



Similar functional structure and encroaching dynamics in two *Juniperus* species with contrasting distribution patterns

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Abstract In the valley of Espot in the central Iberian Pyrenees, two species of juniper, *Juniperus communis* and *J. sabina*, co-occur in the same habitats, showing a similar encroaching ability as prostrate shrubs expanding on former rangeland. Outside of this valley, however, *J. communis* is widespread from the regional to the Holarctic level whereas *J. sabina* is only sparsely found in mutually distant Palaearctic regions, where it remains restricted to scarce locations. We set out to analyse the dynamics of both species as drivers of landscape transformation and to unveil which differences may explain their contrasting biogeographic performance. To do so, we analysed them in terms of plant traits, phenology, primary growth, population structure and their

role in the landscape, all along an elevation gradient. *Juniperus communis* and *J. sabina* showed similar strong investment into stress resistance, according to the functional traits measured (SLA, LDMC, leaf lifespan), and both species expanded laterally at similarly noticeable ratios. Along the elevation gradient, we found shifts in functional traits and performance that respond to environmental differences. The populations of *J. communis* included more balanced age classes and showed good recruiting ability. By contrast, *J. sabina* exhibited a poor recruiting ability, with populations lacking juveniles and including notably old shrubs. The longevity and clonal performance of this species would explain its persistence only in particular locations scattered over distant regions. Therefore, the contrasting plant distribution and ecology of the two species (i.e. a widespread and active colonizer vs a relict growing in secluded locations) appears to be based on a few interspecific developmental and reproductive differences.

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Introduction

In the current patchy landscapes of temperate mountain areas, some shrub species play a prominent role in dynamic vegetation units. The expansion of shrubby

vegetation in grasslands has increased in many European regions in recent decades (MacDonald et al. 2000; Dullinger et al. 2003; Sanz-Elorza et al. 2003; Roura-Pascual et al. 2005; Hallinger et al. 2010; Pedashenko et al. 2015). The ongoing encroachment by shrubs, observed in many places, is mostly a consequence of the abandonment of traditional practices, chiefly extensive livestock grazing and the use of fire to create summer pastures (Lasanta-Martínez et al. 2005; Komac et al. 2013). Although global warming promotes the growth and expansion of woody species in temperature-limited ecosystems (Körner and Paulsen 2004), land use change is the main driver in anthropogenic treeless landscapes of Alpine mountain systems (Palombo et al. 2013; Ameztegui et al. 2016; Cudlín et al. 2017). Generally, the main shrub species driving encroachment feature successful characteristics such as a good colonizing ability (resulting, e.g., from effective seedling establishment, clonal growth, or both), an appropriate combination of stress-resistance traits (tough leaves and twigs, longevity) and an ability to recover after disturbance (active resprouting, persistent or well-dispersed seed banks; Montané et al. 2010; Liu et al. 2013; Ninot et al. 2017; Grau et al. 2019). These characteristics allow such species to be determinative in extensive vegetation shifts, especially those spanning wide environmental niches. In the genus *Juniperus*, different species are good examples of such performance in mountain landscapes in a wide array of Holarctic regions (Houle and Babeaux 1994; García et al. 1999; Thomas et al. 2007; Adams 2014; Grigoriev et al. 2022).

Shrub encroachment is known to cause important changes to the properties of soil and litter in Alpine mountain ranges, mainly where species with evergreen long-lived foliage, such as junipers, are involved (Montané et al. 2010; Grau et al. 2019; Urbina et al. 2020). Unlike in grasslands, essential soil nutrients (N, P, K) mostly decrease in mature shrublands because they become sequestered into biomass and necromass as secondary succession progresses. In turn, this favours the dominance of the same long-lived stress-resistant plant species (Adams 2014; Grau et al. 2019). In the patched landscapes found in the Pyrenees and similar ranges, shrub encroachment leads to a subsequent advance of woodland species, which has been particularly noticeable over the last decades (Ninot et al. 2011; Álvarez-Martínez et al. 2014; Ameztegui et al. 2021). Shrublands are therefore mostly transient vegetation

units at decadal scales, at least below the treeline. Being dynamic ecosystems, shrublands harbour a wide range of characteristic biodiversity, including birds, invertebrates and fungal communities (Thomas et al. 2007; Grau et al. 2019), and thus are of considerable conservation value. In fact, many habitats occurring along encroaching juniper stands include valuable biodiversity components and unique ecological processes, and thus are included in European conservation directives (Giménez Benavides 2009; Montesinos et al. 2009). Acquiring functional knowledge on encroaching scrubs is therefore a *sine qua non* condition for better understanding and managing biodiversity and natural landscapes.

Coexisting shrub species with apparently similar characteristics, such as growth form or leaf habit, may present contrasting colonizing behaviour, which may translate into their contrasting encroachment ability at local and regional scale, and contrasting biogeographic patterns at global scale. This may be a response to differences in functional traits, life strategy and phenological cycle between these species, as has been shown for many plant species in a variety of ecosystems and scales (Murray et al. 2002; Adler et al. 2014; Sporbert et al. 2021; Pinho et al. 2022). The relative advantage of one species over another could be due to (i) traits describing their capacity for carbon acquisition and growth, and thus their colonizing or competition ability, (ii) their life history and population structure, as the base for local persistence, or (iii) their reproductive and dispersal strategy (Lavergne et al. 2004; Syphard and Franklin 2010; Gabriellová et al. 2013; Gaüzère et al. 2023).

The Pyrenean valley of Espot provides an opportunity for analysing two congeneric species, *J. communis* and *J. sabina*, which foster active encroaching processes in the same open habitats in a wide range of elevation and environmental conditions (Ninot and Carrillo 2019). Despite their morphological and functional similarity, and evidence of a similar successional role in the area, these species differ markedly in their overall ecological and biogeographical distribution. Whereas *J. communis* is a Holarctic widespread species, commonly forming active populations in a wide range of habitats, *J. sabina* is restricted to a few scattered Palaearctic regions, where it forms apparently relict, poor populations in open, dry mountain ecosystems (Wesche et al. 2005; Arzac et al. 2016; Ninot and Carrillo 2019). A detailed comparative analysis of these congeneric species is of particular

interest for understanding, on the one hand, the vegetation dynamics dominated by widespread expanding shrub species within encroaching processes occurring worldwide and, on the other, the persistence strategy and fate of rare relicts, which is useful in designing conservation policies. Moreover, the sharp elevation gradient found in the Espot valley should promote varying responses in the two *Juniperus* species, from the lower drought-limiting to the higher cold-limiting sites where they co-occur (Arzac et al. 2016; García-Cervigón et al. 2017), which may help understand their distinct biogeographic roles.

The primary aim of this study is to understand the mechanisms driving the dynamics of *J. communis* and *J. sabina* as leaders of ongoing landscape changes in the mountain area in question. We have studied these dynamics in parallel at sampling sites at distinct elevations, through a wide analysis of their plant traits, phenology, primary growth, population structure, and role in the landscape. In addition, we aimed to unveil whether differences in the aforementioned characteristics may explain the contrasting biogeographic and ecological performance between these species, taking advantage of the fact that they play a similar ecological role in the study area, including a wide elevation gradient. We hypothesized that, in spite of sharing a similar habit, performance and vegetation pattern, the wider distribution and colonization ability of *J. communis* could be driven by small advantages given by plant functional traits better coupled to varying conditions, or by a stronger colonizing ability. Conversely, the apparently lower population dynamics of *J. sabina* should be compensated by other developmental or persistence traits, which would explain its success at least in the area studied and in other scattered locations across its range. Along the elevation gradient, the performance of *J. sabina* is expected to decrease from the low-elevation site (experiencing moderate winter conditions and noticeable summer drought) to the high-elevation site (with longer and harsher winters and mild summers) whereas *J. communis* should show an inverse trend.

Material and Methods

Study Species

The two species studied are similar in most ecological and functional features, being both xeromorphic, slow-growing conifers that, in the area here

considered, develop as diffuse or prostrate shrubs in the form of near-circular, expanding patches. Both species are dioecious and, as is characteristic in the genus *Juniperus*, produce berry-like cones (fruits hereafter) remaining on the plant for months. Both species are resiniferous, heliophilous and tolerant to contrasting temperatures. However, they clearly differ in their biogeographic status and, apparently, in a few morpho-functional traits (Adams 2014).

Juniperus communis L. is widely distributed through Eurasia and North America and from the Arctic to sub-tropical mountain ranges. In the Pyrenees it is typically an erect shrub at lower or moderate elevations (in the submontane and montane belts), but grows as a diffuse or even cushion-shaped shrub at higher elevations (in the subalpine and alpine belts). The latter forms are identified as subsp. *nana* (Wild.) Syme whereas intermediate growth forms, found in the montane and lower subalpine belts, correspond to var. *intermedia* (Schur) Sanio (Bolòs and Vigo 1984). The shrubs here investigated belong to this variety, to which we hereinafter refer to as *J. communis*. It is particularly noticeable in pasture landscapes, where individuals encompass a gradation of habits and sizes, rarely exceeding 6 m in diameter (Ninot and Carrillo 2019). Although their branches are mostly prostrate, one or more stems grow upwards or obliquely. Their leaves are acicular, and thus light is progressively filtered through the canopy.

Juniperus sabina L. is found sparsely from South-Western Europe to Mongolia and from North Africa to the Alps. It occurs mainly in dry, continental mountain ranges around the Mediterranean basin, being very rare or scattered in the Pyrenees from the submontane to the subalpine belt (Adams and Schwarzbach 2006; Bolòs and Vigo 1984; Florapyr 2023). However, it is common in the Espot valley and neighbouring areas (central Iberian Pyrenees), where it plays a noticeable role on rocky slopes (Ninot and Carrillo 2019). Its growth form is creeping, the main branches producing adventitious roots and forming medium-sized to large spots (8–12 m in diameter) tightly adapted to the topography. Leaves are scale-like and cover younger shoots.

Study Area

This study was performed in the Espot valley and surrounding areas, where *J. sabina* and *J. communis* coexist in open or patched landscapes mostly built on south-facing slopes of varying parent material,

inclination and rockiness. The area spans from 1,300 to 2,100 m a.s.l. and encompasses a sharp bioclimatic gradient. This is expressed through key bioclimatic indicators such as the length of the growing period, which shortens along the elevation gradient from 7.5 to 5 months (Ninot et al. 2013); the annual rainfall average, increasing from 690 to some 1,200 mm (Meteocat 2023); and the ratio between summer potential evapotranspiration and summer rainfall (Mediterraneity index), which decreases from 1.3 to 0.9 (Ninot et al. 2013). In any case, the shrubs investigated mostly thrive on poorly developed soils, where the water supply is clearly lower than that assumed in general models for regular soils. Thus, plant life in higher-up areas face a long and cold resting period in winter and a mild summer with moderate drought events. By contrast, at lower elevations winter is shorter and milder, and summer brings harsh drought conditions.

We sampled shrubs at three sites along the elevation gradient described, which we hereafter refer to as the low-, the mid- and the high-elevation site (Fig. 1). The low-elevation site is situated at 1,300–1,450 m a.s.l. ($1^{\circ} 7' 1.707''$ E, $42^{\circ} 36' 4.1724''$ N; 121,500 m²), where xerophilous grasslands of the *Xerobromion erecti* (Br.-Bl. et Moor 1938) Zoller 1954 alliance dominate the landscape, together with rocky shelves and *Pinus sylvestris* L. stands (Fig. S1 in the electronic supplementary material). The mid-elevation site spans between 1,500 and 1,620 m a. s. l. ($1^{\circ} 3' 42.6168''$ E, $42^{\circ} 35' 10.2474''$ N; 134,500 m²) on a slope built of lime schists and ranges from small rocky outcrops to eroded sloping patches to gentle grassland stands with xerophilous and meso-xerophilous pastures (*Xerobromion erecti*, *Bromion erecti* Koch 1926), and to expanding dry forests of *P. sylvestris* (Fig. S2 in the electronic supplementary material). In both locations, found near small villages, the traditionally cultivated landscape consisted of extensive pastures and sown fields until a few decades ago. Nowadays, the abandonment of rural activity has allowed *Juniperus* and other shrubs to encroach into open areas as part of secondary succession leading to pinewoods of *Pinus sylvestris*. The high-elevation site was found upwards on the same main slope at 1,975–2,150 m a. s. l. ($1^{\circ} 4' 44.7702''$ E, $42^{\circ} 35' 27.8586''$ N; 36,900 m²), where shrubby patches alternate with schist rocky spots, eroding dry pastures (*Bromion erecti*) and open stands of *Pinus uncinata* Ramond ex DC. (Fig. S3 in the electronic supplementary material). At this high elevation, the

traditional land use consisted of extensive pasturage and clear-cutting, which decreased from the mid-20th century, resulting in the present-day abandonment.

Therefore, the three sampling sites were found in forest dominions, where encroachment of open areas by *Juniperus* and other shrubs is part of secondary succession leading to pinewoods (Fig. S4 in the electronic supplementary material). In fact, most *Juniperus* stands included other shrub species or tree juveniles, which may indicate facilitation effects (Verdú et al. 2004). Along the same line, young pinewood spots overgrowing older juniper layers are also part of these landscapes.

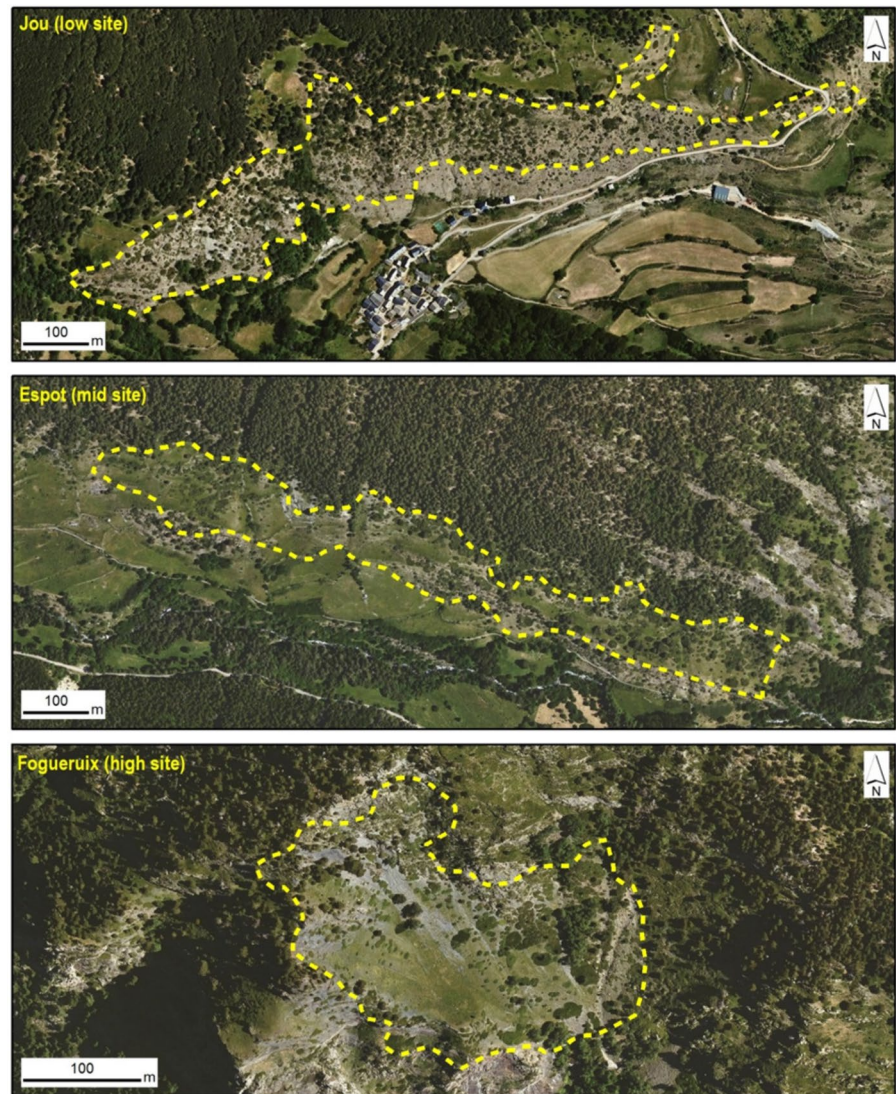
Functional Structure

To gain a comprehensive overview of the functional structure of both *Juniperus* species, we assessed relevant plant traits at the individual scale and the biomass distribution into leaves and stems at the population level at the three sampling sites.

In July 2014 we selected 20 individuals per species representative of each of the sampling sites chosen at given distance intervals along a meandering pathway. For each individual we measured canopy height and collected twigs to calculate specific leaf area (SLA, mm² · mg⁻¹) and leaf dry mater content (LDMC, mg · g⁻¹). The next autumn we also collected ripe fruits from ten female shrubs in each case. This sampling and the subsequent treatments in the laboratory followed the protocols set by Pérez-Harguindeguy et al. (2013). We used sets of five leaves per individual to obtain their fresh weight and scanned them to measure their area with the software *ImageJ* (Abràmoff et al. 2004). In the case of *J. sabina*, we regarded each small leafy twig as a ‘functional leaf’, namely the apical segment of each stem axis plus the scale-like leaves covering it, and calculated the leaf area as twice the twig lateral projection. Dry weight was obtained after drying the leaf subsamples at 60°C for 48 hours. We calculated seed mass as the air-dried seed weight average obtained from sets of 20 (in the case of *J. sabina*) or 40 (in the case of *J. communis*) seeds, each set corresponding to one individual plant.

In representative spots of the shrub communities, we clipped the aerial biomass at the ground level within five distinct subsamples – specifically, detached square areas 40 × 40 cm each. From a significant part of each subsample (at least 20% of its weight), we sorted separately the leaves and stems of the focal

Fig. 1 Aerial ortophotographs of the three sites sampled (taken from the Institut Cartogràfic i Geològic de Catalunya – Vissir3 (<http://srv.icgc.cat/vissir3>, last accessed in November 2023). The polygons outlined correspond to the landscape units considered, where we located the sampling shrubs and evaluated the populations significance per species.



species. We obtained the dry weight of the subsamples after drying them at 70°C for 48 h. Then we extrapolated the weight values of the leaves and stems separated to each subsample and calculated the average dry mass per ground area for each sampling site.

Canopy Expansion

From autumn 2016 to spring 2017 we analysed the two study species for a growth assessment at the three sampling sites. We sampled 16 shrubs per species and site, representative of the diversity of shapes found in each case (i.e. including small, medium-sized and large individuals in similar proportions). Because different

studies dealing with the costs of dioecy with respect to the vegetative growth of female plants give distinct responses depending on the sex of the individual (Obeso 2002; Shetti et al. 2018), we introduced sex as a variable in the growth assessment, considering the canopy expansion rate the most reliable measure of performance response in the mid term. Thus, out of the 16 individuals assessed per species at each of the sampling sites, half were males and half females.

For each shrub we measured two diameters of the canopy (one following the slope gradient, the other perpendicular to it), its maximum height and the basal diameter of the thickest stem. We then selected two ultimate prostrate branches illustrative of the centrifugal expansion of

the shrub (one upslope, the other downslope) to analyse their primary growth (i.e. the elongation ratio per year). For this, we took one small stem segment at 100 cm from the branch tip to the centre of the shrub. Complementarily, we noted relevant site features of each shrub sampled, namely the slope, habitat (categorized as mesophilous grassland, xerophilous grassland or rocky area) and occurrence of other woody species within the shrub stand. We also located and labelled the shrubs sampled on detailed orthoimages.

In the laboratory, we prepared stem sections and counted the annual xylem rings of each stem segment under a stereomicroscope.

We calculated the canopy area of each shrub using the two diameters measured as the axes of an ellipse; and the stem elongation ratio or shrub radial growth per year (hereafter referred to as the primary growth of the shrubs) as the quotient between the length of the stem cut (100 cm) and the number of years at the section level, following the procedure set by García-Cervigón et al. (2017) for the same study species.

Phenomorphology

At the mid-elevation site, where both summer droughts and winter temperatures are moderate, we analysed the phenological performance of the two study species to compare their response to common climatic stress conditions. There, from spring to autumn of the years 2013 and 2014, we recorded roughly each 20 days the status of five male and five female individuals per *Juniperus* species through field notes, detailed photographs and abundant samples of plant material. We then standardized the information gathered using the criteria and phenophases drawn by Orshan (1989), mainly concerning flowering and shoot production. Photos and herbarium samples were also used to refine the field records and to evaluate the average leaf life span, using the procedure established by Pérez-Harguindeguy et al. (2013) for conifers.

In addition, we assessed fruit production in seven female individuals per species at the same mid-elevation site. We clipped the fruiting branches included in three representative square areas of 40 × 40 cm per individual and counted the maturing fruits. Then we obtained an individual value of fruit production in the form of fruits per square metre of projected shrub canopy. Because *J. communis* is reported to be a masting species (Thomas et al. 2007), our evaluation has to be taken as a rough approximation, at least for this species.

Population structure

We characterized the population structure based on data collected from the shrubs sampled for the analysis of canopy expansion, together with data from other shrubs measured in the field. We analysed up to 30–36 shrubs of all sizes per species at each of the sampling sites. The newly measured shrubs were chosen to represent the variety of sizes and habitats occupied at each site. We characterized these shrubs in terms of size (two perpendicular diameters), sex, habitat and co-occurring species of trees or taller shrubs.

Moreover, we analysed the three sites sampled through aerial orthophotographs taken in 2016, available from the on-line facility Vissir3 of the Institut Cartogràfic i Geològic de Catalunya (Fig. 1; ICGC 2020). This tool allowed us to evaluate the extension and landscape structure of each of the sampling sites and to observe the orthoimages in sufficient detail to identify individual trees and shrubs. After locating the shrubs sampled in the field on the orthophotographs, we could identify the other *J. communis* or *J. sabina* shrubs that were not sampled (at least those larger than 2 m) and measure their diameter at 1 m resolution. In this way, we evaluated the ground area covered by the whole populations of the two species studied within each sampling site.

Statistical analyses

To compare plant functional traits (PFT), above-ground structure and fruit production of the two species, we fitted simple linear models and performed analysis of variance (ANOVA). For the analysis of PFT and aboveground structure, we used the shrub species (*J. communis* and *J. sabina*), sampling site (low-, mid- and high-elevation) and their interaction as fixed effects. We used log-transformations to fulfil the assumptions of normality and homoscedasticity. Where transformations did not work, we used a ‘varIdent’ structure (Zuur et al. 2009) to account for heteroscedasticity. For the analysis of fruit production, we used the non-parametric Wilcoxon sum rank test.

Finally, we fitted a linear mixed-effects model to assess the effect of several biotic and abiotic parameters on shrub canopy expansion and used ANOVA to test for significant effects. We fitted the model including primary growth of the branches as the response variable; stem diameter, shrub height and slope as covariates; and sampling site (high-, mid- and

low-elevation), shrub species, sex and their interactions as fixed effects. We included the type of habitat (mesophilous grassland, xerophilous grassland and rocky slope) as a random factor and checked if it contributed to the model fit with AICc. We also tested whether the covariates contributed to the model fits with AICc. The only covariate included in the final model was slope. We visually checked the normality and homoscedasticity of residuals and used Tukey post hoc tests to test the differences between factor levels. We performed all statistical analyses with R v. 4.3.0 (R Core Team 2023), using the packages ‘nlme’ (Pinheiro et al. 2019) for linear mixed-effects models and ‘emmeans’ (Lenth 2020) for post-hoc tests. We used the package ‘ggplot2’ (Wickham 2016) to produce graphics.

Results

Functional Structure

Referring to leaf traits, both *J. communis* and *J. sabina* had similarly low SLA (averaging 5.8 and 4.2 $\text{mm}^2 \cdot \text{mg}^{-1}$, respectively) and high LDMC (491 and 486 $\text{mg} \cdot \text{g}^{-1}$; Fig. 2a, b; Table S1 in the electronic supplementary material). In more detail, there were significant differences in SLA and LDMC between species and sites. Whereas *J. communis* had larger SLA than *J. sabina* at the mid- and high-elevation sites, they did not differ at the low site (Table 1). For LDMC, site-related differences (higher values at the low site) were more evident for *J. communis*.

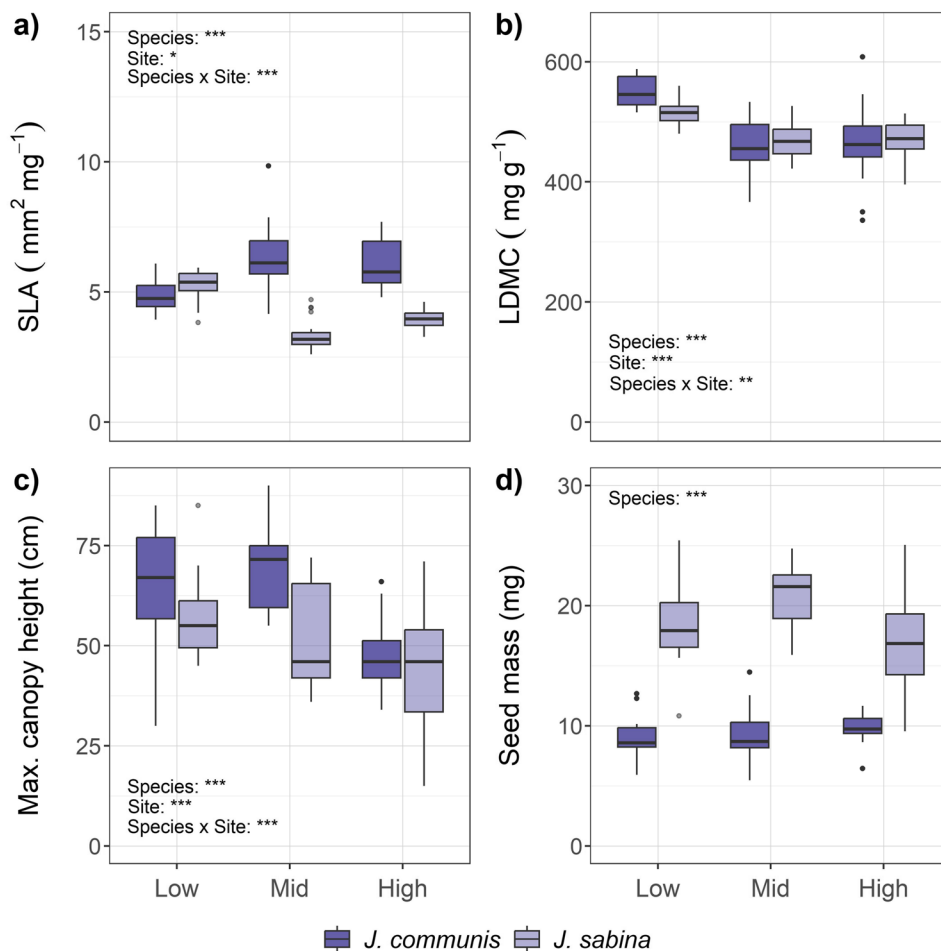


Fig. 2 Plant functional traits studied for each of the *Juniperus* species at each sampling site (low-, mid- and high-elevation; obtained from 20 individuals per site, 10 in the case of seed mass). Each box covers the 50% of the data in each case, and

the horizontal line within it is the median. Asterisks indicate significant differences at $P < 0.001$ (***), at $0.001 \leq P < 0.01$ (**) and at $0.01 \leq P < 0.05$ (*).

There were significant differences between the sampling sites and the species in canopy height, which ranged on average from 47 to 67 cm in *J. communis* and from 45 to 57 cm in *J. sabina*, being smaller at the high-elevation site (Fig. 2c; Table S1 in the electronic supplementary material). Seed mass differed between the species, with *J. sabina* producing seeds twice as heavy as those of *J. communis* across all three sites (20.3 mg vs 9.4 mg on average; Fig. 2d; Table S1 in the electronic supplementary material).

Both species formed dense shrubby communities, considering their low canopy height (dry weight of aboveground biomass averaging $2,409 \text{ g} \cdot \text{m}^{-2}$ in *J. communis* and $3,574 \text{ g} \cdot \text{m}^{-2}$ in *J. sabina*), with leaves playing a noticeable role (27–36% of dry weight in *J. communis*, 41–47% in *J. sabina*; Fig. 3; Table S2 in the electronic supplementary material). The differences between the species were significant, with *J. sabina* forming much denser shrubs (referring to both stems and leaves) at the mid- and high-elevation sites. Differences between the sites were also significant, with *J. sabina* showing a clear maximum at the mid-elevation site (Table 1, Fig. 3).

Canopy Expansion

The canopy expansion during the last decades of the shrubs measured ($N = 88$) varied depending on the species and sampling site. Primary growth or elongation of prostrate branches showed significant differences between the sites ($F_{2,70} = 40.21$, $P < 0.001$) and species ($F_{1,70} = 66.67$, $P < 0.001$), and for the species $\times$ sex interaction ($F_{1,70} = 5.93$, $P = 0.017$; Fig. 4). Primary growth was greater in *J. sabina* than

in *J. communis* (mean $\pm$ SD values of 8.71 ± 0.31 cm per year and 6.48 ± 0.30 cm per year, respectively; more data are presented in Table S3 in the electronic supplementary material), both for males and females. Within each species, we found only a trend towards greater growth in females than in males of *J. sabina* (post-hoc Tukey = 0.051). Post hoc tests showed that primary growth at the high-elevation site was significantly lower than at the mid- ($P < 0.001$) and low-elevation sites ($P < 0.001$), but there were no significant differences between the mid-elevation and the low-elevation sites ($P = 0.963$). Habitat type could not be proven to influence primary growth, because after sampling it did not result in a balanced factor and was partly nested within the effect of the site (Table S4 in the electronic supplementary material).

Based on our field measurements and observations, the performance of the two species differed in a few key aspects. With respect to the size of shrubs and thickness of their main stems, larger shrubs of *J. communis* consisted of one or more thick main stems (e.g. thicker than 40 mm in diameter and sometimes even thicker than 60 mm). By contrast, larger shrubs of *J. sabina* consisted of medium-sized stems (mostly 20–40 mm in diameter; Fig. S5 in the electronic supplementary material). This difference reflects that most *J. communis* shrubs maintained main stems throughout their lifespan whereas in larger *J. sabina* shrubs older stems had vanished. In a few cases this resulted in an empty gap in the central part of the shrub.

Phenomorphology

We have synthesized all the phenomorphological data collected as a simplified phenogram for each species

Table 1 Results of LME ANOVA of data on functional traits (PFT) and aboveground structure. Significant ($P < 0.05$) and marginally significant ($0.05 \leq P < 0.1$) P -values are shown in bold

	<i>D.f.</i>	Species		Sampling site		Species × sampling site	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
1. PFT							
Height	1,109	22.76	< 0.001	18.91	< 0.001	7.67	< 0.001
SLA	1,114	153.14	< 0.001	4.61	0.012	66.65	< 0.001
LDMC	1,114	26.55	< 0.001	64.19	< 0.001	7.29	0.001
Seed mass	1,114	113.21	< 0.001	0.50	0.611	2.20	0.121
2. Aboveground structure							
Stem biomass	1,24	4.28	0.050	11.11	< 0.001	11.52	< 0.001
Leaf biomass	1,24	89.63	< 0.001	5.83	0.009	18.50	< 0.001

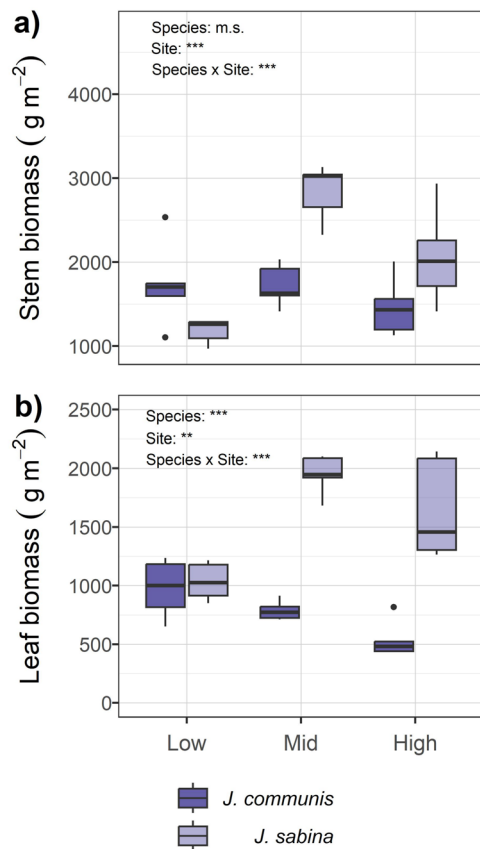


Fig. 3 Aboveground biomass of the two *Juniperus* species at each sampling site (low-, mid- and high-elevation), expressed as the dry weight of stems (a) and leaves (b) per square metre covered. Asterisks indicate significant differences at $P < 0.001$ (***), at $0.001 \leq P < 0.01$ (**) and at $0.01 \leq P < 0.05$ (*); m.s. indicates marginally significant differences at $0.05 \leq P < 0.1$.

(Fig. 5). Both species performed similarly during long phenological phases, which was particularly apparent for shoot elongation. This process took place from early spring to the beginning of winter, with some delay in *J. sabina* with respect to *J. communis*. Leaves were similarly long-lived in both species, with an estimated average lifespan of 42 months for *J. sabina* and 38 months for *J. communis*. In terms of flowering, *J. communis* blossomed massively in spring whereas *J. sabina* produced cones from mid-summer to the following early spring (but not in true winter), albeit at low density and showing substantial variation between individuals and years. Fruit ripening occurred earlier in *J. communis* than in *J. sabina*, and in the second species fruits remained on the plant for a longer time.

As for fruit production, *J. communis* produced significantly more fruits than *J. sabina* in 2021 ($W = 49$, $P = 0.002$). On average, we recorded more than fifteen times more fruits in the former than in the latter ($2,681 \pm 1,012$ fruits $\cdot \text{m}^{-2}$ vs 161 ± 208 fruits $\cdot \text{m}^{-2}$, respectively; Fig. 6). In fact, during the two years of phenomorphological monitoring (2013 and 2014), similar lower fruit production and greater individual heterogeneity were observed in *J. sabina* compared to *J. communis*. Moreover, this numerical difference is magnified in terms of the number of seeds, as *J. communis* produced twice as many seeds as *J. sabina* per fruit (2.62 ± 0.24 vs 1.24 ± 0.14).

Population Structure

The populations of *J. communis* found at the three sampling sites included greater proportions of shrubs of small to medium sizes than those of *J. sabina* (Fig. 7a, c, e). By contrast, the populations of *J. sabina* consisted of larger shrubs, particularly at the mid- and high-elevation sites. There, one-third of the

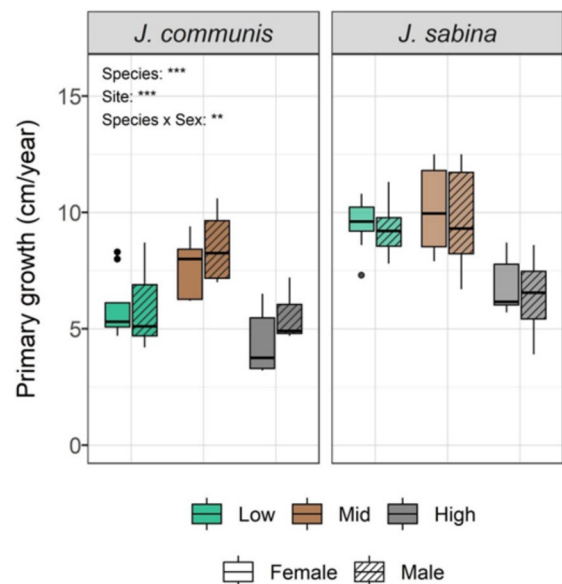


Fig. 4 Expansion of the two *Juniperus* species at each sampling site, expressed as cm of primary growth per year. Data for female individuals are shown on the left side of each boxplot pair, and data for male individuals are presented on the right. Significant differences obtained with the model including both species are shown in the left panel. Asterisks indicate significant differences at $P < 0.01$ (***), and at $0.05 > P > 0.01$ (**).



Fig. 5 Phenology of the two *Juniperus* species under study at the mid-elevation site in terms of vegetative and reproductive main phases.

J. sabina shrubs covered more than 100 m² each –an area not reached by any of the *J. communis* shrubs measured (Fig. S5 in the electronic supplementary material). Indeed, in a few cases we had to discard some groups of poorly detached *J. sabina* spots from the analysis because we could not ensure their distinctiveness, meaning that they might correspond to a single very large clone that fragmented over time.

To describe the age structure of the shrub populations, we transformed the radius length of the shrubs into age, using the average primary growth per year for each species and site stated in the section of canopy expansion. The age patterns obtained were similar to that found for size structure, with *J. communis* showing a larger proportion of young shrubs

and *J. sabina* showing more old shrubs, although the difference is less apparent than that based on size (Fig. 7b, d, f). In both species, we can assume some misdetection of very small individuals hidden in the rugged landscape, which would turn the smaller – and younger – class in each species and sampling site sub-represented in our counting.

In any case, the age structure of both species revealed noticeable recruitment during the last decades. In the case of *J. communis*, the maximum recruitment would have occurred 20–30 years ago at the low- and mid-elevation sites whereas at the high-elevation site the maximum would have peaked 40–50 years ago. Recruitment in *J. sabina* showed less pronounced maxima, which would have occurred one or two decades earlier.

Both *Juniperus* species exhibited varying cover in the three landscapes considered. In the low-, mid- and high-elevation sites, *J. communis* occupied 2.2%, 3.0% and 5.9% of each local area, and *J. sabina* occupied 3.7%, 6.7% and 15.7% of each area (Fig. 1; Table S4 in the electronic supplementary material). Their cover must have increased sharply during the last decades, as illustrated above. Namely, considering the radial expansion rates calculated, the shrubs of *J. communis* analysed have increased their local cover by 82.1%, 123.6% and 53.7% over the course of a single decade (between 2007 and 2017) at the low-, mid- and high-elevation sites, respectively. By contrast, the values for *J. sabina* are 62.9%, 45.8% and 39.1%. Note that, although *J. sabina* showed higher relative cover and individual expansion rates than *J. communis* everywhere, the second species achieved higher percentage increases in global cover, as it was represented by smaller shrubs, in which relative expansion was greater.

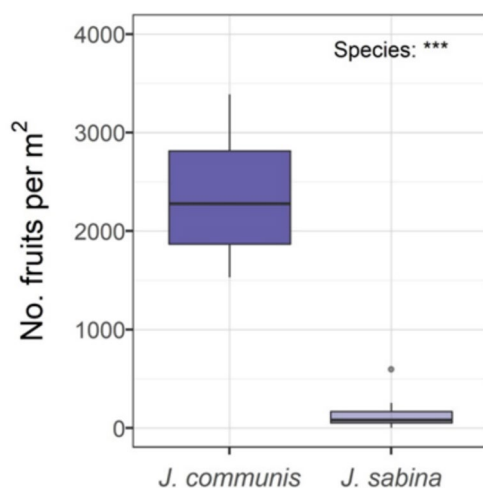


Fig. 6 Fruit production (2021) by the two study species at the mid-elevation site, expressed as the number of fruits per square metre covered by the shrubs. Asterisks indicate significant differences between the species ($P < 0.01$).

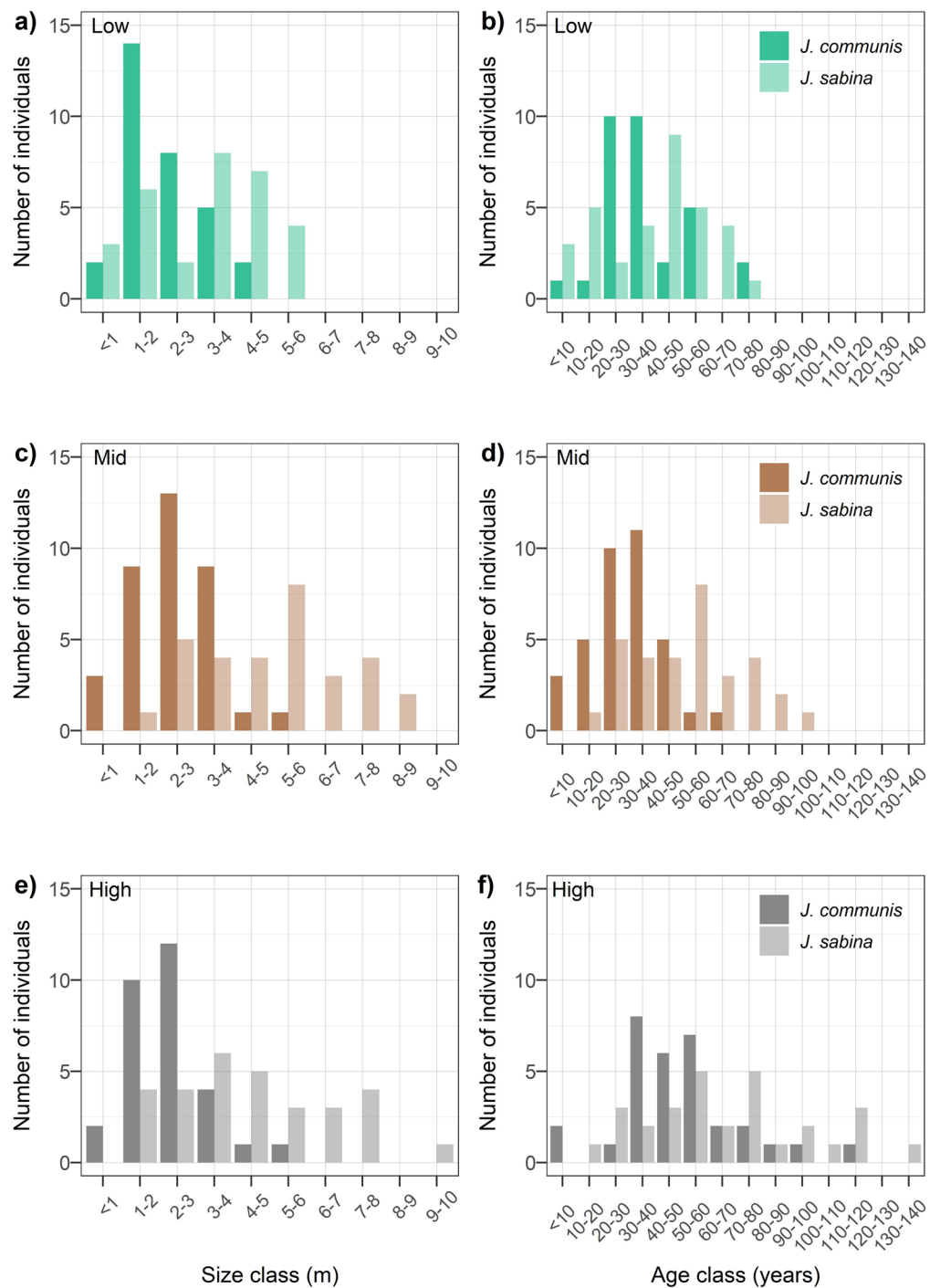


Fig. 7 Population structure of the two *Juniperus* species across the three locations sampled (from top to bottom) at the low-, mid- and high-elevation sites, expressed as the number of

individuals distributed into size classes defined based on average stem radius (left panels, a, c, e) and into decadal age intervals (right panels, b, d, f)

Across the distinct structure of these landscapes, *J. sabina* was more frequently found in rocky areas or on xerophilous grasslands (including outcrop spots) whereas *J. communis* was more frequent in mesophilous grasslands (Table S4 in the electronic supplementary material).

Discussion

Subtle Functional Differences May Result Into Contrasting Species Behaviour

Both *J. communis* and *J. sabina* strongly invest in leaves resistant to stress through distinct morphology and structure, according to the leaf trait values obtained (low SLA, high LDMC, and long lifespan; Westoby et al. 2002; Grime 2006; Pérez-Harguindeguy et al. 2013). The small differences in SLA and leaf lifespan found between the species possibly reflect the greater investment in stress resistance by *J. sabina* and may be related to the distinct leaf morphology between the two species. In any case, the distinct functional structure of leaves allows both species to cope with summer drought stress, which is more pronounced at the low-elevation site, and with frost events, more severe in the high-elevation site. In fact, most *Juniperus* species are associated with environments defined by these factors (Adams 2014). In addition, the greater variance in SLA and LDMC in *J. communis* (Fig. 2; Table S1 in the electronic supplementary material) may reflect a slightly better developmental accommodation ability in this species, which is known for its noticeable phenotypic plasticity (Thomas et al. 2007).

In the populations studied at the mid-elevation site, plants maintained growth (shoot elongation and production of new leaves) over long seasons lasting eight months. This necessarily means a slow growth ratio (i.e. 1 and 1.2 cm per month on average in *J. communis* and in *J. sabina*, respectively), which goes in line with the costly production of such stress-resistant leaves during primary growth (Westoby et al. 2002; Onoda et al. 2017). Moreover, the long growth period allowed the shrubs to achieve noticeable annual growth, amounting to between 4.8 and 9.9 cm of primary growth (i.e. radial expansion) depending on the species and sampling site. These values were higher in *J. sabina* across all sites, apparently due to

its distinct growth pattern. In this species, primary growth obviously occurred in centrifugally expanding branches, which become progressively rooted and ultimately produce a layering shrub. In *J. communis*, growth was more divided between diffuse and vertical main trunks and radially expanding branches of those trunks (pers. obs. and Fig. S1, S2, S4 in the electronic supplementary material). This would indicate that *J. sabina* is more focused on clonal growth and eventual vegetative multiplication, in contrast to *J. communis*. Thus, *J. sabina* would appear to exhibit better adaptation to the effects of disturbance on its aerial parts by factors such as fire, cutting or extreme drought, which seems to compensate for its lower recruiting ability (Bellingham and Sparrow 2000).

The phenological delay in the growth of *J. sabina* compared with *J. communis* suggests that the former needs warmer temperatures than *J. communis* to start vegetative growth and reproduction phases. However, the rates of expansion showed a similar pattern in both species along the elevation gradient, that is, similarly active growth at the mid- and low-elevation sites and less growth at the high-elevation site (Fig. 4). Thus, *J. sabina* growth was not enhanced by warmer conditions at the low-elevation site, likely because of a stronger effect of summer drought events, which limit or interrupt growth (Arzac et al. 2016). The flowering phenology and fruit yield differed markedly between the two species. Contrasting with the seasonal spring blooming in *J. communis*, *J. sabina* showed a diffusely distributed production of male and female cones, starting in late summer and continuing into the following spring, with an interruption in winter, and different behaviour between individuals. This would contribute to the much lower fruit yield observed in *J. sabina*, which has been reported also from other regions (Benito Matías et al. 2012b).

Dioecy did not seem to have a cost on the vegetative fitness of female individuals in the *Juniperus* studied here; in other words, no clear growth differences have been found between the sexes at any of the sampling sites, even in *J. communis*, where female individuals produced so many fruits. This stands in contrast with most dioecious woody species, female plants of which typically show poorer growth (Obeso 2002; Bañuelos and Obeso 2004). However, our results are in line with other studies in northern regions showing a lack of differences in growth or population structure between sexes in *J. communis* (Marion and Houle 1996; Shetti et al. 2018).

The two *Juniperus* species studied here are known for their low rates of seedling emergence, which is related to diverse dysfunctions in seed production and to fruit predation by vertebrate and invertebrate frugivores (García et al. 2000; Wesche et al. 2005; Benito Matías et al. 2012a, 2012b). Nevertheless, the much higher fruit and seed production of *J. communis* may translate into a greater capacity for population expansion. At all the sampling sites, the populations analysed included noticeable proportions of young and moderately aged shrubs of *J. communis*, as has been described in other Pyrenean and Atlantic locations (García et al. 1999). Moreover, *J. communis* has a wide range of habitats, from rocky spots to patches of grassland and scrub; indeed, young individuals were frequently found even within dense *J. sabina* canopies. This may have led to the greater ecological ubiquity observed in *J. communis*, both at local and regional scales (Carrillo and Ninot 1992; Florapyr 2023).

Contrastingly, young individuals of *J. sabina* were very scarce (apparently absent from the mid- and high-elevation sites). A similar population age structure has been reported from other regions, where it has been assumed to be a sign of low seed fertility, competition from herbaceous vegetation and herbivory (Wesche et al. 2005; Benito Matías et al. 2012b). Thus, heavier seeds in *J. sabina* would not result in a stronger colonization ability. In fact, most *J. sabina* individuals originated from rocky outcrops (pers. obs., Table S4 in the electronic supplementary material), from which they currently expand into former pastureland. This suggests a lower competitive ability of the seedlings of this species within established vegetation, which would make rocky spots the most suitable type of microhabitat.

The lower recruitment seen in *J. sabina* may be compensated by greater longevity provided by clonal development. The ageing of shrubs of this species is generally accompanied by the loss of the oldest aerial parts, which are slowly renewed throughout the whole plant, which can thus persist for decades or even centuries (Wesche et al. 2005; De Witte and Stöcklin 2010). The rich rooting system formed by their creeping branches counterbalances the senescence of the older parts of the stems, which facilitates horizontal expansion and the re-colonization of gaps possibly arising within the shrub. *Juniperus communis*, by contrast, retains its main axes for long and lacks

adventitious rooting, so each entire shrub eventually grows old (García et al. 1999), which may be compensated at the population level by higher fruit production and more successful seedling recruitment.

Colonization of Open Habitats and Landscape Encroachment

The abrupt cessation of traditional land use that has occurred in the last decades has promoted the re-colonization of open habitats by marginal populations of the two *Juniperus* species (Ninot and Carrillo 2019). Like in other encroaching shrub species, new, spreading *Juniperus* stands have most likely originated from sparse individuals that had for centuries remained sheltered from grazing and occasional fires in rocky spots occurring in these mountain landscapes (Lasanta-Masrtínez et al. 2005; Roura-Pascual et al. 2005; Ninot et al. 2017).

This process must have progressed differently in the sampling sites located at distinct elevations. The low- and mid-elevation sites formerly corresponded to mosaics of grasslands and arable fields interspersed with rocky spots. These agro-pastoral mosaics were still present until the mid-20th century, when they became an extensive rangeland with noticeable ovine grazing until a few decades ago (pers. obs.). By contrast, the high-elevation site was never cultivated and was kept as a patchwork rangeland with pastures, shrubs and trees until some decades ago (Fig. 1). There, since the disappearance of domestic herbivores, the only large herbivores are wild ungulates (Ninot et al. 2011; Ameztegui et al. 2021). The three sites studied also differ in various ecological factors correlated with the elevation gradient (Ninot et al. 2013). With greater elevation, the growing season becomes shorter, so vegetation dynamics may proceed slower and biotic interactions, such as plant–plant interactions and animal-mediated fruit dispersal, may be less pronounced. This is in accordance with the slower shrub growth and expansion observed in both *Juniperus* species at the high-elevation site (Fig. 4; Arzac et al. 2016) and with the age structure of the corresponding populations (Fig. 7).

At the landscape level, the two species expanded during the last decades at varying rates, and cumulative growth allowed them to reach a significant ground cover, depending on the site (Table S4 in the electronic supplementary material). The expansion of lower

shrubs has facilitated the occurrence of taller shrub species or tree saplings protruding above their canopy, especially at the low- and mid-elevation sites. This is more apparent in the case of *J. sabina* than in that of *J. communis* even though *J. sabina* forms denser canopies (Fig. 3). Most of the plant species benefiting from shrub facilitation may have arrived by ornithochory, since birds use these shrubs as perches in open landscapes when covering medium to long distances (Verdú et al. 2004; Adams 2014). They then successfully established within the moderately shaded environment shrubs provide. Taller recruits of other species do not appear to be detrimental to the mid-term nursing effect provided even by lower *J. sabina* shrubs (pers. obs., Table S4 in the electronic supplementary material), as also found by Verdú et al. (2004). However, denser tree canopies of *Pinus sylvestris*, *P. uncinata* or *Betula pendula* reduce formerly dense scrub into vanishing, etiolated understorey populations of both species (Fig. S4 in the electronic supplementary material). During the process of shrub expansion and densification, the *Juniperus* layers filter the occurrence of understorey species all the while their dense and active rooting system may enhance ecological changes involving soil properties and fungal communities (part C of the electronic supplementary material – Root structure and dynamics; Grau et al. 2019).

Shrub Persistence in Dynamic Landscapes

In Pyrenean landscapes prior to 3.5 millennia ago, when woodlands dominated most mountainous areas (Rodríguez-González et al. 2023), *Juniperus* populations may have inhabited rocky outcrops on mountain slopes. They must have survived in marginal habitats throughout the period of landscape anthropization until the sharp decline in traditional land use, which has made way for their expansion into grasslands on gentler slopes (Komac et al. 2013; Gómez-García et al. 2023). However, the cover of shrubby vegetation has remained low as a result of landscape dynamics that have occurred over the last decades in the Pyrenees and similar mountain ranges. This is due to the fact that what shrubs gain in cover due to grassland encroachment is counterbalanced by losses through shrubland forestation (Monje 2003; Ferré et al. 2005; Roura-Pascual et al. 2005). Thus, although the shrub cover undergoes spatial changes, shrub communities may remain a minority in these mountain landscapes.

Juniperus communis scrubs widely encroach into diverse ecosystems across temperate Europe and Mediterranean mountain ranges (García et al. 1999; Thomas et al. 2007; Benito Matías et al. 2012a). In these areas, this species takes advantage of recent landscape changes allowing it to utilize its good colonization ability and capacity to occupy space, as discussed above. Seedling recruitment counterbalances the loss of populations declining under closing tree canopies. At local scales, *J. sabina* seems to follow similar dynamics, but its whole geographic distribution (it being common in the study area, very sparse in the Pyrenees and irregularly distributed along its entire range) may be related to its population structure. Concretely, the dominance of medium-sized to very large adults and the scarcity or lack of regeneration classes of *J. sabina* in the area studied and in other regions (Wesche et al. 2005; Benito Matías et al. 2012b) suggest that the current populations of this species follow the model of persistence through longevity and vegetative regeneration (García and Zamora 2003). This would be a consequence of its clonal development, an adaptive ability that is very scarce within the genus *Juniperus* and in conifers in general (Adams 2014). Thus, the acquisition of clonality by *J. sabina* may have played a relevant role in the persistence of its populations. In fact, the capacity for adventitious rooting, resulting in clonality, has been described at the population level also in other few conifers, including *J. communis* in suboptimal habitats (Houle and Babeaux 1994; Payette et al. 1994; Thomas et al. 2007). In this way, *J. sabina* populations may have persisted on a few steep, south-facing Pyrenean slopes thanks to their ability to tolerate environmental stress and moderate disturbance by factors such as goat and sheep browsing, fire and erosion. In spite of its low success in recruitment and in colonizing new habitats, these remnant populations must have served as a source for eventual new recruitment and expansion into neighbouring habitats. This would have occurred during ecological windows of opportunity (Eriksson 1996; Bellingham and Sparrow 2000), as evidenced by the populations of *J. sabina* studied here and those scattered in the Pyrenees. As in other relict or rare species, this strategy has proven to be effective at conferring inertia to populations that persist locally despite their apparent reproductive collapse (Picó and Riba 2002; García 2008). This may allow many plant species to persist regionally for even several millennia (Médail and Quézel 1997; García and Zamora 2003), which significantly contributes to explaining the

maintenance of high plant diversity in mountain regions such as the Pyrenees.

In summary, the most commonly considered basic plant functional traits (describing leaf resource use, plant structure and growth) of the two *Juniperus* species studied do not seem to be related to their contrasting distribution, since they showed no substantial differences even across the sharp elevation gradient considered. The more successful dispersion and recruitment in *J. communis*, manifested in a more balanced population structure, would explain the success of this species in many landscapes. On the other hand, the worse recruitment ability of *J. sabina* is apparently compensated by clonality and individual longevity, which allows this species to persist in the form of unbalanced populations in just a few appropriate landscape spots scattered across its range.

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Data Availability Most of the raw data, those referred to Plant Functional Traits, are part of the TTT database, and are available at the GitHub repository (<https://github.com/TundraTraitTeam/TraitHub>).

Declarations

Competing interest The authors declare that they have no known competing interests that could have influenced the work reported in this paper.

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References

- Abràmoff M, Magalhães P, Ram S (2004) Image processing with IMAGEJ. *Biophoton Int* 11:36–42
- Adams RP (2014) *Junipers of the World: The genus Juniperus*, 4th ed. Trafford Publishing Co., Bloomington, Indiana
- Adams RP, Schwarzbach AE (2006) A new variety of *Juniperus sabina* from Mongolia: *J. sabina* var. *mongolensis*. *Phytologia* 88:179–185
- Adler PB, Salguero-Gómez R, Compagnoni A, Hsu JS, Ray-Mukherjee J, Mbeau-Ache C, Franco M (2014) *PNAS* 111:740–745
- Álvarez-Martínez JM, Suárez-Seoane S, Stoorvogel JJ, de Luis Calabuig E (2014) Influence of land use and climate on recent forest expansion: a case study in the Eurosiberian–Mediterranean limit of north-west Spain. *J Ecol* 102:905–919
- Ameztegui A, Coll L, Brotons L, Ninot JM (2016) Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. *Global Ecol Biogeogr* 25:263–273
- Ameztegui A, Morán-Ordóñez A, Márquez A, Blázquez-Casado Á, Pla M, Villero D, García MB, Errea MP, Coll L (2021) Forest expansion in mountain protected areas: Trends and consequences for the landscape. *Landscape Urban Planning* 216:104240
- Arzac A, García-Cervigón AI, Vicente-Serrano SM, Loidi J, Olano JM (2016) Phenological shifts in climatic response of secondary growth allow *Juniperus sabina* L. to cope with altitudinal and temporal climate variability. *Agric Forest Meteorol* 217: 35–45
- Bañuelos MJ, Obeso JR, (2004) Resource allocation in the dioecious shrub *Rhamnus alpinus*: the hidden costs of reproduction. *Evol Ecol Res* 6:397–413
- Benito Matías LF, Villar Salvador P, García Viñas JI, Gastón A, Prada Sáez MA (2012a) *Juniperus communis* L. In Pemán García J, Navarro Cerrillo RM, Nicolás Peragón JL, Prada Sáez MA, Serrada Hierro R (ed.) *Producción y manejo de semillas y plantas forestales, I*, Organismo Autónomo Parques Nacionales, Madrid, pp 632–646

- Benito Matías LF, Villar Salvador P, García Viñas JI, Gastón A, Prada Sáez MA, (2012b) *Juniperus sabina* L. In Pemán García J, Navarro Cerrillo RM, Nicolás Peragón JL, Prada Sáez MA, Serrada Hierro R (ed.) *Producción y manejo de semillas y plantas forestales, I*, Organismo Autónomo Parques Nacionales, Madrid, pp 677–685
- Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. *Oikos* 89:409–416
- Bolòs O, Vigo J (1984) *Flora dels Països Catalans, I*. Barcelona, Barcelona
- Carrillo E, Ninot JM (1992) *Flora i vegetació de les valls d'Espot i de Boí*. Arxius de la Secció de Ciències, 99/1, Institut d'Estudis Catalans, Barcelona, pp 5–475
- Cudlín P, Klopčič M, Tognetti R, Máliš F, Alados CL, Bebi P, Grunewald K, Zhiyanski M, Andonowski V, Hofgaard A, La Porta N, Hlasny T, Bratanova S, Edwards M, Skálák, P, Ninot JM, Kachaunova E, Rigling A, Wielgolaski FE (2017) Drivers of treeline shift in different European mountains. *Clim Res* 73:135–150
- De Witte LC, Stöcklin J (2010) Longevity of clonal plants: why it matters and how to measure it. *Ann Bot* 106:859–870
- Dullinger S, Dirnböck T, Grabherr G (2003) Patterns of shrub invasion into high mountain grasslands of the Northern Calcareous Alps, Austria. *Arctic Antarct Alp Res* 35:434–441
- Eriksson O (1996) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos* 77:248–258
- Ferré A, Carreras J, Carrillo E, Ninot JM (2005) Assessing the natural interest of the landscape of Andorra, a mountain country under contrasting change of land use. *Acta Bot Gallica* 152:443–455
- Florapyr (2023) El atlas de la flora de los Pirineos. Available at <https://atlasflorapyreneaea.eu/src/home/index.php?idma=0> (Accessed November 2023)
- Gabrielová J, Münzbergová Z, Tackenberg O, Chrtek J (2013) Can we distinguish plant species that are rare and endangered from other plants using their biological traits? *Folia Geobot* 48:449–466
- García MB (2008) Life history and population size variability in a relict plant. Different routes towards long-term persistence. *Diversity & Distrib* 14:106–113
- García D, Zamora R (2003) Persistence, multiple demographic strategies and conservation in long-lived Mediterranean plants. *J Veg Sci* 14:921–926
- García D, Zamora R, Gómez JM, Jordano P, Hódar JA (2000) Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe. *J Ecol* 88:436–446
- García D, Zamora R, Hódar JA, Gómez JM (1999) Age structure of *Juniperus communis* L. in the Iberian peninsula: Conservation of remnant populations in Mediterranean mountains. *Biol Conservation* 87:215–220
- García-Cervigón AI, Velázquez E, Wiegand T, Escudero A, Olano JM (2017) Colonization in Mediterranean old-fields: the role of dispersal and plant–plant interactions. *J Veg Sci* 28:627–638
- Gaüzère P, Blonder B, Denelle P, Fournier B, Grenié M, Delalandre L, Münkemüller T, Munoz F, Violle C, Thuiller W (2023) The functional trait distinctiveness of plant species is scale dependent. *Ecography* 2023:e06504
- Giménez Benavides L (2009) 4060 Brezales alpinos y boreales. In *Bases ecológicas preliminares para la conservación de los tipos de hábitats de interés comunitario en España*. Ministerio de Medio Ambiente, y Medio Rural y Marino, Madrid, pp 1–58
- Gómez-García D, Aguirre de Juana AJ, Jiménez Sánchez R, Manrique Magallón C (2023) Shrub encroachment in Mediterranean mountain grasslands: Rate and consequences on plant diversity and forage availability. *J Veg Sci* 34:e13174
- Grau O, Saravesi K, Ninot JM, Geml J, Markkola A, Ahonen SHK, Peñuelas J (2019) Encroachment of shrubs into sub-alpine grasslands in the Pyrenees modifies the structure of soil fungal communities and soil properties. *FEMS Microbiol Ecol* 95:fiz028
- Grigoriev AA, Shalaumova YV, Balakin DS, Erokhina OV, Abdulmanova SY, Moiseev PA, Camarero JJ (2022) Alpine shrubification: Juniper encroachment into tundra in the Ural Mountains. *Forests* 13:2106
- Grime JP (2006) *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley & Sons, Hoboken
- Hallinger M, Manthey M, Wilmking M (2010) Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytol* 186:890–899
- Houle G, Babeux P (1994) Variations in rooting ability of cuttings and in seed characteristics of five populations of *Juniperus communis* var. *depressa* from subarctic Quebec. *Canad J Bot* 74:493–498
- ICGC (2020) Institut Cartogràfic i Geològic de Catalunya – Vissir3. Available at http://www.icc.es/vissir3/index.html?Y=4618175&X=397325&zoom=4&layers=Topographic,vector,Marker&layers_opacity=1,1,1&lang=esl (Accessed November 2020)
- Komac B, Kefi S, Nuche P, Escós J, Alados CL (2013) Modeling shrub encroachment in subalpine grasslands under different environmental and management scenarios. *J Environm Managem* 121:160–169
- Körner C, Paulsen JA (2004) A world-wide study of high altitude treeline temperatures. *J Biogeogr* 31:713–32
- Lasanta-Martínez T, Vicente-Serrano SM, Cuadrat-Prats JM (2005) Mountain Mediterranean landscape evolution caused by the abandonment of traditional primary activities: a study of the Spanish Central Pyrenees. *Appl Geogr* 25:47–65
- Lavergne S, Thompson JD, Garnier E, Debussche M (2004) The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos* 107:505–518
- Lenth L (2020) *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version 1.5.2-1. Available at <https://CRAN.R-project.org/package=emmeans>
- Liu F, Archer SR, Gelwick F, Bai E, Boutton TW, Wu XB (2013) Woody plant encroachment into grasslands: Spatial

- patterns of functional group distribution and community development. *PLoS ONE* 8:e84364
- Marion C, Houle G (1996) No differential consequences of reproduction according to sex in *Juniperus communis* var. *depressa* (Cupressaceae). *Amer J Bot* 83:480–488
- MacDonald D, Crabtree J, Wiesinger G, Dox T, Stamou N, Fleury P, Gutierrez Lazpita J, Gibon A (2000) Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *J Environm Managem* 59:47–69
- Médail F, Quézel P (1997) Hot-spot analysis for conservation of plant biodiversity in the Mediterranean Basin. *Ann Missouri Bot Gard* 84:112–127
- Meteocat (2023) *Servei Meteorològic de Catalunya*. Available at <https://www.meteo.cat> (Accessed November 2023)
- Monje X (2003) Estudio mediante sistemas de información geográfica (GIS) de la evolución de la vegetación natural en Cataluña. Aproximación al caso del Valle del Freser durante el periodo 1956–2000. *Acta Bot Barcinon* 49:421–438
- Montané F, Romanyà J, Rovira P, Casals P (2010) Above-ground litter quality changes may drive soil organic carbon increase after shrub encroachment into mountain grasslands. *Pl & Soil* 337:151–165
- Montesinos D, García D (2009) 5130 Formaciones de *Juniperus communis* en brezales o pastizales calcáreos. In *Bases ecológicas preliminares para la conservación de los tipos de hábitats de interés comunitario en España*. Ministerio de Medio Ambiente, y Medio Rural y Marino, Madrid, pp 1–39
- Montesinos D, García-Fayos P, Verdú M (2012) Genders in *Juniperus thurifera* have different functional responses to variations in nutrient availability. *New Phytol* 193:705–712
- Murray BR, Thrall PH, Malcolm Gill A, Nicotra AB (2002) How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecol* 27:291–310
- Ninot JM, Anadon-Rosell A, Caminal M, Carrillo E, Grau O, Illa E, Lloret F, Nogués S, Talavera M (2017) Los arbustos de alta montaña y los cambios de paisaje en el parque nacional de Aigüestortes i Estany de Sant Maurici. In Amengual P (ed) *Proyectos de investigación en parques nacionales: 2012–2015*. Organismo Autónomo Parques Nacionales, Madrid, pp 209–228
- Ninot JM, Batllori E, Carreras J, Carrillo E, Casals P, Casas C, Grau O, Gutiérrez E, Montané F, Puente A (2011) Reforestación natural en el dominio de *Pinus uncinata* del Parque Nacional de Aigüestortes i Estany de Sant Maurici. In Ramírez L, Asensio B (ed.) *Proyectos de investigación en parques nacionales: 2007–2010*. Organismo Autónomo Parques Nacionales, Madrid, pp 139–158
- Ninot JM, Carrillo E (2019) Contribució al coneixement geobotànic de les comunitats de *Juniperus sabina* i de *Juniperus communis* (Cupressaceae) als Pirineus catalans. *Butl Inst Catalana Hist Nat* 83:159–174
- Ninot JM, Ferré A, Grau O, Font X, Pérez-Haase A, Carrillo E (2013) Environmental drivers and plant species diversity in the Catalan and Andorran Pyrenees. *Lazaroa* 34: 89–105
- Obeso JR (2002) The costs of reproduction in plants. *New Phytol* 155:321–348
- Onoda Y, Wright IJ, Evans JR, Hikosaka K, Kitajima K, Niinemets Ü, Poorter H, Tosens T, Westoby M (2017) Physiological and structural tradeoffs underlying the leaf economics spectrum. *New Phytol* 214:1447–1463
- Orshan G (1989) *Plant pheno-morphological studies in Mediterranean type ecosystems*. Kluwer Academic Publishers, Dordrecht, Boston, London
- Palombo C, Chirici G, Marchetti M, Tognetti R (2013) Is land abandonment affecting forest dynamics at high elevation in Mediterranean mountains more than climate change? *Pl Biosyst* 147:1–11
- Payette S, Delwaide A, Morneau C, Lavoie C (1994) Stem analysis of a long-lived black spruce clone at treeline. *Arctic Alpine Res* 26:56–59
- Pedashenko H, Apostolova I, Oldeland J (2015) The effects of livestock numbers and land cover transformation processes on rangelands in the Balkan Mountains between 1947 and 2012. *Tuexenia* 35:417–32
- Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, van der Heijden MGA, Sack L, Blonder B, Poschold P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC (2013) New handbook for standardized measurement of plant functional traits worldwide. *Austral J Bot* 61:167–234
- Picó FX, Riba M (2002) Regional-scale demography of *Ramonda myconi*: Remnant population dynamics in a preglacial relict species. *Pl Ecol* 161:1–13
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2019) *nlme: Linear and nonlinear mixed effects models. R package version 3.1-139*. Available at <https://CRAN.R-project.org/package=nlme>
- Pinho BX, Trindade DPF, Peres CA, Jamelli D, de Lima RAF, Ribeiro EMS, Melo FPL, Leal IR, Tabarelli M (2022) Cross-scale drivers of woody plant species commonness and rarity in the Brazilian drylands. *Diversity & Distrib* 28:1497–1511
- R Core Team (2023) *R: a language and environment for statistical computing*. Available at <https://www.R-project.org>
- Rodríguez-González JM, Sánchez-Morales M, Nadal-Tersa J, Pélachs A, Pérez-Obiol R (2023) Paleoenvironmental reconstruction for the last 3500 years in the Southern Pyrenees from a peat bog core in Clots de Rialba. *Diversity* 15:390
- Roura-Pascual N, Pons P, Etienne M, Lambert B (2005) Transformation of a rural landscape in the eastern Pyrenees between 1953 and 2000. *Mountain Res Developm* 25:252–261
- Sanz-Elorza M, Dana ED, Gonzalez A, Sobrino E (2003) Changes in the high-mountain vegetation of the central

- Iberian Peninsula as a probable sign of global warming. *Ann Bot (Oxford)* 92:273–280
- Shetti R, Buras A, Smiljanic M, Hallinger M, Grigoriev AA, Wilmking M (2018) Does sex matter? Gender-specificity and its influence on site-chronologies in the common dioecious shrub *Juniperus communis*. *Dendrochronologia* 49:18–126
- Sporbert M, Welk E, Seidler G, Jandt U, Aćić S, Biurrun I, Campos JA, Čarni A, Cerabolini BEL, Chytrý M, Čuštěrevska R, Dengler J, De Sanctis M, Dziuba T, Fagúndez J, Field R, Golub V, He T, Jansen F, Lenoir J, Marcenò C, Martín-Forés I, Moeslund JE, Moretti M, Niinemets Ü, Peñuelas J, Pérez-Haase A, Vandvik V, Vassilev K, Vynokurov D, Bruelheide H (2021) Different sets of traits explain abundance and distribution patterns of European plants at different spatial scales. *J Veg Sci* 32:e13016
- Syphard AD, Franklin J (2010) Species traits affect the performance of species distribution models for plants in southern California. *J Veg Sci* 21:177–189
- Thomas PA, El-Barghathi M, Polwart A (2007) Biological flora of the British Isles: *Juniperus communis* L. *J Ecol* 95:1404–1440
- Urbina I, Grau O, Sardans J, Ninot JM, Peñuelas J (2020) Encroachment of shrubs into subalpine grasslands in the Pyrenees changes the plant-soil stoichiometry spectrum. *Pl & Soil* 448:37–53
- Verdú M, Villar-Salvador P, García-Fayos P (2004) Gender effects on the post-facilitation performance of two dioecious *Juniperus* species. *Funct Ecol* 18:87–93
- Wesche K, Ronnenberg K, Hensen I (2005) Lack of sexual reproduction within mountain steppe populations of the clonal shrub *Juniperus sabina* L. in semi-arid Southern Mongolia. *J Arid Environm* 63:390–405
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Rev Ecol Syst* 33:125–159
- Wickham H (2016) *ggplot2: Elegant graphics for data analysis*. Springer-Verlag, New York
- Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York

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