

Release of *Juniperus thurifera* woodlands from herbivore-mediated arrested succession in Spain

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Abstract

Question: Do abiotic constraints maintain monospecific woodlands of *Juniperus thurifera*? What is the role of biotic (livestock) versus abiotic (climate) drivers in the recruitment and growth of the different tree species?

Location: Cabrejas range, Soria, north-central Spain, 1200 m altitude.

Methods: Stand history was reconstructed using dendro-ecology and spatial pattern analysis, combined with historical data of livestock abundances and climatic records.

Results: *J. thurifera* establishment occurred in two distinct pulses, with a tree component establishing in the late 1800s to early 1900s. *Quercus ilex* and *Pinus sylvestris* establishment was evident only from the late 1970s onward. Recruitment events were related to reductions in livestock browsing. *J. thurifera* spatial structure was clumped and *Q. ilex* showed a short-scale aggregation to *J. thurifera* trees and saplings. Radial growth trends of *J. thurifera* saplings, *Q. ilex* and *P. sylvestris* were negatively related to livestock density. Summer drought limited the radial growth of all the study species, and *P. sylvestris* and *Q. ilex* grew faster than *J. thurifera* even after considering an age effect.

Conclusions: The differences in radial growth patterns and recruitment pulses between species indicate that livestock browsing and not abiotic factors is the main factor controlling plant succession and structural development. In this process, *J. thurifera* acts as a nurse plant, facilitating the establishment of other tree species. Under the current low pressure from herbivores, formerly pure *J. thurifera* woodlands will change towards dense stands of mixed species composition.

Keywords: climate response; dendro-ecology; land-use history; livestock browsing; spatial pattern.

Nomenclature: Castroviejo et al. (1986, 1989).

Introduction

From the 1950s onward, rural landscapes in southern Europe faced rapid land use changes caused by depopulation and agricultural abandonment in some regions, and urbanization and agricultural intensification in others (Westhoek et al. 2006). Traditional management practices have been greatly reduced or abandoned with agrarian activity concentrating on the most fertile soils (De-bussche et al. 1999). In less productive areas, many quasi-natural woodlands historically maintained by traditional practices such as lumbering, tree pollarding and extensive free-ranging livestock, have been affected by changes in land use. Within this framework, the reduction of domesticated animal grazing occurring over large areas is particularly relevant because livestock has been one of the main agents shaping these landscapes for centuries (Barbero et al. 1990; Chauchard et al. 2007).

Changes in traditional land use are a major driver of global change (Vitousek 1994; Chauchard et al. 2007) that, in combination with climate change, may be one of the ultimate factors controlling the future dynamics of forests in southern Europe (Gehrig-Fasel et al. 2007). Consequently, it is necessary to evaluate simultaneously the relevance of both global change drivers to anticipate future ecosystem dynamics.

Juniperus thurifera often forms almost monospecific open woodlands listed as priority habitat by the European Union Directive 92/43/EEC, EUNIS 9560 (Davies et al. 2004). These woodlands are considered to be remnants of the dominant vegetation during drier and cooler past climatic periods (Riera 2006). The dominance of *J. thurifera* is attributed to its tolerance to harsh climatic conditions that

restrict the establishment of other tree species (Blanco et al. 2005). A recent study, however, indicates that both *J. thurifera* growth and recruitment are related to historical changes in livestock density (Olano et al. 2008), suggesting that traditional land use is a key factor shaping the current structure of this ecosystem. Juniper woodlands are changing in community structure and composition throughout Spain following abandonment of traditional land-use practices and, especially as a consequence of the decrease in browsing during the last few decades (Gauquelin et al. 1999).

Succession is commonly described as a linear process where the endpoint is predictable climax vegetation (Whittaker 1953). Natural succession can be arrested when frequent low-severity disturbances occur, and persistent alternative vegetation can dominate (Scheffer et al. 2001). Empirical studies have demonstrated that mammal herbivory can exert a continuous long-term influence on vegetation, whose effects are different from other transitory disturbances such as timber harvesting, blights, insect defoliation or fire (Turner et al. 1998). Arrested succession mediated by long-term livestock grazing might explain the monospecific nature of *J. thurifera* woodlands. The recent decline of livestock pastoralism might therefore have changed community composition because of release of succession following a decrease in herbivory (Sarmiento 1997).

Our aim was to unravel the mechanisms that drive this change, evaluating the effects of both climatic constraints and land-use changes on the dynamics of this community. We intensively surveyed a representative juniper woodland plot historically subjected to traditional land use (Olano et al. 2008). A single plot was focused upon in order to adequately describe intraspecific and interspecific spatial patterns at fine scales, combined with a dendro-chronological approach to gain insight on temporal dynamics. Our specific goals were to (1) reconstruct the past recruitment of tree species in a *J. thurifera* woodland, (2) assess the differential growth dynamics of *J. thurifera* and coexisting species in relation to recent changes of land-use intensity and climate variation, and (3) predict future trends in woodland composition and structure.

Materials and Methods

Study area and species

The study area was located on the upper plain of the Cabrejas range at 1200 m above sea level near

Cabrejas del Pinar (41°47'N, 2°50'W), Soria Province, Spain. The climate is sub-humid supra-Mediterranean (Rivas-Martínez & Loidi 1999), with a mean annual rainfall of 533 mm. Mean monthly temperature ranges from 2.8°C in January to 20.0°C in July. Soils are shallow and calcium rich interspersed with exposed patches of Cretaceous limestone bedrock. Vegetation is dominated by *J. thurifera* L. intermingled with some *Pinus sylvestris* L. and *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. (hereafter *Q. ilex*) individuals.

J. thurifera is a long-lived conifer tree endemic to continental areas of the western Mediterranean and was a dominant species during cold stages of the Pleistocene (Terrab et al. 2008). *P. sylvestris* is a Euro-Siberian species, occupying a wide geographic and ecological range over boreal and temperate Asia and Europe. It reaches its southern extent in the Iberian Peninsula, where its growth is limited by summer drought (Richter et al. 1991). *Q. ilex* is an evergreen tree adapted to a wide variety of soils under continental climate and is native of the western Mediterranean region where it is frequently a dominant species (Blanco et al. 2005).

Plot establishment and sampling

In 2006 a 120 m × 120 m plot was established in an area representative of juniper woodland in this region. Previous studies had already addressed the history of this forest with 107 small plots (Olano et al. 2008; Rozas et al. 2008). Consequently, we concentrated on a single larger plot in order to study inter-tree relationships at a broad spatial scale. All individuals of *J. thurifera*, *P. sylvestris* and *Q. ilex* found in the plot were mapped using a laser total station (Pentax R-325NX, Tokyo, Japan), labelled and measured for their height and diameter. Diameter was measured as (1) DBH (stem diameter measured at 1.3 m above ground) for trees (> 1.5 m tall), or (2) basal diameter (measured at ground level) for saplings (< 1.5 m tall) and all *Q. ilex*. For subsequent analyses *J. thurifera* individuals were divided into tree and sapling categories.

Wood cores were extracted for age estimation and tree-ring analysis. A total of 130 randomly selected *J. thurifera* trees and all *P. sylvestris* trees were cored with increment borers. One core per tree, as close to the ground as possible, was taken. In addition, a basal stem disk was cut from 44 *J. thurifera* saplings and 44 *Q. ilex* saplings and trees up to 3 m tall that were randomly selected from areas surrounding the plot, in order to measure radial growth and estimate the age-diameter relationship.

Dendro-ecological analysis and age estimation

Cores and stem disks were air-dried, cores were glued onto wooden mounts, and all samples were mechanically surfaced and then manually polished with a series of successively finer sandpaper grits. The tree rings were visually dated following a standard procedure (Stokes & Smiley 1968). Total ring-widths were measured at a 0.001 mm resolution using a Velmex sliding-stage micrometer (Bloomfield, NY, US) interfaced with a computer. Measurement and dating errors on *J. thurifera* tree-ring series were detected with the computer program COFECHA (Grissino-Mayer 2001) using a robust master chronology obtained from a sample of stem disks of 107 *J. thurifera* trees (Olano et al. 2008; Rozas et al. 2008). We did not cross-date ring width series derived from *P. sylvestris*, because it showed regular, concentric growth and there were no missing rings. For the stem disks taken from *Q. ilex* and *J. thurifera* saplings, cross-dating was not performed but the tree-ring series were measured along those radii with active growth and without missing rings, keeping dating errors to a minimum.

We estimated the age of cored *J. thurifera* trees and *P. sylvestris* trees from increment cores. The age of *P. sylvestris* saplings was calculated by branch whorls counts; this method has proven to be very accurate for *P. sylvestris* <30 years old (Edenius et al. 1995). The age of *Q. ilex* and *J. thurifera* saplings was estimated using the fitted equations of age against basal diameter obtained from least squares regression. The age of uncored *J. thurifera* trees was estimated from their DBH based on a diameter-age least squares regression obtained from cored trees. A correction for the loss of rings, owing to coring height was implemented based on mean height growth rates obtained from a previous study in this area (Olano et al. 2008).

The Percentage Growth Change (PGC) filter of Nowacki & Abrams (1997) was applied to identify abrupt and sustained growth releases in the raw ring-width series. We used the formula

$$\text{PGC} = [(M2 - M1)/M1]100$$

where *M1* is the preceding and *M2* the subsequent 10-years ring-width means. Individual PGC chronologies were calculated for the individual tree-ring series. The minimum threshold was established 100% as a conservative criterion to confidently recognize abrupt growth releases. We observed that *J. thurifera* trees often experienced an initial suppression of growth rate upon disturbance, followed by a release of growth. Initial radial-growth

suppression has been related to height suppression by herbivory in this area (Olano et al. 2008).

In order to compare individual annual radial growth between species, we used repeated measures analysis of variance, including tree age as a covariate (Moser et al. 1990). We analysed the whole period of common growth and periods of 8 years before a detected growth release for *P. sylvestris* and *Q. ilex* in 1997 (from 1989 to 1996) and after release (from 1998 to 2005) to assess the release impact of browsing cessation on growth change intensity. Differences in individual ring widths between species were tested with *post hoc* Dunnett's test. Within species, differences in mean ring widths before and after release were compared with a pair-related *t*-test.

Spatial pattern analysis

Point pattern analysis was used to analyse univariate and bivariate association and their spatial scale. In order to analyse spatial aggregations, we applied Ripley's *K*-function on completely mapped stem distribution of the study plot (Haase 1995). Because a preliminary visual exploration of the stem map suggested the existence of first-order effects (i.e. the intensity of the pattern is not constant over the study area), the inhomogeneous *K*-function was used (Wiegand et al. 2007). The intensity function were estimated with the maximum pseudo-likelihood algorithm of Baddeley & Turner (2000). For each species, we fitted heterogeneous Poisson models with the heterogeneous intensities modelled as log-linear functions of polynomials of the coordinates *x* and *y* and selected the most parsimonious model using likelihood ratio tests (Baddeley & Turner 2006). Edge effects were accounted for with the local weighting method of Ripley (Haase 1995). For ease of interpretation, we transformed the inhomogeneous *K*-function in the frequently used function $L(r) = [K(r)/\pi]^{1/2} - r$. The observed inhomogeneous *L* functions were tested against the null model of heterogeneous Poisson (Wiegand et al. 2007) by comparing each observed function with the 95% envelopes (i.e. the 2.5% and 97.5% quantiles) of 999 simulated inhomogeneous functions of each fitted heterogeneous model.

As most patterns significantly differed from a heterogeneous Poisson distribution, they were modelled as heterogeneous Poisson cluster processes, using the method of minimum contrast (Waagepetersen 2007). To obtain information about the inter-type association between the *J. thurifera* trees and saplings, and between *J. thurifera*, *Q. ilex* and *P. sylvestris*, bivariate spatial interactions were

examined using the inhomogeneous cross-type K -function (Baddeley & Turner 2005). The observed bivariate functions were tested against the null model of independence (Goreaud & Pelissier 2003) by comparing the observed inhomogeneous L_{12} function with the 95% envelopes of the inhomogeneous L_{12} functions obtained from 999 simulations of the fitted heterogeneous Poisson cluster models. Spatial analyses were conducted with the SPATSTAT package (Baddeley & Turner 2005) in the R environment (R Development Core Team 2007).

Land use history and climate response

Historical information on past livestock density was used to evaluate the effects of browsing on woodland dynamics and tree establishment. It included local and regional documentary archives, interviews with local farmers and a literature review (Gallego et al. 1991; Pérez-Romero 1995).

Mean radial growth of the tree species was compared with the recent variation of livestock numbers as a sum of sheep and goats per year. Individual tree-ring series were standardized with the ARSTAN program (Cook & Holmes 1986) using a spline function with a 50% frequency response of 32 years, which was flexible enough to reduce non-climate variance. The residual chronologies obtained after standardization were compared with seasonal mean temperature and cumulative precipitation considering the previous December, January and February as winter, and the successive 3-month groups as Spring, Summer and Autumn, respectively. Meteorological data were provided by the Spanish Meteorological Agency.

Results

Recruitment, growth dynamics and spatial patterns

A total of 1068 individuals were mapped, of which 890 were *J. thurifera* (448 saplings and 442 trees), 142 were *Q. ilex* and 36 were *P. sylvestris*. We found four dead *J. thurifera* trees and two stumps.

Highly significant relationships were obtained between diameter and age for all tree species. The equations for predicting age from diameter were: *J. thurifera* trees age = $64.04 + 2.55 \times (\text{DBH})$ ($r^2 = 0.46$, $n = 112$, $F = 93.2$, $P < 0.001$); *J. thurifera* saplings age = $13.28 \times (\text{basal diameter})$ ($r^2 = 0.85$, $n = 44$, $F = 231.3$, $P < 0.001$); *Q. ilex* age = $2.98 \times (\text{basal diameter})$ ($r^2 = 0.82$, $n = 44$, $F = 203.1$, $P < 0.001$).

Most of the *J. thurifera* trees recruited during the late 1800s and early 1900s (Fig. 1). An initial period of growth suppression was common in *J. thurifera* during the late 1800s with half of the sampled trees showing suppressed growth (Fig. 2). Most *J. thurifera* saplings occurred during the second half of the 1900s (Fig. 1), although the older saplings established as early as 1870. *P. sylvestris* and *Q. ilex* established only after 1970.

Mean radial growth differed among species ($F_3 = 180.98$, $P < 0.01$) considering the effect of individual age, which was not significant ($F_3 = 0.268$, $P = 0.61$), with larger growth rates for *P. sylvestris* and *Q. ilex* than *J. thurifera*. A distinct release of growth in 1997 was detected in the *Q. ilex* and *P. sylvestris* growth series (Fig. 3a). Curiously growth rates of *J. thurifera* trees decreased since 1997 (Table 1).

Ripley's K -function revealed that *J. thurifera* trees were significantly clumped at distances from 1 to 29 m, with a maximum at 5 m (Fig. 4a). *J. thurifera* saplings also showed a clumped pattern from 0.5 to 28 m (Fig. 4b). *J. thurifera* saplings showed a small-scale positive association with *J. thurifera* trees at distances up to 2.5 m (Fig. 5a). *Q. ilex* also showed a clumped pattern up to 14 m (data not shown), and were also positively associated to *J. thurifera* saplings and trees at distances up to 2.5 and 4 m, respectively (Fig. 5b and c). Spatial analysis of *P. sylvestris* was not performed because of the small sample size.

Livestock pressure and climate effects

Livestock records for the mid-1800s in Cabrejas del Pinar mention 2380 sheep and 500 goats, a high number even taking into account that historical records tend to underestimate livestock abundance. During the late 1800s, a sharp decrease in livestock density occurred in the region (Pérez-Romero 1995). This decreasing trend in browsing pressure was corroborated by local historical events. Livestock density recovered during the World War I (Gallego et al. 1991) and high numbers were probably maintained up until 1945. Livestock abundance peaked in 1951 (4953 sheep and 560 goats) (Fig. 3b) followed by a constant decreasing trend, which intensified in the mid-1960s for goats and in the 1990s for sheep. The lowest values in the whole record of livestock abundance were 17 goats and 459 sheep in 2006, the most recent data year.

Mean radial growth of *J. thurifera* trees was positively correlated to livestock abundance, whereas mean growth of *J. thurifera* saplings, *Q. ilex* and *P. sylvestris* was negatively correlated (Table 2).

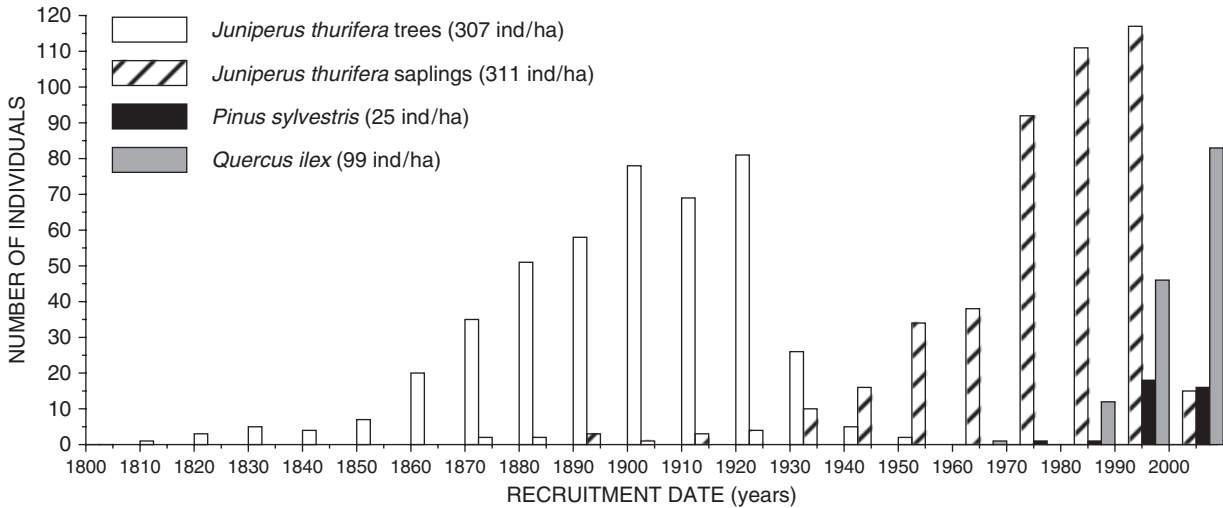


Fig. 1. Recruitment pattern in 10-years classes for the *Juniperus thurifera* trees and saplings, *Pinus sylvestris* and *Quercus ilex* in the study plot.

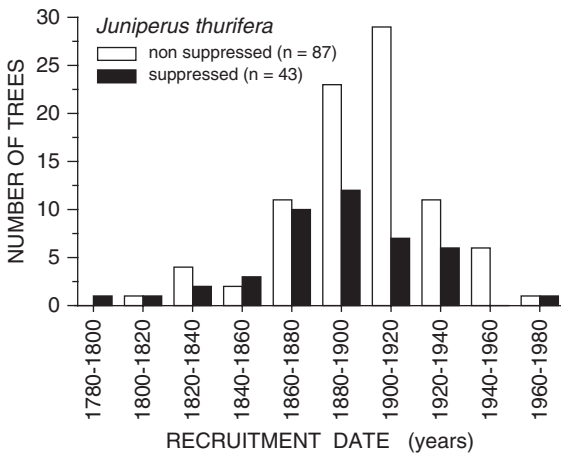


Fig. 2. Number of non-suppressed and suppressed *Juniperus thurifera* trees established in 20-year periods.

The growth of *J. thurifera* trees was positively correlated to winter temperatures and negatively correlated to summer temperatures and winter rainfall (Table 2). *J. thurifera* saplings showed the same pattern in relation to temperature, but radial growth of the *J. thurifera* saplings, *Q. ilex* and *P. sylvestris* was positively related to summer rainfall. However, growth of *Q. ilex* and *P. sylvestris* was not significantly correlated with mean seasonal temperatures.

Discussion

Stressful abiotic conditions associated with droughty, shallow soils have been suggested as the main factors providing *J. thurifera* with a competi-

tive advantage over other tree species, thus explaining the monospecific nature of juniper woodlands in central Spain (Blanco et al. 2005). The larger growth rates of *P. sylvestris* and *Q. ilex*, in comparison with *J. thurifera*, do not support this assertion. Accordingly, *J. thurifera* dominance is best explained by long-term browsing by livestock that suppressed competing tree species. This phenomenon can be considered as a form of herbivore-mediated arrested succession (Sarmiento 1997).

Most *J. thurifera* trees recruited during the late 1800s and early 1900s coinciding with a regional decrease of livestock (Pérez-Romero 1995). However, the browsing pressure might have still been moderate as *J. thurifera* tree growth was often suppressed during early life stages. Moreover, *J. thurifera* trees that established during this period are arranged in clumps – a possible consequence of a nucleation process (Yarranton & Morrison 1974) or as a result of a protection by nurse plants against browsing (Callaway 1995).

The second pulse of recruitment in the 1950s and 1960s coincided with a decrease in the abundance of livestock. *J. thurifera* saplings were clumped in open areas or immediately adjacent to established adult trees. This close proximity between *J. thurifera* trees and saplings may be a consequence of the use of larger tree branches as perches by avian frugivores (Santos et al. 1999; Montesinos et al. 2007). The establishment of *P. sylvestris* and *Q. ilex* commencing in the 1980s coincided with a marked decline in livestock density. This pulse of recruitment was rapid because, by 2006, density had already reached 99 individuals ha⁻¹ for *Q. ilex* and

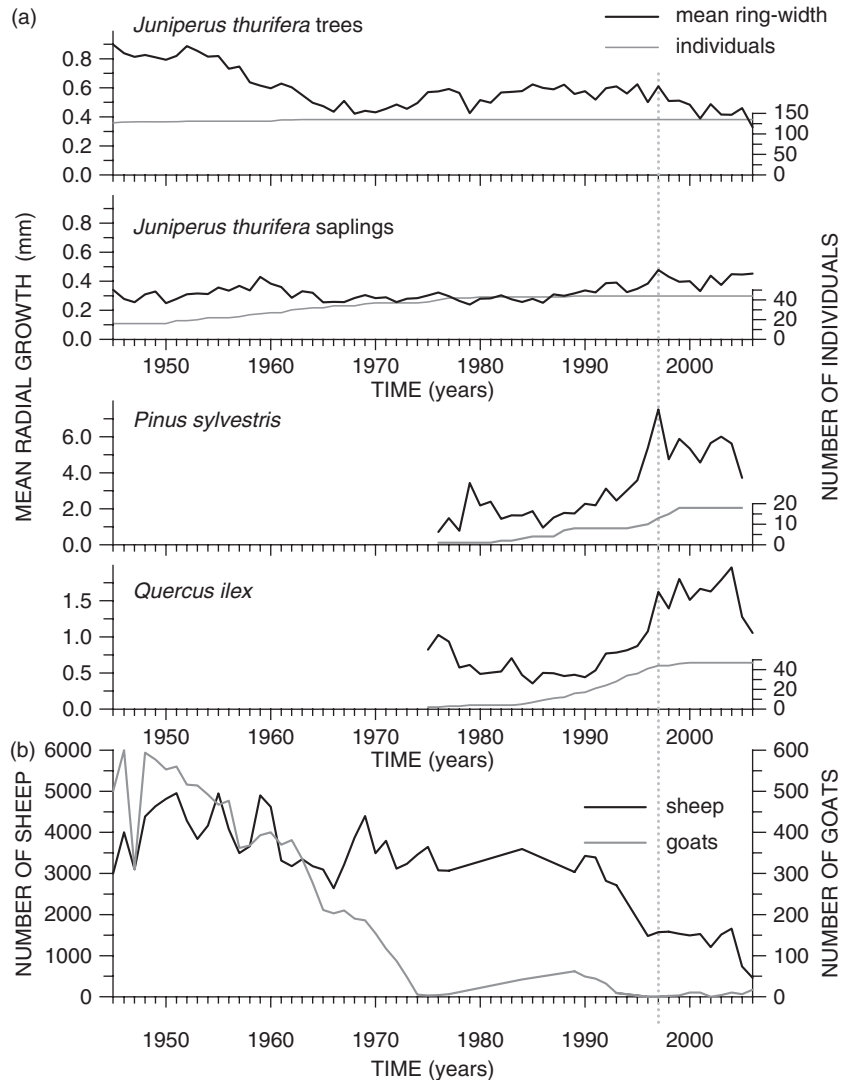


Fig. 3. (a) Mean ring-width chronologies of the species in the stand and temporal variation in the number of individuals used to calculate the chronologies. The vertical line indicates the release of growth in 1997. (b) Temporal variation in the number of sheep and goats in Cabrejas del Pinar.

Table 1. Results of repeated-measures ANOVA on ring width (mm) before (1989–1996) and after (1998–2005) the 1997 release. Letters within a row indicate significant differences in mean ring width, according to Dunnett's test. Last row shows paired-related *t*-test before and after release for each class. * $P < 0.05$; *** $P < 0.001$; n = number of individuals). MRW = mean ring width (mm); SD = standard deviation.

	<i>Juniperus thurifera</i> trees	<i>Juniperus thurifera</i> saplings	<i>Pinus sylvestris</i>	<i>Quercus ilex</i>	$F_{1,3}$
MRW _{1989–1996} (SD)	0.569 ^b (0.354)	0.352 ^c (0.299)	2.973 ^a (1.886)	0.721 ^b (0.455)	81.37***
MRW _{1998–2005} (SD)	0.445 ^c (0.299)	0.414 ^c (0.387)	5.196 ^a (1.315)	1.563 ^b (1.057)	401.10***
<i>t</i> (n)	−6.356 (134)***	1.791 (43)	2.498 (10)*	7.352 (41)***	

24 stems ha^{−1} for *P. sylvestris*. This is in agreement with previous research in Mediterranean areas (Chauchard et al. 2007), which shows that new tree seedling establishment is commonly favoured by reductions of browsing intensity.

The abrupt and sustained increases in radial growth rates observed in *P. sylvestris* and *Q. ilex* since 1997 have occurred simultaneously with a sharp decrease in livestock abundance, suggesting that initial growth was severely limited by browsing.

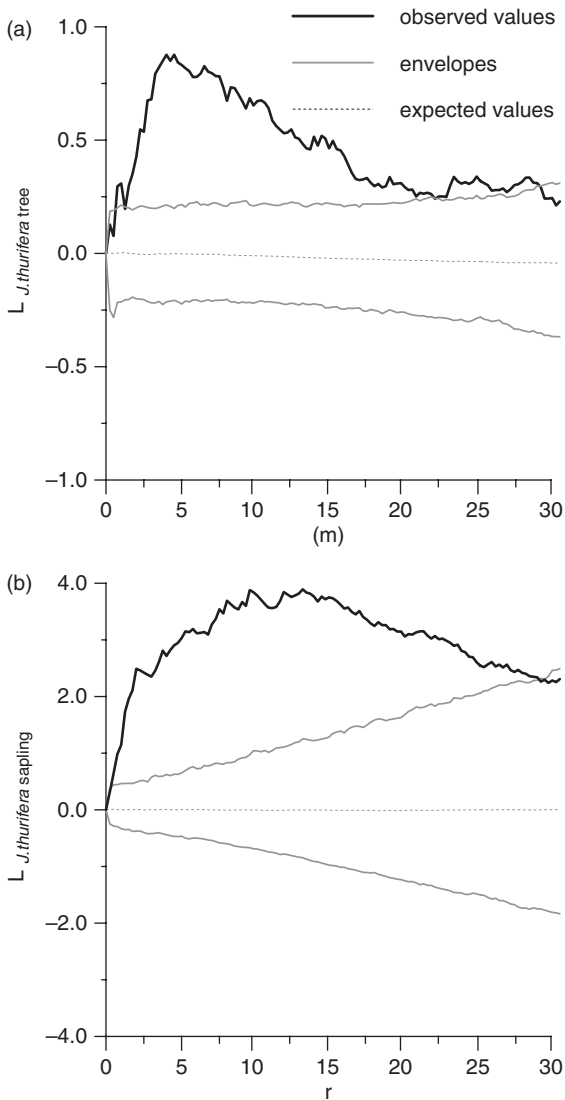


Fig. 4. Univariate point pattern analyses using $L(r)$ function against r distance (metre). (a) *Juniperus thurifera* trees; (b) *J. thurifera* saplings. The confidence interval is composed of 95% envelopes from 999 simulations of heterogeneous Poisson models. The expected values are the mean of the simulations. Observed values greater than the 95% envelopes indicate significant clumped patterns.

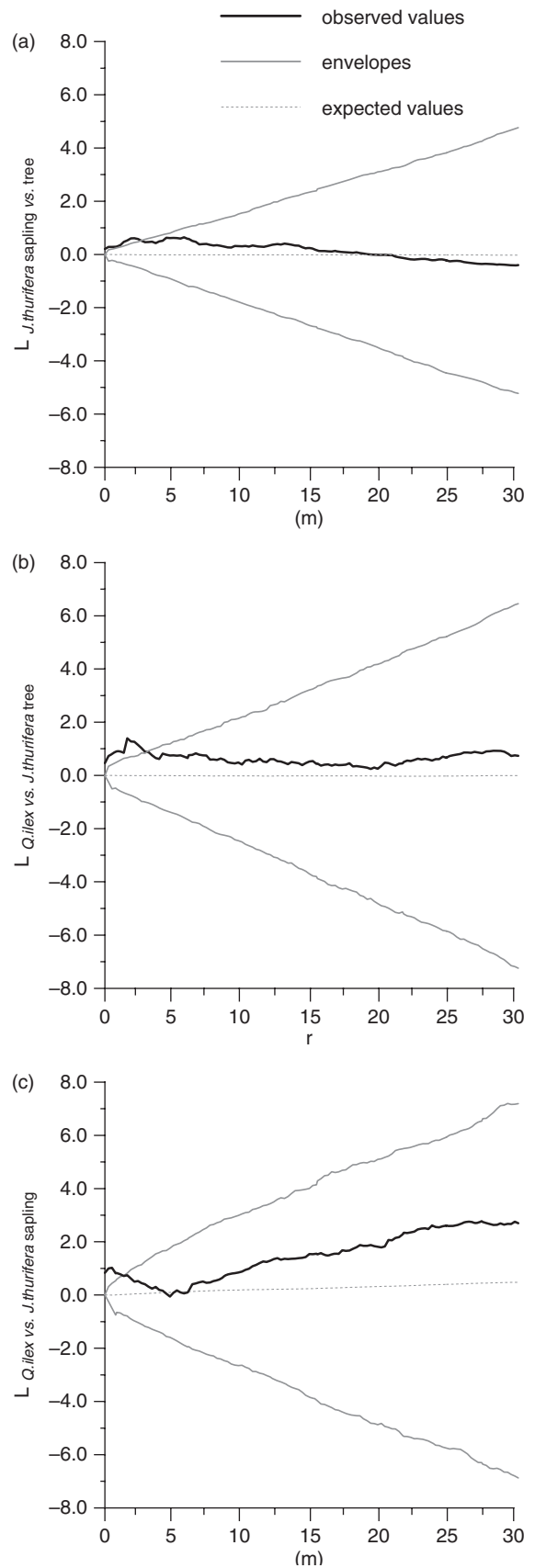


Fig. 5. Bivariate point pattern analyses using $L_{12}(r)$ function against r distance (metre). (a) *Juniperus thurifera* saplings versus trees, (b) *Quercus ilex* versus *J. thurifera* trees; (c) *Q. ilex* versus *J. thurifera* saplings. The confidence interval is composed of 95% envelopes from 999 simulations of the null model of independence. The expected values are the means of the simulations. Observed values greater than the 95% envelopes indicate significant spatial attraction.

Table 2. Spearman correlations of tree species mean radial growth with livestock and growth index with climatic variables. ** $P < 0.01$; *** $P < 0.001$; n = number of years in the common period. Seasons not represented did not show significant correlations.

Tree species	n	Livestock	n	Temperature		Precipitation	
				Winter	Summer	Winter	Summer
<i>Juniperus thurifera</i> tree	50	0.614***	62	0.215**	-0.296**	-0.270**	0.193
<i>J. thurifera</i> sapling	50	-0.403***	62	0.238**	-0.265**	-0.119	0.268**
<i>Pinus sylvestris</i>	18	-0.734***	29	0.086	-0.159	0.069	0.520***
<i>Quercus ilex</i>	20	-0.678***	31	-0.076	-0.218	0.091	0.495**

This is further supported by the negative correlations between livestock numbers and growth rates for both *Q. ilex* and *P. sylvestris*. Although further study of *P. sylvestris* is needed on account of the small sample size in this study, its sensitivity to browsing has been shown in other studies (Zamora et al. 2001). In addition, the spatial association of *Q. ilex* to *J. thurifera* suggests that a facilitation process may be operating at initial stages, with *J. thurifera* saplings and trees providing shelter from herbivores. This process is common in grazed environments (Smit et al. 2006). The relationship between livestock density and *J. thurifera* growth differs depending on size of the individual. A positive relationship exists between livestock density and growth of *J. thurifera* trees and may be a consequence of increased competition with understorey shrubs, herbs and grasses when livestock decreases (Callaway & Walker 1997). *J. thurifera* saplings show the opposite effect, increasing growth with reductions in livestock density (Fig. 3). This is probably because of a decrease in browsing of small saplings.

The role of selective browsing in modifying successional pathways has been reported for Mediterranean forests (Cuartas & García-González 1992; Zamora et al. 2001). The low palatability of *J. thurifera* saplings (Massei et al. 2006) and their tolerance to browsing (Olano et al. 2008) allow this species to recruit and survive even during long periods of sustained high levels of herbivory pressure. Even though the moderate livestock pressure of the 1800s and early 1900s allowed *J. thurifera* to establish and grow into trees, it was still too high and appeared to have hindered establishment of *P. sylvestris* and *Q. ilex*. In addition, these species are more palatable and less tolerant to herbivory than *J. thurifera* (Hester et al. 2004; Espelta et al. 2006). The lack of coexisting species in the forest until the last few decades has been corroborated by interviews with local inhabitants and with an intensive search for mature trees in the neighbouring areas. Indeed, livestock

browsing has been the main ongoing impediment to *P. sylvestris* and *Q. ilex* regeneration and growth. The absence of local seed sources in the surrounding area (closest adult *P. sylvestris* and *Q. ilex* trees were < 1 km from the plot) may have slowed the successional process. However, once *Q. ilex* and *P. sylvestris* reach reproductive age, their representation in this stand will likely benefit tremendously from local seed (Purves et al. 2007).

Although browsing pressure had the strongest influence on tree composition and succession, climate may also affect forest dynamics because of poor conditions (e.g. shallow soils). Water availability in summer is the main climatic factor limiting growth. Differences in sensitivity to summer water stress were evident among species (*J. thurifera* versus *Q. ilex* and *P. sylvestris*) and between size classes (*J. thurifera* trees versus saplings). Tolerance of *J. thurifera* to summer drought increases with increasing age (Rozas et al. 2009). By contrast, *Q. ilex* and *P. sylvestris* become more sensitive to summer drought (Oberhuber et al. 1998; Corcuera et al. 2004), and mortality by xylem embolism has been linked to extreme drought events (Martínez-Vilalta & Piñol 2002; Martínez-Vilalta et al. 2002). An expected increase in drought intensity, owing to climate change, might reduce growth of *J. thurifera* but would probably affect *Q. ilex* and *P. sylvestris* more severely. In addition, future changes in herbivory levels may alter the climate-growth relationship modulating species abundance in juniper woodlands (Trotter et al. 2002).

Open woodlands of *J. thurifera* are an artefact of livestock browsing, essentially representing an arrested state of succession owing to herbivory. Without herbivory, the historical open structure of *J. thurifera* woodlands readily converts to a closed-canopy forest with increasing representation of other tree species. There is evidence that this phenomenon is occurring over a wide area. Spanish Forest Inventory data show that 20% of *J. thurifera*-dominated stands in Castilla y León region, which

includes a quarter of the forested surface of this species around the world, turned into mixed stands from 1992 to 2002 as a result of the establishment of *Pinus* spp. and *Quercus* spp. (J. M. Olano unpubl. data).

The dominance of other juniper species is also influenced by herbivory and drought resistance. For example, in NW and central USA, a reduction of fire frequency, mediated by livestock removing fine fuels, or an increase of drought events has promoted *Juniperus* spp. recruitment in open grasslands (Knapp & Soulé 1998; Briggs et al. 2002) and its persistence in piñon-juniper and oak-juniper woodlands (Mueller et al. 2005; Engle et al. 2006). This process appears to be a form of arrested succession resulting from cessation of fire and severe droughts, although the consequences for *Juniperus* spp. abundance are the opposite of our findings.

In a broader perspective, our study exemplifies how recent land-use changes caused by socio-economic trends may lead to rapid ecosystem change in composition, structure and function (Jackson 2006). Much interest has been focused on the role of climate change as a driving force for succession of terrestrial ecosystems (Booth & Jackson 2003); however, the recent debate about the role of large herbivores in determining the past structure and composition of North European Quaternary forests (Svenning 2002) has highlighted the relevance of the biotic component in this global change context.

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References

Baddeley, A. & Turner, R. 2000. Practical maximum pseudo-likelihood for spatial point patterns (with discussion). *Australian and New Zealand Journal of Statistics* 42: 283–322.

- Baddeley, A. & Turner, R. 2005. Spatstat: an R package for analyzing spatial point patterns. *Journal of Statistical Software* 12: 1–42.
- Baddeley, A. & Turner, R. 2006. Modelling spatial point patterns in R. In: Baddeley, A., Gregori, P., Mateu, J., Stoica, R. & Stoyan, D. (eds.) *Case studies in spatial point process modelling*. pp. 23–74. Springer, Heidelberg, DE.
- Barbero, M., Bonin, G., Loisel, R. & Quezel, P. 1990. Changes and disturbances of forest ecosystems caused by human activities in the western part of the Mediterranean basin. *Vegetatio* 87: 151–173.
- Blanco, E., Casado, M.A., Costa, M., Escribano, R., García, M., Génova, M., Gómez, A., Gómez, F., Moreno, J.C., Morla, C., Regato, P. & Sáinz, H. 2005. *Los Bosques Ibéricos: una interpretación geobotánica*. Planeta, Madrid, ES.
- Booth, R.K. & Jackson, S.T. 2003. A high-resolution record of Late Holocene moisture variability from a Michigan raised bog. *The Holocene* 13: 865–878.
- Briggs, J.M., Hoch, G.A. & Johnson, L.G. 2002. Assessing the rate, mechanisms and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forests. *Ecosystems* 5: 578–586.
- Callaway, R.M. 1995. Positive interactions among plants. *Botanical Review* 61: 306–349.
- Callaway, R.M. & Walker, L.R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities: positive interactions in communities. *Ecology* 78: 1958–1965.
- Castroviejo, S., Lainz, M., López-González, G., Montserrat, P., Muñoz-Garmendia, F., Paiva, J. & Villar, L. (eds.) 1986. *Flora Ibérica Vol. I*. Real Jardín Botánico, C.S.I.C., Madrid.
- Castroviejo, S., Lainz, M., López-González, G., Montserrat, P., Muñoz-Garmendia, F., Paiva, J. & Villar, L. (eds.) 1989. *Flora Ibérica Vol. II*. Real Jardín Botánico, C.S.I.C., Madrid.
- Chauchard, S., Carcaillet, C. & Guibal, F. 2007. Patterns of land-use abandonment control tree-recruitment and forest dynamics in Mediterranean mountains. *Ecosystems* 10: 936–948.
- Cook, E.R. & Holmes, R.L. 1986. User's manual for program ARSTAN. In: Holmes, R.L., Adams, R.K. & Fritts, H.C. (eds.) *Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin*. pp. 50–65. Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ, US.
- Corcuera, L., Camarero, J.J. & Gil-Pelegrin, E. 2004. Effects of a severe drought on *Quercus ilex* radial growth and xylem anatomy. *Trees Structure and Function* 18: 83–92.
- Cuartas, P. & García-González, R. 1992. *Quercus ilex* browse utilization by Caprini in Sierra de Cazorla and Segura (Spain). *Vegetatio* 99–100: 317–330.
- Davies, C.E., Moss, D. & Hill, M.O. 2004. *EUNIS habitat classification revised 2004*. European Environment Agency, Copenhagen, DK.

- Debussche, M., Lepart, J. & Dervieux, A. 1999. Mediterranean landscape changes: evidence from old postcards. *Global Ecology and Biogeography* 8: 3–15.
- Edenius, L., Danell, K. & Nyquist, H. 1995. Effects of simulated moose browsing on growth, mortality, and fecundity in Scots pine: relations to plant productivity. *Canadian Journal of Forest Research* 25: 529–535.
- Engle, D.M., Bodine, T.N. & Stritzke, J.E. 2006. Woody plant community in the cross timbers over two decades of brush treatments. *Rangeland Ecology & Management* 59: 153–162.
- Espelta, J.M., Habrouk, A. & Retana, J. 2006. Response to natural and simulated browsing of two Mediterranean oaks with contrasting leaf habit after a wildfire. *Annals of Forest Science* 63: 441–447.
- Gallego, D., Jiménez, J.I., Roca, E.A., Sanz, J., Zambrana, J.F. & Zapata, S. 1991. *Estadísticas Históricas de la Producción Agraria Española, 1859–1935*. Ministerio de Agricultura, Pesca y Alimentación, Secretaría General Técnica, Madrid, ES.
- Gauquelin, T., Bertaudiere, V., Montes, N., Badri, W. & Asmode, J.F. 1999. Endangered stands of thuriferous juniper in the western Mediterranean basin: ecological status, conservation and management. *Biodiversity and Conservation* 8: 1479–1498.
- Gehrig-Fasel, J., Guisan, A. & Zimmermann, N.E. 2007. Tree line shifts in the Swiss Alps: climate change or land abandonment? *Journal of Vegetation Science* 18: 571–582.
- Goreaud, F. & Pelissier, R. 2003. Avoiding misinterpretation of biotic interactions with the intertype K12-function: population independence vs. random labelling hypotheses. *Journal of Vegetation Science* 14: 681–692.
- Grissino-Mayer, H.D. 2001. Assessing crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree Ring Research* 57: 205–221.
- Haase, P. 1995. Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. *Journal of Vegetation Science* 6: 527–534.
- Hester, A.J., Millard, P., Baillie, G.J. & Wendler, R. 2004. How does timing of browsing affect above- and below-ground growth of *Betula pendula*, *Pinus sylvestris* and *Sorbus aucuparia*? *Oikos* 105: 536–550.
- Jackson, S.T. 2006. Vegetation, environment, and time: the origination and termination of ecosystems. *Journal of Vegetation Science* 17: 549–557.
- Knapp, P.A. & Soule, P.T. 1998. Recent *Juniperus occidentalis* (Western Juniper) expansion on a protected site in central Oregon. *Global Change Biology* 4: 347–357.
- Martínez-Vilalta, J. & Piñol, J. 2002. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *Forest Ecology and Management* 161: 247–256.
- Martínez-Vilalta, J., Piñol, J. & Beven, K. 2002. A hydraulic model to predict drought-induced mortality in woody plants: an application to climatic change in the Mediterranean. *Ecological Modelling* 155: 127–147.
- Massei, G., Watkins, R. & Hartley, S.E. 2006. Sex-related growth and secondary compounds in *Juniperus oxycedrus macrocarpa*. *Acta Oecologica* 29: 135–140.
- Montesinos, D., Verdú, M. & García-Fayos, P. 2007. Moms are better nurses than dads: gender biased self-fertilization in a dioecious *Juniperus* tree. *Journal of Vegetation Science* 18: 271–280.
- Moser, E.B., Saxton, A.M. & Pezeshki, S.R. 1990. Repeated measures analysis of variance, application to tree research. *Canadian Journal of Forest Research* 20: 524–535.
- Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter, R.T., Gehring, C.A. & Whitham, T.G. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology* 93: 1085–1093.
- Nowacki, G.J. & Abrams, M.D. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67: 225–249.
- Oberhuber, W., Stumbock, M. & Kofler, W. 1998. Climate tree-growth relationships of Scots pine stands (*Pinus sylvestris* L.) exposed to soil dryness. *Trees Structure and Function* 13: 19–27.
- Olano, J.M., Rozas, V., Bartolomé, D. & Sanz, D. 2008. Effects of changes in traditional management on height and radial growth patterns in a *Juniperus thurifera* L. woodland. *Forest Ecology and Management* 255: 506–512.
- Pérez-Romero, E. 1995. *Patrimonios comunales, ganadería trashumante y sociedad en la Tierra de Soria. Siglos XVIII–XIX*. Consejería de Educación y Cultura, Junta de Castilla y León, Salamanca, ES.
- Purves, D.W., Zavala, M.A., Ogle, K., Prieto, F. & Rey-Benayas, J. 2007. Environmental heterogeneity, bird-mediated directed dispersal, and oak woodland dynamics in Mediterranean Spain. *Ecological Monographs* 77: 77–98.
- R Development Core Team. 2007. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, AT.
- Richter, K., Eckstein, D. & Holmes, R.L. 1991. The dendrochronological signal of pine tree (*Pinus* spp.) in Spain. *Tree-Ring Bulletin* 51: 1–13.
- Riera, S. 2006. Cambios vegetales holocenos en la región mediterránea de la Península Ibérica: ensayo de síntesis. *Ecosistemas* 15: 17–30.
- Rivas-Martínez, S. & Loidi, J. 1999. Bioclimatology of the Iberian Peninsula. *Itinera Geobotánica* 13: 41–47.
- Rozas, V., Olano, J.M., DeSoto, L. & Bartolomé, D. 2008. Large-scale structural variation and long-term growth dynamics of *Juniperus thurifera* trees in a managed woodland in Soria, central Spain. *Annals of Forest Science* 65: 809.

- Rozas, V., DeSoto, L. & Olano, J.M. 2009. Sex-specific, age-dependent sensitivity of tree-ring growth to climate in the dioecious tree *Juniperus thurifera*. *New Phytologist* 182: 687–697.
- Santos, T., Tellería, J.L. & Virgos, E. 1999. Dispersal of Spanish juniper *Juniperus thurifera* by birds and mammals in a fragmented landscape. *Ecography* 22: 193–204.
- Sarmiento, F.O. 1997. Arrested succession in pastures hinders regeneration of Tropicandean forests and shreds mountain landscapes. *Environmental Conservation* 24: 14–23.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591–596.
- Smit, C., Den Ouden, J.A.N. & Muller-Scharer, H. 2006. Unpalatable plants facilitate tree sapling survival in wooded pastures. *Journal of Applied Ecology* 43: 305–312.
- Stokes, M.A. & Smiley, T.L. 1968. *An introduction to tree-ring dating*. University of Chicago Press, Chicago, IL, US.
- Svenning, J.-C. 2002. Review of natural vegetation openness in north-western Europe. *Biological Conservation* 104: 133–148.
- Terrab, A., Schönswetter, P., Talavera, S., Vela, E. & Stuessy, T.F. 2008. Range-wide phylogeography of *Juniperus thurifera* L., a presumptive keystone species of western Mediterranean vegetation during cold stages of the Pleistocene. *Molecular Phylogenetics and Evolution* 48: 94–102.
- Trotter, R.T. III, Cobb, N.S. & Whitham, T.G. 2002. Herbivory, plant resistance, and climate in tree ring record: interactions distort climatic reconstructions. *Proceedings of the National Academy of Sciences of the United States of America* 99: 10197–10202.
- Turner, M.G., Baker, W.L., Peterson, C.J. & Peet, R.K. 1998. Factors Influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1: 511–523.
- Vitousek, P.M. 1994. Beyond global warming: ecology and global change. *Ecology* 75: 1861–1876.
- Waagepetersen, R.P. 2007. An estimating function approach to inference for inhomogeneous Neyman-Scott processes. *Biometrics* 63: 252–258.
- Westhoek, H.J., Van den Berg, M. & Bakkes, J.A. 2006. Scenario development to explore the future of Europe's rural areas. *Agriculture, Ecosystems and Environment* 114: 7–20.
- Whittaker, R.H. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecological Monographs* 23: 41–78.
- Wiegand, T., Gunatilleke, S. & Gunatilleke, N. 2007. Species associations in a heterogeneous Sri Lankan Dipterocarp forest. *The American Naturalist* 170: 77–95.
- Yarranton, G.A. & Morrison, R.G. 1974. Spatial dynamics of a primary succession: nucleation. *Journal of Ecology* 62: 417–428.
- Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J. & García, D. 2001. Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. *Forest Ecology and Management* 144: 33–42.

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