

Being an annual plant in a water-limited Mediterranean-alpine mountain; the case of rare-endemic and threatened *Arenaria nevadensis*

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ARTICLE INFO

Keywords:

Plant conservation
Population dynamic
Functional traits
Climate change
Water supply
Sierra Nevada

ABSTRACT

Mountain ecosystems are proving to be particularly vulnerable to the effects of global change, with Mediterranean high mountains standing out as among the most susceptible regions worldwide. The impact of climate change on biota operates across key levels: metabolism, phenology, evolution, and spatial distribution. Monitoring species within these ecosystems is crucial to establish early warning indicators for effective mitigation and adaptation strategies. Within this context, annual plants, like the critically endangered species *Arenaria nevadensis* endemic to Sierra Nevada, could offer advantages as indicators due to their rapid life cycles and dependence on water sources.

This study aims to investigate the impact of climatic change on this specific annual, endemic, and threatened species while assessing its potential as an indicator for shifting snow patterns affecting alpine biota. Analyzing data collected between 2005 and 2021 from four populations of *Arenaria nevadensis* alongside hydro-meteorological data revealed notable variations in population parameters linked to climatic fluctuations. Factors such as precipitation and snowpack significantly influenced plant size, reproductive potential, and population size, with neighboring populations showing distinct responses to climatic variations.

The observed unpredictability in population trends across consecutive years underscores the climatic stochasticity inherent in Mediterranean mountains, particularly Sierra Nevada. Forecasts of decreased precipitation and increased temperatures are expected to diminish snowpack depth and duration, posing a severe threat to this critically endangered species. Conservation efforts should prioritize managing higher elevation populations and exploring new suitable habitats for restoration or assisted migration.

While *Arenaria nevadensis* demonstrates promise as a climate change indicator owing to its short life cycle, restricted distribution, and sensitivity to climatic shifts, comprehensive understanding of its germination ecology, seed bank role, and reproductive biology remains lacking. Addressing these knowledge gaps is crucial to enhance its effectiveness as an indicator species.

1. Introduction

Mountain biodiversity is of paramount importance worldwide (Körner, 2004; 2021). The intricate interactions by climate and mountains produces highly environmental heterogeneity that ultimately leads to the high species diversity patterns observed in many mountains worldwide (Körner, 2004; Perrigo, Hoorn, & Antonelli, 2020). In fact, many mountain regions are considered biodiversity hotspots of alpine flora and boast great richness and a considerable number of endemic species (Körner, 2021).

Mountain ecosystems are proving to be particularly susceptible to global change, particularly climate change with temperatures raising faster than in lowland areas (Nogués-Bravo, Araújo, Errea, & Martínez-Rica, 2007; Lenoir, Gégout, & Marquet, 2008; Martín-Esquivel, Marrero-Gómez, & Cubas, 2020). In fact, global warming is strongly affecting the mountain climate, altering the snowfall patterns and, consequently, altering seasonal runoff patterns as well (IPCC, 2021). These changes also lead to changes in the albedo of the mountains, gradually shifting hydrological cycles from being dominated by snow and ice to being determined by rainfall (Kohler, Wehrli, & Jurek, 2014). As a result,

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<https://doi.org/10.1016/j.jnc.2024.126597>

Received 14 December 2023; Received in revised form 7 February 2024; Accepted 8 March 2024

Available online 11 March 2024

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climate change may impact biota at four levels: metabolism, phenology, evolution, and spatial distribution (Hughes, 2000). The first three may lead to adaptation (both via individual adaptation and/or natural selection) to the new conditions, the last one could pose local extinctions and/or migrations. For this reason, as mountain plant species are often cold-adapted, migration leads mainly to upward movement, as suitable thermal and bioclimatic conditions also migrate upward, and causing major shifts in altitudinal distribution (Benito, Lorite, & Peñas, 2011; Steinbauer, Grytnes, & Jurasinski, 2018). However, in some cases this migration is not possible because the suitable habitat for the species is lost (Bello-Rodríguez, Hamann, & Martín-Esquível, 2023). In addition, when upward migration is possible, for many mountain species this leads to a reduction of the suitable habitats and could result in increased interspecific competition. This fact could be very detrimental to alpine species, which could be outnumbered, specially in small massifs with limited vertical extent, where suitable conditions for this species are increasingly scarce (Benito, Lorite, & Pérez-Pérez, 2014).

According to the literature, this trend is exacerbated in the Mediterranean (Thuiller, Lavorel, & Araújo, 2005; Nogués-Bravo, Araújo, & Lasanta, 2008). This fact, together with the high biological diversity of Mediterranean-type ecosystems (Medail & Quezel, 1999), makes Mediterranean high mountains among the most vulnerable to global warming (Grabherr, Gottfried, & Pauli, 1994; Nogués-Bravo et al., 2008).

Different studies point Sierra Nevada (SE Spain) as a paradigmatic example of these trends in a typical water-limited Mediterranean mountain (Lamprecht, Pauli, & Fernández Calzado, 2021). In fact, a sharp decrease in snowfall with a highly unpredictable pattern is currently being reported (Pérez-Palazón, Pimentel, & Polo, 2018).

Due to that, the monitoring of key species is of paramount importance in order to have early warning indicators for mitigation and adaptation strategies. In this regard, annual plants offer some advantages as key species for monitoring programs in mountain regions. Annual plants are very rare at alpine conditions due to the obvious difficulties of seedling establishment under the adverse climatic conditions and the limitation to complete the entire life cycle in the typical short growing period, thus they have to respond very quickly to climatic fluctuations, making them scarce and typically confined to warm microhabitats (Reynolds 1984; 1984; Körner, 2021).

In Mediterranean mountains, annual species are also very scarce. For instance, in Sierra Nevada there are only 39 annual species out of 362 growing above 2,400 m. asl. (Lorite, Ros-Candeira, Alcaraz-Segura, & Salazar-Mendías, 2020). Whereas in alpine areas the length of the growing season at treeline generally ranges from 90 days in the Arctic to ca.365 days at Equatorial mountains, in the Mediterranean high mountains it is only 90 days, with snow disappearing in July and growth then being water-limited (Körner, 2012). Consequently, annual plants here have either an early life cycle, or they are linked to any source of water. This is the case of *Arenaria nevadensis* Boiss. & Reuter, a rare species endemic to Sierra Nevada and Critically Endangered (Gutiérrez & Blanca, 2003). The species presents a curious adaptation to overcome this water limitation during vegetative period, inhabiting the edge of melting snowfields and germinating very quickly when the snow melts, taking advantage of the water supplied by the snowmelt (Blanca, López-Onieva, & Lorite, 2001).

This species, besides the importance for conservation purposes, can act as a good indicator on the effects of a decreasing snowfall predicted for the area (Pérez-Palazón et al., 2018). The species has been monitored by the Agencia de Medio Ambiente y Agua (Environment and Water Agency) of the Regional government for the last 20 years. For the first time, we analyzed data on this species seeking trends and assessing the potential of the species as an indicator on the effects of global change, and particularly the effects of climatic change. We hypothesize that this species suffers drastic changes in their populations and that these changes may be related to climatic trends, especially in a water-limited mountain such as Sierra Nevada.

The aims of this study are: i) to relate climatic data with population

variables on this species, searching for evidence of the effect of climatic change on an annual, endemic and threatened species and ii) to look for the potential of using the species to track the influence of changing snow patterns on alpine biota.

2. Material and methods

2.1. Study area

Sierra Nevada, in southeastern Spain (from 36°50'24" to 37°15'0"N in latitude, and 3°44'24" to 2°35'24" W in longitude) is a paradigmatic example of a small and isolated Mediterranean high mountain, constituting the only true alpine region between the North African mountains (High and Middle Atlas), the Spanish Central Range, and the Pyrenees, which are all several hundreds of kilometers away (Lamprecht et al., 2021). Within its limited area of 2,100 km², it boasts a complex orography with a broad altitudinal range (from 200 m to 3,479 m at Mulhacén peak). The climate is typically Mediterranean, characterized by cold, wet winters and hot, dry summers (with strong summer drought in July-August; Gómez-Ortiz, 2002). Temperature usually ranges from −10 °C to 10 °C above 2000 m a.s.l. during the snow season (Pérez-Palazón et al., 2018), with a snowpack that can persist for up to 8 months in the highest elevations (occasionally up to 10 months in small patches of snowbeds; Lamprecht et al., 2021). Average annual rainfall is highly irregular, with values ranging from 220 to 1000 mm per year, with a high spatial variability due to changes in elevation, longitude, and contrasting exposures (north-south) (Algarra, Cariñanos, & Herero, 2019). Geologically, the core area is composed of siliceous rocks, mainly mica-schists, surrounded by limestone and dolomite (Jabaloy, Galindo, & Sanz, 2008).

This mountain marks the southernmost limit of the influence of the Quaternary glaciations in Europe, being covered by glaciers only in areas above 2,500 m., while large areas remained free of glacial ice (Gómez-Ortiz, Oliva, Salvà-Catarineu, & Salvador-Franch, 2013). Thus, Sierra Nevada acted as refuge for many plant species during glacial ages, as well as for isolated populations that have evolved under particular conditions, not only climatic, but also specific soil types or isolated summit habitats (Blanca, Cueto, Martínez-Lirola, & Molero-Mesa, 1998; Médail & Diadema, 2009). This has encouraged speciation, resulting in 2,348 taxa from a total of 756 genera and 146 families, with 95 endemic or subendemic taxa (Lorite et al. 2007; 2020; Lorite, 2016). For this reason, it is considered one of the most important plant hotspots within the Mediterranean region (Blanca et al., 1998; Médail & Quezel, 1999; Médail & Diadema, 2009; Cañadas, Fenu, & Peñas, 2014; Peñas & Lorite, 2019).

2.2. Studied species

Arenaria nevadensis Boiss. & Reuter, annual plant up to 9(15) cm., is a narrow endemic to Sierra Nevada, growing in screes within the upper alpine zone from 2,950 to 3,200 m asl. The species take advantage of the water coming from the snowmelt. It flowers in July-August and fructifies in August and early September. The species presents only 6 small patches forming three populations (see Fig. 1 and Table 1), and has been assessed as Critically Endangered (CR). The number of individuals is around 2,500, though there are important interannual fluctuations in both individuals and occupation area (Gutiérrez & Blanca, 2003).

2.3. Field data collection

Data collection has been carried out from 2005 to 2021, coinciding with the flowering peak of the populations, highly variable among years (typically the end of July or the first half of August). We designed a monitoring program to take both individual and population data. For the individual-based data we selected 4 patches (Mulhacén1, Mulhacén 3, Mulhacén 4, and Veta_Grande) within the 6 existing population patches

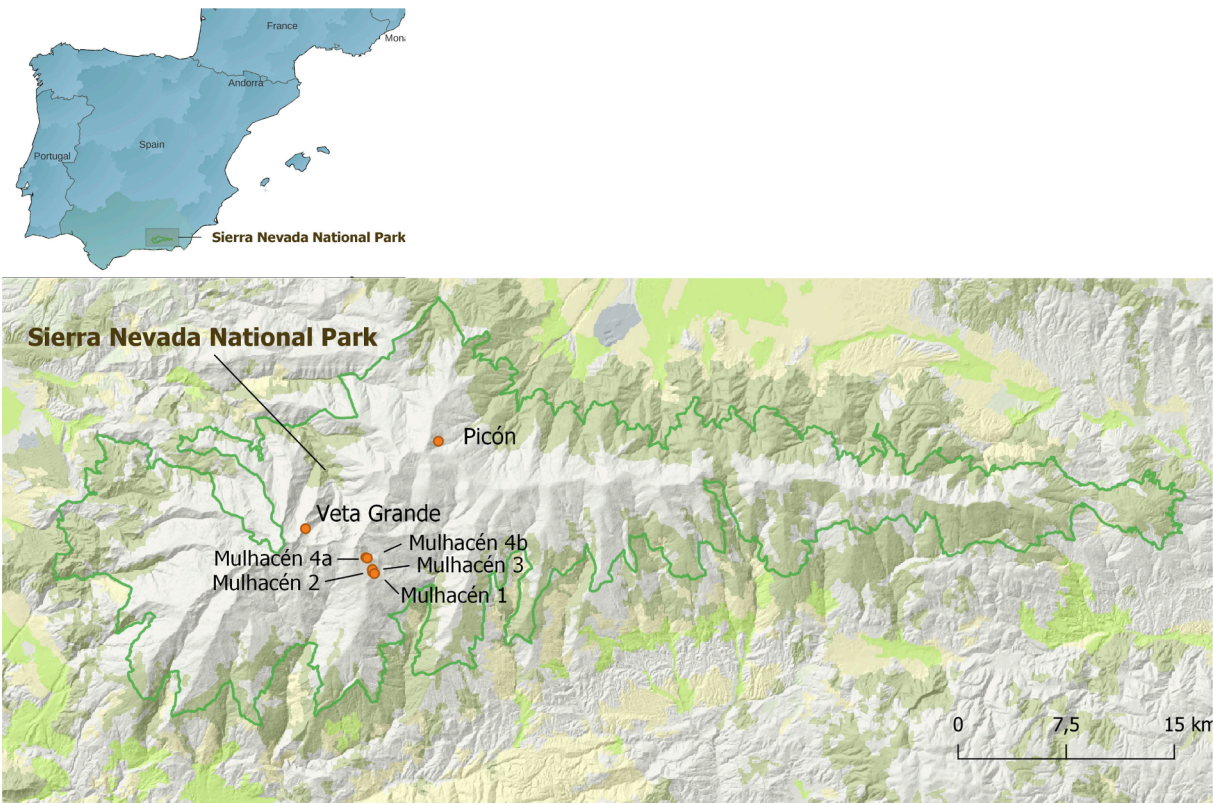


Fig. 1. Location of the populations of *Arenaria nevadensis* in Sierra Nevada (SE Spain; see Table 1 for further details).

Table 1
Main features of *Arenaria nevadensis* populations (partially taken from FAME; <https://www.juntadeandalucia.es/medioambiente/servtc2/fame>, plus own unpublished data). ¹Altitude of the population centroid. ²Historical occupation area in m² (years 2008–2021, see material and methods for details). ³Average number of individuals for the period 2008–2021 (except for Picon population with data only for 2021). ⁴Main species threats per population: 1. Low ecological plasticity, 2. Grazing and trampling (wild), 3. Grazing and trampling (domestic). 4. Poor reproductive capacity, 5. Low ecological plasticity, 6. Outdoor recreation activities (trampling and artificialization by hicking). ⁵Main species threats per population: 1. Climate change, 2. Grazing and trampling (wild), 3. Grazing and trampling (domestic). 4.Substrate instability (rock movements on screes). 5. Outdoor recreation activities (trampling and artificialization by hicking).

Population	Alt. ¹	Area ²	N.ind. ³	species threats ⁴	habitat threats ⁵
Mulhacén 1	3020	6,869	470	1,2,3,4,5,6	1,2,3,5
Mulhacén 2	3060	7,300	199	1,4,5	1
Mulhacén 3	3030	11,893	2,526	1,4,5	1
Mulhacén 4	3180	16,562	157	1,4,5	1,4
Veta Grande	2960	9,443	932	1,2,4,5,6	1,2,4,5
Picon	2860	1,086	64	1,4,5	1

(see Table 1 and Fig. 1). In each of the patches we randomly selected 30 individuals and took the following variables: 1) height, 2) width (maximum diameter in cm), 3) number of flowers, 4) number of flower buds, 5) number of fruits. Variables 1 and 2 were used to estimate the individual size as biolume (calculated as the volume of the cone formed, see Lorite, Peñas, & Benito, 2010). Variables 3 to 6 were added to obtain reproductive potential (i.e. as total number of reproductive structures formed by individual).

For population data we selected three patches (Mulhacén 1, Mulhacén 3, and Veta Grande). We calculated the historic occupation area for the three populations by overlapping and summarizing the cloud of points taken with GPS (±5 m bias) for the entire period surveyed (from 2001 to 2021). Within these three populations, we placed a series of

permanent transects of 2 m width and variable length (from 21 to 48 m) depending on the area of each population and its geomorphological characteristics. Data from these transects have been recorded from 2007 to 2021. Also, we have added some data prior for 2005 (Mulhacén 1 population) taken by non-permanent transects, although taken with the same type of transect. We recorded the number of individuals of the species encountered within each transect. Finally, the data were standardized by calculating the density (i.e. individuals per square meter) for each transect in a given year. Using the density-per-patch (i.e. average density per population obtained from the different transects) data and historical occupation area, we have estimated the total number of individuals per patch and year for the surveyed period. In order to calculate the tendencies of the three populations we calculated Lambda, defined as the finite rate of increase of the population in one-time step, often 1 year (Menges, 1990). $\Lambda = N_t + 1/N_t$; where N_t = number of individuals in time t , and $N_t + 1$ = Number of individuals in time $t + 1$). When $0 < \lambda < 1$, the population decreases; $\lambda = 1$, population stable; and $\lambda > 1$, the population increases.

2.4. Hydro-meteorological data

Hydro-meteorological data for the populations were obtained from the WiMMed hydrological model (Watershed Integrated Model in Mediterranean Environments; Herrero, Millares, & Aguilar, 2014). WiMMed is a fully distributed and physically based hydrological model that combines hourly and daily meteorological data with soil physical properties to simulate the hydrological cycle, including snow accumulation and ablations, soil moisture evolution, aquifer recharge and watershed flow circulation (see Herrero et al. 2014 for details). For this study, we use meteorological data from 1999 to 2021 for temperature, precipitation, solar radiation, wind speed, and relative humidity provided by a network of meteorological stations in the study area (Pérez-Palazón et al., 2018), including a high-elevation network of Automated Weather Stations specially focused on snow monitoring (Polo, Herrero,

Pimentel, & Pérez-Palazón, 2019).

WiMMed outputs provided us with 11 representative hourly scale hydro-meteorological variables that were averaged on a daily or monthly basis for each population of the studied species. These data series can be grouped into 6 meteorological (atmospheric) variables and 5 hydrological (snow and soil moisture related) variables. The meteorological variables were: 1) monthly maximum temperature (Tmx), 2) monthly minimum temperature (Tmn), 3) mean daily temperature (T_m), 4) monthly global solar radiation (Rad), 5) monthly snowfall (P_n) 6) monthly total precipitation as the sum of snowfall and rainfall (Pre). The hydrological variables were: 1) monthly snowmelt (Fus), and 2) daily snow water equivalent – the amount of snow accumulated on the surface in mm (Ean). 3) daily soil humidity at first 25 cm of the soil (HSol1) 4) daily soil humidity at bottom soil layer (from 25 cm to rock) (HSol2), and 5) monthly water infiltrated into the soil (Inf).

2.5. Data analysis

Statistical analyses were performed using R version 4.1.2 (R Core Development Team, 2021). Reproductive potential and biovolume per individual were adjusted by GAM models using mgcv function in “vegan” Package (Oksanen, Blanchet, & Friendly, 2018).

To test differences in climatic variables among the populations we performed a permutational multivariate analysis of variance

(PERMANOVA) with the “adonis” function in R package vegan 2.5–2 (Oksanen et al. 2018).

To address relationship among: size (biovolume), reproductive potential and density of individuals (ind./m²) as dependent variables, and the different climatic variables as independent ones (see former section for further details on variables), we have adjusted different models using permutational ANOVAs by means of “lmPerm” R package (Wheeler & Torchiano, 2016), a flexible and very robust analysis that could cope with heterocedasticity and a wide variety of statistical distributions. Multiple comparisons after permutational ANOVAs were performed by means of Tukey’s *post-hoc* test using “multcomp” package (Hothorn, Bretz, & Westfall, 2008). Afterwards, with each model for the response variables (size, reproductive potential and density) we performed a stepwise model selection by AIC using “stepAIC” function from library MASS (Venables & Ripley, 2002), in order to choose the best final model in each case.

Since differences in density strongly depends in the seed production of the former and due to that can have a delayed response in time, we transformed density into two new variables, “Densitylag1” in which the climatic data of the year was made to coincide with the plant density obtained the following year (i.e. applying a lag of 1 year).

For graphs included we used ggplot2 package (Wickham, 2009). Data across the text were expressed as mean \pm SE.

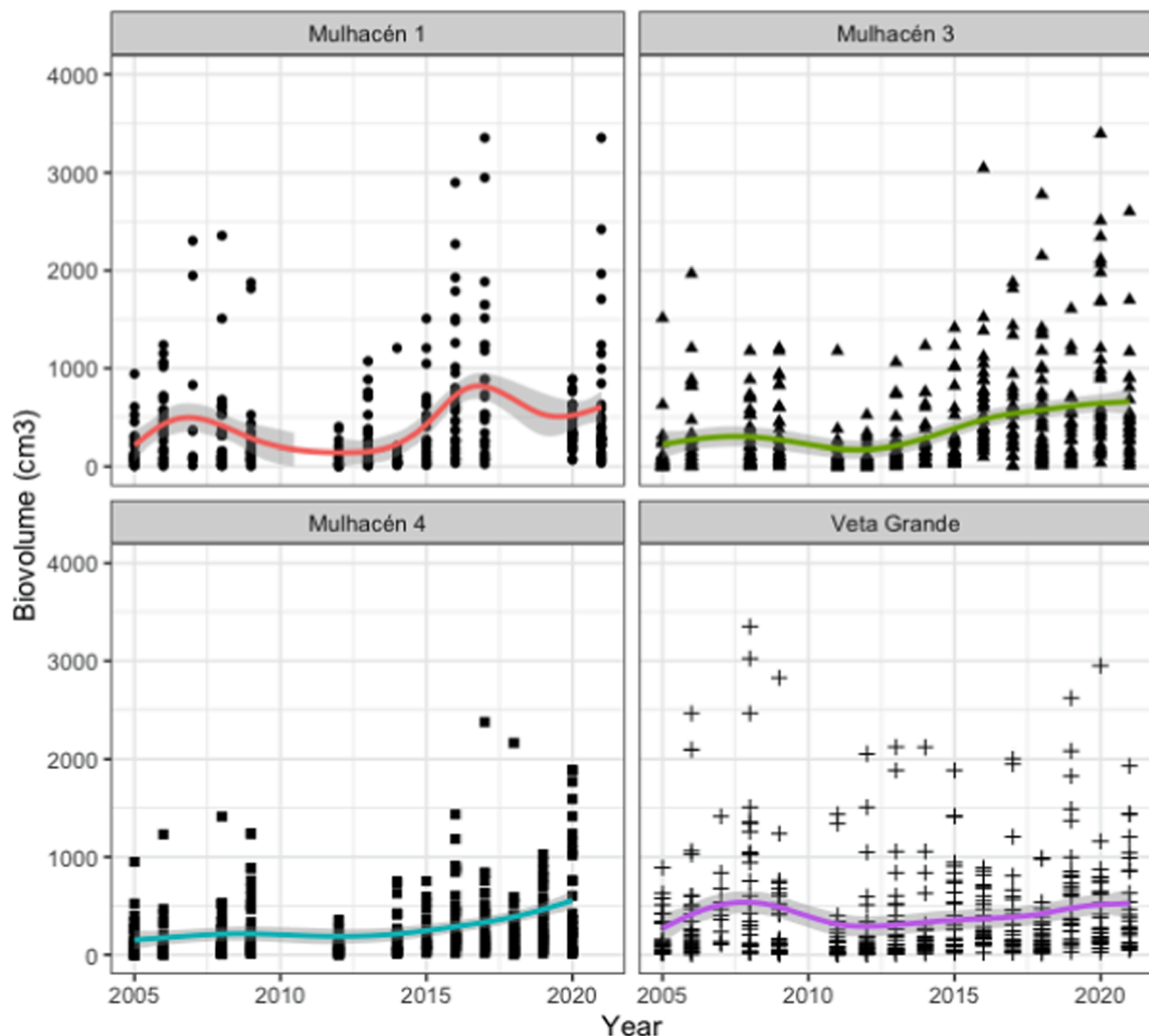


Fig. 2. Individual size (as biovolume in cm³) by years (data adjusted by GAM model; $p < 0.0001$).

3. Results

3.1. Plant size

The average individual size (in biovolume) for the entire period (2005–2021) was 389.80 cm^3 . However, the individual size (Fig. 2 and Figure S1) varied greatly among years, reaching a maximum in 2020 ($660.67 \pm 66.86 \text{ cm}^3$) and a minimum in 2012 (140.59 ± 23.91), representing more than 4-fold difference between the two years. Regarding the populations, the maximum was reached at Mulhacén 3 in 2020 ($944.35 \pm 160.43 \text{ cm}^3$) and the minimum at Mulhacén 1 in 2012 ($94.01 \pm 19.53 \text{ cm}^3$), which entails a tenfold difference. Considering the four different populations (Fig. 2) notable differences can be noticed. While Mulhacén 1 showed sharp variations with different periods of 3–4 years with increasing or decreasing trend, Mulhacén 3, Mulhacén 4 and Veta Grande showed a flatter response that tends to increase in the last four-five years assessed.

3.2. Reproductive potential

Reproductive potential (i.e. number of flower buds + flowers + fruits) per individual for the whole period cover in this study was highest for Mulhacén 3 population with the largest number of reproductive structures of 48.38 ± 2.07 (Figure S1). This parameter showed significant differences among years, being lower than 25 structures per plant for the period 2009–2013, and dropping to a minimum in 2012 with 22.51 ± 1.66 structures per plant (Figure S1). This period was followed by an increasing of more than double for the period 2016–2020, reaching its peak in 2020 with 63.96 ± 3.83 (Figure S1). Although this pattern was consistent across all the studied populations (Fig. 3), the lowest reproductive potential was reached in Mulhacén 1-year 2013

with 18.97 ± 2.19 , while the highest was Mulhacén 3 -year 2016 with 106.97 ± 13.95 .

3.3. Population size

Permanent transects to estimate populations size were placed in only three populations as indicated above. Mulhacén 3 presented the highest mean individuals over the period surveyed with $2,526 \pm 333$, followed by Veta Grande 932 ± 113 , and Mulhacén 1 with 470 ± 96 . The total number of individuals estimated in the three populations reached a minimum in 2017 with 1,294 and a maximum in 2014 with 9,468.

Fig. 4 shows important differences in population size among years, with a worrisome situation for Mulhacén 1 with no individuals in several years of the serie (2009, 2012 and 2019) despite showing a minor increase in the last two years of the serie (2020 and 2021). Mulhacén 3 presented a better situation even though there were significant fluctuations among years. This population peaked at $8,883 \pm 956$ individuals in 2014.

Regarding Lambda (finite growth rate) values (Fig. 5), we observed the typical fluctuating pattern described for other variables with positive trend (Lambda > 1) in 2007, 2009, 2012, 2018, 2019, 2021, and specially in 2014 (Lambda > 6). Whereas in 2011, 2013, 2015, 2016, 2017 and 2020 the trend was negative, highlighting the negative trend for three years in a row (2015–2017) which can be very detrimental to the species.

3.4. Influence of climatic variables

We obtained significant differences after PERMANOVA for the climatic variables among years ($P < 0.01$; $R^2 = 0.75$), but also among populations ($P < 0.01$; $R^2 = 0.29$) despite all populations assessed are

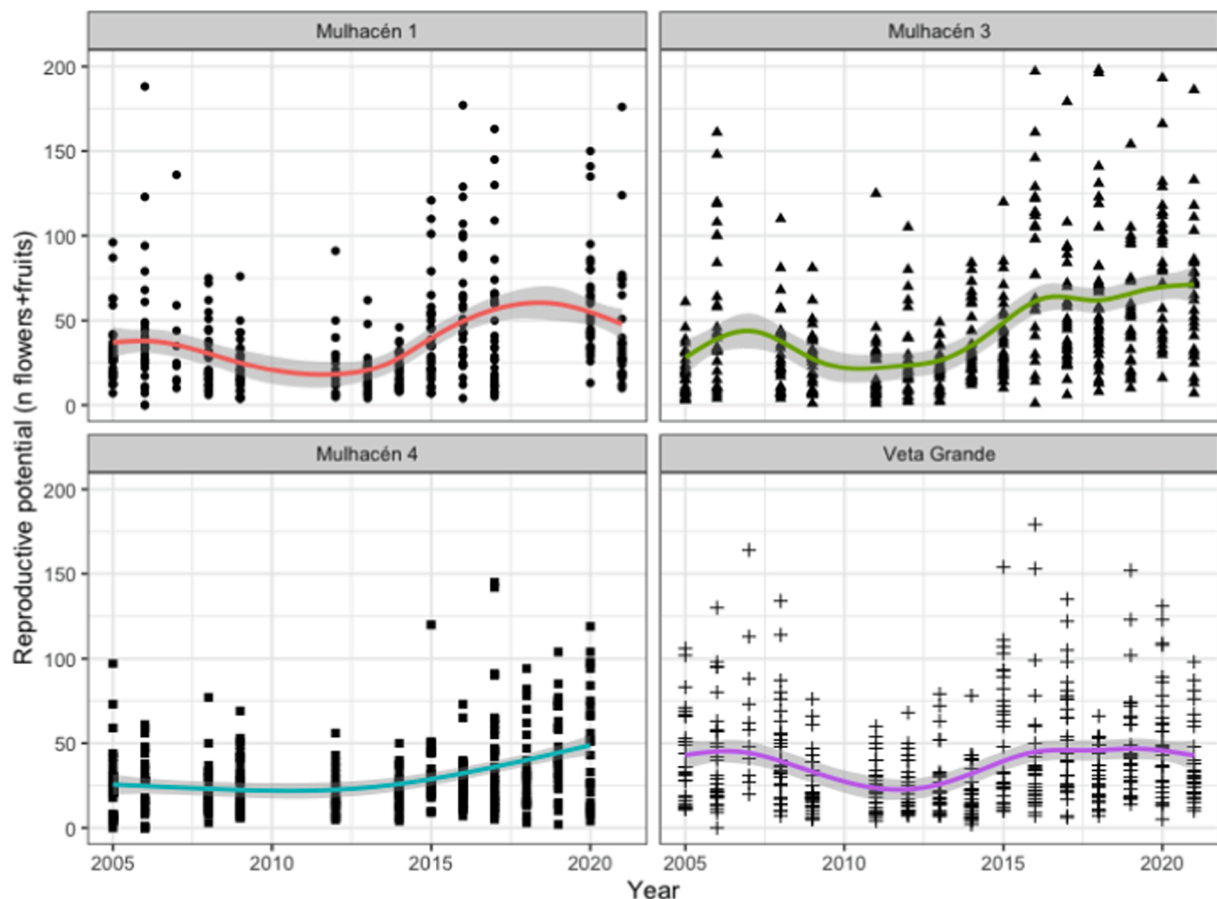


Fig. 3. Reproductive potential (i.e. number of flower buds + flowers + fruits per individual) by years (data adjusted by GAM model; $p < 0.0001$).

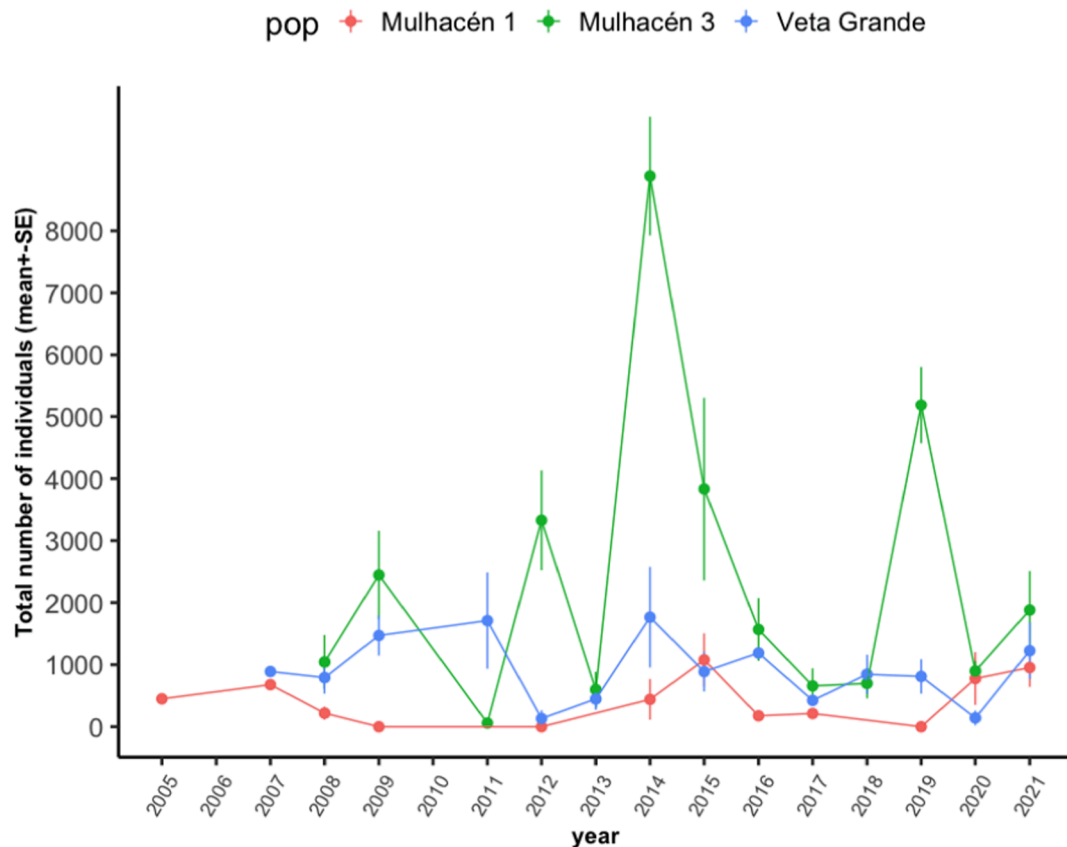


Fig. 4. Estimated number of individuals (mean \pm SE) for the three studied populations per year.

relatively close to each other. The combination of both showed the typical stochastic and topographically complex behavior of Mediterranean climate.

Climatic variables (see Table 2) strongly influenced individual size (as biovolume) ($P < 0.01$; $R^2 = 0.87$). Particularly, soil humidity at first 25 cm had a positive influence on plant size, on the contrary soil humidity in July and specially in August negatively influenced plant size. Soil humidity in deeper layer (HSol2) was less influential. The amount of snow accumulated on the surface positively influenced the plant size, especially in September. The total amount of precipitation, and precipitation in June favored plant growth. Also, mean temperatures were very influential, and while the annual mean, and the September mean were positively related with growth, high temperatures in July and August strongly and negatively affected plant size. The annual monthly maximum temperatures for June and September were negatively related to growth, and on the contrary these maximum temperatures in July and August favored plant growth.

The development of flower structures (buds, flower and fruit) was also strongly related to climatic variables ($P < 0.01$; $R^2 = 0.92$). Soil humidity (annual) did not favor reproductive potential, however soil humidity in June showed a positive relationship with reproductive potential, while the relationship in August was strongly negative. The amount of snow accumulated in September (EAnSep) exerted strong and negative influence on reproductive potential. Mean temperature positively affected plant reproductive potential, except for August, which was strongly negative. Monthly minimum temperature negatively affected the reproductive potential, except for August where it showed a positive relationship. In contrast, monthly maximum temperature was negative in general, though positive in August.

The model for density of individuals after the studied populations was not significant, proving that there is no relationship between climatic variables of the year and the density obtained, from which a one-

year lag would be expected. For this reason, we introduced a 1-year lag in the data (see material and methods) to seek for relationship between the observed density of individuals and the climatic variable of the former year (Table 2). In this case, the model was significant ($p = 0.002$), although the multivariate adjust was lower than observed for other response variables ($R^2 = 0.42$). In this case, only a few variables were retained after model selection based on the AIC.

4. Discussion

4.1. Plant performance

Even though annual plants make up one third of plant diversity in the European Mediterranean (Médail & Verlaque, 1997), Mediterranean mountains are particularly harsh for annual short growing season typical of mountains is also partly water-limited (Lamprecht et al., 2021). Our results contribute to support the explanations for the scarcity of the annuals in Mediterranean-alpine areas. In fact, in the area only around 10 % of the species are annual, with only three annual species above 3,000 m a.s.l., *Euphrasia willkommii* Freyn, *Sedum candollei* Raym.-Hamet and *Arenaria nevadensis* Boiss. & Reut., all of them linked to moist places (Lorite et al., 2020), trying to overcome this water limitation. This behavior is different in other temperate mountains where these annual plants are typically confined to warm microhabitats, which are more favorable for an annual life cycle ((Reynolds 1984; 1984; Körner, 2021).

The size and reproductive potential of annual plants are typically highly variable from within years, especially in arid and semi-arid environments (Aronson, Kigel, Shmida, & Klein, 1992), where water pulses can largely determine plant performance and thus plant assemblages (Luzuriaga, Gonzalez, & Escudero, 2015). In line with the expectations, we found very sharp variations among years in size and subsequently in

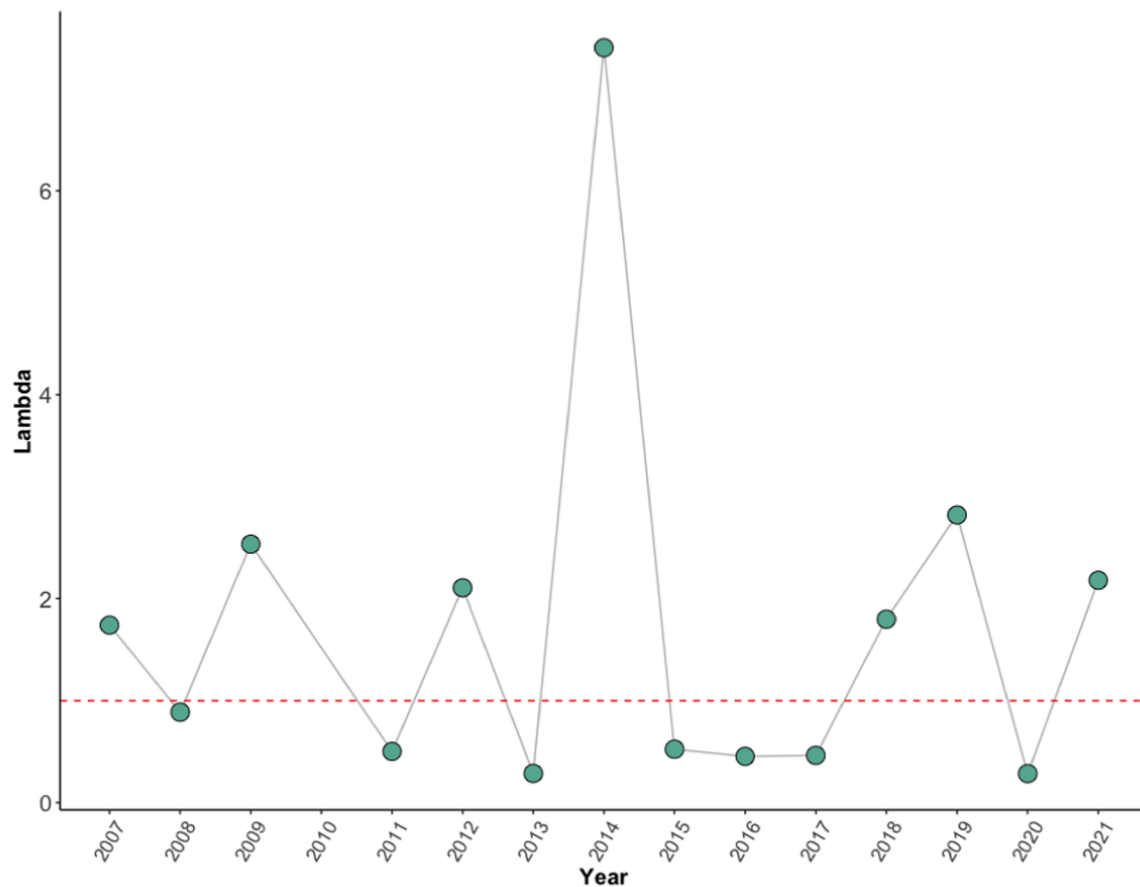


Fig. 5. Finite growth rate (Lambda) for the period 2007–2021 (the three populations pooled). Red dotted line shows stasis (Lambda = 1) as a reference.

reproductive potential in this water-limited mountain area. Besides, with 3–4 years in a row with negative or positive trends. However, the scarce literature on alpine annual plants does not assess these interannual differences and the effects of this multi-year cycles in the long or even mid-term (eg. (Reynolds, 1984)). These chains of several years in a row can be very detrimental if seeds do not persist in the seed bank and can lead to a local extinctions. Such seed bank persistence, though existing, has proved to be very small for some alpine annual species, with around 80 % of the seeds germinating in the first year (Reynolds, 1984).

The typical unpredictable Mediterranean climate, particularly marked in Sierra Nevada (Esteban-Parra, García-Valdecasas Ojeda, & Peinó-Calero, 2022), combined with the harsh alpine conditions, may exacerbate the differences in seed production among years. Subsequently, the major loss of individuals for alpine annuals occurs between seed dispersal and germination (Reynolds, 1984), all resulting in large differences in population size among years. In fact, in our case we found drastic differences in population size of up to 10-fold between the largest and the smallest population size for the assessed period, even differences between consecutive years being up to 6-fold. Such extreme fluctuations in population size may enhance the extinction likelihood (Lande, 1993), especially in short-lived species (Morris, Pfister, & Tuljapurkar, 2008). Furthermore, the lowest altitude population showed the lowest number of individuals. This lower altitude population in fact constitutes the rear edge of the distribution area, and thus prone to experience the worst effects of climate change, as cold-adapted species (Benito et al., 2014).

4.2. Influence of hydro-meteorological

Hydro-meteorological variables specially those related to snow occurrence and persistence, play key role in alpine ecosystems (Körner,

2021). In our case, we obtained marked differences among years, but also among neighboring populations concerning relevant climatic variables. This fact informs us not only of the strong climatic stochasticity in a typical Mediterranean mountain but also the high spatial heterogeneity of climatic variables in Sierra Nevada (Polo, Herrero, & Millares, 2022).

Differences among years have proved to be highly influential in alpine annual plants (Reynolds 1984; 1984; Cui, Meng, & Suonan, 2017). In this line, hydrological variables were also very influential in *Arenaria nevadensis* in terms of individual size, fitness and population size (the last in a lesser extent). Specifically, the amount of snow accumulated and soil humidity at first 25 cm had a positive effect. Also, soil humidity in June had a positive effect in species fitness, though humidity in July or August did not favour biovolume of fitness, perhaps because it means late snow melting and a late plant cycle development. As regards temperature, even though mean temperature had a positive effect on species, the increase of mean temperatures in July and August, together with an increase of annual maximum temperatures, and in June were negative. Thus, warmer years with higher summer temperatures will be determinant in the fate of the species. The negative trend forecasted for the area in terms of snowpack and thus the soil moisture in early and mid-summer (Polo et al., 2022) combined with the rising temperatures (Esteban-Parra et al., 2022) may lead to a worsening of the species, exacerbated by a highly unpredictable pattern (Pérez-Palazón et al., 2018).

4.3. Conservation of the species

Arenaria nevadensis is linked to snow beds and germinates very quickly as the snow melts, taking advantage of the water supplied by the snowmelt (Blanca et al., 2001). However, in a context of climatic change

Table 2

Results of permutational ANOVAs with AIC model selection for response variables: biovolume, reproductive potential (rep_pot), and density of individuals obtained with a lag of one year (densitylag1). Significant variables at $p < 0.05$ marked in bold. Independent variables (predictors): 1) **HSol1**: Daily (monthly averaged) soil humidity at first 25 cm of the soil (HSol1Jun = HSol1 in June; HSol1Jul = HSol1 in July; HSol1Aug = HSol1 in August; HSol1Sep = HSol1 in September); 2) **HSol2**: Daily (monthly averaged) soil humidity at bottom soil layer (from 25 cm to rock) (HSol2Jul = HSol2 in July; HSol2Aug = HSol2 in August; HSol2Sep = HSol2 in September); 3) **EAn**: Daily (monthly averaged) snow water equivalent – the amount of snow accumulated on the surface in mm (EAnJun = EAn in June; EAnJul = EAn in July; EAnSep = EAn in September); 4) **Fus**: monthly snowmelt (FusJun = Fus in June; FusJul = Fus in July; FusSep = Fus in September); 5) **Pre**: monthly total precipitation as the sum of snowfall and rainfall (PreJun = Pre in June; PreJul = Pre in July; PreSep = Pre in September; PreSum = Pre in Summer); 6) **T_m**: mean daily temperature (T_mJun = T_m in June; T_mJul = T_m in July; T_mAug = T_m in August; T_mSep = T_m in September); 7) **T_{mn}**: monthly minimum temperature (T_{mn}Jul = T_{mn} in July; T_{mn}Aug = T_{mn} in August; T_{mn}Sep = T_{mn} in September); 8) **T_{mx}**: monthly maximum temperature (T_{mx}Jun = T_{mx} in June; T_{mx}Jul = T_{mx} in July; T_{mx}Aug = T_{mx} in August; T_{mx}Sep = T_{mx} in September).

Predictors	biovolume		rep_pot		densitylag1	
	Estimates	p	Estimates	p	Estimates	p
(Intercept)	1570.29	<0.001	37.22	<0.001	0.14	0.002
HSol1	352.38	<0.001	-7.08	0.009	-0.06	0.002
HSol1Jun	39.39	0.160	3.30	0.022	–	–
HSol1Jul	-157.24	0.003	-0.82	0.186	–	–
HSol1Aug	-277.48	<0.001	-9.43	<0.001	–	–
HSol1Sep	–	–	2.67	0.118	–	–
HSol2	14.56	0.040	0.27	0.065	-0.00	0.921
HSol2Jul	-8.95	0.745	-0.61	0.0223	–	–
HSol2Aug	–	–	2.09	0.017	–	–
HSol2Sep	–	–	-1.69	0.119	–	–
EAn	22.31	0.029	0.27	0.534	–	–
EAnJun	7.99	0.076	0.38	0.002	–	–
EAnJul	23.30	<0.001	0.16	0.220	–	–
EAnSep	800.68	<0.001	-16.46	<0.001	–	–
Fus	-17.21	0.001	–	–	–	–
FusJun	-8.92	0.069	-0.51	<0.001	–	–
FusJul	-7.24	0.8431	-0.51	0.003	–	–
FusSep	-122.29	0.028	4.41	0.009	–	–
Pre	13.41	<0.001	0.06	0.516	–	–
PreJun	131.53	<0.001	-0.64	0.421	–	–
PreJul	-98.27	0.037	–	–	–	–
PreSep	–	–	-3.07	<0.001	–	–
PreSum	-28.20	0.003	4.00	<0.001	–	–
T _m	864.87	0.023	52.20	0.030	-0.35	0.006
T _m Jun	401.66	0.024	21.13	0.1353	–	–
T _m Jul	-2374.23	<0.001	8.27	0.495	–	–
T _m Aug	-3197.38	<0.001	-69.50	<0.001	–	–
T _m Sep	1806.45	<0.001	19.43	0.206	–	–
T _{mn}	–	–	-21.95	0.037	0.06	0.473
T _{mn} Jul	433.70	0.005	-14.12	0.023	–	–
T _{mn} Aug	–	–	11.90	<0.001	–	–
T _{mn} Sep	–	–	3.78	0.102	–	–
T _{mx}	-1358.55	<0.001	-22.71	0.033	0.11	0.044
T _{mx} Jun	-255.57	0.040	-6.93	0.156	–	–
T _{mx} Jul	1844.07	<0.001	–	–	–	–
T _{mx} Aug	1201.54	<0.001	32.95	<0.001	–	–
T _{mx} Sep	-1080.37	<0.001	-13.65	0.025	–	–
Observations	57		49		25	
R ² /R ² adjusted	0.870/ 0.731		0.925/ 0.760		0.420/ 0.268	

this water supply is by no means guaranteed. With predicted decrease in precipitation and increase in temperature, the depth and duration of snowpack is expected to decrease. This fact seems to be very detrimental and constitutes one of the main conservation challenges for the species, which is currently critically endangered (Gutiérrez & Blanca, 2003).

This worsening of conditions is expected to be more pronounced in populations at the lower altitudinal limit (Benito et al., 2011). The results meet the expectations as the Mulhacen 1 population at the lower altitudinal limit showed the worst situation (lower individual size, lower reproductive potential, and population size), while Mulhacen 3 the upper studied population showed the best overall situation. As the species inhabits the summit area there is no room for an altitudinal migration (Gómez, González-Megías, & Lorite, 2015) and potential habitat is increasingly scarce (Benito et al., 2014). This fact poses a conservation issue for the species that is difficult to overcome. Conservation policies should be aimed at concentrating management measures on higher elevation populations, which will be the only viable in the mid to long term, and also at seeking for potential new suitable habitats for population restoration (reinforcements or reintroductions) or assisted

migration/colonization (Vitt, Havens, & Kramer, 2010; IUCN-Species ISSG, Invasive Species Specialist Group, 2013).

4.4. Interest of the species for climatic change monitoring

As mountains are particularly prone to suffer the effects of climate change (Pepin, Bradley, & Diaz, 2015), especially Mediterranean ones (Pauli, Gottfried, & Dullinger, 2012), the use of early warning indicators of these changes and their effects on biota are especially important. In this sense, the short life cycle, restricted distribution, its sensitivity to changes in climatic parameters, as well as the long monitoring period available, spanning 20 years, all make *Arenaria nevadensis* an excellent candidate for monitoring changes arising from climatic change. However, many crucial aspects in an annual species, such as its germination ecology, the role and extent of the seed bank, or even those related to reproductive biology, remain poorly known. Moreover, studies addressing annual plant dynamics should consider an integrated perspective that includes not only climatic and environmental factors, but also genetic, and biotic factors, to gain a comprehensive and

accurate understanding of their behavior. Filling these knowledge gaps would therefore be particularly relevant for the species in order to be a good indicator.

With rising temperatures, the appearance of novel annual plant species has been detected in warmer sites in alpine areas in general, and in particular in Sierra Nevada (Lamprecht et al., 2021). They are very common species (eg. *Bromus tectorum*, *Polygonum aviculare*, etc.) that are escalating as mountain climate becomes warmer. Consequently, it is crucial to follow with long-term monitoring, adding basic knowledge of the species and including not only “losers”, such as *Arenaria nevadensis*, but also “winners”, such as new common species migrating upwards.

Credit authorship contribution statement

Cristina P. Sánchez-Rojas: Conceptualization, Data curation, Investigation, Visualization. **Javier Herrero:** Writing – review & editing, Validation, Investigation, Data curation. **Juan Lorite:** Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

The Agencia de Medio Ambiente y Agua, Junta de Andalucía, financed the field sampling and the staff of the agency led it over the assessed period.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jnc.2024.126597>.

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