. squamatum* showed a higher number of heavier seeds in the milder year, differences between years in *C. hyssopifolia* were exclusively due to higher seed mass (Supporting Information 16). These interspecific differences could be related to the different longevity, life history, and a potential trade-off between reproduction and survival (e.g. Harshman & Zera, 2007). Long- and medium-lived species (like *C. hyssopifolia*) usually base their lifetime fitness on survival, in contrast to annual and short-lived perennials (like *H. squamatum*), which maximize their fitness by a high reproductive output that guarantees a persistent seed bank (Adler et al., 2014; García & Zamora, 2003). Indeed, reproduction has been reported in *H. squamatum* even under very stressful conditions and at the expense of individual survival (Aragón et al., 2009). However, we did not detect such trade-off between reproduction and survival at the intraspecific level as demonstrated by the lack of differences in reproductive output between dead and surviving individuals in both slopes and species (Supporting Information 15).

Similar to the contrasting selection patterns acting through reproduction and survival, fitness components were differentially affected by individual traits and environmental conditions. While reproductive output was determined by individual phenotypic expression and microenvironmental conditions in both species, survival was not associated with either functional trait variation, microenvironmental conditions, reproductive output or plant size, suggesting that individuals progressively died due to differences in other unmeasured traits or environmental conditions (Supporting Information 6 and 15). Future studies are needed to understand the determinants of plant survival at the intraspecific level in gypsum specialists.

5 | CONCLUSIONS

Our results provide evidence that a drought-escape, acquisitive strategy was linked to higher reproductive fitness in our study system at the intraspecific level. This pattern was mostly consistent across species, environmentally contrasting slopes and climatically contrasting years. Such an acquisitive strategy may be adaptive in these stressful environments if it allows rapid individual development and reproduction before the most limiting climatic conditions encountered in mid-late summer. Further studies should aim to identify the precise physiological mechanisms that maintain this strategy in highly stressful Mediterranean environments. Additionally, our study showed remarkable differences in patterns of selection depending on

the fitness component used (reproduction or survival), emphasizing the importance of studies quantifying selection on the same trait, considering more than one fitness component, and spanning more than 1 year to fully understand the temporal and spatial dynamics of selection in natural populations. Finally, our study provides insights into phenotypic evolution and plant responses to rapid environmental change, and underlines that studies focused on the intraspecific level are key to unveil unexplored adaptive strategies.

AUTHORS' CONTRIBUTIONS

S.M. and A.E. conceived the idea; M.B.-S., M.R.-M., B.P., L.D.-G. and S.M. collected the data; M.B.-S. and J.A.R.-V. analysed the data; all authors discussed the main results; M.B.-S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY STATEMENT

Phenotypic and environmental data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.tb2rbp037> (Blanco-Sánchez et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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