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Age structure of *Juniperus communis* L. in the Iberian peninsula: Conservation of remnant populations in Mediterranean mountains

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Abstract

We examined the demographic structure of *Juniperus communis* L. populations in the Mediterranean high mountains of southern Spain in order to analyse its population viability. For this, we compared the age structure of these Mediterranean populations with those of northern Spain (Atlantic), and, on a local scale, the populations of different habitats within the Sierra Nevada. The populations from northern Spain showed age structures with high proportions at young stages. In contrast, the Mediterranean populations proved to be dominated by adult and senescent individuals, except for the few habitats with higher water availability during the summer, which have larger proportions of seedlings and juveniles. Dry habitats showed a lower seedling survival rate than did wet ones, mainly due to summer drought. Both the difference between Atlantic and Mediterranean categories, and the difference between habitats in Sierra Nevada reflect a serious limitation on recruitment of *J. communis* in Mediterranean mountains due to climatic stress imposed by summer drought. The Mediterranean populations provide a clear example of remnant dynamics, surviving for long periods due to great individual longevity which partially offsets losses to unfavourable environmental conditions. The low ability to recover after anthropic disturbances emphasizes the need for conservation of *J. communis* populations in south-eastern Spain. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Age structure; Iberian peninsula; *Juniperus communis*; Mediterranean high mountain; Remnant populations; Sierra Nevada

1. Introduction

The mountain areas of the Mediterranean Basin contain the highest plant species diversity in Europe and one of the greatest plant species richness on earth (Cox and Moore, 1993; Castro-Parga et al., 1996; Cowling et al., 1996). This diversity, related both to historical causes and to high local environmental heterogeneity, has resulted in the coexistence of old taxa, from palaeotropical and boreoalpine climates, with new taxa appearing under the current Mediterranean climate (Herrera, 1992; Cox and Moore, 1993; Greuter, 1994). Consequently, Mediterranean mountains are equivalent to ecological islands containing, in their coldest and wettest habitats, species which were distributed in southern Europe during the glacial periods, and which currently are abundant in boreal areas (Bennett et al., 1991). Juniper *Juniperus communis* L. (Cupressaceae), is one of the gymnosperms with the widest distribution in

the Holarctic. It is a clear example of a plant species abundant today in boreal and northern areas but isolated in the mountain areas of Mediterranean Europe. In the Iberian Peninsula, it covers a continuous area in northern Spain but is increasingly fragmented southwards in mountain ranges (Castroviejo et al., 1986).

Although *J. communis* is still a common species in Europe, its populations have suffered serious regression processes in certain insular areas (Ward, 1973, 1981; Clifton et al., 1997). In the Mediterranean mountains, such as the Sierra Nevada, juniper is a major species of the xeroacanthic shrublands above the treeline (Vigo and Ninot, 1987). These juniper shrublands have a high ecological value, mainly in relation to their soil-retaining ability, their associated endemic flora and fauna, and their traditional use as summer grazing areas (Molero et al., 1992). Despite their ecological value, no study has yet evaluated the conservation of juniper populations in the Mediterranean area. The present work was performed to determine the population viability of juniper in the Spanish Mediterranean mountains, in relation to the species status throughout the Iberian

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peninsula. Taking into account that the age structure of populations provides an indication of their regeneration process and their conservation status (Hutchings, 1986; Andrzejczyk and Brzeziecki, 1995; Primack, 1995), we analysed the population viability using two different spatial scales. First, we compared regional differences between the Mediterranean populations and those of northern Spain, and secondly, between habitats with different soil-water availability within the Sierra Nevada. Both the populations of northern Spain and the populations in wetter habitats of Sierra Nevada are considered here to be representative of *J. communis* dynamics in the European Atlantic climatic region, and suitable in order to analyse comparatively the status of Mediterranean high mountain populations.

2. Methods and study area

During 1995 and 1996 we visited 15 populations of *J. communis* located in medium and high altitudes throughout the Iberian peninsula, covering a latitudinal gradient from 37 to 42°N (Fig. 1, Table 1). We classified these populations into two biogeographical categories on the basis of climate: 'Atlantic' for those in the north, and 'Mediterranean' for those extending into the Mediterranean summer drought domain (Fig. 1; Font,

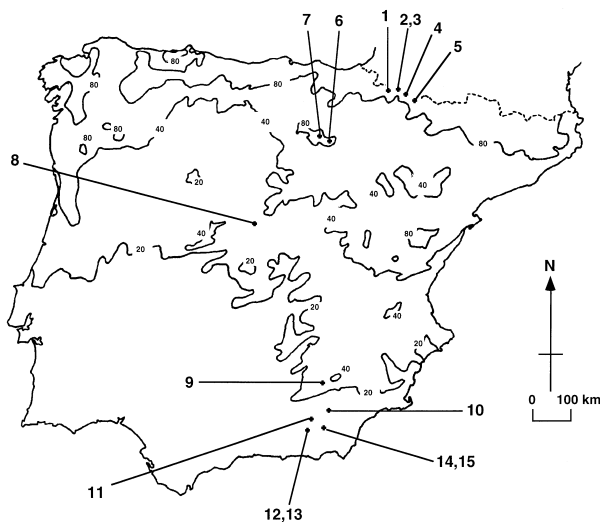


Fig. 1. Location of the populations studied in the Iberian peninsula: 1, Orhy; 2, Lakora; 3, Belagoa; 4, Piedra de San Martín; 5, Hecho; 6, Puerto de Piqueras; 7, Puerto de Santa Inés; 8, Puerto de Navacerrada; 9, Collado Cabañas; 10, Boleta; 11, Maitena; 12, Dornajo; 13, Prados del Aire; 14, Campos de Otero; 15, Valle de San Juan. The lines represent the rainfall isohyets of values 80, 40 and 20 mm, respectively, calculated as the sum of July and August precipitation (Font, 1983). We used the criterion " $2 \times (\text{mean temperature of July} + \text{mean temperature of August}) < (\text{rainfall of July} + \text{rainfall of August})$ ", using the values of temperature and rainfall from climatic diagrams, to determine the presence of summer drought. This criterion fits roughly with the area with < 80 mm rainfall isohyet in the figure.

1983; Polunin and Walters, 1985; Greuter, 1994). All the populations were shrubland, climax communities above the treeline, except at Belagoa, which lies in a successional ecotone between grasslands and forest. In two Mediterranean populations (Campos de Otero and Valle de San Juan) we differentiated between the main dry hillside habitat (with *Genista versicolor* Boiss. and *Hormathophylla spinosa* (L.) Küpfer) and wet meadows, close to streams and abandoned irrigation channels, which cover $< 10\%$ of the area (García et al., 1996). Both Atlantic and Mediterranean populations are in undisturbed areas grazed extensively by summer livestock (sheep, goats and cattle) which leave the mountains during winter. The wet meadow areas in the Sierra Nevada support a proportionally higher grazing pressure than do hillsides (Molero et al., 1992). There is no evidence of differences in burning or management between populations, and both regions have undergone a general decrease in land use during the last few decades, due to demographic shift away from mountain areas (Molero et al., 1992; Gómez-Sal et al., 1993).

In all locations, we recorded all the juniper populations covering an area of c. 2–3 ha. We determined the age structure by assigning each individual to one of the following age classes: established seedling, juvenile, reproductive adult and senescent (see Ward, 1973, 1981; Gatsuk et al., 1980; Clifton et al., 1997). We considered each age category to correspond, respectively, to the size classes of < 0.25 m, 0.25–1 m, 1–5 m and > 5 m, because individual size correlates significantly with age in this species, even when considering populations along environmental gradients (Marion and Houle, 1996). *J. communis* shows a stunted morphology in mountain areas, with multiple trunks which are usually inaccessible due to the interlaced branching system. Therefore age was estimated by measuring the largest diameter of the plant. The correspondence between different plant sizes and age classes could be affected by two main factors: the microenvironment where the individual plant develops and the density of individuals in the stands; lower resource availability or higher density would promote lower sizes for a specific age (Hutchings, 1986). In order to take account of these possible factors, we also judged the age of some individuals from the basal diameter of main trunks, the presence/absence of reproductive organs and the quantity of dead wood (i.e. an individual of size 0.90 m showing reproductive structures would be assigned to reproductive adult, and an individual of size 4.80 m showing a high proportion of dead wood would be assigned to senescent; see also Clifton et al., 1997). In most populations from each region, we estimated the density of individuals in the stand, using a variable number of transects of 50×2 m arbitrarily located in the study area.

Mortality of first-year juniper seedlings was compared between the two habitats of the Sierra Nevada.

Table 1

Characteristics of 15 *J. communis* populations studied in the Iberian peninsula: location, mean density of individuals (number of transect units in parentheses), total number (*N*) of individuals measured per population and age structure. The habitat of dry hillside (DH) and wet meadow (WM) are distinguished in two localities of the Sierra Nevada. See also Fig. 1 for location

Map no.	Population	Mountain range	Altitude m a.s.l.	Density plants/100 m ²	<i>N</i>	Age classes (%)			
						Seedling	Juvenile	Adult	Senescent
<i>Atlantic</i>									
1	Orhy	Western Pyrenees	1450	23.8 ± 4.5 (5)	188	4.79	30.32	61.70	3.19
2	Piedra de San Martín	Western Pyrenees	1750	7.5 ± 1.0 (5)	178	16.29	44.94	38.20	0.56
3	Lakora	Western Pyrenees	1500	12.5 ± 1.5 (10)	277	5.42	35.02	57.76	1.81
4	Belagoa	Western Pyrenees	1000	–	110	37.27	41.82	20.91	0
5	Hecho	Central Pyrenees	1700	5.4 ± 0.8 (5)	140	8.57	40	50.71	0.72
6	Puerto de Piqueras	Sierra Cebollera	1450	–	98	7.14	45.92	46.94	0
7	Puerto de Santa Inés	Sierra de Urbión	1650	14.1 ± 4.6 (5)	192	27.60	32.29	39.58	0.52
<i>Mediterranean</i>									
8	Puerto de Navacerrada	Sierra Guadarrama	1900	–	85	1.18	12.94	57.65	28.24
9	Collado Cabañas	Sierra de Cazorla	1800	5.9 ± 0.5 (10)	118	1.70	8.47	39.83	50.00
10	Boleta	Sierra de Baza	1800	–	251	0	1.99	58.16	39.84
11	Maitena	Sierra Nevada	2100	14.2 ± 1.2 (10)	142	0	0	61.97	38.03
12	Dornajo	Sierra Nevada	1800	1.9 ± 0.9 (10)	50	0	6.52	86.96	6.52
13	Prados del Aire	Sierra Nevada	2100	–	60	1.67	3.33	80.00	15.00
14	Campos de Otero DH	Sierra Nevada	2230	9.3 ± 0.7 (20)	372	0.81	2.69	64.25	32.26
	Campos de Otero WM			11.0 ± 1.4 (15)	331	34.44	23.87	41.69	0
15	Valle San Juan DH	Sierra Nevada	2250	7.5 ± 1.3 (10)	75	0	6.67	58.67	34.67
	Valle San Juan WM			7.6 ± 3.6 (5)	77	40.26	22.08	33.77	3.90

For this comparison, in June 1996, we tagged 204 first-year seedlings on dry hillsides and 76 in wet meadows at the locality of Campos de Otero. We recorded the survival rate of the seedlings in October 1996, identifying, when possible, the causes of death.

We compared the density of individuals using Mann–Whitney tests, both between biogeographical categories (using the population mean values of each region, to avoid pseudoreplication) and between habitats within population. The age structure and the seedling mortality was analysed by χ^2 test. We used a Nominal Logistic Model with interaction to study the effect of habitat and population (Campos de Otero and Valle de San Juan) in the age structure. When statistically analysing more than one related variable, we used the sequential Bonferroni test for determining significance level (Rice, 1989).

3. Results

Atlantic populations showed, as a whole, a density similar to Mediterranean ones, with no significant differences between biogeographical categories (mean \pm se: 12.66 ± 3.20 vs 7.76 ± 2.02 individuals/100 m², respectively, $U=8.00$, $p=0.35$, $df=9$; Table 1). Similarly, hillside areas showed densities comparable to those of wet meadows in Sierra Nevada, both in Campos de Otero ($U=119.00$, $p=0.30$, $df=34$) and Valle de San Juan ($U=20.00$, $p=0.54$, $df=14$; Table 1). Since

there were no differences in plant density we could ignore this factor in comparing age structures between regions and habitats.

All the hillside Mediterranean populations were dominated by adult and senescent individuals, showing percentages of up to 50% for the oldest age class (Table 1). In contrast, all the Atlantic populations showed markedly high percentages of seedlings and juveniles, ranging from 35 to 80%. Thus, the age distributions differed significantly between the two biogeographical categories ($\chi^2=1014.41$ $p<0.0001$, $df=3$, Fig. 2). Likewise, the proportions of seedlings and juveniles in wet meadows in the Sierra Nevada exceeded

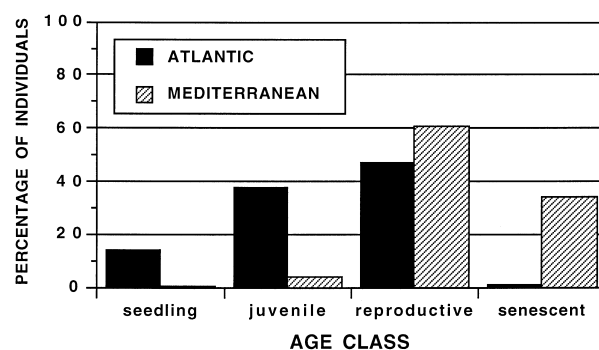


Fig. 2. Age structure of *J. communis* populations in the Atlantic and Mediterranean biogeographical categories of Iberian peninsula, represented as the percentage of individuals corresponding to different age classes.

50%, both in Campos de Otero and Valle de San Juan, with very few senescent individuals (Table 1). The habitat differences in age structure were significant (Table 2).

The seedling-mortality percentage was significantly higher for the dry hillsides than for the wet meadows at Campos de Otero (82.84 vs 50.00%, respectively; $\chi^2=31.53$, $p<0.0001$, $df=1$). On the dry hillsides, 73.07% of seedlings died from drought, 23.07% from trampling by livestock and 3.84% from being eaten by ungulates ($n=78$ seedlings with identified cause of death). The distribution of causes of seedling mortality was significantly different in the wet meadow ($\chi^2=24.36$, $p<0.0001$, $df=2$), 26.92% of seedlings dying from drought, 34.61% from trampling and 38.46% from herbivory ($n=26$ seedlings).

4. Discussion

We found two different age structures for *J. communis*, depending on the biogeographical category considered. Atlantic populations were composed of a notable proportion of young individuals, showing a pattern similar to that of northern European and boreal populations with high recruitment rates (Falinski, 1980; Rosén, 1988; Austad and Hauge, 1990; Marion and Houle, 1996). Conversely, Mediterranean populations are dominated by adult and, above all, senescent individuals, thus indicating a strong recruitment limitation of juniper in Mediterranean mountains. This regeneration bottleneck can be imposed by several, non-mutually exclusive, factors. For example, limited regeneration can be due to reproductive failure at the seed-set level; the old age of most individuals in southern Spanish populations might reduce their reproductive output, as was suggested by Ward (1982) for some English populations, where old age was associated with low seed viability. It is known that, through the combined effect of seed abortion and predispersal seed predation, *J. communis* produces a low proportion of viable seeds in Mediterranean mountains compared to northern populations (García et al., 1996; García, 1997). However, the potential effect of low seed quality

limiting recruitment could be quantitatively offset by the large crop sizes of this species, where a typical reproductive plant can bear several hundreds of thousands of seeds in a masting year. Overgrazing by domestic herbivores, combined with changes in land use, has been charged with limiting juniper recruitment and leading populations to extinction in England (Ward, 1973; Ward, 1981; Gilbert, 1980; Clifton et al., 1997). The Sierra Nevada also supports high densities of domestic and wild herbivores, which, in fact, negatively affect juniper recruitment by eating, and especially by trampling, seedlings.

The differences between Mediterranean and Atlantic populations reported here suggest that the recruitment bottleneck relates less to reproductive failure or herbivory than to the Mediterranean climate. In contrast with the rainy summers of the mountains of northern Spain and central Europe, those in southern Spain are characterised by summer drought (Fig. 1). Water limitation during the summer, a cause of juniper-seedlings mortality even in boreal populations (Rosén, 1995), imposed an extremely low survival rate for most juniper seedlings on the dry hillsides of Sierra Nevada. The scattered wet meadows are the only patches in the Mediterranean high mountain mosaic which provide relatively higher water availability during summer, and show higher seedling survival and recruitment rate than the predominant hillside areas. Because of livestock concentration during summer, wet meadows support a proportionally higher grazing pressure compared with the hillsides. Although herbivores are the main cause of seedling mortality in wet meadows, these wet areas have higher recruitment rate than do hillsides. Therefore, wet meadows are equivalent to islands of Atlantic climate within a sea of Mediterranean environment, reproducing, at a local scale, the demographic structure of the northern juniper populations.

Juniper populations in SE Spain are a clear example of marginal or border populations within the overall plant distribution area, a factor commonly associated with regression dynamics due to climatic stress (Silverton and Lovett-Doust, 1993; Eriksson, 1996). In this sense, the situation of *J. communis* in Mediterranean mountains is similar to that of other *Juniperus* species in the southern border of their range, where population decline is associated with drought (Fisher, 1997, and references therein). *J. communis* habitats in Sierra Nevada, like those of *J. excelsa* in the mountains of Oman (Fisher and Gardner, 1995; Gardner and Fisher, 1996), consist of a few sites with wetter soils and higher population regeneration, surrounded by a wider matrix of hillsides having very low regeneration.

According to the demographic characteristics, *J. communis* populations in Mediterranean mountains exemplify remnant dynamics, that is, local populations surviving for long periods under ecological conditions

Table 2
Results of Nominal Logistic Model considering habitat and population to be independent variables and individual age a dependent variable

	df	Wald χ^2	p
Habitat (H)	3	43.50	<0.0001*
Population (P)	3	3.13	0.37 n.s.
H×P	3	1.94	0.59 n.s.
Model	9	464.91	<0.0001*

* $p < 0.05$ after Bonferroni adjustment.

unfavourable for recruitment (Eriksson, 1996). 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. This inertia would maintain populations through the unfavourable regression period imposed by the current Mediterranean climate with persistent drought periods, between two favourable phases presumably during glacial periods. In this sense, it is commonly assumed that the flora now found in northern Europe was located in the south during glacial periods, moving to the north in the interglacial periods from southern refugia (Cox and Moore, 1993). Bennett et al. (1991) suggested that the populations of many woody species became extinct in boreal areas during Ice Age phases, as there is no palinological evidence of north-to-south movements. Therefore, the survival of woody species such as *J. communis* in the Quaternary Europe, may depend on these populations remaining in the Circum-Mediterranean areas, where they survive both in glacial and interglacial phases.

4.1. Ecological implications for conservation

Although *J. communis* is still abundant in Mediterranean mountains such as the Sierra Nevada, this species shows almost no ability to recover from anthropic disturbances in these areas (Zamora et al., 1996). After burning, *J. communis* is unable to sprout and most of their seeds die; therefore the only way to recolonize open areas after fire destruction is the arrival of seeds from plants in the surrounding undisturbed areas. However, the probability of recolonizing these disturbed areas is very low, considering that open patches receive < 1% of the total juniper seed-shadow dispersed by birds (García et al., 1996). Disturbances associated with ski runs and road clearances present a similar situation in Sierra Nevada, because they destroy the superficial soil layer, removing the seed bank and the organic matter. Moreover, large stones and boulders are removed, eliminating natural perches for avian dispersers and therefore places where the juniper seed-rain is higher. Furthermore, seedling survival in these open areas is almost nil (García et al., 1996). Consequently, the natural regeneration in disturbed areas, either by burning or by clearance, is practically non-existent and the bare ground is the dominant feature of the landscape in both types of disturbance.

In conclusion, given both remnant-population dynamics and low resilience against disturbances, the distribution area of *J. communis* in the high mountains of southern Spain declines after burning and clearing. Furthermore, the stress imposed by Mediterranean summer drought to population recruitment would hinder almost any feasible attempt at man-made

restoration of *J. communis* populations. Therefore, the maintenance of unaltered montane shrublands is an indispensable requisite for the conservation of *J. communis* under the current Mediterranean climate.

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