

# The decreased competition in expanding versus mature juniper woodlands is counteracted by adverse climatic effects on growth

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**Abstract** World-wide deforestation is being reversed in Mediterranean continental areas, where abandonment of traditional practises favours the expansion of valuable habitats, like *Juniperus thurifera* woodlands. We hypothesised that pre-existing trees facilitate establishment in expanding woodlands, whereas in mature woodlands, competition leads to patch disaggregation. We compared the imprint of these processes on growth, demographic and spatial structure of expanding and mature *J. thurifera* woodlands. We selected plots where we geopositioned, aged and quantified the morphological characteristics of all trees. In the mature woodland, trees arranged in clumps and randomly in the expanding woodland. Competition negatively affected growth, was greater in the mature woodland

and led to disaggregation of juvenile clumps. Differences in growth between the mature and the expanding woodland disappeared in climatically unfavourable years, suggesting that adverse climate constrains growth more in expanding than in mature woodlands. We suggest that change in the dispersal agents and a decrease of facilitation underlay differences in spatial patterns between the expanding and the mature woodland. Observed effective recruitment in less than 30 years into the expanding woodland evidenced that propagule arrival and sapling survival do not constrain woodland expansion. Furthermore, growth of juveniles established in these new areas is favoured by reduced intra-specific competition. However, we expect growth in expanding woodlands to be negatively impacted by climate change. We conclude that under current global change scenario, conservation of *J. thurifera* woodlands is favoured by changes in land use, but greater frequency and severity of drier than usual episodes could hamper natural reforestation.

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## Introduction

Change in habitat use is a major global change driver that involves loss of natural habitats (Millennium Ecosystem Assessment 2005), but also natural reforestation of abandoned lands (Bonet 2004; Chauchard et al. 2007). Some studies have found that colonisation of former grasslands by woody species is a relevant type of habitat loss (Briggs et al. 2002; Kunstler et al. 2007; Richardson and Rejmánek 2004) because it implies loss of biodiversity and altered

ecosystem services (Moore and Owens 2006; Roland and Matter 2007; Schroter et al. 2005). Nevertheless, natural reforestation has potentially positive effects on biodiversity—increasing connectivity between isolated forest remnants and habitat availability for forest species (Schroter et al. 2005)—and on provisioning of ecosystem services—preventing desertification and increasing carbon sink capacity (Maestre et al. 2009; Van Auken 2009).

Natural expansion of woodlands into abandoned lands has been broadly studied (e.g. Briggs et al. 2002; Breshears 2006), so the underlying mechanisms and consequences of woodland expansion are well known for particular cases such as the expanding juniper woodlands in North American plateaus (Van Auken 2008). However, little is known about the expansion of juniper woodlands in other regions, like the Mediterranean. In contrast to North America, in the Mediterranean, woodland expansion is not driven by increased grazing pressure and changes in fire regime (Briggs et al. 2002). Mediterranean woodlands have a long history of intense exploitation (Barbero et al. 1990; Valladares 2004), which has largely ceased now in mountainous and continental areas in the northern half of the Mediterranean Basin (Bonet 2004; Chauchard et al. 2007). In scarcely populated areas in central Spain, this is leading to the colonisation of abandoned agricultural fields and livestock pastures by expanding Spanish-juniper (*Juniperus thurifera* L.) woodlands (Blanco et al. 2005). *J. thurifera* woodlands are priority habitats for conservation, act as refuge for endemic species and account for a high cultural value (Olano et al. 2008), which makes their expansion particularly interesting not only from the scientific but also from the conservation and management point of view.

Several factors determine woodland expansion: properties of the propagule source (Pueyo and Alados 2007; Santos et al. 1999), dispersal mode of the target species (Aparicio et al. 2008; Kunstler et al. 2007), the existence of disturbances (Briggs et al. 2002; Smit et al. 2007; Van Uytvanck et al. 2008), species-specific traits (Gomez-Aparicio et al. 2006; Quero et al. 2008; Valladares et al. 2002) and plant–plant interactions, frequently a crucial factor (see Gomez-Aparicio 2009 and references herein). In grasslands, pre-existing plants will compete with tree seedlings for resources, but they can also facilitate their establishment, particularly under limiting abiotic conditions [e.g. high irradiance and drought (Berkowitz et al. 1995)]. Facilitation by pre-existing plants can take place either actively, nursing effect (Gomez-Aparicio et al. 2005; Montesinos et al. 2007), or passively, perch effect (Pausas et al. 2006; Verdú and García-Fayos 1996). Facilitation can drive initial steps of woodland expansion leading to a patchy distribution (clumped) of established trees (Duarte et al. 2010), but competition for resources between nursed

and nursing trees and among nursed trees in one patch can lead to patch disaggregation as trees grow (Escudero et al. 2004; Franco and Nobel 1989; Soliveres et al. 2010).

*Juniperus thurifera* woodland expansion can be constrained, first, by propagule arrival into abandoned fields, because perch scarcity negatively affects *J. thurifera* dispersal (Santos et al. 1999); remnant *J. thurifera* trees, thus, play a major role in woodland expansion by attracting seed dispersers into abandoned fields (Manning et al. 2006). Second, further sapling survival in expanding *J. thurifera* woodlands might be constrained by the availability of safe sites for recruitment, as adult *J. thurifera* trees facilitate the establishment of their conspecifics (Montesinos et al. 2007). Here, we studied the imprint of these processes on growth, demographic and spatial structure in a mature and an expanding *J. thurifera* woodland. We sought for evidences of different underlying ecological processes dominating in each woodland type (like dispersal and plant–plant interactions). We hypothesised that: (1) in the expanding woodland, trees arrange in clumps due to facilitation of sapling establishment by nurse trees (remaining adult trees and early established young adults); (2) in mature woodlands, juvenile trees arrange in clumps, but adults do not (due to competition) and (3) intra-specific competition is greater in the mature woodland, negatively affects radial growth and leads to disaggregation of clumps as trees grow.

## Materials and methods

### Study species and site

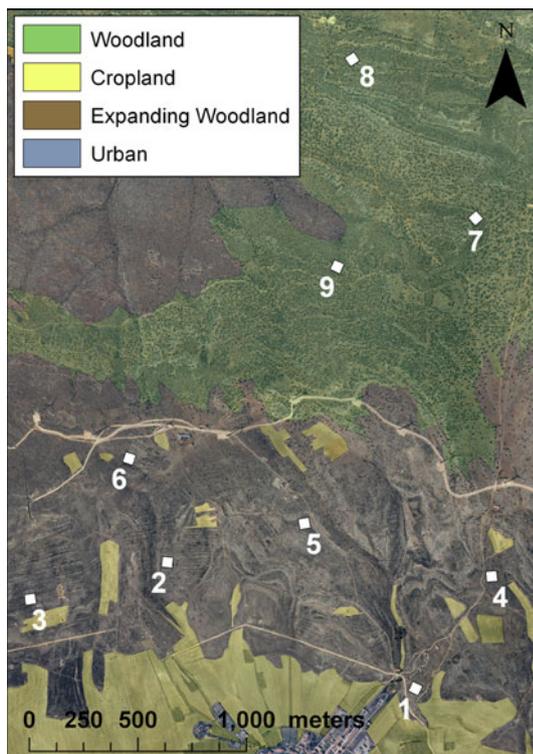
*Juniperus thurifera* L. (Cupressaceae) is a dioecious tree species with a relict Tertiary distribution confined to the western Mediterranean Basin. It is usually the dominant species in low-density woodlands on poor, shallow, rocky soils (both acidic and calcareous, although more abundant in the latter), at a variety of altitudes (300–3,200 m a.s.l.) in climates that range from semi-arid to sub-humid Mediterranean types (Gauquelin et al. 1999). Trees are usually 5–10 m tall. Males and females flower at the end of the winter and wind-pollinated female cones mature during 20 months. Mature cones are then dispersed by birds of the genus *Turdus* and some mammals like red foxes (*Vulpes vulpes*), rabbits (*Oryctolagus cuniculus*) or wild boars (*Sus scrofa*, Santos et al. 1999).

The study was conducted near Maranchón, in the province of Guadalajara, Spain. The climate is continental Mediterranean with hot and dry summers and cold and cloudless winters. Mean annual rainfall is  $649 \pm 23$  mm, and mean annual temperature is  $9.4 \pm 0.1^\circ\text{C}$  (mean  $\pm$  SE,  $n = 39$ , data from Maranchón:  $41^\circ03'03''\text{N}$ ,  $2^\circ12'37''\text{W}$ , 1,254 m a.s.l., 1964–1975, and completed with data from

Molina de Aragón: 40°50'40"N, 1°53'07"W, 1,063 m a.s.l. 1951–2007, all data provided by the Spanish Agencia Estatal de Meteorología). The soils are shallow, poorly developed and formed mainly from Cretaceous and Jurassic limestone. In the past, this area was subjected to an intense human exploitation of different types: agricultural, free-ranging livestock and wood harvest. This exploitation has largely ceased, due to socio-economic changes and rural exodus occurring since the beginning of the twentieth century and even more since the 1960 s (Alonso Ponce et al. 2003). Land-abandonment has led to the expansion of juniper woodlands into former agricultural fields and livestock pastures and to increased tree density in mature woodlands (Fig. 1 and S1). Current landscape consists of a mature woodland continuum that borders on an area of abandoned agricultural fields where Spanish-juniper woodland is expanding. The mature woodland was formerly used for cattle grazing and timber harvest. There are some adult *J. thurifera* remnants that landowners used to separate properties within the matrix of abandoned agricultural fields.

#### Study plots and morphological measurements

In 2008, after surveying current satellite images and aerial photographs of the past century (from 1957 to 1985), we haphazardly selected nine study plots located in different



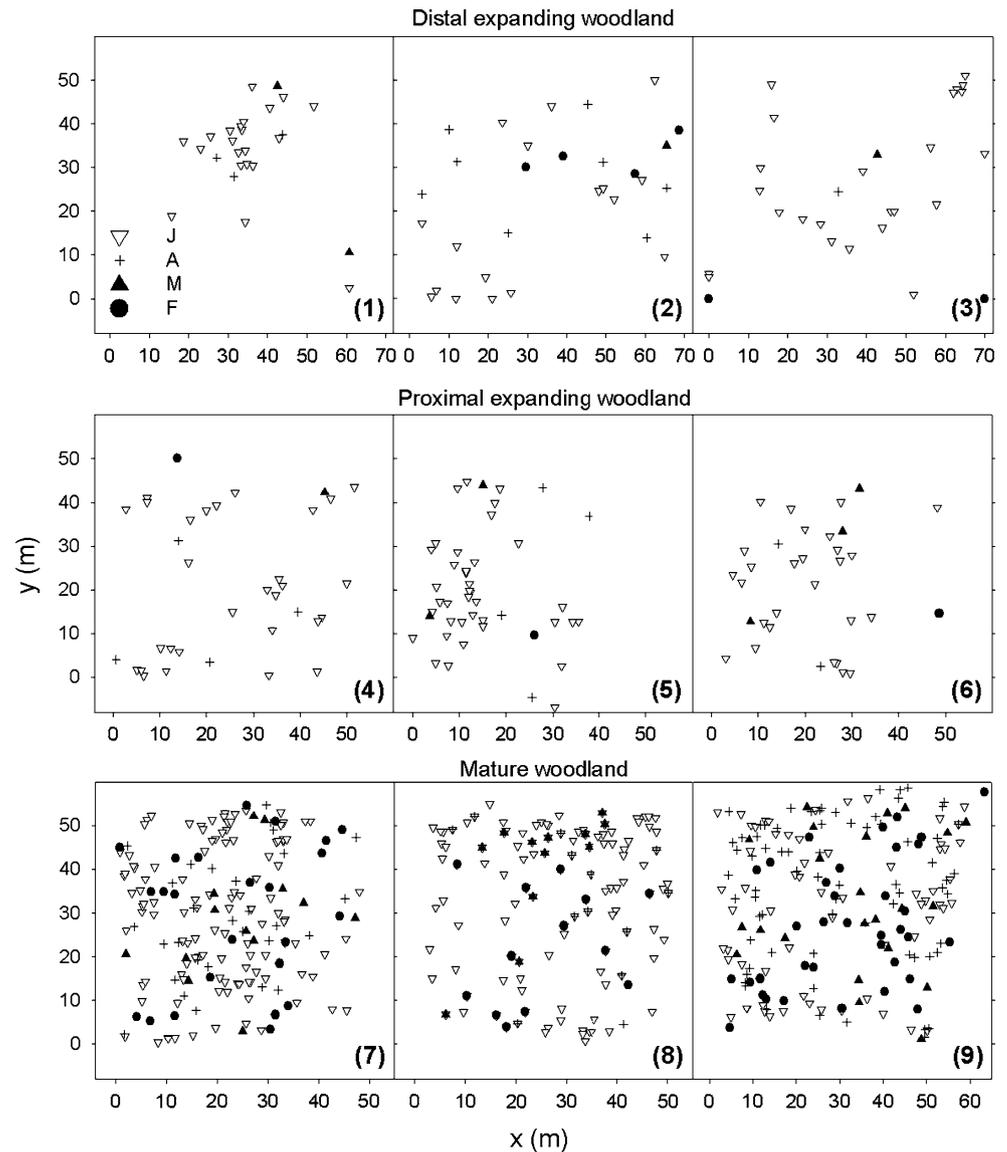
**Fig. 1** Map of soil use of the study area with the location of the nine study plots

habitat types representing different stages of woodland expansion (Fig. 1 and S1): non-bordering mature juniper woodland (plots 7–9); proximal expanding woodland, located at 500 m from the edge of the mature woodland (plots 4–6) and distal expanding woodland, located at 1,000 m from the edge of the mature woodland (plots 1–3). Within each habitat type, we selected three plots located at least 1,000 m away from each other. Plots number 3–9 were squares of 50 × 50 m. Plots number 1–3 were extended to 50 × 70, this was done to achieve a minimum total tree number of 30 (Fig. 2). All trees taller than 5 cm in the plots were geopositioned. We excluded individuals shorter than 5 cm because we only sought for effectively recruited individuals and in the Mediterranean area highest mortality occurs during the first years after emergence (Gomez-Aparicio et al. 2008). For all trees, we measured canopy radius, height, trunk diameter (d) at breast height (1.3 m) for trees higher than 2 m (hereafter adults) and diameter at base for trees below 2 m height (hereafter juveniles). For adult trees, we also recorded gender.

#### Age estimation and radial growth

In February 2009, we selected 13 trees, covering all height ranges, at each study plot. We chose tree height, instead of tree trunk diameter as our criteria, because in trees with anemophilous pollination (as it is the case of *J. thurifera*), reaching a certain height threshold will determine the transition to sexual maturity (Montesinos et al. 2006). Our premise did not prove to be wrong, since we found that tree height was the morphological variable that was best correlated to tree age (Figure S2). These were bored at breast height (adults) or at 25 cm height (juveniles) to obtain wood cores, using a Pressler increment borer (Haglöf, Långsele, Sweden). Among trees bored at breast height, we chose three trees per plot and these were bored also at 25 cm height to estimate the number of rings missed from 25 cm to breast height. Two complete radii were extracted from each tree, and pith was reached in 80% of them. The cores were air dried, glued onto wooden mounts and polished using sand paper of progressively finer grain until tree rings were visible. Wood samples were visually cross-dated (Stokes and Smiley 1968) to estimate tree age; tree-ring width was then measured on a Lintab measuring system (Rinntech, Heidelberg, Germany) with a resolution of 0.001 mm. Cross-dating was checked with the program COFECHA (Holmes 1983). Number of missing rings (in radii where the pith was not reached) was estimated geometrically according to Duncan (1989). Additionally, one radial wood mini-core was collected from each juvenile (at 25 cm height) and reproductive adult (at breast height) in all plots using a Trephor, a specially designed increment puncher with a thin piercing tube (Rossi et al. 2006). Mini-

**Fig. 2** Map of all trees (*J* juveniles, *A* non-reproductive adults, *M* males, *F* females) of the nine study plots located at three different habitat types



cores were also air dried, glued onto mini-wooden mounts and polished and then cross-dated and measured the same way as normal wood cores. Mini-cores extraction is a non-destructive, easy and fast technique that provides samples that allow measuring tree-ring width of the past 5–10 years in *J. thurifera*. To compare growth of trees of varying ages and sizes, tree-ring width was converted to basal area increment according to the formula:  $BAI = \pi (r_t^2 - r_{t-1}^2)$ ; where  $r$  is the tree radius and  $t$  is the year of tree-ring formation, then BAI of each year was normalised by dividing between tree diameter ( $d$ ).

#### Spatial pattern analyses and competition index

Point pattern analyses were used to assess univariate and bivariate (adults vs. juveniles) association patterns and their spatial scale at each plot. Prior to analyses, spatial

homogeneity and isotropy were visually checked (De la Cruz 2008). To analyse the global pattern of all trees, we calculated Ripley's  $K$  function [ $K(r)$ ] and its normalised version [ $L(r)$ ]. Similarly, bivariate point patterns (relative spatial arrangement of juveniles and adults) were analysed with the bivariate  $K$  function [ $K_{aj}(r)$ ], which estimates the number of juveniles ( $j$ ) surrounding an adult ( $a$ ) in a radius  $r$  (Wiegand et al. 2007). To test for complete spatial randomness (CSR, in the case of univariate patterns) and independence between adults and juveniles (for bivariate patterns) at each  $r$ , we generated 999 Poisson patterns and represented the critical values delimiting the 95% confidence interval. We applied the isotropic method to correct for border effects (Haase 1995). Additionally, we performed analyses of contingency tables. This approach tests whether there is spatial segregation of a given type of point, based on the observed and expected frequencies this

type of point has as nearest neighbour the other type of point. Expected frequencies are calculated with the random labelling approach with 999 simulations (Dixon 2002). For each plot, we tested for global segregation and for segregation of juveniles and adults.  $P$  values were calculated with Monte Carlo simulations (Dixon 2002).

A competition index (CI) was calculated for each sampled tree ( $i$ , focal) according to  $CI_i = \sum_{j=1}^{N(r)} [(d_j/d_i)/\text{dist}_{i-j}]$ , where  $d_j$  is the diameter of all neighbouring trees within a  $r$  distance,  $d_i$  is the diameter of the focal tree, and  $\text{dist}_{i-j}$  is the distance between the focal tree and each neighbouring tree (Lorimer 1983). The  $r$  value corresponding to the effective neighbourhood competition was tested by linear regression analyses as follows: the CI values obtained using radii from 1 to 10 m (in 1 m increments) were fit against the mean annual radial growth (according to the mini-cores) of each focal tree. Then, the distance  $r$  with the highest correlation coefficient was chosen: 7 m. This was done only using trees located away from the border of the plot, from the nine studied plots. To obtain a value of CI for all trees, we divided the CI at the calculated distance by the area of influence, i.e. a whole circle of radius  $r$  for trees away from the border of the plot and the proportional area included in the plot for trees close to the border. All spatial analyses were performed in the R environment (R Development Core Team 2009) using packages SPATSTAT (Baddeley and Turner 2005) and ECESPA (De la Cruz 2008).

### Statistical analyses

We performed a one-way ANOVA to test for differences among habitats in percentage of surface covered by trees; male, female and juvenile tree densities (variables measured at the plot level). We performed a linear mixed model [LMM (Bolker et al. 2008)] to test for differences among habitat types in CI, tree height, tree diameter and canopy radius (variables measured at the tree level) with one fixed factor (habitat type with three levels) and one random factor (plot, nested within habitat type). We used two LMMs to test for differences in growth (BAI/d, measured at the tree-ring level). One model only with adult trees, to test for the effects of tree gender (males vs. females) and a second model, with all trees, to test for the effect of tree age class (adults vs. juveniles). We included four factors as fixed (year, habitat type, age class or gender and CI), tree age as a covariate and plot (nested within habitat type) and tree (nested within plot) as random factors. Prior to analyses, normality and homogeneity of variance were checked using Levene's test and when necessary, variables were log-transformed. We used the restricted maximum-likelihood method (REML). We used the log-likelihood test to test for random effects (Zuur et al.

2009). These analyses were performed in the R environment (R Development Core Team 2009) using package nlme (Pinheiro et al. 2009).

## Results

### Tree age and morphology at the different habitat types

We found significant positive linear correlations between all measured morphological characteristics: height and trunk diameter ( $R^2 = 0.43$ ,  $P < 0.001$ ), height and canopy diameter ( $R^2 = 0.70$ ,  $P < 0.001$ ) and canopy and trunk diameter ( $R^2 = 0.42$ ,  $P < 0.001$ ). As expected, tree density and total surface covered were higher in the mature woodland (Fig. 2,  $F = 35.43$ ,  $P < 0.001$  and  $F = 55.28$ ,  $P < 0.001$ , respectively) than in the expanding woodland (Table 1). There was higher density of males ( $F = 80.35$ ,  $P < 0.001$ ), females ( $F = 21.24$ ,  $P = 0.002$ ) and juveniles ( $F = 8.08$ ,  $P = 0.020$ ) in the mature than in the expanding woodlands. The percentage of juveniles from all trees did not differ among habitat types ( $F = 3.05$ ,  $P = 0.122$ , Table 1). Mean tree age (Fig. 3), height and trunk diameter were higher in the mature than in the expanding woodland ( $F = 15.0$ ,  $5.9$  and  $5.3$ , respectively, and  $P < 0.001$ , Table 1). Mean tree canopy radius did not differ among habitat types ( $F = 1.2$ ,  $P = 0.307$ ). We found that CI was highest in the mature woodland and higher in the proximal than in the distal expanding woodland ( $F = 4.0$ ,  $P < 0.001$ , Table 1). Within habitat types, plots significantly differed ( $P < 0.01$ ) in all morphological variables.

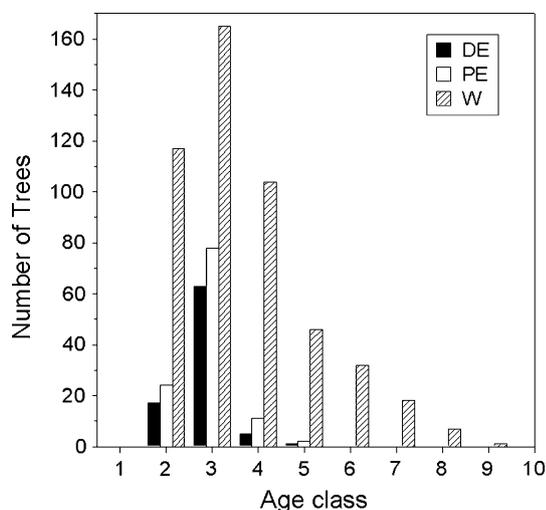
We did not find any significant effect neither of habitat type ( $F = 2.82$ ,  $P = 0.109$ ) nor of tree height ( $F = 0.58$ ,  $P = 0.568$ ) on the number of missed rings from 25 cm to breast height (for adult trees). Therefore, mean number of missed rings ( $7.1 \pm 0.9$ , mean  $\pm$  SE,  $n = 25$ ) was added to all adult trees bared at breast height to estimate age at 25 cm height (hereafter age). We found that age was best correlated to tree height, among all morphological variables (height, trunk and canopy diameter), in all plots from all habitat types. Analysis of homogeneity of slopes showed that the effect of height was not significantly different among habitat types ( $F = 0.06$ ,  $P = 0.938$ ), hence, we pooled data of age and height from all habitat types to estimate age with linear regression and obtained: age =  $14.9 + 0.068 \cdot \text{height}$  ( $R^2 = 0.54$ ,  $P < 0.001$ ,  $n = 114$ ).

All ages classes were not uniformly distributed in all woodland types. In all woodland types, trees between 20 and 30 years were the most abundant, followed by trees between 20 and 30 years. As expected, older age classes (trees between 40 and 100 years) were found only in mature woodlands.

**Table 1** Mean (SE,  $n = 3$ , except for competition index, age, height, trunk and canopy diameter where  $n = 86, 115$  and  $490$ , total number of trees at each habitat type) characteristics of the different habitat types

| Habitat type                                | Distal expanding woodland      | Proximal expanding woodland     | Mature woodland                  |
|---|--------------------------------|---------------------------------|----------------------------------|
| Tree density (N ha <sup>-1</sup> )          | 78.1 (4.1) <sup>a</sup>        | 151.5 (18.3) <sup>a</sup>       | 529.7 (68.0) <sup>b</sup>        |
| Female tree density (N ha <sup>-1</sup> )   | 5.6 (3.3) <sup>a</sup>         | 3.9 (0.01) <sup>a</sup>         | 76.3 (15.2) <sup>b</sup>         |
| Male tree density (N ha <sup>-1</sup> )     | 4.5 (0.8) <sup>a</sup>         | 10.5 (0.3) <sup>a</sup>         | 51.5 (4.7) <sup>b</sup>          |
| Juvenile tree density (N ha <sup>-1</sup> ) | 57.8 (5.0) <sup>a</sup>        | 123.8 (14.1) <sup>a, b</sup>    | 288.6 (70.8) <sup>b</sup>        |
| % Juvenile trees                            | 74.8 (9.1)                     | 81.8 (0.6)                      | 54.4 (10.8)                      |
| % Surface covered                           | 1.7 (0.3) <sup>a</sup>         | 2.8 (0.3) <sup>a</sup>          | 22.6 (2.7) <sup>b</sup>          |
| Competition index (CI)                      | 55.4 (8.9) <sup>a</sup>        | 105.8 (16.9) <sup>b</sup>       | 574.6 (71.6) <sup>c</sup>        |
| Age (year) (max–min)                        | 24.8 (0.5) <sup>a</sup> (7–42) | 24.3 (0.5) <sup>a</sup> (12–40) | 31.5 (0.7) <sup>b</sup> (10–145) |
| Height (cm)                                 | 145.92 (21.11) <sup>a</sup>    | 139.13 (7.56) <sup>a</sup>      | 242.84 (9.36) <sup>b</sup>       |
| Tree trunk diameter (cm)                    | 5.77 (0.36) <sup>a</sup>       | 5.74 (0.28) <sup>a</sup>        | 7.73 (0.29) <sup>b</sup>         |
| Canopy diameter (cm)                        | 143.4 (8.51)                   | 129.6 (7.43)                    | 185.7 (6.7)                      |

Different letters indicate significant differences ( $P < 0.05$ ) according to Tukey HSD



**Fig. 3** Histogram of age classes of the different habitat type (DE distal, PE proximal expanding woodland, W mature woodland). Age classes are 1 0–10, 2 10–20 ... and 10 90–100 years

### Spatial pattern analyses

*Juniperus thurifera* trees were clumped in all mature woodland plots at varying distances from 4 to 11 m (Figure S3). We also found a clumped pattern for trees at plot one (distal expanding woodland) from 3 to 10 m distance. The observed univariate point patterns, in the rest of the plots, did not differ significantly from spatial randomness. The analyses of the bivariate  $K$  function did not reveal any significant associations of juveniles to adults in any of the study plots (Figure S4). Global tests of analyses of contingency tables showed that in plots seven, eight (mature woodland) and three (distal expanding woodland) juveniles were significantly segregated (Table 2), i.e. juveniles were more likely to have other juveniles as nearest neighbour. In

these same plots, overall segregation was significant (marginally significant for plot seven, Table 2).

### Radial growth

Results of the linear mixed models showed that there was a significant effect of the habitat type on growth (BAI/d) and that growth was greatest in distal expanding woodland plots and lowest in mature woodland plots, for both genders and age classes (Table 3, Fig. 4a). Growth varied significantly between years (Table 3), it was greater in the more recent years on both genders and age classes (Fig. 4). Besides, we found that the interaction between habitat type and year had a significant effect on both genders and age classes (Table 3). The differences among habitat types were greatest in 2004, 2007 and 2008, compared to the driest years 2003 and 2005 (Fig. 4a).

Competition index (CI) had a significant negative effect on growth, for both genders and age classes (Table 3). Tree age also had a significant effect on growth, for both genders and age classes (Table 3). There were no significant differences in growth between males and females (Table 3, Fig. 4b), and the interactions of gender with habitat type and year did not have any significant effect either (Table 3). Age class had a significant effect on growth: juveniles grew more than adults (Table 3, Fig. 4c) and adults and juveniles responded similarly to the effect of habitat type and year (Table 3). For both models (first: males vs. females and second: adults vs. juveniles), we found that there was a significant effect of the random factor tree [log-likelihood ratio ( $L$ -ratio) = 508.08,  $P < 0.001$  for the first model and  $L$ -ratio = 950.26,  $P < 0.001$ , for the second]. The random factor plot did not have any significant effect ( $L$ -ratio = 1.95,  $P = 0.163$  for the first model and  $L$ -ratio = 1.17,  $P = 0.279$  for the second).

**Table 2** Results for each study plot of the global segregation test (statistical parameters:  $\chi^2$  and  $P$ ) based on the observed and expected frequencies of nearest neighbours, for the whole plot (overall) and for each age class

| Habitat type                | Plot            | Segregation | $\chi^2$  | $P$          |              |
|-----------------------------|-----------------|-------------|-----------|--------------|--------------|
| Distal expanding woodland   | 1               | Overall     | 1.17      | 0.530        |              |
|                             |                 | Adults      | 0.58      | 0.519        |              |
|                             |                 | Juveniles   | 0.74      | 0.412        |              |
|                             | 2               | Overall     | 1.61      | 0.442        |              |
|                             |                 | Adults      | 0.47      | 0.536        |              |
|                             |                 | Juveniles   | 0.54      | 0.425        |              |
|                             | 3               | Overall     | 5.92      | <b>0.037</b> |              |
|                             |                 | Adults      | 0.34      | 0.640        |              |
|                             |                 | Juveniles   | 3.73      | <b>0.037</b> |              |
| Proximal expanding woodland | 4               | Overall     | 2.39      | 0.299        |              |
|                             |                 | Adults      | 0.73      | 0.479        |              |
|                             |                 | Juveniles   | 1.14      | 0.279        |              |
|                             | 5               | Overall     | 0.26      | 0.888        |              |
|                             |                 | Adults      | 0.00      | 0.871        |              |
|                             |                 | Juveniles   | 0.26      | 0.575        |              |
|                             | 6               | Overall     | 2.64      | 0.239        |              |
|                             |                 | Adults      | 0.75      | 0.535        |              |
|                             |                 | Juveniles   | 1.16      | 0.250        |              |
|                             | Mature woodland | 7           | Overall   | 5.65         | 0.060        |
|                             |                 |             | Adults    | 0.47         | 0.450        |
|                             |                 |             | Juveniles | 5.5          | <b>0.010</b> |
| 8                           |                 | Overall     | 6.71      | <b>0.049</b> |              |
|                             |                 | Adults      | 2.56      | 0.110        |              |
|                             |                 | Juveniles   | 6.3       | <b>0.019</b> |              |
| 9                           |                 | Overall     | 0.95      | 0.661        |              |
|                             |                 | Adults      | 0.73      | 0.421        |              |
|                             |                 | Juveniles   | 0.64      | 0.476        |              |

Significant segregations are indicated in bold ( $P < 0.05$ )

## Discussion

### Spatial patterns and characteristics of the different habitats

We had hypothesised that facilitation would lead to clumping of *J. thurifera* trees in the mature and the expanding woodland. However, spatial patterns revealed a difference in the underlying nucleation processes from the expanding to the mature woodland. We found clumped patterns in the mature woodland, but we did not find clear evidence of nucleation in the expanding woodland. Clumped patterns have been reported in other *J. thurifera* woodlands (DeSoto et al. 2010; Montesinos et al. 2007). These authors suggested that clumping was due to direct facilitation of seedling and sapling establishment by conspecific adults (Montesinos et al. 2007) and nucleation

driven by zoochorous dispersal and perching effect (Pausas et al. 2006; Verdú and García-Fayos 1996). Zoochorous dispersal by birds (*Turdus* sp., thrushes) could underlay clumped patterns in mature *J. thurifera* woodlands, where pellets of thrushes loaded with seeds, and emerged seedlings, are found more often under the canopy of adult trees than in the open (Montesinos et al. 2007; Santos et al. 1999; Pías et al. unpublished data). Direct facilitation of sapling establishment by adult *J. thurifera* trees might play a role in the observed pattern, as it has been shown experimentally that *J. thurifera* sapling performance is improved under the canopy of adults (Montesinos et al. 2007; Gimeno et al. unpublished data). Nurse trees would facilitate sapling establishment by modifying the microhabitat underneath them and alleviating abiotic stress (Gomez-Aparicio et al. 2005; Smit et al. 2007; Verdú and García-Fayos 1996). Yet, since intra-specific competition negatively affected radial growth, direct facilitation would only be effective in the very early stages of tree establishment where competition is low. We propose that the observed clumping in the mature woodland is due mainly to perching and to a lesser extent to nursing effects of adult trees. Clumping can also be due to spatial heterogeneity of resource availability (Bestelmeyer et al. 2006). However, spatial heterogeneity of resource availability would have led to clumping in all types of studied plots, which was not the case, although it cannot be totally discarded as a structuring agent.

Differences between the expanding and the mature woodlands in the spatial patterns can be due to, first, a change in *J. thurifera* dispersers. In expanding woodlands, lack of adult trees, which serve as perches, limits bird attraction (Santos et al. 1999). Under this scenario, dispersal would rely more on mammals, whose depositions are independent of adult tree locations (Santos et al. 1999). Second, differences in spatial patterns could be due to reduced facilitation of sapling establishment due to lack of trees that serve as nurses (Kunstler et al. 2007). There was, however, some evidence of clumping in the distal expanding woodland, suggesting that isolated nucleation processes could take place in the early stages of woodland expansion (Pausas et al. 2006).

According to our predictions, competition was greatest in the mature woodland and negatively affected *J. thurifera* growth. Thus, we could expect that as saplings grow, competition increases and overrides facilitation, and trees in clumps (formed as a result of facilitation at early stages) would overcompete each other. This would indicate an ontogenetic shift in the nature of intra-specific interactions (Quero et al. 2008), which would explain the significant segregation found for juveniles that was not mirrored by adults in mature *J. thurifera* woodlands.

We found that tree age and demographic structure in our mature woodland were different from other Spanish-

**Table 3** Results of the linear mixed models (statistical parameters, degrees of freedom of the numerator and the denominator, *F* and *P*) of the fixed effects of the linear mixed models fitted for normalised basal area increment (BAI/d, d = tree diameter)

| Factor              | Males vs. females |                   |          |                  | Adults vs. juveniles |                   |          |                  |
|---------------------|-------------------|-------------------|----------|------------------|----------------------|-------------------|----------|------------------|
|                     | DF <sub>num</sub> | DF <sub>den</sub> | <i>F</i> | <i>P</i>         | DF <sub>num</sub>    | DF <sub>den</sub> | <i>F</i> | <i>P</i>         |
| Habitat type        | 2                 | 6                 | 11.1     | <b>0.010</b>     | 2                    | 6                 | 13.4     | <b>0.006</b>     |
| Gender              | 1                 | 110               | 0.1      | 0.802            | –                    | –                 | –        | –                |
| Age class           | –                 | –                 | –        | –                | 1                    | 291               | 6.5      | <b>0.012</b>     |
| Year                | 5                 | 519               | 153.7    | <b>&lt;0.001</b> | 5                    | 1,258             | 420.9    | <b>&lt;0.001</b> |
| Tree age            | 1                 | 110               | 12.3     | <b>0.001</b>     | 1                    | 291               | 17.6     | <b>&lt;0.001</b> |
| CI                  | 1                 | 519               | 14.9     | <b>0.000</b>     | 1                    | 1,258             | 38.0     | <b>&lt;0.001</b> |
| Habitat × year      | 10                | 519               | 10.7     | <b>&lt;0.001</b> | 10                   | 1,258             | 26.1     | <b>&lt;0.001</b> |
| Habitat × gender    | 2                 | 110               | 1.3      | 0.272            | –                    | –                 | –        | –                |
| Habitat × age class | –                 | –                 | –        | –                | 2                    | 291               | 1.3      | 0.287            |
| Gender × year       | 5                 | 519               | 1.6      | 0.152            | –                    | –                 | –        | –                |
| Age class × year    | –                 | –                 | –        | –                | 5                    | 1,258             | 0.2      | 0.944            |

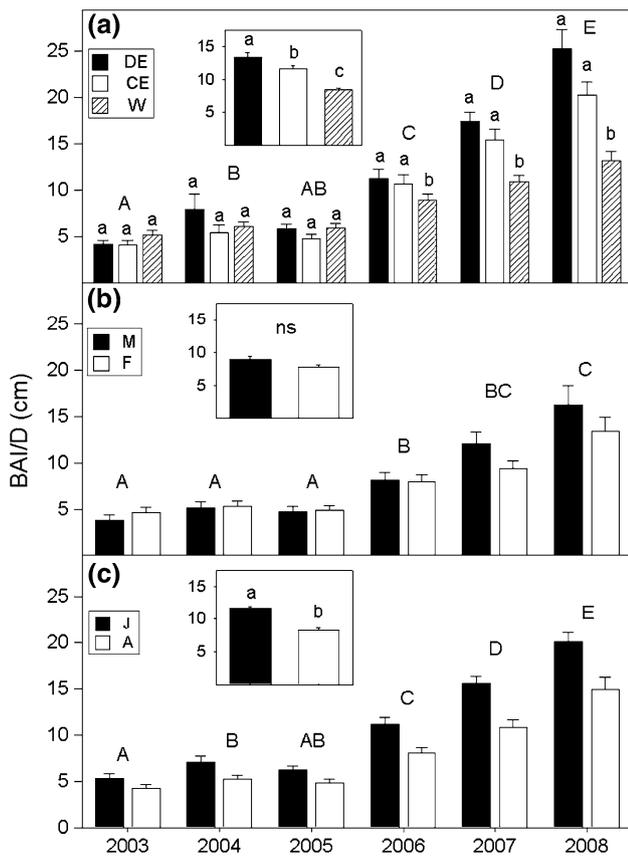
Fixed variables were: habitat type, gender, age class, year, tree age and competition index (CI). Significant effects ( $P < 0.05$ ) are indicated in bold

juniper stands (Montesinos et al. 2006; Olano et al. 2008; Rozas et al. 2009). Most of our trees were younger than 50 years, and we did not find trees older than 100 years. Age estimations from our study site agreed with measured ages in three nearby locations from another study (Gimeno et al. unpublished data). Our approach to estimate tree age from height was reliable. First, because no signs of growth suppression were detected in any of the bored trees and, second, because according to Olano et al. (2008), *J. thurifera* tree height increases linearly with age for trees under 100 years. Lack of aged trees, together with the higher proportion of juveniles, suggests a different impact of land use (growth suppression, wood harvest and browsing by cattle) on growth and recruitment dynamics at our study site than in previous studies in other juniper woodlands (Montesinos et al. 2006; Olano et al. 2008; Rozas et al. 2009). Spanish-juniper woodlands have been regarded traditionally as open formations (Olano et al. 2008), but increased tree density and the observed population structure in our study site could indicate a transition to a more closed forest-like formation, with important consequences for ecosystem processes, community assemblage and species composition (Maestre et al. 2009; Moore and Owens 2006; Van Auken 2009). For *J. thurifera*, forest closure could imply increased stress due to intra-specific competition, which could reduce resistance and adaptation to other disturbances such as pathogenic infection or drought (Linares et al. 2010). However, changes in land use (reduced grazing and fire frequency) are likely to increase inter-specific competition with grasses and woody shrubs, such as *Genista* sp., *Thymus* sp. and *Lavandula* sp. (Briggs et al. 2002; Van Uytvanck et al. 2008), which would impose a limit to forest closure.

#### Effects of habitat type, age and gender on radial growth

As expected, we found that radial growth was greatest in the distal expanding woodland, and lowest in the mature woodland. Higher growth in the expanding woodland is partially due to lower intra-specific competition (Lorimer 1983), as evidenced by the significant negative effect of competition index on growth, but other ecosystem traits related to land previous history (e.g. soil properties or species community composition) might also affect tree growth (Van Uytvanck et al. 2008). Interestingly, our results showed that there was a significant interactive effect on growth of habitat type and year: differences among habitats were maximised in the favourable years (2004, 2007 and 2008) and disappeared in the more climatically unfavourable years (like 2003, and especially 2005). In the expanding woodlands, *J. thurifera* radial growth proved more plastic than in the mature woodlands; it increased more under favourable climatic conditions, such as mild winters or rainy springs (Rozas et al. 2009), and decreased more in response to unfavourable climatic conditions (rainfall scarcity) experienced during 2005. Differences in climatic responsiveness could be modulated by competition intensity, as competition can affect growth response to climate (Linares et al. 2010). This result also suggests that increased drought associated to climate change (Christensen et al. 2007) could impair *J. thurifera* growth in the early stages of woodland expansion.

Previous studies showed that *J. thurifera* males and females differed in their radial growth patterns (Montesinos et al. 2006) and climate sensitivity (Rozas et al. 2009). However, this was not the case in our study: gender did not significantly affect radial growth, and it did not have any



**Fig. 4** Mean ( $\pm$ SE) radial growth (normalised basal area index, BAI/D, D = tree diameter) over the past six years for **a** different habitat types: DE distal, PE proximal expanding woodland, W mature woodland; **b** different genders: M male, F female and **c** different age classes: J juveniles, A adults. Inserts are the means ( $\pm$ SE) of each class without accounting for the different years. Different letters indicate significant differences among years (capital letters) and among habitat types within years (lower case letters)

interactive effect neither with year nor with habitat type. Notably, these previous studies were conducted in older *J. thurifera* stands than ours. We argue that gender does not influence radial growth in young stands of *J. thurifera*, which agrees with our results from three nearby *J. thurifera* stands of similar ages to this (Gimeno 2011, unpublished data).

**Conclusions**

Our results suggest that the mechanisms underlying the dynamics of expanding *J. thurifera* woodlands differ from those structuring mature woodlands. Contrary to our expectations, in the expanding woodland, we did not find clear evidence for underlying nucleation processes. We suggest that this is due to, first, the replacement of birds by mammals as main dispersers in expanding woodlands and, second, to reduced importance of intra-specific facilitation

by adult trees in expanding woodlands. It should be noted that woodland expansion was favoured in our study site by the proximity to a propagule source, but in very isolated fields, lacking remnant adults of *J. thurifera*, propagule arrival, emergence and seedling establishment might be seriously compromised (Santos et al. 1999). We propose that growth of established *J. thurifera* juveniles will be favoured in the early stages of expansion due to reduced intra-specific competition, but significantly constrained by unfavourable years, which are expected to become more frequent under climate change scenarios.

Our results highlight that in the Mediterranean, expansion of juniper woodlands is not limited to woody encroachment of grasslands by juniper trees. Spanish-juniper woodland expansion into abandoned agricultural fields and livestock pastures is coupled to an increase in effective recruitment and total cover in mature, partially degraded woodlands, formerly devoted to timber extraction and cattle grazing. This effective woodland expansion and rapid recuperation of the mature woodland are a broader phenomenon than simple woody encroachment (see Maestre et al. 2009) for which we propose the term *woodlandisation*. In this particular case, woodlandisation translates into a net gain of a valuable habitat from a conservation perspective, increased habitat availability for forest species and increased carbon sink capacity, but it will also impact on other ecosystem services, such as water and nutrient cycling. Finally, the net impact of woodlandisation on ecosystem services and biodiversity conservation will depend on its interaction with other global change drivers such as biological invasions (Siemann and Rogers 2003) and changes in the climate and the fire regime (Breshears 2006).

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