Contrasting population dynamics in the boreo-alpine *Silene acaulis* (Caryophyllaceae) at its southern distribution limit

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Classical theory predicts a high demographic vulnerability and diminished performance of peripheral plant populations, but recent studies highlight the fact that environmental factors may override that geographical pattern. In this study, we compare the density, population structure and population dynamics of the boreo-alpine *Silene acaulis* (Caryophyllaceae) in two locations at its southern European distribution limit, using matrix projection models. One population was close to the species' lower altitudinal limit, and thus exposed to more ecologically marginal conditions (higher intraspecific competition and temperature) than the population higher up. The low-altitude population was sparser and its members were older as a result of lower recruitment and survival of new individuals. Additionally, this population's growth rate was lower, mainly due to a shorter permanence of large plants. The contrasting demographic differences between two closely located, southern peripheral populations highlight the importance of distinguishing between geographical periphery and ecological marginality.

Introduction

Peripheral populations are characterized by singular genetic diversity (Safriel *et al.* 1994, Thompson *et al.* 2010), as a consequence of isolation and adaptation to different environmental conditions relative to those in central

areas of species' ranges. Such isolated location and exposure to extreme environments are also supposed to lead to a higher demographic vulnerability (Lesica & Allendorf 1995). The abundance-center model, for example, predicts a decrease in the abundance of populations from the distribution center towards the peripheries due to harsher local conditions in the latter locations (Hengeveld & Haeck 1982, Brown 1984). Similarly, it has traditionally been accepted that peripheral populations are more demographically variable and less reproductively successful than the central ones (Dorken & Eckert 2001, Jump & Woodward 2003, Guo et al. 2005). Overall, these differences in conditions and population behavior can lead to aging of peripheral populations (García et al. 2000, Dorken & Eckert 2001). However, recent reviews have not found clear patterns across ranges in abundance (Sagarin & Gaines 2002, Sexton et al. 2009, Abeli et al. 2013), and an increasing body of evidence shows that, as compared with core populations, similar or even higher reproductive success (García et al. 2010), recruitment (Yakimowski & Eckert 2007, Villellas et al. 2013), survival (Kluth & Bruelheide 2005), individual plant growth (Doak & Morris 2010), and overall population growth rates (Doak & Morris 2010, García et al. 2010, Villellas et al. 2013) are also possible in peripheral populations. Thus, classical theoretical expectations should not be taken for granted when analyzing demographic differences throughout ranges.

Several factors may help to understand inconsistent trends in population performance across species distributions. A possible explanation could be that towards the distribution edges conditions become disadvantageous to certain species' features while promoting other features, a phenomenon known as demographic compensation (Doak & Morris 2010). Originally found at continental scales, demographic compensation among populations is also common at smaller, local scales (García-Camacho et al. 2012, Villellas et al. 2015). On the other hand, most central vs. peripheral population studies were carried out along purely geographical gradients, without taking into account that not all geographically peripheral populations are also ecologically marginal, and vice versa (Soulé 1973). While geographical location can have a strong influence on genetic patterns across species ranges through meta-population dynamics (Eckert et al. 2008), fitness components such as individual vital rates (e.g., survival and reproduction) and population-growth rates are more likely to

respond to local environmental conditions. Some authors have adopted this view and analyzed central vs. marginal patterns by focusing on ecological gradients determined by changes in habitat or altitude (Grant & Antonovics 1978, Herrera & Bazaga 2008). There is indeed recent evidence of discrepancies in plant responses to central-peripheral gradients when analyzed from geographic vs. ecological points of views (Gerst et al. 2011, Martínez-Meyer et al. 2012, Pironon et al. 2015). Considering differences in environmental conditions, rather than only focusing on the relative position of populations within the range, will thus provide a better insight into the patterns of intraspecific variation in population dynamics.

Alpine plants, often exposed to steep altitudinal and environmental gradients in relatively small areas, provide the opportunity to analyze variation in population performance along central-peripheral environmental gradients. Indeed, many studies have analyzed the effects of altitude on life history traits and population dynamics (e.g., Neuffer & Bartelheim 1989, Kelly 1998, Jonas & Geber 1999, Angert 2009). Information on alpine-plant performance is of high interest, considering the strong effects that climatic warming and land-use change may have on these species (Engler et al. 2011, Pauli et al. 2012). Several studies carried out at the southern edge of mountain plants' distributions have shown a trend for population decline at the lowest part of their altitudinal range (Jump et al. 2006, Giménez-Benavides et al. 2011, Matías & Jump 2015). However, these edge populations have a long history of persistence and adaptations (as opposed to younger populations in more northern latitudes; Hewitt 2000, Hampe & Petit 2005), and deserve special attention due to their potential evolutionary role in the context of changing environmental conditions.

Here, we study the population dynamics of the boreo-alpine plant *Silene acaulis* at the southern edge of its distribution. The demographic performance of this cushion-forming species has been studied in detail across North America (Doak & Morris 2010), but it remains largely unknown in Europe. In our study, we analyzed and compared the density, demographic structure of populations, and dynamics of S. acaulis in the Pyrenees, at the southern edge of the species' European distribution. To analyze its demographic variability at a regional scale, we studied the plant at two altitudes differing in ecological conditions. The high location - a rocky area subject to relatively low interspecific competition — represented ecological conditions typical for many populations of the species at northern latitudes. The other location, close to the low altitudinal limit, is characterized by conditions which are less favorable (e.g., higher temperatures and intensive interspecific competition). With such comparative analyses, we aimed to broaden our knowledge of the demographic performance of alpine plants at the edges of their geographic ranges, and to test whether ecological conditions typical to the edges of distribution lead to lower densities and population performance in S. acaulis.

Material and methods

Species and study area

Silene acaulis (Caryophyllaceae; "moss campion") is a long-lived perennial plant that forms cushions composed of small rosettes of triangular leaves. The species is gynodioecious, with female and hermaphrodite individuals. In our study, however, we did not consider the two reproductive forms separately, because they have been found not to differ in their survival and growth (Morris & Doak 1998, 2005). This species, typical to alpine and arctic-tundra habitats, is a good colonizer but cannot withstand intense competition from other taxa (Griggs 1956, Benedict 1989, Gehring & Delph 1999). According to some studies, S. acaulis facilitates establishment of other taxa in harsh environments (Antonsson et al. 2009). Silene acaulis occurs throughout the northern hemisphere (Jones & Richards 1962), and has its southern distribution limit in high mountain ranges such as the Pyrenees and the Apennines in Europe, and the southern Rocky Mountains in North America.

Our study was carried out at the species' southwestern limit in Europe, in the Ordesa

Fig. 1. (A) Distribution of Silene acaulis in Europe (in green, based on Jones & Richards 1962); the location of the two study populations, in the Ordesa and Monte Perdido National Park in the Pyrenees, is marked with a black dot (image produced with ModestR; García-Rosello et al. 2013). (B) Mean monthly temperatures in the populations (measured with data-loggers placed above ground at the level of plants; temperature was not recorded in August).

and Monte Perdido National Park (central Pyrenees in Spain; Fig. 1A). The alpine zone of the National Park has a mean annual temperature of 5.1 °C (range = 3.6-6.1 °C) and a mean annual precipitation of 1676 mm (range = 1103-2506 mm; climatic data for the period 1982-2012 from the meteorological station in Góriz, 2160 m a.s.l.). As many mountains worldwide, in the last decades the area experienced a significant increase in the mean annual temperature (in the Pyrenees, on average 0.3 °C per decade between 1950 and 2006; Lopez-Moreno et al. 2010). Our study was conducted in the years 2010 and 2011, and the mean annual temperature (5.1 °C) and precipitation (1358 mm) in that period were more or less representative of the current climate of the region. An important characteristic of the study area is that in the last five decades in addition to low overall anthropogenic influence due to legal restrictions, also livestock pressure decreased considerably resulting in an increase in vegetation biomass and in compe-



tition among species (García-Ruiz et al. 1996, Lasanta-Martínez et al. 2005).

Monitoring and characterization of populations

The altitudinal range of S. acaulis in the Pyrenees extends from ca. 1400 m a.s.l. to the highest elevations at 3300 m (Atlas of the Pyrenean flora: http://www.atlasflorapyrenaea.org/florapyrenaea/index.jsp). For this study, we monitored two populations located on the same mountain range: one at high altitude (2700 m a.s.l.; location: 42°40′20′′N, 0°01′14′′E; hereafter population H) and other closer to the species' low altitudinal limit (1950 m a.s.l.; location: 42°36'32''N, 0°02'01''E; hereafter population L). The distance between the two populations is less than 10 km (Fig. 1), which makes the altitude (and the underlying ecological and climatic differences) the key factor in the study. Population H is larger (thousands of individuals), and grows in stone crevices and areas with poorly developed soils and low vegetation cover, common conditions across the species' distribution area in northern Europe and North America (Jones & Richards 1962, Morris & Doak 2005). Thus, this population can be considered central from an ecological perspective. In contrast, population L comprises only hundreds of individuals and occurs in ecologically unfavorable conditions: grassland with deeper soil and much higher interspecific competition.

Data were collected between late July and early August (the period when S. acaulis fruits ripen) of 2010 and 2011. A total of 86 permanent, 1-m² plots arranged along transects were established. There were 36 plots in population H and 50 in L. The transects (4 in H and 6 in L) were randomly placed within an area of ca. 0.5 ha in each population, ensuring a good representation of environmental variability. Plants occurring within the plots were individually marked with toothpicks and plotted on gridded maps to replicate the real cushion areas. Plant sizes were later digitally calculated from the scanned maps using the ImageJ software (http://rsb.info.nih. gov/ij/). Photographs were not useful for plant size estimation in population L due to the presence of other plants, which covered significant parts of the S. acaulis cushions. A total of 544 individuals (368 in H and 176 in L) were monitored to estimate plant survival and growth. In order to estimate recruitment, we identified in the first year the individuals that produced fruit (reproductive plants). In the second year, a subset of those reproductive plants (19 in H, 32 in L) were randomly chosen as "focal plants"; their seedlings were carefully searched for in the nearest 10 cm-wide belt outside the perimeter of each focal plant, which served to calculate the average number of descendants produced per reproductive plant. This method assumes that new recruits come from the nearest reproductive plant, because S. acaulis has no adaptations to biotic or long-distance dispersal (Jones & Richards 1962; see also Doak & Morris 2010). Seed bank was not considered in our study, because it has been shown that only a small percentage of seeds remain alive for two years (Morris & Doak 2005). Finally, we estimated the density of S. acaulis individuals in the populations by dividing the total number of plants by the total area of the plots.

We measured temperature and interspecific competition to characterize abiotic and biotic conditions in both populations. Temperature was measured every four hours throughout the year with one iButton data-logger per population, situated above ground at the level of plants (data from August were absent due to errors in data logging). Interspecific competition was quantified visually, by estimating the percentage of vegetation cover other than *S. acaulis* in each plot (four categories: 0%-25%, 25%-50%, 50%-75%, and 75%-100%). Differences in vegetation cover between the two populations were tested with a two-sample Wilcoxon test (*wilcox. test* function of the *stats* package in R).

Analyses of plant performance and projection matrices

In a preliminary analysis, we studied the relationship between plant size and plant survival and reproduction with Generalized Linear Models (GLM; binomial distribution), including population as a factor, and found significant effects



Fig. 2. (A) Life-cycle graph and (B) transition matrix of *Silene acaulis*. In **A**, nodes correspond to size classes and arrows indicate transitions among them (dashed lines correspond to shrinkage transitions between non-consecutive classes). Matrix elements represent the transition from stages in year *t* (second number in subscript) to stages in year *t* + 1 (first number in subscript). Each matrix value shows the probability of an average plant in a given class to move to a different class (growth or shrinkage) or remain in the same one (stasis). In **B**, the matrix elements in the first row also include recruitment, i.e. the new recruits (1-year seedlings) estimated to be produced from each size class, according to the proportion of reproductive plants in each size class and the average number of seedlings found around reproductive plants. S = stasis, G = growth, K = shrinkage, F = recruitment.

(survival: Z = 2.75, p = 0.006; reproduction: Z =4.61, p < 0.001). Hence, to evaluate the effect of plant size on the performance of S. acaulis individuals, the plants were assigned to the following plant-size (x) classes for the matrix analyses (Fig. 2): (1) $x < 4 \text{ cm}^2$, (2) $4 \le x < 17.5 \text{ cm}^2$, (3) $17.5 \le x < 35.5 \text{ cm}^2$, (4) $35.5 \le x < 66 \text{ cm}^2$, (5) $66 \le x < 140 \text{ cm}^2$, and (6) $x \ge 140 \text{ cm}^2$. The class limits were established so as to have enough classes to detect among-class transitions, but also to keep the number of classes at a minimum for easier detection of among-class transitions, but also to avoid having too few individuals in a size class for reliable estimates of performance. We calculated annual transition probabilities among the different classes (stasis, growth, shrinkage and recruitment) (Fig. 2A), and we constructed Lefkovitch matrices (Caswell 2001) for each population between 2010 and 2011 (Fig. 2B).

We obtained various demographic parameters from the population matrices. To investigate the population structure, we calculated the projected stable-stage distribution, which is the abundance of individuals in each class whose vital rates do not change in time (Caswell 2001). The stable stage distribution was compared with the observed distribution by means of a χ^2 -test, in order to explore to what extent past ecological conditions (responsible of the observed structure) resemble the conditions observed in the study period (used to calculate the projected stable structure). Another output of the matrix analyses was the deterministic population growth rate (λ) , which corresponds to the matrix dominant eigenvalue and provides an overall assessment of the population dynamics. The closer λ is to 1, the more stable the population dynamics is, while the values of λ above or below 1 indicate that the population is growing or shrinking, respectively. We also obtained the elasticity matrix, which indicates the theoretical relative importance of each matrix element for λ (de Kroon *et al.* 1986). It is a proportional measure of sensitivity of λ to changes in matrix elements, and the total sum of elasticities for all matrix elements equals 1. Finally, to study the contribution of each demographic process to the actual differences found in population growth rates, we used a retrospective analysis: the life table response experiment (LTRE) of fixed design (Caswell 2001). This analysis takes into account (1) the differences between populations in the values of the matrix elements, and (2) the sensitivity of λ to changes in the matrix elements. Matrix analyses were performed with PopTools ver. 3.2.3. (http://www.poptools.org/), but the LTRE analysis was performed with R (package popbio, R Development Core Team



Fig. 3. Observed Stage Distribution for the two study populations of *Silene acaulis* in the Ordesa and Monte Perdido National Park (Pyrenees, Spain), and Stable Stage Distribution according to deterministic models (*see* Material and methods for further details).

(2011); sensitivities were calculated on the mean matrix).

Results

Environmental conditions and population structure

Mean annual temperatures were 1.2 °C and 5.9 °C in populations H and L, respectively. The difference in mean monthly temperature for the studied populations was on average 4.6 °C (SD = 2.6), and was greater in the warmest months (Fig. 1). Vegetation cover was significantly greater in population L than in H (two-sample Wilcoxon test: W = 72, n = 86, p < 0.001): in 94% of the plots in L, the vegetation cover was higher than 50%; whereas in H, the vegetation cover in 92% of the plots was smaller than 50%.

The density of S. acaulis individuals in the monitored plots was ca. 6 times higher in H (33.2 indiv. m^{-2}) than in L (5.3 indiv. m^{-2}). Regarding population structure, large differences were found between the two populations (Fig. 3): H was dominated by small individuals (89% in classes 1 and 2), whereas in L more than half of the individuals belonged to classes 3-6. The stable-stage structure showed a similar pattern (Fig. 3): a higher proportion of small individuals in H than in L. There were no significant differences between observed and expected structures for any population (H: $\chi^2 = 8.87$, p = 0.11; L: $\chi^2 = 2.75, p = 0.73$, indicating that our study year would be representative of the overall period that shaped the observed population structures.

Population dynamics

In smaller size classes, survival of individuals was higher in H than in L, while survival of large classes was very high in both populations (Table 1). Recruitment and stasis were also higher in H, and shrinkage was more frequent in L. Individual plant growth was higher in L in the smallest class, but higher in H in larger classes. Annual population growth rates indicated that H was growing at a rate of 10.9% ($\lambda = 1.109$) whereas L was suffering a sharp decline of 16.9% ($\lambda = 0.831$).

In the prospective analysis, elasticity revealed that stasis, particularly in the largest class, is the process with the highest potential capacity of modifying λ in both populations, whereas recruitment and shrinkage had in general the lowest values (Table 1). In L, transitions among and within the two largest classes (5 and 6; stasis, growth and shrinkage) accounted for more than half of the total elasticity. In H, however, the greatest elasticity values were more widespread along the matrix diagonal elements (stasis) and growth of class 1, and classes 1 and 6 had the highest sum of elasticities across rates. The retrospective LTRE analysis showed that the differences in population growth rates between the two sites were mainly due to differences in the probability of stasis and shrinkage of class 6, and stasis and growth of class 1, although stasis and growth in other classes had also moderate contributions to differences between populations (Fig. 4). Most rates had a negative contribution to population growth rate in L, although the higher probability of growth from class 1 to 2

in L than in H (Table 1) led to a high positive contribution.

Discussion

Silene acaulis in the Pyrenees had some characteristics typical of long-lived boreo-alpine plants, such as low recruitment rates and high survival of large individuals (Morris & Doak 1998, Forbis & Doak 2004). However, despite their close proximity to the species' southern range limit, the two studied populations differed in structure and dynamics, probably due to the contrasting ecological conditions. Plants in the low-altitude population were exposed to e.g., higher interspecific competition and higher temperatures. The consequences of living in a peripheral environment seem to be a lower density and lower population growth rate in the study year, as well as prevalence of older individuals in the population in comparison with the population at the higher altitude. Our results

provide an example of distinct variation in population dynamics within a plant taxon at a small spatial scale.

The ecologically-central population H was denser than population L, which agrees with the abundant-center model (Brown 1984) at a local scale. Similarly, we found higher recruitment and survival in population H. Other authors have reported decreased abundance or performance of mountain species at low-altitude altitudes (Beals 1969, Brown 1984, Giménez-Benavides et al. 2011). One exception to the overall worse performance of S. acaulis in population L in the Pyrenees was higher growth rate of small-sized plants, which agrees with what was found for southern peripheral populations of the species in N America (Doak & Morris 2010). Differences in the growth rate of small plants in L had indeed a moderate but positive contribution to this population growth rate. However, in contrast to the pattern found in N America, the level of demographic compensation between Pyrenean populations was weak, considering the low over-

Table 1. Transition and elasticity matrices based on size classes, for the two studied populations of *Silene acaulis* in the period 2010–2011, in the Ordesa and Monte Perdido National Park, Spain. For each matrix, stasis is reported along diagonals, growth and decline are represented below and above the diagonals, respectively, and the first row reports recruitment + shrinkage. For further details *see* Fig. 2.

	Population H						Population L					
	1	2	3	4	5	6	1	2	3	4	5	6
Transition matrix												
1	0.51	0.51	1.15	1.15	1.41	1.29	0.11	0.27	0.33	0.37	0.32	0.50
2	0.15	0.52	0.23	0.09	0.03	-	0.33	0.33	0.26	0.10	0.02	_
3	0.05	0.09	0.31	0.09	0.03	-	-	0.13	0.35	0.32	0.10	_
4	_	0.02	0.29	0.55	0.17	-	-	-	0.13	0.32	0.24	0.11
5	-	-	_	0.18	0.57	0.12	-	-	-	0.06	0.45	0.29
6	_	0.03	_	0.09	0.20	0.88	-	-	-	0.06	0.19	0.57
<i>S</i> *	0.71	0.86	0.86	1.00	1.00	1.00	0.44	0.67	0.78	0.90	1.00	0.96
N**	41	65	35	22	30	25	9	24	23	31	42	28
Elasticity matrix												
1	0.10	0.03	0.02	0.02	0.01	0.03	< 0.01	0.01	0.01	< 0.01	< 0.01	< 0.01
2	0.07	0.08	0.01	< 0.01	< 0.01	-	0.03	0.03	0.01	< 0.01	< 0.01	-
3	0.05	0.03	0.03	0.01	< 0.01	-	-	0.03	0.04	0.02	0.01	-
4	_	0.01	0.05	0.07	0.01	-	-	-	0.04	0.06	0.03	0.02
5	_	_	_	0.03	0.05	0.03	_	_	_	0.03	0.15	0.10
6	_	0.02	_	0.02	0.02	0.21	-	-	-	0.04	0.08	0.26
Σ	0.22	0.16	0.12	0.14	0.11	0.27	0.03	0.07	0.10	0.15	0.28	0.38

* Total survival for each class (it does not match the sum of column elements if any matrix element of the upper row includes recruitment).

** Total number of individuals monitored in each size class at the beginning of the study.



Fig. 4. Contribution of matrix elements to observed differences in the population growth rates between the two study sites of *Silene acaulis* (Life Table Response Experiment analysis, random design). Matrix elements are named as a_{ij} indicating transitions from class *j* in 2010 (columns in Fig. 2B) to class *i* in 2011 (rows). *See* Material and methods for further details.

all population L growth rate. Studies of other plant taxa provide examples of better performance either in central (e.g., Carey *et al.* 1995, García *et al.* 2000, Jump & Woodward 2003) or in peripheral populations (Kluth & Bruelheide 2005, Samis & Eckert 2009), and trends might vary depending on the vital rate studied (Villellas *et al.* 2013), which highlights the need for studies in different geographic and ecological conditions to find patterns of demographic variation across species' ranges.

We only monitored S. acaulis for two years, and environmental conditions may change across time, affecting long-term population dynamics. Thus, the exact values of individual and population growth rates obtained in this study should be taken cautiously. For example, both populations showed growth rates that are far from equilibrium ($\lambda = 1$) as compared with those reported in previous studies on the same species elsewhere (Doak & Morris 2010). Nevertheless, some evidence suggests that our study captured the common situation in both populations. First, S. acaulis has a very long lifespan (Benedict 1989, Morris & Doak 1998), and long-lived plants have very stable population dynamics (García et al. 2008, Jongejans et al. 2010) and long-term population growth rates that are little sensitive to short-term (e.g., annual) changes in plant performance (Morris et al. 2008). On the other hand, the meteorological parameters recorded during our study period, such as temperature, were typical for the current climate in the study area. All this strongly suggests that our results are illustrative of the overall state of populations, especially considering the striking differences found among the central and peripheral sites in density, size structure and population growth rates.

Differences in the life cycle of S. acaulis between the two locations seem to underlie population structures. The low-altitude population was comprised of older individuals and juveniles were scarce, a similar pattern to its congener S. ciliata in the mountains of central Spain (Giménez-Benavides et al. 2011). This fact, together with the lower density than in population H, could be attributed to a lower recruitment rate and lower survival of small classes. due to a higher interspecific competition and a harsher environment. Low recruitment rates at the range margin have been suggested as an explanation for low densities and aged population (García et al. 2000, Dorken & Eckert 2001, Jump & Woodward 2003, Giménez-Benavides et al. 2008, 2011), and low survival of small individuals can only exacerbate low recruitment. In fact, population L had higher mortality rates of smaller individuals than many populations elsewhere (Morris & Doak 1998, Doak & Morris 2010). By contrast, population H was younger and had higher survival rates of the smallest and the largest plants.

Comparing the observed population structures with predicted ones can also help to evaluate recent changes in population dynamics. In longlived species, for example, the stable structure predicted by matrix models is often similar to the observed one unless considerable environmental changes have taken place in recent time (Doak & Morris 1999). In our study, the differences found between observed and projected abundances in the two populations of S. acaulis were not statistically significant. Such pattern, combined with the population growth rates far from equilibrium, suggests that whatever the factor leading to expansion or decline of populations is, it must have been acting for a period of time long enough to produce a similar structure to the one predicted for the last years. Projections inferred from our study, therefore, seem to be in line with the overall trends in the past. Such assertion, however, should be taken cautiously, as it remains to be tested whether the differences recorded between central and peripheral sites are persistent.

Assessing plant performance in the context of climate change requires analyzing present population trends in different environments, but also discussing possible responses to future changes. Although Alatalo and Totland (1997) found that increases in temperature improved some reproductive rates of some subarctic and alpine populations of S. acaulis, increasing temperatures in the long term have been suggested to cause an overall decline in southern peripheral populations in N America (Doak & Morris 2010). In the Pyrenees, the mean temperature has increased on average 0.3 °C per decade since 1950 (López-Moreno et al. 2010). Demographic performance of the low-altitude population of S. acaulis, which is currently subject to higher temperatures, may thus be further reduced if global warming persists. For an alpine plant, this can lead to a contraction of the distribution range by local extinctions near the lower boundary, which cannot be compensated by a parallel expansion in the high extreme, since the species is already occupying the mountain summits. Adaptation to these accelerated changes seems unlikely, and numerous studies have indeed reported upward shifts in altitudinal ranges in alpine plants (e.g., Walther et al. 2005, Cannone et al. 2007, Lenoir et al. 2008, Kullman 2010, Pauli et al. 2012).

Besides temperature, other factors, such as increasing interspecific competition due to a decrease in cattle grazing, may affect boreoalpine plants in the Pyrenees and other European mountains (García-Ruiz *et al.* 1996, Lasanta-Martínez *et al.* 2005), may affect boreo-alpine plants. Silene acaulis is a non-palatable species that benefits if large herbivores browse on palatable plants nearby (Ishii & Crawley 2011), and thus may be indirectly affected by changes in grazing intensity. Population L monitored in this study was located in a grassland, an area that was intensively grazed in the past, with high interspecific competition. Poor soils and harsh environmental conditions in population H, on the other hand, keep interspecific competition low. If levels of grazing in the Pyrenees are maintained or further reduced as a consequence of abandonment of the rural life style, populations near the low limits of the range of S. acaulis may collapse. Overall, both high temperatures and interspecific competition seem to have negative effects on population L, but only long-term experimental studies of the effects of global change on alpine plants will enable us to understand and predict future plant responses with more accuracy.

The future of boreo-alpine plants under global change scenarios is not promising, and species and populations located at the southern mountain ranges have been demonstrated to be of particular concern at a European scale (Pauli et al. 2012). In the present work, we found large differences in population structure and dynamics between two closely located populations of a boreo-alpine plant, a potential mechanistic process underlying a species range contraction. If the environmental conditions change any further, the range of S. acaulis in the Pyrenees may indeed shrink through altitudinal contraction. In any case, our study showed a differing demography between ecologically central and peripheral populations of a boreo-alpine plant in its geographical southern periphery. This highlights difficulties of accurately predicting the future of S. acaulis even at a regional scale. Being at the geographical limit of distribution does not necessarily entail extinction risk, since not all populations respond in the same manner to global climate change.

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