



Tracing five decades of junipers' responses to global changes in Mediterranean high mountains

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ABSTRACT

Persistent and long-lived species, such as *Juniperus communis* and *Juniperus sabina*, base their population survival strategy on a great individual longevity under extreme environmental conditions. In the high Mediterranean mountain, global change stressors may challenge such persistence strategy by reducing growth and survival. This study identifies how global change is affecting the growth of juniper shrubs over five decades in Sierra Nevada (southern Spain). For this, we analysed the growth rates and foliage damages of 900 juniper shrubs by manual digitalization of their crowns in historical orthoimages from 1970's to 2020's. Almost all small junipers (96 %) and most larger junipers (86 %) increased their size, particularly at lower elevations, favoured by the lengthening of the growing season and by the abandonment of traditional land uses. Such finding supports the persistence strategy hypothesis, highlighting not only junipers' survival, but also the maintenance of growth even under harshening conditions. Despite the loss of snow cover protection, we also found good juniper foliage health, with a low proportion (~12 %) of damaged shrubs. Damages only occurred at the highest elevations, particularly on larger shrubs (> 7 m²). However, these findings should be seen as an early warning of increasing risks associated with ongoing climate change, such as heightened exposure to mechanical damage due to the increased wind speeds at high elevations and severe droughts affecting species recruitment. Using historical aerial and satellite orthoimages, we have been able for the first time to track the fate of hundreds of juniper individuals over the last 50 years.

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1. Introduction

How do persistent, long-lived species struggle for survival in global change scenarios? Persistent species base their population survival strategy on an extreme longevity of individuals, which have to be able to survive over hundreds of years even under high environmental stresses conditions (Camarero and Ortega-Martínez, 2019; García and Zamora, 2003; Grime, 2006). Typical examples of persistence by longevity and/or vegetative reproduction are more frequent among stress-tolerant species inhabiting arid, alpine and tundra habitats (Grime, 2006; Rosbakh and Poschold, 2021, 2018; Tumajer et al., 2021), as well as other poor but stable habitats such as cliffs and ravines (García et al., 1999; Larson et al., 2000, 1999). In this sense, persistence is a major ecological trait determining the long-term viability of peripheral populations of relict species as well as the inertia against extinction of many threatened plants, thereby contributing to the maintenance of the high biodiversity of the Mediterranean region.

The common juniper (*Juniperus communis* L.) and the savin juniper (*Juniperus sabina* L.) are two clear examples of long-lived species that can survive due to the remarkable survival ability and longevity of mature individuals, which can be as long as millennia (Camarero and Ortega-Martínez, 2019; Sangüesa-Barreda et al., 2022; Ward, 1982). They are widely distributed around the world, e. g., the common juniper occupies large extensions in North America, Europe and northern Asia while the savin juniper is widespread from central and southern Europe to western and central Asia. Both species currently exist as relicts from the last Ice Age in the Mediterranean mountains, as it is the case of Sierra Nevada (south-eastern Spain). Juniper scrublands have a high ecological value due to their capacity to retain soils, their abundant associated endemic flora and fauna, and their traditional use as summer grazing areas (Lorite, 2002). For these reasons, these high-mountain scrublands are protected in the European Union under the Habitats Directive (Directive 92/43/CEE).

The landscape of Mediterranean high mountains has been shaped for centuries by traditional human activities (e.g., deliberate burning, livestock grazing or agricultural practices), which have reduced the distribution area of juniper shrubs (García et al., 1999; Zamora et al., 2022). Mediterranean juniper populations are dominated by adult and senescent individuals, thus indicating a strong recruitment limitation (García et al., 1999). Water limitation during the summer drought, a cause of juniper-seedlings mortality even in boreal populations (Rosén, 1995), imposes an extremely low survival rate for most juniper seedlings on the dry hillsides of high Mediterranean mountains. According to the demographic characteristics, juniper populations in Mediterranean mountains exemplify remnant dynamics, that is, local populations surviving for long periods under ecological conditions unfavourable for recruitment (Eriksson, 1996; Zamora et al., 2022). Juniper populations in the Mediterranean area survive due to great individual longevity, an inertia which partially offsets losses to unfavourable environmental conditions and delays the possible extinction process, even in a declining population. Junipers are very slow growing, but once they reach a size large enough to escape the vagaries of the environment, they become persistent plants (García and Zamora, 2003; Herrero and Zamora, 2014). This inertia would allow it to maintain populations during the long unfavourable droughts typical of the current Mediterranean climate (García et al., 1999).

The Mediterranean region is highly vulnerable to the effects of climate change due to projected increases in temperature and substantial declines in precipitation, which are expected to be particularly pronounced during the summer months, exacerbating the region's already arid conditions (Giorgi and Lionello, 2008; IPCC, 2023; Ozturk et al., 2015). Indeed, high Mediterranean mountains have already experienced significant warming and drying trends in recent decades (Esteban-Parra et al., 2022; Pérez-Luque et al., 2015; Sigro et al., 2024) and snow cover has experienced a decrease in its duration and extension, with greater negative trends in the highest altitudes (Bonet et al., 2016; Pérez-Luque et al., 2016). This reduction in snow cover has ecological implications, since it plays a key role in insulating alpine plants from macro-climatic atmospheric conditions, maintaining milder conditions under the snowpack (De Frenne et al., 2021; Körner and Hiltbrunner, 2021) and protecting junipers from mechanical damage of windstorms and blizzards (Zamora et al., 2022). Furthermore, climate projections indicate that Mediterranean mountain ecosystems will experience an increase in temperature and a reduction in precipitation by more than 15 %, accompanied by slightly longer and more frequent droughts (Esteban-Parra et al., 2022; García-Valdecasas Ojeda et al., 2021). This, together with the confluence of abiotic stressors associated with altitude (e.g., abbreviated growth periods and severe frosts) exacerbates a severe regeneration bottleneck of juniper populations, increasing the species' sensitivity and vulnerability to supply ecosystem functions and services (IPBES, 2019).

This study aims to identify how global change is affecting the persistence strategy of juniper shrubs in the high Mediterranean mountain of Sierra Nevada (Spain) during the 1977–2020 period. Major changes in land use that have occurred during the last decades, together with climate change (Esteban-Parra et al., 2022; Pérez-Luque et al., 2015; Sigro et al., 2024), represent a substantial alteration in the ecological scenario.

Juniper shrubs base their persistence strategy on the survival of established individuals, but they could also adapt to the new conditions imposed by global changes, i.e., taking advantage of the window of opportunity offered by human land use abandonment and a warming climate. In this sense, juniper shrubs should exhibit a size-dependent response to global change drivers, where larger individuals, those having accumulated greater biomass and structural complexity, would be more resilient to environmental fluctuations than smaller ones. Therefore, hypothesis H1 postulates that while larger juniper shrubs would exhibit greater temporal stability in size, experiencing fewer fluctuations in growth or shrinkage, smaller junipers would be more sensitive to favourable (or unfavourable) conditions, exhibiting greater size changes over time.

The abandonment of traditional land uses has favoured recent recovery of juniper cover in Mediterranean regions, being particularly evident in areas historically subjected to greater human disturbances, compared to remote regions with minimal historical human influence. Therefore, we postulate (hypothesis H2) that junipers in areas previously subjected to human influence will now exhibit greater growth rates as junipers recover from these pressures, compared to remote regions where human activity already had minimal influence on them.

On the other hand, climate change is expected to have dual and opposing effects on juniper shrubs in high Mediterranean

mountains. Global warming would be lengthening the growing season, so we postulate that this positive effect on growth should be greater at lower elevations, where the growing season is longer (hypothesis H3a). At the same time, we hypothesise that the loss of snow cover due to climate change would increase crown damage due to increased exposure to windstorms and blizzards, particularly at higher elevations (hypothesis H3b).

Testing these hypotheses over the last five decades in Sierra Nevada would allow us to provide insights on how global changes might be already shaping growth and population structure of persistent shrubs in high Mediterranean mountains, a global hotspot of biological diversity.

2. Material and Methods

2.1. Study area

The study area covers the entire range of the Sierra Nevada National Park (south-eastern Spain), extending approximately 2000 km² and reaching up to 3480 m.a.s.l. (Fig. 1). Climate is Mediterranean, with cold-humid winters and hot-dry summers, and characterised by high fluctuations in temperature and precipitation. Average annual temperatures are typically above 12°C at lower altitudes (<1500 m.a.s.l.) and below 0°C at the highest peaks (>3000 m.a.s.l.). Average annual precipitation also varies significantly, with values ranging from less than 250 mm in the lower elevations to above 700 mm at summits. Winter precipitation predominantly falls as snow above 2000 m.a.s.l. In addition to the wetter and cooler climate of the northern slopes compared to the southern ones, there is also a precipitation increase from east to west (Esteban-Parra et al., 2022; Pérez-Luque et al., 2015). Due to its orographic and environmental features, Sierra Nevada is the most biodiverse area in vascular flora of the Western Mediterranean Region (Blanca et al., 1998; Cañadas et al., 2014). Such uniqueness is protected as Natural and National Park, as Natura 2000 Special Protection Area for Birds and Special Area of Conservation, and as UNESCO Biosphere Reserve and Geopark, being also included in the IUCN Green List of protected areas.

Deliberate burning of juniper shrublands to increase the area of pastures for livestock were common until the designation of the Sierra Nevada as protected area in 1986 (Lorite et al., 2022; Zamora et al., 2022). Nowadays, traditional land uses have been abandoned following rural exodus (Jiménez-Olivencia et al., 2016; Martín Civantos et al., 2022), though new disturbances such as ski slopes and tourist pressure have emerged (Zamora et al., 2022).

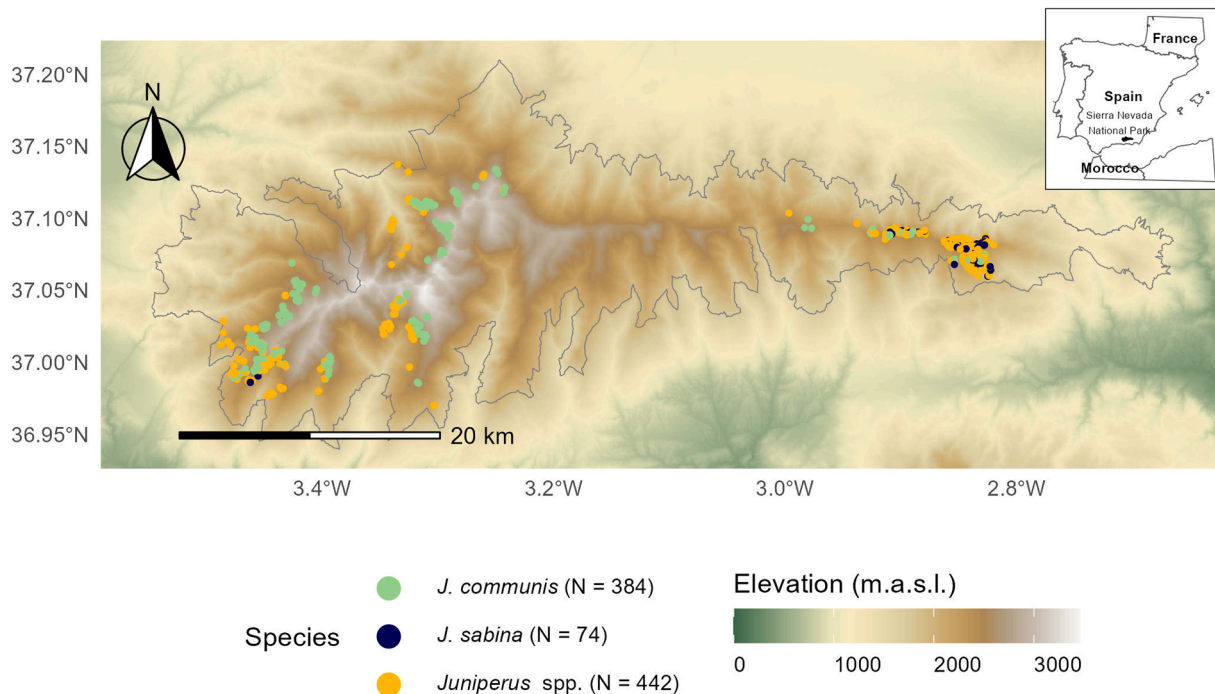


Fig. 1. Study area, location and number (N) of 900 manually digitised *Juniperus* L. shrubs in historical orthoimages from 1970's to 2020's. The two *Juniperus* species present were differentiated using a Random Forest (RF) model trained with field survey data consisting of 659 *J. communis* and 93 *J. sabina* individuals. Probability values above a 0.79 threshold were uniquely classified as *J. communis* or *J. sabina*, while those below this threshold were simply classified as *Juniperus* spp. See [Supplementary Material](#) for details. The black outline represents the boundaries of the Sierra Nevada National Park (Spain).

2.2. Ortho-imagery, juniper crown delineation, and growth estimation

To assess junipers' growth over the last five decades, the crown area of 900 junipers was tracked over time using historical aerial orthophotography from the Spanish National Plan for Aerial Orthophotography (PNOA) along with the 2020 high-resolution satellite imagery of Google Earth. To get a balanced and representative dataset across the environmental conditions of Sierra Nevada, six sampling areas were chosen: North and South faces of East, Central, and West parts. Within each stratum, the crown of 150 (900 in total) random junipers was manually digitised along altitudinal and slope gradients. We started with the image of 2020 (Figure S1), since it offered the highest quality, and the crown area of each selected juniper was subsequently digitised for previous decades (Fig. 2). If a shrub was not visible in one year (e.g., due to snow cover), its surface area was linearly interpolated between the previous and following decades. In 2020, hundreds of junipers suffered from such severe foliage damage that it could even be observed in the satellite image (i.e., their foliage appeared brownish or reddish in the image). Hence, the health status of each shrub crown was recorded as damaged (>5 % of shrub crown in red or brown colours) or undamaged (>95 % of crown in green colours) foliage. These processes were carried out in UTM-30N WGS84 projection within the QGIS 3.10.3 software.

To determine changes in shrub crown area over time (growth or shrink, but hereafter referred only as growth for simplification), we compared two approaches. None of them implied assessing tree rings or trunk widths, just crown areas. In the first approach, we computed crown growth just by comparing shrub size estimated from the first and last available images in the time series and expressed growth rate as the percentage of change in crown area between first and last images (Eq. 1). This method provides a straightforward and simpler assessment of the net change in shrub size over time.

However, comparing the crown areas from just the first and last images could introduce artifacts in shrub growth estimation due to different viewing angles or to experts' subjectivity during shrub crown delineation. To minimize such potential artifacts we tested a second approach. First, we chose the highest-quality image representing each of the five decades to estimate shrub size in each decade (Table 1). Then, we used the non-parametric linear Theil–Sen's slope and the significance test of Mann–Kendall to get a trend slope of shrub size across decades. Sen's method (Sen, 1968), unlike ordinary least squares regression, computes the median of the slopes of all lines through pairs of points, thus allowing to reduce the influence of outliers, extremes, missing data and serial dependence on the slope estimations (Gilbert, 1987). Sen's slope was divided by the initial crown area and multiplied by 100 to express it as a percentage of growth per decade that could be compared to the first approach (Eq. 2). This second approach is particularly valuable to provide a nuanced and consistent measure of long-term growth trends over time, reducing the errors when the data are irregular (e.g., different viewing angles) or contain variability (e.g. possible digitalisation errors). Theil–Sen's slope statistics were computed with the *trend* package (Pohler, 2023) within the R 4.1.2 software (R Core Team, 2024). Finally, juniper shrubs were grouped into quartiles based on their initial crown area.

$$\text{Growth rate(\%)} = \frac{\text{last} - \text{first digitised crown area}}{\text{first digitised crown area}} * 100 \quad (1)$$

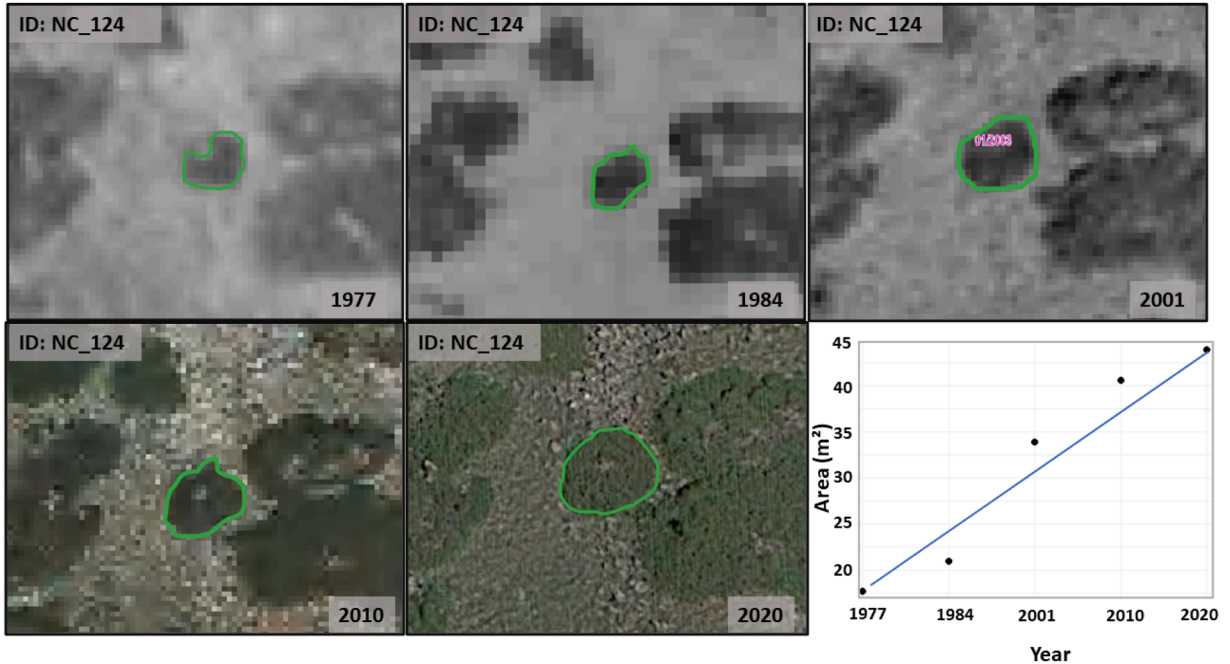


Fig. 2. Example of digitization of the same shrub at different decades in the time series, along with a scatter plot illustrating the changes in shrub area over time. The crowns are delineated in light green.

Table 1

List of selected orthoimages from each decade used to manually delineate 900 juniper crowns.

Decade (year)	Spatial resolution (m)	Spectral resolution	Product name	Source
1970's (1977)	0.5	Panchromatic	IRYDA (1977–1983)	PNOA
1980's (1984)	1	Panchromatic	Panchromatic Historical Digital Orthophoto of Andalusia (1984–1985)	PNOA
2000's (2000)	0.5	Panchromatic	Panchromatic Orthophoto of Andalusia (2000–2001)	PNOA
2010's (2010)	0.5	Red, Green, Blue	Colour Orthophoto of Andalusia (2010–201)	PNOA
2020's (2020)	0.15	Red, Green, Blue	Google Satellite image	Google Earth

$$\text{Sen's growth rate}(\%) = \frac{\text{Sen's slope}}{\text{first digitised crown area}} * 100 \quad (2)$$

2.3. Environmental change predictors

To assess how global change is affecting the persistence strategy of the two juniper species, we considered topographical, vegetation, human and climate-related predictors that could influence growth rates (Table 2). Manually, we determined the presence of surrounding vegetation or bare soil around each target shrub, as well as the presence or absence of nearby (<250 m) historical human land uses (i.e., human infrastructures such as old crops, cattle tracks, vehicle tracks, trails, roads, houses, shelters or other infrastructures). Using the centroid of each polygon, we extracted for each shrub the elevation and slope, the percentage of snow days per year (as the average for the 1985–2022 period), and the trends in percentage of snow days per year (as Theil–Sen's slope for the 1985–2022 period). Elevation was extracted from the two-meter resolution digital elevation model (DEM) provided by REDIAM, which was also used to compute topographic slope using the Horn's method (Horn, 1981). For the percentage of snow days per year, we processed in Google Earth Engine the Landsat 5, 7, and 8 collections of surface reflectance, covering the period 1985–2022 at 30 m/pixel with a temporal resolution of up to 16 days. Snow presence was determined by using the Normalised Difference Snow Index (NDSI) (Dozier, 1989), which ranges from -1 to 1, indicating low to high probability of snow. For that, we considered NDSI values > 0.35 as snow. To reduce cloud noise, we discarded scenes tagged as having more than 20 % of clouds and applied pixel-based cloud-removal algorithms using the quality-band specific bits (QA_PIXEL). Then, for every pixel of all the images captured between October and June of the following year (i.e. the hydrological year), we calculated the percentage of clear scenes that contained snow. Finally, we computed the average percentage of snow days for the 1985–2022 period and the trend in snow cover as the Theil–Sen's slope.

2.4. Statistical analyses

To assess the impact of global change predictors on shrub growth or shrink rates, we performed linear mixed models (LMMs) and linear regression models (LM) using either growth or shrink rates as a dependent variable. The LMM results from the two approaches for estimating growth (see Section 2.2) were compared. LMMs are designed to accommodate a normal and homoscedastic distribution of residuals and encompass both fixed and random effects in their analysis (Bolker et al., 2009). Unlike LM, LMMs can address potential lack of independence between observations (Cnaan et al., 1997). In our case, this was achieved by acknowledging the spatial autocorrelation of observations (growth rate) within specific locations, i.e. six sampling zones across Sierra Nevada, through the incorporation of random effects. Consequently, random effects in LMMs accounted for variations in experimental observations replicated across different sampling zones (Bolker et al., 2009). In the case of shrinkage trends, there existed a very limited number of shrinking shrubs and they were not equally distributed along the sampling zones, so the unbalanced sample and lack of variability in random effects (Table S1) impeded for their inclusion in an LMM and we therefore had to fit linear regression models (LM). In all cases, all

Table 2

Environmental change predictors used to explore the drivers of crown growth in juniper shrubs during the 1977–2020 period and the 2020 foliage damage. Expected effects were established regarding previous studies.

Variable	Description	Units	Spatial resolution (m)	Expected effect over growth rates
Elevation	Elevation of each shrub extracted from a DEM	m.a.s.l.	2	-
Slope	Slope of each shrub computed from DEM using the Horn's method	%	2	-
Pct_SnowCover	Mean of the percentage of clear-sky scenes that had snow each hydrological year (October–June) for the 1985–2022 period	% of snow-days (scenes) /year	30	-
SnowSenSlope	Sen's slope of the percentage of snow days per year along the time-series (1985–2022)	Yearly change in % of snow-days/year	30	-
Vegetation	Whether plant species other than <i>J. communis</i> and <i>J. sabina</i> were close next to the shrub	Bare soil / Vegetation	-	(-) Bare soil (+) Vegetation *Depending on shrub size
HumanImpact	Whether within a radius of 250 m, or less, historic human influence was observed	Anthropised / Non anthropised	-	(+) Anthropised (-) Non anthropised

predictors were standardised to have zero mean and unit variance. To test the hypotheses, all predictors were retained in the final models regardless of their statistical significance. Additionally, the interaction between the presence of surrounding vegetation and shrub size was included in the models to account for the possible presence of the known change from facilitation to competition interactions of nursery plants along junipers lifecycle in Mediterranean mountains (Zamora et al., 2004).

To assess the influence of global change predictors on foliage damage, we constructed a Logistic Regression (LR) model with the presence or absence of foliage damage as the dependent variable, and incorporated all standardised predictors as independent variables. To facilitate the ecological interpretation of the LR results, the model coefficients were expressed as the odds ratio (OR). OR is defined as the ratio of the odds of an event occurring in one group versus another group, or in ecological terms, the damaged versus undamaged shrubs and *vice versa*. Thus, when interpreting odds ratios (ORs) for damaged versus undamaged, ORs greater than 1 indicate that the independent variable is associated with a higher probability of damage. Conversely, ORs lower than 1 suggest that the independent variable is associated with a lower probability of damage. ORs equal to 1 imply that there is no association between the independent variable and the probability of damage. In that case, the most parsimonious model was selected after removing non-significant variables by type-II analysis-of-variance (ANOVA). In all cases, the models' goodness of fit was computed with the root mean squared error (RMSE). For model fitting, we used the lme4 library (Bates et al., 2015) implemented within the R software environment (R Core Team, 2024).

3. Results

3.1. Growth rates

For simplicity, we present the summary statistics on growing or shrinking shrubs according to the second approach, based on the Sen's slope and Mann-Kendall trend test, since it is more robust than the first one. Throughout the last five decades, most shrubs exhibited increases in shrub crown area, with 90.3 % displaying positive Sen's slopes (Fig. 3; see Figure S3 for general distribution of growth rates by quartiles). Among these, 46.5 % exhibited a significant Mann-Kendall p-value, lower than 0.1, indicating notable growth trends. Conversely, only 9.7 % showed negative slopes, with 6.9 % having a significant p-value, lower than 0.1. Notably, significant shrink trends accounted for only 0.67 % of the total shrubs.

The average positive growth rate was 3.53 m² per decade (± 3.11 m² SD), representing a 33 % increase per decade. Conversely, the average shrink was -1.95 m² per decade (± 4.37 m² SD), which is equal to a 5.63 % decrease per decade. Categorization of shrub initial sizes into quartiles showed the following distribution: Q1: 0.5–7 m²; Q2: 7–14.5 m²; Q3: 14.5–27.5 m²; Q4: 27.5–292.6 m². In this regard, the relative change in crown area over time showed statistically significant differences between quartiles (Table 3, Table 4 and Figure S4). Gains in crown area were less pronounced in larger shrubs compared to smaller ones. Specifically, the largest shrubs (Q4) exhibited approximately 56 % smaller growth rates compared to the smallest shrubs (Q1), with a growth rate of 11.28 % in Q4 versus 67.27 % in Q1.

3.2. Consequences over growth rates

The results of the LMMs explained 30 % and 27 % (of the relative and Sens' growth rates, first and second approach, respectively)

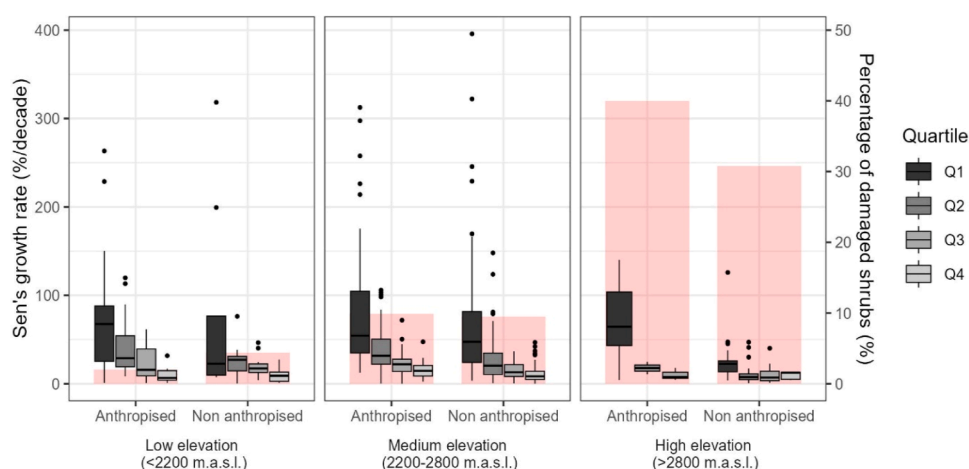


Fig. 3. Distribution of growth rates and percentage of damaged juniper shrubs with respect to human influence and elevation. Growth rates are grouped in the following quartiles: Q1: 0.5–7 m²; Q2: 7–14.5 m²; Q3: 14.5–27.5 m²; Q4: 27.5–292.6 m². Box-and-whisker (mean; 25 % and 75 % quartile) and violin plots represent the distribution and values, represented in the left y-axis. The black dots represent outliers. Percentage of damaged shrubs is represented by the red bar and should be interpreted in the right y-axis. For assessment of statistically significant effects in growth trends refer to Table 4, and, Table 5 for statistically significant effects in damage.

Table 3

Detailed summary of growth and shrink trends categorised by quartiles. The following quartiles are considered: Q1: 0.5–7 m²; Q2: 7–14.5 m²; Q3: 14.5–27.5 m²; Q4: 27.5–292.6 m². Growth and shrink trends correspond to positive and negative growth rates obtained with the two approaches (see Method). N: number of shrubs. [Table S3](#) shows equivalent results using only the shrubs that experienced positive and negative Mann-Kendall-significant growth trends.

Method	Trend	Size quartile	N	Mean growth (m ² /decade)	SD of growth (m ² /decade)	Growth rate (%/decade)
Sen's growth rate	Growth	Q1	217	2.16	1.9	67.27
		Q2	205	3.13	2.55	31.47
		Q3	198	3.37	2.32	17.03
		Q4	193	5.67	4.2	11.28
	Shrink	Q1	8	−0.33	0.23	−5.64
		Q2	20	−0.57	0.61	−5.58
		Q3	27	−1.53	1.73	−7.33
		Q4	32	−3.56	6.75	−4.22
Relative growth rate	Growth	Q1	213	1.77	1.61	54.78
		Q2	203	2.46	2.07	24.69
		Q3	190	2.61	1.98	13.07
		Q4	173	4.66	3.47	9.24
	Shrink	Q1	12	−0.36	0.25	−6.64
		Q2	22	−0.58	0.38	−5.36
		Q3	35	−1.28	1.09	−6.07
		Q4	52	−3.22	8.15	−3.86

Table 4

LMM results for positive growth trends obtained with the two approaches (see Response variable) in juniper shrub crown area during the 1977–2020 period. The random effect was the six sampling zones over Sierra Nevada. R²c and R²m mean the conditional and marginal R². Statistical significance: *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$; ****: $p \leq 0.0001$. Number of samples = 813 for Sen's growth rate and 779 for Relative growth rate response variables. [Table S2](#) shows equivalent results using only the shrubs that experienced positive and Mann-Kendall-significant growth trends.

Response variable	Predictor variables	Coefficient	p. value	R ² c	R ² m	RMSE
Sen's growth rate (%/decade) = Sen's slope / initial crown area * 100	<i>J. communis</i> - Anthropised - Q1 - Bare soil - Vegetation*Q1 (Intercept)	70.63	****	0.31	0.30	35.66
	Elevation	−9.37	****			
	Slope	−0.65				
	Vegetation	5.95				
	Q2	−35.53	****			
	Q3	−41.67	****			
	Q4	−49.92	****			
	Non anthropised	−6.59	*			
	Pct_SnowCover	4.80				
	SnowSenSlope_1985_2022	4.29	*			
	<i>J. sabina</i>	−15.90	*			
	<i>Juniperus</i> spp.	−7.13	*			
	Vegetation*Q2	1.23				
	Vegetation*Q3	−8.82				
	Vegetation*Q4	−6.70				
Relative growth rate (%) = (final - initial crown area) / (initial crown area) * 100	<i>J. communis</i> - Anthropised - Q1 - Bare soil - Vegetation*Q1 (Intercept)	243.53	****	0.29	0.27	134.08
	Elevation	−32.18	***			
	Slope	−1.65				
	Vegetation	27.83				
	Q2	−116.39	****			
	Q3	−139.04	****			
	Q4	−165.86	****			
	Non anthropised	−25.57	*			
	Pct_SnowCover	21.63	*			
	SnowSenSlope_1985_2022	20.16	**			
	<i>J. sabina</i>	−72.64	**			
	<i>Juniperus</i> spp.	−33.63	*			
	Vegetation*Q2	−8.98				
	Vegetation*Q3	−40.62				
	Vegetation*Q4	−34.35				

of the variance by fixed factors, while the zone as a random factor just explained around 1–2 % of variability ([Table 4](#); see [Table S4](#) for similar LMM results obtained using only the shrubs that experienced positive and significant growth trends according to Mann-Kendall trend test). Shrub size, elevation, human impact and the juniper species emerged as influential fixed terms, all of them showing

negative coefficients (see Figure S4 to see growth rates distribution with respect to human influence). Climate predictors showed positive effects, being the decreasing trends in snow cover more influential than the average percentage of snow cover. Despite not statistically significant, vegetation interaction with shrub size showed slight positive effects for small juniper shrubs, but the effect shifted to negative for larger ones. Regarding species, *J. communis* showed higher growth rates than *J. sabina*, while *Juniperus* spp. displayed an intermediate growth rate.

The LM models for shrinkage trends (Table S5) explained a low percentage of variance, varying from 12 % to 19 % (of the relative and Sens' growth rates, first and second approach, respectively). Only climate related predictors, snow cover and decreasing trends in snow cover, showed statistically significant coefficients. Both coefficients were negative, indicating that the shrinkage was lower with greater average snow cover and with lower decreases in snow cover. Although not statistically significant, *J. communis* showed lower shrinkage rates than *J. sabina*.

3.3. Environmental drivers of foliage damage

Out of the 900 digitised shrubs, 105 (~12 %) exhibited foliage damage, of which 86 were *J. communis*, one *J. sabina*, and 18 undetermined *Juniperus* spp. Regarding shrub size, 10 damaged shrubs were categorised within Q1, 23 in Q2, 34 in Q3, and 38 in Q4.

The LR results indicated that one in 35 *J. communis* and one in 38 *J. sabina* experienced foliage damage, which means that, without considering other variables, shrubs are much more likely to be undamaged than damaged (Table 5 and Figure S5). However, several factors, including elevation, climate-related variables, presence of surrounding vegetation, and shrub size, significantly influenced the likelihood of foliage damage. First, larger shrubs (Q4) showed almost six times more damaged individuals compared to smaller shrubs (Q1). Second, damage was three times more frequent with increasing elevation. On average, damaged shrubs were found at 2697 m.a.s.l., while undamaged shrubs were located at 2444 m.a.s.l.

4. Discussion

In this study, we digitised 900 juniper shrubs along environmental gradients to assess the potential effects of global change on *J. communis* and *J. sabina* growth rates and foliage damage in the high Mediterranean mountain of Sierra Nevada (Spain) during five decades (1970's-2020's). The manual photo-interpretation of *Juniperus* shrubs using aerial and satellite imagery highlighted that, over the last five decades, the Sierra Nevada juniper shrubs mainly increased in size, being shrinkage trends much less common. As hypothesised (H1), growth rates were found to be more pronounced in small and juvenile shrubs than in larger and adult-senescent ones, while no differences in size were found for shrinkage trends. Growth rates increased with the abandonment of traditional land uses and at lower elevations. Our results also displayed that elevation and shrub size did significantly increase the risk of crown damage in the year 2020. Fig. 3 shows a summary of growth by elevation and human influence, as well as the percentage of damage shrubs by elevation. Overall, these insights offer a better understanding of the resilience and adaptive strategies of *Juniperus* shrubs in the face of ongoing global changes in high Mediterranean mountains.

4.1. Growth rates

Practically all junipers have changed in size in the last decades. Almost all small junipers (96 %) and the majority of larger junipers (86 %) have grown. However, approximately 14 % of larger shrubs have experienced shrinkage. As a result, over the past five decades, there has been a notable transition of a significant number of juvenile individuals to reproductive stages, leading to a demographic shift where reproductive individuals become predominant within the population. This transition also involved an increase in juniper reproductive investment as reproductive individuals increase in size (García et al., 1999). Consequently, a larger number of reproductive individuals of greater size ensures a higher seed production. Conversely, shrinkage trends can be attributed to several factors such as trampling and browsing by herbivores, burial by loose stones on steep slopes, frost damages, and the loss of vegetative vigour in senescent individuals. This damage can lead to the thinning of their crowns and the establishment of faster growing grasses and other shrub species, such as cushion-like plants (*Genista versicolor* and *Cytisus galianoi* in Sierra Nevada) (Zamora et al., 2022).

Table 5

Logistic regression results of environmental variables modulating the probability of presence of undamaged over damaged canopies (and vice versa) of *Juniperus* shrubs in Sierra Nevada in the year 2020. Statistical significance: *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$; ****: $p \leq 0.0001$. Number of samples = 900.

Response variable	Predictor variables	Odds ratio (undamaged / damaged)	Odds ratio (damaged / undamaged)	p. value	R ²	RMSE
Damaged or undamaged shrubs	<i>J. communis</i> - Q1 - Bare soil (Intercept)	34.63	0.03	****	0.20	0.29
	Elevation	0.32	3.08	****		
	Vegetation	0.51	1.98	**		
	Q2	0.47	2.13			
	Q3	0.29	3.41	**		
	Q4	0.17	5.88	****		
	<i>J. sabina</i>	3.75	0.27			
	<i>Juniperus</i> spp.	3.21	0.31	****		

The persistence by longevity of junipers can be manifested in different ways. At one extreme, vegetative stasis (i.e., zero growing) may predominate and senescent individuals end up dying off, according to the species' lifespan, without replacement. Conversely, established individuals may grow, and a significant portion of juveniles may transition to reproductive stages, resulting in a population predominantly composed of long-lived reproductive individuals with a higher seed production capacity (García and Zamora, 2003). The demographic consequences are that the remaining population following this second pathway (as observed in our junipers) will be much better prepared to take advantage of the next recruitment window, which may occur during exceptionally rainy years (approximately every 40–50 years according to historical records in Sierra Nevada, Matías et al., 2022, 2012). This readiness is due to the presence of more reproductive individuals throughout the entire altitudinal gradient, serving as sources of seeds.

4.2. Controls of growth rates

In this study, we employed two approaches to calculate the change in crown size of established individuals (i.e., growth rates). The first approach, which calculates the growth rate between the first and last images, captures broad changes over time and is relatively simple to compute, but it may be subjected to unrealistic growth estimations (e.g., artifacts due to different viewing angles between images or errors during manual photo-interpretation). In contrast, by requiring a time series, the Theil-Sen's slope method provides a nuanced and consistent measure of long-term growth trends over time, minimising the impact of outliers and irregularities (Gilbert, 1987; Sen, 1968), but it implied almost three times more work time than the first approach. Here, our results demonstrate that both approaches provide consistent insights into juniper growth, with no significant discrepancies between them, probably due to the lack of digitization errors or inconsistencies between satellite images. Therefore, while the Theil-Sen method can be more accurate in some contexts, the simpler first-to-last image method was equally effective in our study. However, if the digitization process is more complex, there are inconsistencies between digitizers or satellite images, or if sufficient data and time are available, we recommend using the Theil-Sen slope for enhanced accuracy.

Overall, our results suggest that small juniper shrubs have a greater capacity for rapid growth under favourable conditions. Larger shrubs have a greater cost of maintaining their aboveground and belowground biomass (Collalti et al., 2020; Ryan et al., 1994), which may limit their growth rate. Conversely, small shrubs have a greater capacity for faster growth under favourable conditions. Despite that, our results suggest that larger and adult-senescent shrubs are still growing, which highlights the persistence strategy of the species in harsh environments such as the Mediterranean mountains (García and Zamora, 2003).

Our results confirm that the abandonment of traditional land uses positively influenced juniper growth rates (hypothesis H2), which has favoured the recent recovery of the juniper cover. *Juniperus* shrubs close to human infrastructures (old crops, cattle and vehicle tracks, trails, roads, houses, shelters or other infrastructures) and burned areas, which therefore were historically more disturbed, have experienced a higher growth rate during the last five decades than those located in more remote and natural areas. Here, the declaration of Sierra Nevada as protected area in 1986 limited the traditional use of fire to favour grazing, thus forbidding shrub burning and favouring the survival and growth of junipers that had been established. In addition, rural abandonment has decreased the effect of traditional land uses (Martín Civantos et al., 2022). Thus, our findings suggest that the interplay of limited traditional high-mountain land uses and protective legislation has facilitated the recovery and growth of juniper cover in Sierra Nevada.

Regarding climate change, our results also confirmed that lower elevations were associated with higher juniper growth rates (hypothesis H3a). While elevation is not a climate change predictor *per se*, the elevation gradient influences local climatic conditions. This supports the hypothesis that in a high mountain scenario, lower elevations benefit the most from increased temperatures (Pérez-Luque et al., 2015; Sigro et al., 2024) which extend the growing season and provide more favourable conditions for growth. As mentioned above, adaptive strategies to climate change in Mediterranean regions allow for higher growth rates in junipers through the extension of the growing season in spring and autumn, when water is not a limiting factor and due to increasing temperatures (Tumajer et al., 2021). The predicted winter warming in Mediterranean high mountains may enhance juniper growth by reducing thermal constraints and, consequently, lengthening the growing season (Castagneri et al., 2018; Dobbett et al., 2022). In junipers, meristems are protected by snow cover during winter, limiting the risk of freezing and mechanical damage (Körner, 2012; Rixen et al., 2010). Given that, the increasing temperatures together with the loss of the snow cover may facilitate the growth of saplings at higher elevations, promoting an upward shift (Lenoir et al., 2008). At the same time, the extended growing season and favourable conditions at lower elevations support the growth of larger shrubs. This explains recent findings by Khaldi et al., (2024), who found that the distribution of small *Juniperus* shrubs in Sierra Nevada is biased towards the highest elevations while the larger ones occupy the lowest elevations, thus supporting an upward shift of the species. Indeed, these juvenile junipers probably colonised the high mountains at the end of the last century and have transitioned to reproductive stages, now supplementing the continuous seed rain from adult junipers established at lower altitudes.

4.3. Drivers of foliage damage

Our results showed that approximately 12 % of digitised shrubs exhibited crown damage and that foliage damage was greater at higher elevations (hypothesis H3b) and for larger shrubs. Mechanical damage caused by windstorms and blizzards should increase with altitude due to higher wind speeds and lower minimum temperatures (Zamora et al., 2022). However, our results did not show that areas experiencing more snow losses would be experiencing the greatest foliage damages (hypothesis H3b). This is probably due to the fact that greater snow losses are not occurring at the highest summits but at lower ones, where blizzards are less frequent. Thus, *J. communis*, located at a higher altitude than *J. sabina*, ends up suffering greater mechanical damage due to a greater exposure to frost

and wind at higher elevations. We did not find evidence that the shorter duration of snow cover had increased the risk of crown damage (H3b), despite the decreasing precipitation and increasing maximum temperatures have reduced snow cover in Sierra Nevada, particularly at higher elevations (Bonet et al., 2016; Pérez-Luque et al., 2016; Pérez-Palazón et al., 2018; Polo et al., 2022).

In the long term, climate projections indicate that high Mediterranean mountain ecosystems will face rising temperatures and reduced precipitation, accompanied by longer, more severe, and frequent droughts (Esteban-Parra et al., 2022; García-Valdecasas Ojeda et al., 2021; Gonzalez-Hidalgo et al., 2024). The loss of snow cover (Pérez-Palazón et al., 2018; Polo et al., 2022), driven by warming temperatures and declining precipitation, will remove the protective layer that currently prevents shrubs from extreme cold and wind and, plants will be more vulnerable to mechanical damage (De Frenne et al., 2021; Zamora et al., 2022). Prolonged droughts will further disrupt the water balance, reducing the ability of plants to recover from physical damage and making them more susceptible to pests, diseases, and wildfires. Additionally, as wind speeds intensify under changing climate conditions (Shaw and Miyawaki, 2024), the mechanical stress on shrubs, particularly at higher elevations, is expected to increase, leading to higher rates of crown damage.

5. Conclusions

Using historical aerial orthophotography together with recent high-resolution satellite imagery from Google Satellite, we have been able for the first time to track the fate of hundreds of juniper individuals over the last 5 decades. Our findings show that: 1) junipers grow faster where human disturbance (e.g., juniper burning to produce pastures) has ceased, 2) shrub size and elevation display a key role influencing growth rates, with lower elevations offering more favourable conditions due to extended growing seasons due to global warming, 3) junipers have expanded altitudinally in recent decades, and a good proportion of juveniles and small reproductive adults now occur above 2600 m.

These results offer a more precise diagnosis of the conservation status of juniper populations in the Mediterranean high mountains than that previously carried out by García et al., (1999) using only demographic data over a specific period. Our study tracking the fate of hundreds of juniper individuals over the last 50 years allows us to make a much more accurate and, in some ways, more positive diagnosis considering plant responses to land use change and climatic change. However, the fact that individuals are mostly growing in size, does not imply that recruitment may be taking place to warrant the long-term fate of the species in Mediterranean high mountains.

This study should also serve as an early warning of the damage observed in *Juniperus* spp. shrubs at high elevations. Climate change may pose greater risks in the coming years, driven by the accelerating loss of snow cover, the increasing wind speeds caused by a more unstable atmosphere (Shaw and Miyawaki, 2024), and the more frequent and severe droughts. In 2020, these damages affected a small percentage of junipers in Sierra Nevada, but considering that the juniper population is moving to higher elevations (Khaldi et al., 2024), and that this type of damage occurs mainly there, we can predict that such damage will become more frequent, especially in larger junipers. Therefore, as climate change continues to unfold, understanding these dynamics becomes increasingly crucial for conservation efforts and ecosystem management in high mountain ecosystems from the local to the global scales. Currently, tracking shrub growth at the individual level and the associated changes in population structure and distribution across the globe might be possible thanks to the application of freely available artificial intelligence models and very-high-resolution imagery (Guirado et al., 2022; Khaldi et al., 2024). This is our pursuit for future works.

Ethics statement

Not applicable: This manuscript does not include human or animal research.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Regino Zamora reports financial support was provided by University of Granada. Regino Zamora reports financial support was provided by Spain Ministry of Science and Innovation. Domingo Alcaraz-Segura reports financial support was provided by Spain Ministry of Science and Innovation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03426](https://doi.org/10.1016/j.gecco.2025.e03426).

Data availability

Data will be made available on request.

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