Journal of Ecology

Demographic, developmental and life-history variation across altitude in *Erysimum capitatum*

Eunsuk Kim¹* and Kathleen Donohue²

¹Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford St, Cambridge, MA 02138, USA; and ²Biology Department, Duke University, Box 90338, Durham, NC 27708, USA

Summary

1. Natural variation in life history provides the opportunity to examine its correlated population performance. Alpine systems are considered to be vulnerable to climate change as high-altitude conditions are predicted to become more similar to those at low altitude. Comparing natural populations that exhibit variation in life history across altitude can provide information on how life history may influence the demography of alpine plants under a range of altitudinally or climatically variable conditions.

2. We compared the abundance, demography, life history and morphological development of *Erysimum capitatum* populations in alpine and lower-altitude habitats in the Colorado Rocky Mountains.

3. Mortality of all life stages was higher at lower elevation than in alpine sites, and low-elevation plants reproduced more quickly and expressed a semelparous life history more frequently than did alpine plants. Significant variation in post-reproductive survival, i.e. the opportunity for iteroparity, was also found across regions.

4. Several life stages contributed comparably to projected population growth in high-altitude, iteroparous populations, whereas low-elevation semelparous populations depended primarily on seedling recruitment and rapid reproductive maturation for population maintenance. Populations with intermediate levels of iteroparity differed from each other in their demography, suggesting that transitional states between iteroparity and semelparity are unpredictable.

5. Morphological development also differed between iteroparous and semelparous plants, with iteroparous plants producing more vegetative rosettes and maintaining those rosettes in a vegetative state more frequently than semelparous plants. Sites with lower soil water content were more semelparous.

6. *Synthesis.* These combined results suggest that changes in developmental rates and morphology may promote changes in fundamental life history. Altitudinal variation in morphology and parity is strongly associated with demographic variation across altitude, indicating that plastic or evolutionary changes in these traits would influence population performance across altitudinally or climatically variable conditions.

Key-words: alpine, climate change, demography, elasticity, iteroparity, life-history traits, plant development, semelparity

Introduction

Life history is a fundamental determinant of population demography. Schedules of reproduction and patterns of age-specific mortality combine to determine the relative contribution of different life stages to population growth and persistence. In some plants, life history varies geographically.

*Correspondence author. E-mail: eunsukkim2@gmail.com

Such natural variation in life history provides the opportunity to examine its effects on population performance and enables analyses of causes and demographic consequences of lifehistory variation.

Considerable attention has recently been paid to the demography of alpine and arctic species because they are thought to be especially vulnerable to future climate change; being at the edges of climatic gradients, their geographic ranges are projected to decrease rapidly (Theurillat & Guisan 2001; Walther

 $[\]ensuremath{\mathbb C}$ 2011 The Authors. Journal of Ecology $\ensuremath{\mathbb C}$ 2011 British Ecological Society

2003; Parmesan 2006; Diaz & Eischeid 2007). With decreasing opportunities for environmental tracking via migration, predicting how the distribution of such plant species and the viability of their populations respond to climate change is an urgent agenda in current ecological studies (Parry *et al.* 2007).

Characterizing the demography of a population is the first step toward inferring its likelihood of persistence. Demographic analysis can identify key life stages that contribute to population growth and maintenance (Caswell 2001; Morris & Doak 2002). By comparing populations inhabiting different altitudes, moreover, key life stages for population growth in different altitudes can be identified, differences in mortality of those life stages can be determined, and morphological or developmental traits that differ and contribute to demographic differences can be characterized.

Plant life history as well as demography has been shown to vary across altitude. In alpine environments, plant demography is often characterized by low seedling recruitment and high mortality at early developmental stages compared with lower-elevation populations (Billings & Mooney 1968; Bliss 1971; Hautier et al. 2009; Milla et al. 2009), although this is not always the case (Chambers 1995; Forbis 2003; Forbis & Doak 2004; Giménez-Benavides, Escudero & Iriondo 2007; Venn & Morgan 2009). Altitudinal differences in stage-specific mortality correspond with differences in life history, especially at the interspecific level, such that long-lived, frequently iteroparous, perennials are dominant in alpine habitats (Billings & Mooney 1968; Körner 2003). Consequently, survival of adult plants has been suggested to be a key demographic parameter for maintaining alpine plant populations and a key contributor to the evolution of life histories that are characteristic of high altitudes. In contrast, the lower adult survival that is frequently observed at lower altitude would select for faster reproduction and more semelparous life histories at low altitude. Changes in adult survival, as a consequence of migration to different altitudes or of climate change that would cause high-altitude sites to experience environmental conditions increasingly similar to those at low altitude (Dunne et al. 2004; Etterson 2004), are therefore predicted to alter selection on life histories and to directly influence population demography.

Demographic parameters, in turn, such as age-specific survival and reproduction, result from interactions among organismal traits and environmental conditions (Ricklefs & Wikelski 2002; Lambrecht et al. 2007). Given the strong correlation between life history and population demography (Franco & Silvertown 1996), it is of special interest to identify traits that are associated with life-history expression. Morphological or developmental traits may evolve in response to natural selection, or they may exhibit phenotypic plasticity to altered environments. In turn, those altered traits can induce changes in life history. It is important to know what demographic consequences may result from such responses (Gomulkiewicz & Holt 1995; Saccheri & Hanski 2006; Reusch & Wood 2007). Knowing which traits are associated with particular life-history strategies would provide insight into the potential demographic consequences of adaptation and plasticity of traits likely to be subject to novel selection across an altitudinal range or novel selection that accompanies climate change.

While fundamental life-history differences are commonly documented between species that inhabit different altitudes, as discussed above, intraspecific variation in life history across altitude offers an especially useful context for investigating the causes and demographic consequences of life-history variation, while controlling for taxonomic variation. By comparing populations of the same species that inhabit different altitudes, morphological and developmental traits that are associated with altitudinal variation in life history can be characterized, and traits that contribute to demographic differences can be identified. Such systems also provide a framework for interpreting how threatened high-altitude populations may respond to climate change, since abundant evidence predicts that highaltitude conditions will become increasingly more similar to low-altitude conditions with respect to temperature and precipitation regimes (Dunne et al. 2004; Etterson 2004). While in situ comparisons cannot distinguish between plasticity versus genetic differentiation as causes of demographic and life-history differences without further experimental manipulations, they can generate informed hypotheses concerning how life history and demography may respond, in the short- and long term, to changes in altitudinally variable environmental factors.

Here, we report a comparative study that characterizes demographic, life-history, and morphological and developmental differences between alpine and low-altitude populations of Erysimum capitatum (Douglas ex Hook. Brassicaceae) in the Colorado Rocky Mountains. Erysimum capitatum is a rosette-forming herbaceous plant found in the western United States and Mexico, in a wide variety of habitats, from coastal dunes to deserts, chaparral, forests and alpine tundra (Price 1987; Rollins 1993). In the Rocky Mountains, it occurs mainly in open habitats from 1500 m to over 4000 m a.s.l. A taxonomic study based primarily on herbarium specimens (Price 1987) reported natural variation in morphological and life-history traits, with plants in alpine habitats exhibiting a perennial life cycle, multiple basal stems and rosettes, and low statue while those at lower altitude being biennial with fewer basal stems and taller inflorescences. In all populations, rosettes that produce inflorescence from their apical meristems degenerate during the reproductive period (E. Kim, personal observation). However, no field study has confirmed this variation nor investigated the population dynamics associated with this variation. We took advantage of the wide altitudinal distribution of E. capitatum to examine natural variation in demography, morphology and developmental traits, and the associations among morphology, life history and demography. Specifically, the following questions were addressed: (i) Does population demography differ between alpine and low-elevation habitats? (ii) Do high- and low-elevation populations differ in life history, morphology and developmental traits? (iii) What is the relationship of morphological or developmental variation to variation in life history and demography?

Materials and methods

STUDY SITES AND EXPERIMENTAL DESIGN

Six natural populations of *E. capitatum* in the Colorado Rocky Mountains, USA, were used for this study. In each of three watersheds, one population was chosen in an alpine tundra environment above tree-line (altitude > 3200 m) ('H1', 'H2', 'H3'), henceforth referred to as 'high-elevation sites', and one population was chosen below tree-line (altitude < 2650 m) ('L1', 'L2', 'L3'), henceforth referred to as 'low-elevation sites' (Table 1). L1 was in an open area in sagebrush scrub, and L2 and L3 were in open area in ponderosa pine forest.

Depending on the spatial extent of the populations, three or four 1×1 m permanent plots were established in L2, L3, H2 and H3 in July, 2004, with the goal of marking at least 50 individuals within each population. In H1, the density of *E. capitatum* was much sparser, so four 1×3 m plots were established there. Plots at the L1 site were set up in 2005 because we could not find a natural population below tree-line near the H1 site in 2004.

All individuals of *E. capitatum* in each plot were marked with numbered aluminium tags that were fixed in the ground near each plant. The total numbers of tagged plants that were followed were comparable across all sites (Table S1 in Supporting Information). At the L1, H1 and H2 sites, all seedlings within permanent plots were marked in 2005. At the L2, L3 and H3 sites, one 0.25×1 m subplot was randomly selected within each plot because of high seedling densities, and seedlings within the subplots were marked with numbered aluminium tags. Regular censuses were conducted during the growing season (May to August), approximately every 2 weeks from 2005 to 2008, except for 2006 when monthly censuses were conducted.

The number of fruits produced by each reproductive plant was counted from 2004 to 2008. The number of leaves on all vegetative rosettes and the length of the largest leaf were recorded in 2004. The number of rosettes at the vegetative stage, number of rosettes at the reproductive stage, and number of leaves and diameter of each rosette were measured in every census from 2005 to 2008 in all populations.

Census to census survivorship was recorded for each tagged plant, as was transition to reproduction. Plant mortality during the summer was extremely high in low-elevation sites (see Results), and mortality appeared to be caused by drought stress as indicated by the desiccation of rosettes and wilting and yellowing of leaves. Therefore, volumetric soil water content of the six natural populations was measured every 2 weeks from June to August in 2007. Three to four locations were randomly chosen near permanent plots within each site, and soil water content was measured using a Hydrosense with a 12-cm rod (Campbell Scientific, UT, USA).

STATISTICAL ANALYSIS

All statistical analyses used the sAs statistical package ver. 9.2 (SAS Institute Inc., Cary, NC, USA). For demographic analyses, life stages were defined as follows: (i) 'seedlings' were plants that were less than 1 year old, (ii) 'juveniles' were non-reproductive plants that were older than 1 year, (iii) 'adults' were plants that were in the reproductive state ('reproductive adults') or had been reproductive in the past but were not reproductive at present ('non-reproductive adults'). A plant was designated as juvenile in 2005 if it did not reproduce in both 2004 and 2005 and if it did not have a dried inflorescence from previous years during 2004 and 2005. While censuses started in 2004 in five out of six sites (all but L1), most analyses below were conducted using data starting in 2005 in order to include all the sites.

To compare plant density (number of plants per square metre) between high- and low-elevation sites, repeated-measures analysis of variance was conducted (SAS PROC GLM; SAS Institute Inc.). At the beginning of a growing season, the densities of seedlings, juveniles, adult plants (reproductive plus non-reproductive), fruits and the sum of plants at all life-cycle stages (except fruits) were averaged across plots at each site. Seedling density was measured again at the end of the growing season. Plant densities were natural-log-transformed for the analysis. The model included year as the repeated factor, and habitat (high vs. low), region and Habitat × Region as independent variables. For the year, Year × Habitat, Year × Region and Year × Habitat × Region effect, F-ratios based on Wilk's λ were evaluated. To interpret Habitat × Region and Habitat × Year interactions, additional sub-analyses of variance were conducted to compare plant densities between habitats within each region and year. To interpret three-way interactions involving inter-annual variation in plant densities, effects of year were tested for in each population separately. To compare the proportion of adult plants between high- and low-elevation habitats, analysis of variance using a logistic model was

Region	Population	Location (latitude/longitude)	Altitude (m)	Plant density in 2004 (no. m ⁻²)
1	H1	Emerald Lake, Gothic (39°00'32.3" N, 107°02'26.3" W)	3191	4.0 ± 0.5
	Ll	Near Co Rd 743, Gunnison Public Land (38°36'16.8" N, 106°49'27.7" W)	2630	18.0 ± 2.9
2	H2	Summit of Loveland Pass (39°39'49.5" N, 105°52'48.2" W)	3636	14.5 ± 1.5
	L2	Near Lookout Mountain Nature Center (39°43'54.7" N, 105°14'30.8" W)	2234	17.0 ± 2.3
3	H3	Niwot Ridge (40°03'11.6" N, 105°35'20.1" W)	3505	18.0 ± 1.7
	L3	South Fork of Shanahan Trail, Boulder Open Space (39°57'40.0" N, 105°16'16.5" W)	1831	19.3 ± 2.0

Table 1. *Erysimum capitatum* natural populations in the Colorado Rocky Mountains, USA. Location and plant density $(\pm SE)$ at the start of experiment are shown

1240 E. Kim & K. Donohue

conducted (SAS PROC LOGISTIC; SAS Institute Inc.) with the same independent variables as those used for the analysis of plant densities. Year was treated as a fixed factor instead of a repeated factor. The logit function was used as the link function, and the exact permutation distribution was used as the error function (Stokes, Davis & Koch 2000).

To compare stage-specific (seedling, juvenile, adult) survival between high- and low-elevation habitats, analysis of variance using a logistic model was conducted (sAS PROC LOGISTIC; SAS Institute Inc.). The model included as the dependent variable the survival probability (0 or 1) of individual plants from the beginning of one growing season to the beginning of the next growing season. The habitat, region and Habitat × Region interaction were included as independent variables. The logit function was used as the link function, and the exact permutation distribution was used as the error function (Stokes, Davis & Koch 2000). The full model was evaluated only for data collected in 2005 because plants at all life stages existed in all sites only in 2005. Separate analyses were conducted for each year and each region, with habitat as an independent variable. To test for interannual variation in survival within each population, analysis of variance was conducted with year as the independent factor.

To compare survival curves between habitats, survival functions were compared between high- and low-elevation habitats within each region (sas proc LIFETEST; SAS Institute Inc.). A life table of cohorts for each year (2005, 2006 and 2007 cohorts) was constructed, and log-rank tests were conducted. The L1 site had only four germinants during the study years, so it was not included in the analysis, and the comparison between habitats within Region 1 was not conducted.

To compare the relative contribution of life-cycle components to the projected population growth rate, transition matrices were constructed for each population, and elasticities of the matrix elements were calculated following Caswell (2001) and using a Matlab code provided by Morris & Doak (2002). Seedlings were formulated as a direct production from reproductive adults, and a seed bank was not included in the model because of a lack of information on the seed life stage. Omitting the seed stage from the transition matrix could influence the population growth rate especially in declining populations (Kalisz & McPeek 1992). However, combining the seed and seedling stage is common in single-year matrix models (Caswell 2001), and such combining may have a modest effect on elasticity analysis (Silvertown et al. 1993). Since no juvenile or adult plants existed in 2005 and/or 2006 at the L2 and L3 sites, transition matrices for 2005 and 2006 at those sites could not be calculated. Therefore, a stochastic model using between-year variation in vital rates could not be applied. Instead, the average transition probabilities from 2004 to 2008 were used in the transition matrices, although tests for interannual variation in vital rates that could be compared across years are also presented.

To test whether life-history reproductive strategy differed across elevation, two key indicators of iteroparity – the post-reproductive survival and number of reproductive episodes by individual plants – were compared between habitats and across regions using analysis of variance (SAS PROC LOGISTIC and SAS PROC GLM; SAS Institute Inc.). The model included habitat, region and Habitat \times Region as independent variables. Separate analyses of variance were then conducted within each region. Since no reproductive plant was present at L2 and L3 in 2006 and 2007, and since the L3 population was not found in 2004, only data collected in 2005 were analysed.

To test for differences in morphological, developmental and reproductive trajectories across altitude, analyses of variance (SAS PROC GLM; SAS Institute Inc.) compared rosette ontogeny and fruit production between habitats. The number of rosettes present at the beginning of

reproduction, the average number of leaves of those rosettes, the proportion of rosettes that was allocated to reproduction within a growing season, the number of rosettes produced during reproduction, and fruit production per reproductive plant were compared. The number of vegetative rosettes that were produced during the reproductive period was estimated by subtracting the number of vegetative rosettes present at the beginning of reproduction from the number of vegetative rosettes after reproduction. The model included habitat, region and Habitat × Region interaction as independent variables. To satisfy normality assumptions, all traits were natural-log-transformed except the proportion of rosettes allocated to reproduction, which was arcsine square root transformed. Due to significant Habitat × Region interactions, additional analyses were conducted within each region. The leaf number and rosette diameter of seedlings at the end of the growing season, and the probability of reproductive maturation were also compared. Only the 2007 cohorts could be compared because of extremely high mortality of the 2005 and 2006 cohorts in the L2 and L3 sites. Since no germinant was found in the L1 site in 2007, habitat effect was tested within Region 2 and Region 3. Additional analyses were conducted to compare iteroparous H1 and H2 populations and semelparous L2 and L3 populations. To satisfy normality assumptions, leaf number was natural-log-transformed. Soil water content was also compared across altitude using the same model

To test for associations between morphological traits and postreproductive survival (the opportunity for iteroparity), two analyses were conducted. First, to evaluate iteroparity at the population level, linear regression analysis was conducted using population means of traits as the independent variables, and population means of postreproductive survival as the dependent variable (SAS PROC GLM; SAS Institute Inc.). Only data in 2005 could be used in this analysis. Secondly, the association at the individual level within populations was evaluated using logistic regression (SAS PROC GENMOD; SAS Institute Inc.). The post-reproductive survival probability (0 or 1) of individuals was the dependent variable, and the following traits were independent variables: the number of rosettes present at the beginning of reproduction, average leaf number of rosettes at the beginning of reproduction, proportion of rosettes allocated to the reproduction, fruit production, and number of vegetative rosettes that were produced during reproduction. Data were combined over populations and years, and the model included population and year to control for yearly and population variation in post-reproductive survival. One analysis was conducted with each independent variable ('Total'), and another analysis was conducted with all independent variables ('Direct') to control for correlations among traits. All independent variables were standardized with zero means and one standard deviation. Pearson correlation coefficients among traits were also calculated. We compared the number of leaves on reproductive versus non-reproductive rosettes. A separate t-test was conducted within each population (SAS PROC TTEST; SAS Institute Inc.). The comparison was not conducted in the L2 and L3 populations since most reproductive plants did not have non-reproductive rosettes for comparison.

Results

PLANT DENSITY AND POPULATION AGE STRUCTURE

The overall density of plants was lower in high-elevation than low-elevation sites (Table 2, Fig. 1a), especially the density of new seedlings. However, the densities of juveniles and adults were higher in high-elevation sites. Altitudinal differences in

Table 2. Results of repeated-measures analysis of variance to compare (natural-log-transformed) plant density between high- and low-elevation sites for each year from 2005 to 2008. d.f. = numerator/denominator degrees of freedom. *F*-ratios based on ANOVA and *F*-ratios based on Wilk's λ (for year and its interactions) are presented

	d.f.	Seedlings at the beginning of the growing season	Seedlings at the end of the growing season	Juvenile plants	Adult plants	Fruit
Habitat	1	8.22*	22.04***	17.84***	7.70*	1.58
Region	2	30.15***	24.98***	11.33**	0.26	1.28
Habitat × Region	2	11.53**	2.06	10.07**	11.21**	7.06**
Year	3/12	30.17***	48.23***	55.12***	6.81**	2.47
Year × Habitat	3/12	5.29*	6.02**	28.3***	5.56*	4.26*
Year × Region	6/24	8.17***	7.26***	12.63***	3.41*	5.52**
Year \times Habitat \times Region	6/24	3.57*	8.12***	9.4***	2.46(*)	1.87

(*)P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001.

plant densities varied across regions and among years, as indicated by significant Habitat × Region and Year × Habitat interactions (Table 2). The density of particular life stages also differed significantly across regions within a given altitude. Notably, plant densities at the L1 site differed from those in the other low-elevation sites, such that only four germinants were observed during the study years, and overall plant density decreased from 18 plants m⁻² in 2005 to 2 plants m⁻² in 2008. The density of adult plants showed significant temporal variation only in the low-elevation habitat [L1 site, F(year) = 4.30, P < 0.05; L3 site, F(year) = 29.33, P < 0.001], but temporal variation in the density of juvenile plants was significant only in the high-elevation habitat (H2 site, F(year) = 26.76, P < 0.001; H3 site, F(year) = 48.87, P < 0.001) (Table S2).



Fig. 1. Plant densities (the number of plants m^{-2}) and life-stage structure of each population. Average proportion of life-cycle stages during study years (2005–2008) is presented. Life-stage structure for each year is given in Fig. S1. Statistical analyses are given in Table 2.

© 2011 The Authors. Journal of Ecology © 2011 British Ecological Society, Journal of Ecology, 99, 1237-1249

Although pre-reproductive stages were usually more numerous than adult stages in both habitats, the proportion of adult plants in the high-elevation habitat (H1 site, 24–33%; H2 site, 19–54%; H3 site, 3–18%) was higher than in the low-elevation habitat (L1 site, 3–56%; L2 site, 0–6%, L3 site, 0–23%) ($\chi^2 = 17.34$, P < 0.001) while the L1 site showed a higher proportion of adult plants, similar to the high-elevation sites (Figs 1b and S1). In addition, altitudinal difference in the adult proportion varied across regions [Region 1, Score statistic (habitat) = 2.68, P = 0.26; Region 2, Score statistic (habitat) = 222296, P < 0.001; Region 3, Score statistic (habitat) = 1.34, P = 0.43]. A high proportion of new seedlings characterized the L2 and L3 sites.

AGE-SPECIFIC SURVIVAL AND REPRODUCTION: VARIATION IN ITEROPARITY AND DEMOGRAPHIC PROJECTIONS

The survival of plants at all life-cycle stages was higher in highelevation than low-elevation habitats in 2005 [seedling, Score statistic (habitat) = 492.6, P < 0.001; Juvenile, Score statistic (habitat) = 5.23, P < 0.1; Adult, Score statistic (habitat) = 30.50, P < 0.001] (Table S3), and this pattern was



Fig. 2. Survival curve of the 2005 cohort. The L1 population was not included in the analysis since they had only one germinant in 2005. Survival curves of the 2006 and 2007cohorts showed similar patterns to that of the 2005 cohort (Fig. S2). χ^2 values from log-rank test are given to compare the survival curves between high- and low-elevation sites in each region for which a comparison was made and sample sizes are presented in parenthesis. (*)P < 0.1, *P < 0.05, **P < 0.01.

consistent across years (Fig. S2). Fewer than 56% of the new seedlings died in the H1, H2 and H3 sites, but more than 73% died in the L2 and L3 sites during their first year (Figs 2 and S2). The probability of juvenile survival was also higher in the high-elevation than low-elevation habitat in Regions 2 and 3. Because of high mortality of seedlings and juveniles, no plants of the 2005 and 2006 cohorts survived in the L2 and L3 sites at the end of this study in 2008. Mean adult survival was also higher in the high-elevation than low-elevation sites, and this difference was driven by the extremely low survival of reproductive plants in the low-elevation habitats (Fig. 3a). All reproductive plants in the L2 and L3 sites died after reproduction in 2005 and 2006. The survival probability of reproductive adult plants was similar to that of vegetative adult plants in all high-elevation sites. The survivorship of seedlings showed significant temporal variation in low-elevation sites when it could be measured [L2 site, Score statistic (year) = 9.55, P < 0.05; L3 site, Score statistic (year) = 36.09, P < 0.001 (Table S3). The survival probability of seedlings in the H3 site also varied significantly across years [Score statistic (year) = 12.64, P < 0.001]. In contrast, no temporal variation was detected for the survival probability of adult plants except in the H2 site [H2 site, Score statistics (year) = 13.99, P < 0.001].

Post-reproductive survival provides an opportunity for iteroparity – more than one reproductive episode during an organism's lifetime. Average survival of reproductive individuals in high-elevation populations was six to seven times higher than those in low-elevation sites in 2005 [Score statistic (habi-



Fig. 3. Natural variation in iteroparity. Post-reproductive survival and the number of reproductive episodes during the study years are two indicators of iteroparity. *F*-ratios are given for the comparison of the number of reproductive episodes between habitats. (*)P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001.

tat) = 17.52, P < 0.001] (Fig. 3a), although it differed across regions in high-elevation [Score statistic (region) = 15.93, P < 0.001] and low-elevation sites [Score statistic (region) = 6.78, P < 0.05]. Over 83% of the reproductive plants survived in the H1 and H2 sites, and 23–32% of them survived in the H3 and L1 sites. In contrast, post-reproductive survival was extremely low in the L2 and L3 sites: all reproductive plants died in 2005.

Variation in post-reproductive survival was associated with differential reproductive strategies among populations. Extremely low post-reproductive survival in the L2 and L3 sites removed the opportunity for multiple reproductive episodes, so 98% of the adult plants reproduced only once during the period of study (Fig. 3b). In contrast, 37% of adult plants in the H1 site and 68% of adult plants in the H2 site reproduced more than two times during the course of the study. Although 63% of adult plants reproduced only once during the period of observation in the H1 site, 40% of those plants survived until the end of the study, providing an opportunity for additional reproductive episodes in the future. Like post-reproductive survival, the number of reproductive episodes in the H3 and L1 sites was somewhat intermediate, such that 6-24% of adult plants reproduced at least twice, but no plant reproduced more than three times. In short, L2 and L3 populations were essentially semelparous (but see below), and H1 and H2 were unambiguously iteroparous, while H3 and L1 were of intermediate parity.

On average, no significant net effect of elevation was found for fruit number m⁻² during any year, but a significant Habitat × Region effect was detected (Table 2). Fruit density in the H2 site was higher than in the L2 site, likely due to fewer reproductive plants in the L2 site in 2005–2007. Fruit density varied year to year in the H2 [*F*(year) = 9.55, *P* < 0.01] and L3 sites [*F*(year) = 16.61, *P* < 0.001]. Similar to fruit density, no effect of habitat was detected for the number of fruits per reproductive plant [*F*(habitat) = 3.49, *P* = 0.19] (Fig. 4). The number of fruits per reproductive plant varied significantly across years in the H2 [*F*(year) = 6.89, *P* < 0.001], L1 [*F*(year) = 5.07, *P* < 0.01] and L3 sites [*F*(year) = 5.90, *P* < 0.05].



Fig. 4. Fruit production per reproductive plant in each population. Statistical analysis for fruit production per reproductive plant is given in text and Table S3.

© 2011 The Authors. Journal of Ecology © 2011 British Ecological Society, Journal of Ecology, 99, 1237-1249

то	Transition	Transition matrices				Elasticity matrices From			
	From								
	S	J	RA	VA	S	J	RA	VA	
(a) H1 (λ =	= 1.022)								
S	0.000	0.000	1.809	0.000	0.000	0.000	0.141	0.000	
J	0.916	0.554	0.000	0.000	0.141	0.167	0.000	0.000	
RA	0.000	0.114	0.415	0.188	0.000	0.141	0.148	0.076	
VA	0.000	0.000	0.473	0.605	0.000	0.000	0.076	0.110	
(b) H2 (λ	= 0.802)								
S	0.000	0.000	1.256	0.000	0.000	0.000	0.145	0.000	
J	0.825	0.431	0.000	0.000	0.145	0.168	0.000	0.000	
RA	0.000	0.085	0.330	0.335	0.000	0.145	0.161	0.086	
VA	0.000	0.000	0.242	0.343	0.000	0.000	0.086	0.065	
(c) H3 (λ =	= 1.371)								
S	0.000	0.000	9.859	0.000	0.000	0.000	0.264	0.000	
J	0.666	0.538	0.000	0.000	0.264	0.171	0.000	0.000	
RA	0.000	0.218	0.067	0.417	0.000	0.264	0.014	0.011	
VA	0.000	0.000	0.138	0.225	0.000	0.000	0.011	0.002	
(d) L1 (λ =	= 0.396)								
S	0.000	0.000	0.071	0.000	0.000	0.000	0.004	0.000	
J	0.003	0.395	0.000	0.000	0.004	0.982	0.000	0.000	
RA	0.000	0.446	0.106	0.500	0.000	0.004	0.002	0.002	
VA	0.000	0.000	0.064	0.125	0.000	0.000	0.002	0.001	
(e) L2 (λ =	= 1.230)								
S	0.000	0.000	115.444	0.000	0.000	0.000	0.459	0.000	
J	0.028	0.125	0.000	0.000	0.074	0.008	0.000	0.000	
RA	0.011	0.083	0.000	0.000	0.385	0.074	0.000	0.000	
VA	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
(f) L3 (λ =	1.395)								
S	0.000	0.000	26.762	0.000	0.000	0.000	0.476	0.000	
J	0.102	0.125	0.000	0.000	0.044	0.004	0.000	0.000	
RA	0.066	0.083	0.000	0.000	0.432	0.044	0.000	0.000	
VA	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	

Table 3. Transition matrices and elasticities for *Erysimum capitatum* transition elements in six populations. Developmental stages are:S = seedling, J = juvenile, RA = reproductive adult and VA = vegetative adult

Elasticity analysis indicated that all non-zero life-stage transitions contributed comparably to projected population growth rates in two high elevation, iteroparous populations (H1 and H2) (Table 3). At high elevation, survival at all stages, seedling recruitment, the transition to reproduction of nonreproductive plants, as well as the continued reproduction of adults all had elasticities between 0.141 and 0.168. Combined elasticities of pre-reproductive survival were 0.308-0.313. In contrast, in the low-elevation semelparous populations (L2 and L3), seedling recruitment had the highest elasticity, followed by the transition of seedlings (first-year plants) directly into reproductive plants in their second year. Unlike iteroparous populations, juvenile and adult survival contributed little to projected population growth rates of semelparous populations, with combined survival elasticities of only 0.082-0.048. Instead, seed and seedling survival followed by rapid reproduction was projected to lead to higher population growth rates. In sites with intermediate degrees of iteroparity (L1 and H3), demographic patterns differed greatly. In H3, as in iteroparous populations, many life-stage transitions contributed comparably to projected population growth. However, successive

reproduction contributed comparatively little, in contrast to truly iteroparous populations, because of high adult mortality. In L1, only juvenile survival contributed strongly to projected population growth, most likely because of high adult mortality and low seedling recruitment.

Projected population growth rate (λ) was greater than 1 in the low-elevation semelparous populations (L2 and L3), but close to or slightly smaller than 1 in the high-elevation iteroparous populations (H1 and H2) (Table 3). In the intermediate H3 population, λ was similar to those in semelparous populations. Projected population growth rate (λ) of the intermediate L1 population was far smaller than 1, reflective of the fact that the population declined during the study period, most likely due to high adult mortality and low seedling recruitment.

NATURAL VARIATION IN ONTOGENETIC TRAITS AND THEIR CORRELATION WITH ITEROPARITY

Developmental rates of juvenile plants differed across altitude in Regions 2 and 3 (Fig. 5a–c). Seedlings of the 2007 cohort



attained a larger size by the end of their first growing season at the L2 and L3 sites than at the H1 and H2 sites (leaf number of the apical rosette, F = 22.14, P < 0.001; Diameter of apical rosette, F = 56.90, P < 0.001). All plants of the 2007 cohort had a single apical rosette at the end of first growing season in all sites. Plants in the semelparous L2 and L3 populations also reproduced more quickly than those in other populations $(\chi^2 = 11.44, P < 0.001)$, with 24–35% of them initiating reproduction in their second year compared with no reproduction of second-year plants in the other populations. The H3 site with intermediate parity had seedlings that were intermediate in size between those of semelparous (L2 and L3) and iteroparous populations (H1 and H2). Faster development was associated with lower opportunity for iteroparity (post-reproductive survival) at the population level $[R^2(\text{leaf number of }$ rosette) = 0.80, P < 0.05; R^2 (diameter of apical rosette) = 0.84, P < 0.05].

Traits of reproductive plants also differed between highand low-elevation sites, and such variation was associated with the reproductive strategy of the populations (Fig. 5d–f). Reproductive plants in high-altitude sites had more, but smaller rosettes, allocated a smaller proportion of rosettes to reproduction, and produced more rosettes during reproduction. Like iteroparity, morphological traits of reproductive plants in

Fig. 5. Natural variation in seedling developmental rate (a-c) and morphological traits of reproductive plants (d-f). Morphological traits that were measured from the 2007 cohort are shown as an index of seedling developmental rate. Non-adjusted standard error is shown as bars. For seedling developmental rate, the L1 site is not shown since no germinant was found in 2007. F-ratios and χ^2 values are given for comparison of seedling development between habitats. Morphological traits of reproductive plants that were measured in 2005 are presented. F-ratios are given for comparison between habitats. See Table S4 for analysis of each region and year separately. (*)P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001.

the H3 and L1 sites were intermediate between semelparous (L2 and L3) and iteroparous populations (H1 and H2). Populations with higher mean post-reproductive survival (opportunity for iteroparity) had reproductive plants that had more ($R^2 = 0.84$, P < 0.05) but smaller rosettes ($R^2 = 0.62$, P < 0.1) at the beginning of reproduction, allocated a lower proportion of rosettes to reproduction ($R^2 = 0.91$, P < 0.01), and produced more rosettes during reproduction ($R^2 = 0.98$, P < 0.001). All reproductive plants except one in the semelparous populations (L2 and L3) allocated all rosettes to reproduction, while 83% did so in the intermediate populations (H3 and L1), and less than 17% plants did so in the iteroparous populations (H1 and H2). No correlation was detected between population mean fruit number per individual and post-reproductive survival ($R^2 = 0.14$, P > 0.1).

Results of logistic regression at the individual level within populations supported the significant associations between post-reproductive survival and morphological traits at the population level (Table 4). In addition, regression analysis showed that the multiple regression coefficient of the number of rosettes at the beginning of reproduction was non-significant, whereas its simple regression coefficient was significant. Since the number of rosettes at the beginning of reproduction was negatively correlated with the proportion of rosettes

Table 4. The association between morphological traits and post-reproductive survival at the individual level. Simple ('Total') and multiple ('Direct') logistic regression coefficients are also shown with their standard errors. The logistic regression model included year and population to control for yearly variation and population variation in the post-reproductive survival. Data collected from 2005 to 2007 were used. No significant interaction between population and trait was detected unless indicated

	Total	Direct
Log (rosette number at the beginning of reproduction)	0.56* (0.28)	-0.13 (0.49)
Log (leaf number per rosette at the beginning of reproduction)	0.17 (0.24)	0.49 (0.34)
Arcsine square root (proportion of rosettes allocated to reproduction)	-0.82** (0.27)	$-1.39^{**}(0.50)$
Log (number of rosettes produced during reproduction)	0.61*† (0.24)	0.89** (0.28)
Log (fruit number per individual)	-0.19 (0.21)	0.01 (0.27)

[†]Significant interaction with population.

(*)P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001.



Fig. 6. Size differences between vegetative and reproductive rosettes. Plants with both vegetative and reproductive rosettes in 2006, 2007 and 2008 were analysed. The comparison could not be conducted in semelparous populations (L2 and L3) since most reproductive plants did not have vegetative rosettes for comparison. (*)P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001.

allocated to reproduction (correlation coefficient = -0.86, P < 0.001), the association of the number of rosettes at the beginning of reproduction with post-reproductive survival is likely due to its effect on the proportion of rosettes allocated to reproduction. In contrast, the effects of the proportion of rosettes allocated to reproduction and the production of rosettes produced during reproduction remained significant after controlling for correlations among traits, suggesting they are likely two key predictors of iteroparity in *E. capitatum*.

In iteroparous and intermediate populations, not all rosettes of a reproductive individual were allocated to reproduction. The mean leaf number of vegetative rosettes was smaller than that of reproductive rosettes, suggesting that the transition of rosettes from vegetative to reproductive may depend on its size (Fig. 6).

Plants that produced more rosettes during reproduction had higher post-reproductive survival in intermediate populations (H3: regression coefficient = 1.40, SE = 0.66, P < 0.05; L1: regression coefficient = 0.91, SE = 0.35, P < 0.01) but not in completely iteroparous populations ($\chi^2 = 8.82$, P < 0.05)



Fig. 7. Soil water contents measured during growing season in 2007. Soil water content differed between high- and low-elevation sites (F = 72.25, P < 0.001), although soil water content of the L1 site was similar to high-elevation sites.

for Trait \times Population effect). Since 83% of the reproductive plants in intermediate populations allocated all rosettes to reproduction, and since rosettes that were allocated to reproduction degenerated during the reproductive period, the production of vegetative rosettes during reproduction is likely a key developmental mechanism for maintaining vegetative tissues.

Low-elevation sites were drier than high-elevation sites in Regions 2 and 3 (Fig. 7). The degree of iteroparity of a population was correlated with soil water content, especially that in August ($R^2 = 0.78$, P < 0.05) compared with June ($R^2 = 0.18$, P = 0.39) or July ($R^2 = 0.24$, P = 0.32).

Discussion

In *E. capitatum*, demography differed across altitude, as did life history, morphological and developmental traits. Lowelevation populations tended to be semelparous and highelevation populations iteroparous: some populations exhibited intermediate parity. With high mortality in low-elevation sites, selection for rapid growth to increase survival long enough to reproduce is likely to be extremely important for maintaining populations there. Some morphological traits, such as rosette production and rosette size, are associated with iteroparity, suggesting that selection on those traits may influence adult life-history expression. This life-history expression, in turn, is predicted to influence population growth and maintenance.

DEMOGRAPHIC DIFFERENCES ACROSS ALTITUDES AND THEIR RELATION TO LIFE HISTORY

In E. capitatum, adult life stages contributed more to projected population growth at high altitude than at lower altitude, but juvenile life stages had contributions that were comparable with those of adult life stages at high altitude. Juvenile plants constituted a relatively high proportion (10-80%) of the standing density in high-elevation sites, and the elasticity of their survival and reproductive maturation was comparable with the elasticity of adult plants. Even though stressful environmental conditions in the high-elevation habitat are often expected to cause low seedling recruitment as well as low plant survival at early life stages (Billings & Mooney 1968; Bliss 1971; Bingham & Orthner 1998), recent demographic studies have shown relatively high recruitment and survival of plants at early life stages (Chambers 1995; Forbis 2003; Forbis & Doak 2004; Venn & Morgan 2009). Moreover, elasticity of survival and growth of juvenile plants has been shown to be high in some alpine herbaceous plants, such as Artemisia genipi (Svensson et al. 1993; Marcante, Winkler & Erschbamer 2009). Seedling recruitment and survival of plants at early life stages seems to play an important role in maintaining the size of high-elevation populations in at least some plant species.

Mortality of seedlings and juvenile plants in low-elevation sites was significantly higher than in high-elevation sites. In addition, temporal variation in survival was significant, which is expected to increase the population extinction risk over the long term. A similar pattern has been observed in other temperate mountains (Rochow 1970; Giménez-Benavides, Escudero & Iriondo 2007; Venn & Morgan 2009). Climatic conditions at higher altitudes are predicted to become more similar to those at lower altitudes, and such changed climatic conditions in high-elevation habitats could substantially increase mortality of plants at early life stages. Given the high elasticity of pre-reproductive survival in high-elevation populations, changed climatic conditions could cause decreased population size as well as higher variation in population size at high elevations in the short term if the stage structure of the populations there remains similar to that observed in this study.

Iteroparity was more prevalent in high-elevation sites, and semelparity was more prevalent in low-elevation sites, implying that the demographic differences among populations discussed above are due to differential life histories. Survival of juvenile and adult plants and the continued reproduction of adult plants were the most critical life-cycle components with respect to projected growth rates of the iteroparous populations (H1 and H2). In contrast, seedling recruitment and early reproductive maturation of seedlings were the most critical components for semelparous populations (L2 and L3). Such contrasting elasticity between iteroparous and semelparous populations conforms to results from comparative studies among species (Silvertown *et al.* 1993). Therefore, changes in parity appear to have a profound effect on population demography.

The trajectory through which transitions between iteroparity and semelparity occur, however, is not known. Populations of intermediate parity, such as the H3 and L1 populations observed in this study, can be useful for examining possible transitional or intermediate states. Such intraspecific variation in iteroparity is not uncommon, especially in short-lived herbaceous plant species (Van Baalen & Prins 1983; Verkaar & Schenkeveld 1984; Hautekèete, Piquot & Van Dijk 2001). The elasticity patterns of these intermediate populations of E. capitatum differed from those of iteroparous and semelparous populations, but also differed greatly from each other. Even though the confidence interval of elasticity might be broad due to the small sample size used for the transition matrix, this result suggests that such intermediate populations have variable demographic properties, and that demographic trajectories of populations in transition between iteroparous and semelparous life histories are not easily predictable.

DEMOGRAPHIC FACTORS FAVOURING SEMELPARITY VERSUS ITEROPARITY

Life-history theories predict that the mean and/or the variance of age-specific survival influence the evolution of parity (Stearns 1992). Iteroparity has been hypothesized to be a bet-hedging strategy that distributes reproductive effort across years in a temporally variable environment although empirical support for this is poor (Schaffer & Rosenzweig 1977; Orzack & Tuljapurkar 1989). Similarly, this study provides no support for this hypothesis since significant temporal variation in reproductive output was not detected at sites with a high degree of iteroparity, and iteroparous populations exhibited higher survival at all life stages than did semelparous populations.

Models suggest that semelparity is more likely to evolve in environments in which population growth rate is high and/or adult survival is low relative to juvenile survival (Charnov & Schaffer 1973; Young 1981). The high λ values of the L2 and L3 populations, and even of the H3 population, are consistent with the high occurrence of semelparity in those populations although the confidence interval of λ might be broad due to the small sample size used for the transition matrix. The low λ of L1 is not consistent with the prevalence of semelparity there, despite some iteroparity. While the high adult mortality observed at low elevation is consistent with theoretical expectation, the high post-reproductive mortality in these semelparous populations could be due to external environmental factors, internal physiological factors, or both. The results from this experiment therefore could not test this theoretical prediction. However, when plants were grown in benign greenhouse conditions, 40–50% of the reproductive plants from semelparous populations survived after reproduction (E. Kim & K. Donohue, unpubl. data), suggesting that sites with semelparity Semelparous *E. capitatum* populations experienced lower soil moisture during the summer. Notably, the soil water availability was positively associated with the degree of post-reproductive survival in the population. A similar pattern was reported in *Lobelia* species (Young 1984), suggesting that low soil water availability may produce demographic conditions (low adult survival) that favour semelparity or may impose selection on traits (such as rosette size or number, see below) that promote semelparity. More study is required to test this hypothesis.

The faster growth and earlier reproduction of plants in semelparous populations of *E. capitatum*, compared with those in iteroparous populations, is consistent with the 'fast-slow continuum' hypothesis that is based on similar patterns observed in other species (Franco & Silvertown 1996; Bielby *et al.* 2007). According to this hypothesis, differential adult survival is the causal factor of such correlations among life-history traits; low adult survival selects for faster growth, accelerated reproduction and high reproductive investment in a single reproductive episode. Thus, as adult mortality increases, a suite of life-history traits associated with semelparity is expected to evolve.

Without experimental transplants, it is not possible to determine the degree to which semelparity in E. capitatum reflects the predicted suite of trait covariation and the degree to which it is imposed by extrinsic mortality or by intrinsic monocarpic scenescence. Semelparity is often defined as a programmed process of high fecundity followed by post-reproductive scenescence (Hautekèete, Piquot & Van Dijk 2001). Post-reproductive survival of 'semelparous' populations was higher under benign greenhouse environments than in the field, as mentioned above, yet post-reproductive senescence was still higher in semelparous populations (E. Kim, unpubl. data). These results suggest that both intrinsic and extrinsic factors increase post-reproductive mortality in semelparous populations. In addition, high reproductive output per reproductive episode is a characteristic trait of semelparous plants, yet fruit number per plant did not differ between high- and low-elevation populations in this study. However, environmental quality may have been poorer at low elevation and/or fruit production may increase with plant age; relative reproductive output of semelparous versus iteroparous plants with similar age needs to be determined in a common environment in order to draw conclusions concerning whether reproductive allocation differs among these populations. Thus, it remains unclear the extent to which some low-elevation populations of E. capitatum have evolved a complete semelparous syndrome, despite exhibiting functional semelparity in the field.

THE DEVELOPMENTAL AND MORPHOLOGICAL BASIS OF ITEROPARITY

Iteroparity depends on whether plants have a developmental mechanism for renewed vegetative growth after reproduction (Townsend *et al.* 2006). In *E. capitatum*, iteroparous plants

had multiple rosettes at the beginning of reproduction and allocated only a subset of those rosettes to reproduction. Rosettes with inflorescences from their apical meristems invariably degenerated during the reproductive period, but those without inflorescences maintained viable leaves. In addition, iteroparous plants continued to produce vegetative rosettes during the reproductive period. Thus the production of rosettes and the maintenance of rosettes in a vegetative state are key developmental mechanisms of iteroparity in this species. Such a developmental pattern of rosette production has been reported in many other iteroparous rosette plants (Verkaar & Schenkeveld 1984; Silvertown 1989; Young & Augspurger 1991; Wang *et al.* 2009).

In many plants, rosettes require a period of cold temperature in order to initiate reproduction, a process called 'vernalization', and rosette sensitivity to vernalization is associated with life-history variation in diverse plants. Erysimum capitatum responds to vernalization (E. Kim & K. Donohue, unpubl. data), and it receives winter vernalization across its elevational ranges, so vernalization likely regulates rosette transitions to the reproductive state. Iteroparous E. capitatum seems to have mechanisms that prevent rosettes from becoming reproductive after vernalization. First, not all rosettes that were present before reproduction - and therefore experienced vernalization over the winter - became reproductive, especially the smaller rosettes. In some plant species, the size or developmental state of rosettes influences its 'competence' to respond to environmental stimuli for reproduction, such as vernalization (Wesselingh et al. 1997; Rees et al. 1999; Searle et al. 2006) while the physiological and genetic mechanisms that regulate 'competence' to respond to vernalization is not known. In iteroparous E. capitatum, rosettes that did become reproductive were larger than those that did not, suggesting that the competence for a rosette to become reproductive depends on its size. Alternatively, size may be correlated with some other factors, such as developmental or physiological state, or growth rate itself, which governs the competence of a rosette (Young 1985).

Secondly, rosettes that are produced during the reproductive period do not receive vernalization, and they may require vernalization in order to flower. In many semelparous plants, such as Arabidopsis thaliana, all rosettes that are produced after vernalization of the plant become reproductive, even if the rosettes themselves did not experience vernalization because they were produced after the plant was vernalized. In contrast, iteroparous plants like Arabis alpina keep rosettes that are produced after vernalization in a vegetative state. It is suggested that differential expression of the floral repressor, Flowering Locus C (FLC) or its analogue PEP1, may induce such a different transition of rosettes to reproduction in response to vernalization (Grbić & Bleecker 1996; Wang et al. 2009). In A. thaliana, vernalization represses FLC irreversibly, which induces newly produced rosettes after reproduction to become reproductive. In contrast, in A. alpina, while vernalization represses PEP1, enabling the rosettes that experienced vernalization to flower, PEP1 becomes active again during the growing season, preventing newly produced rosettes from becoming reproductive. Expression studies of FLC or its analogue in

1248 E. Kim & K. Donohue

E. capitatum can reveal whether its expression also plays an important role in iteroparity.

In summary, the iteroparous life history in *E. capitatum* appears to be enabled by the ability of new rosettes not to be induced to flower immediately even if the plant experienced vernalization, and a decreased sensitivity of some rosettes to respond to vernalization, possibly due to a size effect on rosette competence to respond to chilling.

Conclusions and future directions

In conclusion, altitudinal variation exists in developmental morphology, which is associated with variation in life history. Populations with different life histories, moreover, also exhibited different population demography. Thus, if selection and mortality at high altitude become more similar to those at lower altitude, populations are expected to suffer greater mortality, a semelparous life history is likely to be favoured, and viable populations are expected to depend heavily on early survival and rapid reproduction.

Among traits correlated with iteroparity, some pre-requisites for iteroparity are expressed at the juvenile stage – such as the production and growth of rosettes. Future studies that measure natural selection on such juvenile traits would provide insight into the evolution of life-history differences across altitude.

While this study documented morphological, developmental and life-history differences among populations growing at different altitudes, it was not able to determine whether those differences were due to phenotypic plasticity or genetic adaptation. If the observed variation reflects past adaptive genetic differentiation, rapid climate change is likely to have detrimental effects on the persistence of alpine populations since genetic adaptation to changed environmental conditions will likely be slow compared with the rate of climate change. Plastic responses, in contrast, will occur more quickly, and if adaptive, they can increase population performance in the face of environmental change (Baldwin 1896; Bradshaw, Caspari & Thoday 1965; Sultan 1987; West-Eberhard 1989; Schlichting & Pigliucci 1998). Thus a priority in predicting plant responses to environmental change is to distinguish between genetic and plastic responses and to evaluate the adaptive value of those responses.

Acknowledgements

We are grateful to N. Pierce and K. Jones for their comments throughout this experiment. We thank H. Hyun for her wonderful help in the field, W. Bowman at the University of Colorado Mountain Research Center, S.J. Popovich at the USDA Forest Service, C. Wanner at Boulder Co. Parks and Open Space, Jefferson County Open Space, and C. Dawson at the Bureau of Land Management in Gunnison Co. for their warm support in getting research permits. We also thank two anonymous referees for proving valuable comments on a previous version of the manuscript. We are grateful to T. Kim and K. Kang for their financial support. Funding was provided by the Department of Organismic and Evolutionary Biology at Harvard University.

References

Baldwin, J.M. (1896) A new factor in evolution. American Naturalist, 30, 441– 451.

- Bielby, J., Mace, G.M., Bininda-Emonds, O.R.P., Cardillo, M., Gittleman, J.L., Jones, K.E., Orme, C.D.L. & Purvis, A. (2007) The fast-slow continuum in mammalian life history: an empirical reevaluation. *American Naturalist*, 169, 748–757.
- Billings, W.D. & Mooney, H.A. (1968) The ecology of arctic and alpine plants. *Biological Reviews*, 43, 481–592.
- Bingham, R.A. & Orthner, A.R. (1998) Efficient pollination of alpine plants. *Nature*, 391, 238–239.
- Bliss, L.C. (1971) Artic and alpine plant life cycles. Annual Review of Ecology and Systematics, 2, 405–438.
- Bradshaw, A.D., Caspari, E.W. & Thoday, J.M. (1965) Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics, 13, 115–155.
- Caswell, H. (2001) *Matrix Population Models*. Sinauer Associates Inc., MA, USA.
- Chambers, J.C. (1995) Disturbance, life history strategies, and seed fates in alpine herbfield communities. *American Journal of Botany*, 82, 421–433.
- Charnov, E.L. & Schaffer, W.M. (1973) Life-history consequences of natural selection: Cole's result revisited. *The American Naturalist*, **107**, 791–793.
- Diaz, H.F. & Eischeid, J.K. (2007) Disappearing "alpine tundra" Köppen climatic type in the western United States. *Geophysical Research Letters*, 34, L18707–L18711.
- Dunne, J.A., Saleska, S.R., Fischer, M.L. & Harte, J. (2004) Integrating experimental and gradient methods in ecological climate change research. *Ecology*, 85, 904–916.
- Etterson, J.R. (2004) Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. I. Clinal patterns of selection along an environmental gradient in the Great Plains. *Evolution*, 58, 1446–1458.
- Forbis, T.A. (2003) Seedling demography in an alpine ecosystem. American Journal of Botany, 90, 1197–1206.
- Forbis, T.A. & Doak, D.F. (2004) Seedling establishment and life history trade-offs in alpine plants. *American Journal of Botany*, 91, 1147–1153.
- Franco, M. & Silvertown, J. (1996) Life history variation in plants: an exploration of the fast-slow continuum hypothesis. *Philosophical Transactions: Biological Sciences*, 351, 1341–1348.
- Giménez-Benavides, L., Escudero, A. & Iriondo, J.M. (2007) Local adaptation enhances seedling recruitment along an altitudinal gradient in a high mountain Mediterranean plant. *Annals of Botany*, **99**, 723–734.
- Gomulkiewicz, R. & Holt, R.D. (1995) When does evolution by natural selection prevent extinction? *Evolution*, 49, 201–207.
- Grbić, V. & Bleecker, A.B. (1996) An altered body plan is conferred on Arabidopsis plants carrying dominant alleles of two genes. *Development*, **122**, 2395– 2403.
- Hautekèete, N.C., Piquot, Y. & Van Dijk, H. (2001) Investment in survival and reproduction along a semelparity-iteroparity gradient in the *Beta* species complex. *Journal of Evolutionary Biology*, 14, 795–804.
- Hautier, Y., Randin, C.F., Stocklin, J. & Guisan, A. (2009) Changes in reproductive investment with altitude in an alpine plant. *Journal of Plant Ecology*, 2, 125–134.
- Kalisz, S. & McPeek, M.A. (1992) Demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. *Ecology*, 73, 1082–1093.
- Körner, C. (2003) Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. Springer-Verlad, Berlin, Germany.
- Lambrecht, S.C., Loik, M.E., Inouye, D.W. & Harte, J. (2007) Reproductive and physiological responses to simulated climate warming for four subalpine species. *New Phytologist*, **173**, 121–134.
- Marcante, S., Winkler, E. & Erschbamer, B. (2009) Population dynamics along a primary succession gradient: do alpine species fit into demographic succession theory? *Annals of Botany*, **103**, 1129–1143.
- Milla, R., Giménez-Benavides, L., Escudero, A. & Reich, P.B. (2009) Intraand interspecific performance in growth and reproduction increase with altitude: a case study with two *Saxifraga* species from northern Spain. *Functional Ecology*, 23, 111–118.
- Morris, W.F. & Doak, D.F. (2002) *Quantitative Conservation Biology*. Sinauer Associates Inc., MA, USA.
- Orzack, S.H. & Tuljapurkar, S. (1989) Population dynamics in variable environments VII. The demography and evolution of iteroparity. *American Naturalist*, 133, 901–923.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics, 37, 637–669.
- Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J. & Hanson, C.E. (2007) Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007. Cambridge University Press, New York, USA.

- Price, R.A. (1987) Systematics of the Erysimum capitatum alliance (Brassicaceae) in North America. PhD Thesis, University of California, Berkeley.
- Rees, M., Sheppard, A., Briese, D. & Mangel, M. (1999) Evolution of sizedependent flowering in *Onopordum illyricum*: a quantitative assessment of the role of stochastic selection pressures. *The American Naturalist*, **154**, 628– 651.
- Reusch, T.B.H. & Wood, T.E. (2007) Molecular ecology of global change. *Molecular Ecology*, 16, 3973–3992.
- Ricklefs, R.E. & Wikelski, M. (2002) The physiology/life history nexus. Trends in Ecology and Evolution, 17, 462–468.
- Rochow, T.F. (1970) Ecological investigations of *Thlaspi alpestre* L. along an elevational gradient in the central rocky mountains. *Ecology*, **51**, 649–656.
- Rollins, R.C. (1993) The Cruciferae of Continental North America: Systematics of the Mustard Family from the Arctic to Panama. Stanford University Press, CA, USA.
- Saccheri, I. & Hanski, I. (2006) Natural selection and population dynamics. *Trends in Ecology and Evolution*, 21, 341–347.
- Schaffer, W.M. & Rosenzweig, M.L. (1977) Selection for optimal life histories. II: multiple equilibria and the evolution of alternative reproductive strategies. *Ecology*, 58, 60–72.
- Schlichting, C. & Pigliucci, M. (1998). Phenotypic Evolution: A Reaction Norm Perspective. Sinauer, Sunderland, USA.
- Searle, I., He, Y., Turck, F., Vincent, C., Fornara, F., Kröber, S., Amasino, R.A. & Coupland, G. (2006) The transcription factor FLC confers a flowering response to vernalization by repressing meristem competence and systemic signaling in *Arabidopsis. Genes & Development*, 20, 898–912.
- Silvertown, J. (1989) A binary classification of plant life history and some possibilities for its evolutionary application. *Evolutionary Trends in Plants*, 3, 87– 90.
- Silvertown, J.W., Franco, M., Pisanty, I. & Mendoza, A. (1993) Comparative plant demography – relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology*, 81, 465–476.
- Stearns, S.C. (1992) The Evolution of Life Histories. Oxford University Press, Oxford, UK.
- Stokes, M.E., Davis, C.S. & Koch, G.G. (2000) Categorical Data Analysis using the SAS System. SAS Institute Inc., NC, USA.
- Sultan, S.E. (1987) Evolutionary implications of phenotypic plasticity in plants. Evolutionary Biology, 21, 127–178.
- Svensson, B.M., Carlsson, B.A., Karlsson, P.S. & Nordell, K.O. (1993) Comparative long-term demography of three species of *Pinguicula*. *Journal of Ecology*, 81, 635–645.
- Theurillat, J.-P. & Guisan, A. (2001) Potential impact of climate change on vegetation in the European Alps: a review. *Climate Change*, **50**, 77–109.
- Townsend, T., Albani, M., Wilkinson, M., Coupland, G. & Battey, N. (2006) The diversity and significance of flowering in perennials. *Flowering and its Manipulation* (ed. C. Ainsworth), pp. 181–199. Wiley-Blackwell, Sheffield, UK.
- Van Baalen, J. & Prins, E.G.M. (1983) Growth and reproduction of *Digitalis purpurea* in different stages of succession. *Oecologia*, 58, 84–91.
- Venn, S.E. & Morgan, J.W. (2009) Patterns in alpine seedling emergence and establishment across a stress gradient of mountain summits in south-eastern Australia. *Plant Ecology and Diversity*, 2, 5–16.
- Verkaar, H.J. & Schenkeveld, A.J. (1984) On the ecology of short-lived forbs in chalk grasslands: semelparity and seed output of some species in relation to various levels of nutrient supply. *New Phytologist*, **98**, 673–682.
- Walther, G.-R. (2003) Plants in a warmer world. Perspectives in Plant Ecology, Evolution and Systematics, 6, 169–185.

Altitudinal variation in the life history of a mustard 1249

- Wang, R., Farrona, S., Vincent, C., Joecker, A., Schoof, H., Turck, F., Alonso-Blanco, C., Coupland, G. & Albani, M.C. (2009) PEP1 regulates perennial flowering in *Arabis alpina. Nature*, 459, 423–427.
- Wesselingh, R.A., Klinkhamer, P.G.L., de Jong, T.J. & Boorman, L.A. (1997) Threshold size for flowering in different habitats: effects of size-dependent growth and survival. *Ecology*, **78**, 2118–2132.
- West-Eberhard, M.J. (1989) Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics, 20, 249–278.
- Young, T.P. (1981) A general model of comparative fecundity for semelparous and iteroparous life histories. *American Naturalist*, 118, 27–36.
- Young, T.P. (1984) The Comparative demography of semelparous Lobelia telekii and iteroparous Lobelia keniensis on Mount Kenya. Journal of Ecology, 72, 637–650.
- Young, T.P. (1985) Lobelia telekii herbivory, mortality, and size at reproduction: variation with growth rate. Ecology, 66, 1879–1883.
- Young, T.P. & Augspurger, C.K. (1991) Ecology and evolution of long-lived semelparous plants. *Trends in Ecology and Evolution*, 6, 285–289.

Received 28 June 2010; accepted 17 February 2011 Handling Editor: Mark Rees

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Number of plants censused during study years.

 Table S2. Variation in (natural log-transformed) density of different life stages.

Table S3. Variation in survival and reproduction.

 Table S4. Morphological differences of reproductive plants between habitats and across regions.

Figure S1. Life-stage structure of each population for all years of observation. Statistical analyses are given in Table 2.

Figure S2. Survival probabilities of seedlings, juveniles and adults, and survival curves of 2006 and 2007 cohorts.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.