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Disruption of *Juniperus thurifera* woodland structure in its northwestern geographical range: potential drivers and limiting factors

José M. Olano · Miguel A. Zavala · Vicente Rozas

Abstract Enhancement of *Juniperus thurifera* recruitment and colonisation by oak and pine species has been related at the local level to changes in livestock pressure. We used forest inventory data from Castilla y León Autonomous Region (Central Spain), an area comprising 34% of the world range of *J. thurifera*, to assess whether this process is occurring at a larger scale. We compared tree composition and density in a set of 659 permanent plots over a 10-year period. Logistic models and redundancy analysis were used to assess the effect on this process of parameters such as livestock pressure, propagule availability and climatic conditions. Between 1992 and 2002, juniper woodlands became denser (1.31% juniper stem year^{-1}) and tree diversity increased due to rapid colonisation by oaks and pines (2.21% occupied plots year^{-1}). In addition, the presence of juniper increased in other types of forests at a moderate rate (0.6% y^{-1}). Thus, we observed both a disruption of the borders between current forest types and a generalised increase in α-diversity of tree species. The seed source was the main factor explaining colonisation rate, suggesting that the pace of colonisation is critically constrained by the spatial configuration of the landscape and the local propagule availability of the colonising species. If the current colonisation trends continue, monospecific juniper woodlands will become very scarce by the end of the twenty-first century.

Keywords Abrupt compositional shift · Juniper · Land-use change · Seed source · Tree colonisation · Markov models

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Introduction

Understanding the mechanisms underpinning geographical ranges is a key issue in ecology and biogeography (Gaston 2003). The range of distribution of a species is largely driven by environmental correlates as well as population interactions and seed dispersal (e.g. Pacala and Hurtt 1993). With the global changes currently expected, major shifts in species distribution may become the rule. In fact, range variations due to climatic conditions have already been described (Brommer 2004; Wilson et al. 2007), although data in relation to plants are scarcer and mainly centred on shifts of species ranges along altitudinal gradients (Jump et al. 2009). Moreover, widespread changes in land use may be leading to additional sources of variation, such as habitat fragmentation or reduced habitat quality (Matesanz et al. 2009).

In Mediterranean countries, human activities have long-shaped ecosystem structure and functions (e.g. Urbieta et al. 2008), and the transition from traditional labour-intensive agriculture driven by self-consumption to industrialised market-oriented agriculture has involved profound

changes in land-use patterns (Gellrich et al. 2007). Production has been intensified in the most fertile spots, while vast areas of marginal lands have been neglected. Hence, formerly productive areas in mountain regions—used for traditional agriculture or by free-ranging livestock—are experiencing landscape changes and undergoing secondary succession due to recent changes in land use (Mazzoleni et al. 2004, Chauchard et al. 2007).

The interaction between successional reactivation and other drivers of global change may involve the onset of novel vegetation trajectories. Currently, dominant species may be replaced by other taxa from the regional species pool, which could lead to a new equilibrium state of the ecosystem *sensu* Rietkerk et al. (2004). These phenomena are contingent on the spatial configuration of the ecosystem and on historical effects determining demographic thresholds in community dynamics (Rietkerk et al. 2004). There is growing evidence of the dramatic role of dispersal syndromes and local seed pools in current forest community reorganisation (Montoya et al. 2008).

Most of the studies describing potential changes in species distributions in response to global change are focused on the margins of their distribution range (Anderson et al. 2009). Much less attention has been paid, however, to the effects of global change across a significant fraction of the range of a species (Purves 2009). This line of research is particularly exciting given that plant species usually do not cover their potential climatically defined range, and its actual distribution is normally defined by other factors, such as human activity or the availability of seed sources (Svenning and Skov 2004).

Spanish juniper (*Juniperus thurifera* L.) woodlands are one of the dominant plant communities in the sparsely populated mountain regions of the central Iberian Peninsula (Blanco et al. 1997). In previous centuries, monospecific juniper woodlands have represented a stable component of Iberian vegetation and even a climax state (Peinado and Rivas-Martínez 1987). These woodlands have been traditionally managed as grazed systems combined with timber production for firewood or construction (Gauquelin et al. 1999; Olano et al. 2008; Rozas et al. 2008). Recently, a process of densification and colonisation by oak and pine species was described in *J. thurifera* woodlands at a local scale (DeSoto et al. 2010), as a consequence of the decline in traditional practices. We hypothesise that changes in *J. thurifera* woodland structure may be a widespread phenomenon along its distribution range. We tested this hypothesis using forest inventory data (Second and Third Spanish Forest Inventory in 1992 and 2002, respectively) for the *J. thurifera* distribution range in the Castilla y León region in Spain. We focused on Castilla y León because it encompasses 34% of the world range of *J. thurifera* and includes the most representative and extensive areas of formerly managed *J. thurifera* woodland in Spain. Our specific questions were: (1) Are the structure and composition of *J. thurifera* woodlands changing? (2) What is the speed and future direction of these changes? (3) What is the role of key potential factors controlling this process, such as climate, livestock density and propagule availability?

Methods

Study species

Spanish juniper is a long-lived tree, endemic to the western Mediterranean basin. Its most important populations are located in Spain (95.1% of the world surface cover of this species) and Morocco (4.8%) with isolated populations in Argelia, Italy, and France (Blanco et al. 1997). It forms open woodlands that have been traditionally managed in a wood-pasture system, in which the understorey is grazed by sheep and goats. During the past century, social transformations have caused a progressive abandonment of these traditional management practices in the European range. At the same time, juniper woodlands are considered a priority habitat according to European Union Directive 92/43/EEC, EUNIS 9560 (Davies et al. 2004). Our study is focused on the Community of Castilla y León, a region of Spain, with 214,000 ha of *J. thurifera* woodland, comprising 34.2% of the total world surface cover of this habitat type. Most of these woodlands are located at the eastern half of the region (Fig. 1), at altitudes between 800 and 1,300 m under Mediterranean continental climate, on shallow and stony soils.

Data collection

The Spanish Forest Inventory (SFI) consists of a systematic recording of permanent plots distributed over a grid of 1 × 1 km on forested areas (Ministerio de Medio Ambiente 2003). In every plot, all trees were recorded according to both their diameter at breast height (dbh, measured at 1.3 m above ground) and their distance to the centre of the plot: trees showing a dbh of 7.5–12.5 cm were recorded within a 5-m radius, 12.5–22.5 cm, within a 10-m radius, 22.5–42.5 cm, within a 15-m radius and >42.5 cm, within a 25-m radius. This sampling schema allows estimation of the density of every species in the plot. In the study area, the Second Forest Inventory (2-SFI) and the Third Forest Inventory (3-SFI) were accomplished in 1992 and 2002, respectively. A time-span of 10 years may be considered short to study long-lived woody species; however, it is long enough to detect changes in forest ecosystems (Olano et al. 2009b), particularly given the large sample size of study plots and the wide study area considered in this work.
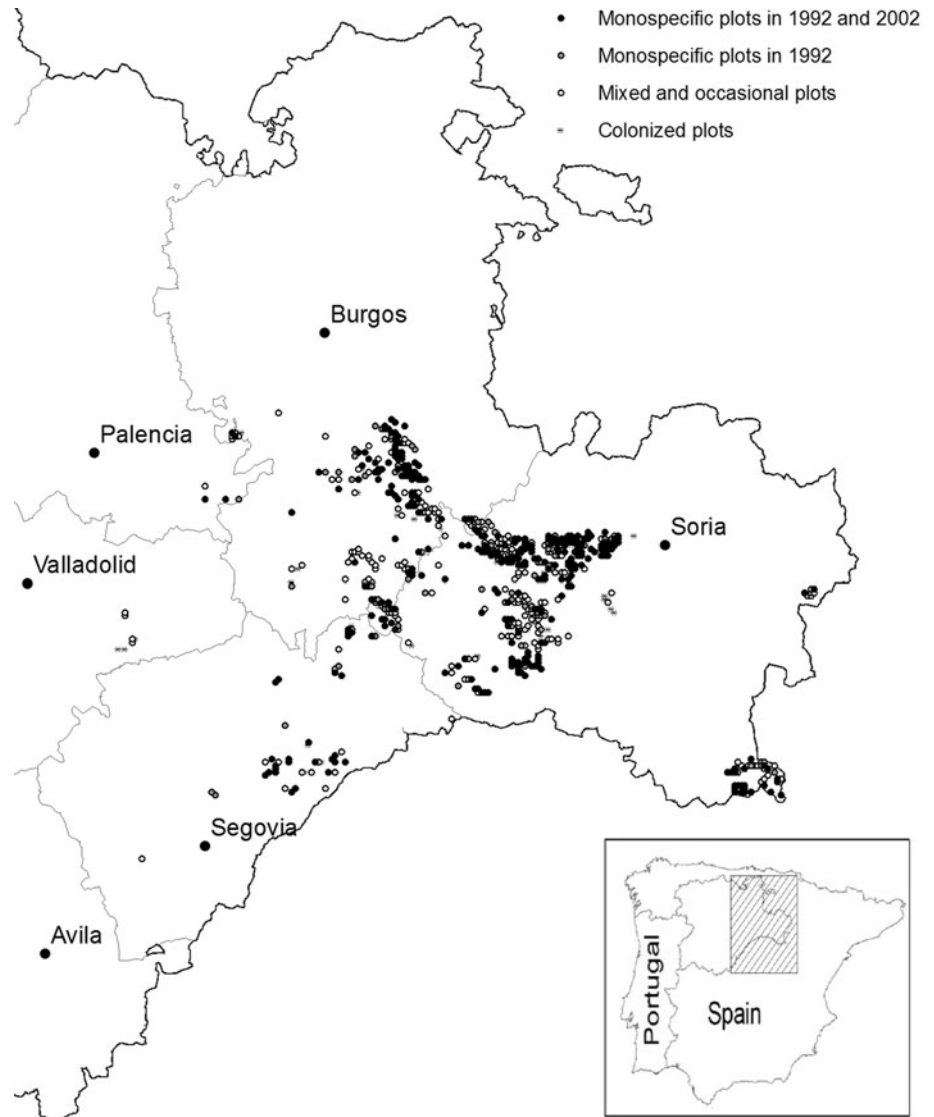
Plots sampled in both inventories and containing *J. thurifera* individuals in at least one were included. We discarded those plots whose recorded position in 1992 was not correctly identified in 2002. Consequently, data corresponding to 659 plots were included in analysis. For each plot, UTM coordinates, municipality and tree density for each species were considered. A digital terrain elevation model with 10-m resolution was used to obtain physiographic information such as altitude, slope and aspect for every plot. Climatic data for each plot were obtained by using Estclima, a multiple regression model based on meteorological-station data (Sánchez-Palomares et al. 1999) that provides monthly averages for temperature and precipitation with a geographical resolution of 1 × 1 km. For subsequent analysis, we selected a reduced group of informative climatic parameters: mean July and December temperatures, total spring rainfall, the Gorezynski

Continentality Index (Gorczynski 1920) and the Mediterraneity Index-Im3 (Rivas-Martínez 1987).

To assess the potential effects of livestock density on tree establishment, we used the Agrarian Census from the Spanish National Statistics Institute (http://www.ine.es). Although this census has a high level of uncertainty, it is the only nationwide register available on livestock density at a local (municipality) scale. We focused on goats and sheep numbers because cows are restricted to flat areas in valley bottoms away from juniper woodlands. We obtained information on goats and sheep abundance per municipality for 1982 (the first year with data available) and 1999. Livestock has an immediate effect on *J. thurifera* growth, restricting primary and secondary growth (Olano et al. 2008; DeSoto et al. 2010). However, the effect of livestock on forest composition shows a temporal lag because trees need several years to reach minimal sampling size.

Therefore, we selected these dates to estimate the trend in livestock density.

The distance of every plot to a potential seed source was estimated as the shortest distance to a 2-SFI plot containing at least 1 adult pine (pineseed), 1 adult oak (oakseed) or both 1 pine and 1 oak (treeseed). Based on the UTM coordinates of the SFI plots, the nearest neighbourhood distances between the sampling points were calculated with the Hawth Tool extension of Arc GIS 9.2. Using the source *Juniperus,* averages of the 3 smallest distances to plots with pines, oaks and the set pines + oaks was calculated. Because source trees would also be present in the space between sampling plots, our parameter obviously provides a very conservative estimate of the available seed source.

Data analysis

The plots were classified into 4 classes according to the dominance of *J. thurifera*: (a) monospecific plots; (b) plots with ≥2 tree species, with *J. thurifera* representing more than 10% of the stems, (hereinafter: mixed plots; (c) plots with *J. thurifera* comprising <10% of the stems (hereinafter: occasional plots); and (d) plots without *J. thurifera*.

To evaluate changes in tree species diversity with the Shannon diversity index (Magurran 1989), changes in plot class and composition between 2-SFI and 3-SFI were compared for every plot using a Wilcoxon nonparametric test for paired data. Changes in the number of occupied plots and average stem density were compared for the most abundant species.

To ascertain future changes in plot composition, we calculated a transition matrix (Caswell 1989) describing the probability of transition between the different *J. thurifera* woodland classes. This matrix was used to predict the future composition of *J. thurifera* plots using a Markov model for the twenty-first century. The number of plots in each class in time $t + 1$ was obtained by multiplying plots in each class in time t by the transition matrix. We assumed that regeneration and mortality rates of the different tree species during the next century would be similar to those recorded during the study period, so that this prediction would constitute an approximation to future trends in the composition and extent of *J. thurifera* woodlands in Castilla y León. Because estimation of the parameters for the model is sensitive to the numbers of nonoccupied plots (i.e. potentially available habitat), and 3 nonoccupied plots (500, 1,000, and 2,000) were arbitrarily established to evaluate the effect of this parameter on the results.

If plot colonisation by other tree species is occurring due to a change in climatic conditions, recently colonised plots will show differences in their climatic conditions from previously occupied plots. This hypothesis was tested via redundancy analysis (RDA) (Legendre and Legendre 1998). This test was performed separately for *Quercus ilex* L. and *Q. faginea* Lam because the two species show different climatic preferences. Pine species were not tested due to the smaller number of plots colonised by these species. A data set for each species was created, including the previously mentioned climatic variables and all the plots where the species had been present at either of the two sampling dates. A dummy parameter indicating presence or absence of *Q. ilex* or *Q. faginea* in 1992 was used as a constraining matrix for each data set. This dummy parameter was randomly assigned by a Monte Carlo permutation test with 999 randomisations to determine whether there were differences in multivariate climatic space between groups. The canonical eigenvalue was used to build the *F*-ratio statistic (ter Braak 1990). This analysis was conducted using CANOCO for Windows v. 4.0 (ter Braak and Smilauer 1997).

A logistic model (Legendre and Legendre 1998) was used to determine which factors provided better prediction of tree colonisation in the monospecific plots in 2-SFI. Four groups of variables were considered: (1) climatic variables affecting *J. thurifera* growth (Rozas et al. 2009; Camarero et al. 2010): July and December temperatures, spring rainfall, Gorezynski Continentality Index and Mediterraneity Index; (2) physiographic variables: altitude, slope and aspect; (3) variables related to land use: population in 1999/(population in 1961 + 1), goats + sheep number in 1999/(goats + sheep number in 1982 + 1); and 4) variables related to seed source distance: pineseed, oakseed and treeseed. Variables were included in the model by the Wald forward stepwise selection. The cut-off value for inclusion in the model was 0.05, and 0.1 to exclude a previously included variable. The overall model significance was evaluated using the log-likelihood ratio (Hosmer and Lemeshaw 2000). Additionally, a receiver operating characteristic (ROC) curve was employed to test the validity of the logistic regressions. ROC curves provide an evaluation of the model sensitivity (rate of true positives) and specificity (rate of false positives). The validity is estimated by the c statistic, which measures the area under the curve and compares it with the null hypothesis (Hosmer and Lemeshaw 2000).

Results

The number of plots including *J. thurifera* increased by 6.1% (0.6% plots y^{-1}) between 1992 and 2002. Most plots were monospecific (62.7% in 1992; 48.5% in 2002) with a smaller percentage of mixed plots (30.3% in 1992; 38.5% in 2002) and a lower number of occasional plots (6.9% in 1992; 13% in 2002). The richness of tree species per plot increased during the study period (1.47 in 1992; 1.71 in 2002; $Z = -11.648$, $P < 0.0001$), even after excluding

monospecific plots ($Z = -6.468$, $P < 0.0001$). The same pattern holds for tree diversity (0.199 in 1992; 0.317 in 2002; $Z = -10.404$, $P < 0.0001$), even after excluding monospecific plots ($Z = -4.132$, $P < 0.0001$).

The number of monospecific plots declined from 389 to 319 (Fig. 2); because *J. thurifera* individuals were recorded in all these plots in 2002, this decline (18% of the plots, 2.21% plots year^{-1}) is explained by colonisation by other tree species. The transition matrix showed an increase in the number of mixed plots at the expense of monospecific plots (Fig. 2), with the incorporation of 39 newly colonised plots. Markov models predict very similar results in spite of the colonising threshold (Fig. 3). According to models, the number of monospecific plots will be surpassed by that of mixed plots as early as 2012 and by the number of occasional plots in 2042, thus becoming increasingly rare. *J. thurifera* will significantly increase its area occupied in the 3 scenarios, from 33 to 44%.

This increase in species richness and diversity is related to rapid colonisation by oaks (*Q. ilex* and *Q. faginea*) and to a lesser extent by pines (*P. pinaster* Ait., *P. sylvestris* L. and *P. nigra* Arnold) (Table 1). The number of pine individuals increased substantially from 13.63% for *P. nigra* to 52.42% for *P. sylvestris*. Plot colonisation was faster than species recruitment in *Q. faginea* and *P. nigra*, leading to a decrease in mean stem density per occupied plot. The other tree species, however, increased their densities. *J. thurifera* showed a relevant increase in total tree number and density per occupied plot from 197 stems ha^{-1} in 1992 to 220 in 2002 ($Z = -7.110$, $P < 0.001$).

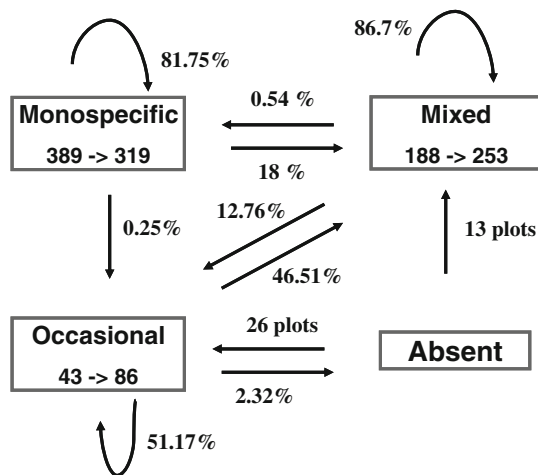Climatic parameters did not differ between newly colonised plots and those previously occupied by *Q. ilex*

Fig. 3 Observed (1992–2002) and predicted (>2002) number of occupied plots for different plot classes between 1992 and 2002. *Different lines* represent different colonising thresholds (*dashed black* for 500 potentially colonised plots, *grey* for 1,000 and *solid black line* for 2,000)

($F = 0.169$, $P = 0.199$) or *Q. faginea* ($F = 0.72$, $P = 0.419$). We achieved a satisfactory logistic model (Table 2) that included two parameters, namely, distance to seed source (treeseed) and altitude. Colonisation was slower in areas far from an available seed source (*Quercus* or *Pinus*) or at higher altitudes. The ROC curve showed that the logistic model predicted colonisation reasonably well ($C = 0.683$, $P < 0.001$).

Discussion

As we hypothesised, the composition of juniper woodlands is changing across the whole area studied. Oaks and pines are colonising monospecific plots at a rapid pace (2.21% year^{-1}) and at the same time that a sharp increase in juniper stem density is occurring (1.31% year^{-1}). Although most Juniper plots were monospecific in 1992, the Markov models consistently predict that *J. thurifera* monospecific plots will become extremely rare during the twenty-first century.

Monospecificity of *J. thurifera* woodlands has been traditionally attributed to environmental constraints, such as harsh continental climate and shallow soils, which could limit the performance of other tree species (Peinado and Rivas-Martínez 1987). The colonisation of juniper woodlands by species such as oaks and pines might be interpreted as a result of an improvement of climatic conditions, as has already been reported for other plant species in the Iberian Peninsula (Sanz-Elorza et al. 2003). However, because climate factors were excluded from the logistic model as drivers for plot changes, and colonised plots do not differ in their climatic conditions from those previously occupied by *Q. ilex* and *Q. faginea*, no support was

Fig. 2 Transition matrix among different plot classes in *J. thurifera* woodlands in Castilla y León, Spain, 1992–2002. *Numbers in boxes* indicate number of plots in each state in 1992 and 2002. *Arrows* show probability of transition, in percentage, of the 1992 plots. Exception is transition from absent to occasional *J. thurifera* plots, which shows absolute number of plots
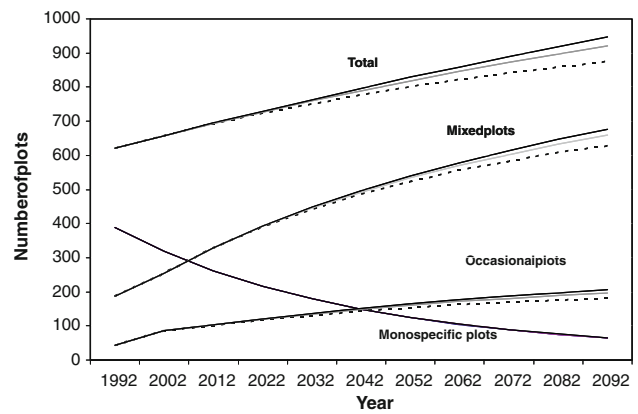
Table 1 Number of occupied plots, stems and stem density per occupied plot in 1992, and percentage change per tree species between 1992 and 2002

	Plots in 1992	Change (%) 1992–2002	Total stem number	Change (%) 1992–2002	Density in 1992 (stems ha^{-1})	Change (%) 1992–2002
Juniperus thurifera	620	6.13	122,382	22.46	197	15.38
Pinus nigra	49	22.45	17,405	13.63	370	−10.99
Pinus pinaster	92	11.96	12,857	36.14	139	21.60
Pinus sylvestris	50	21.95	4,370	52.42	106	24.98
Quercus ilex	111	36.94	36,427	13.63	328	12.48
Quercus faginea	34	50.00	8,489	19.86	249	−20.10

Note that density is based on number of occupied plots, so it can decrease even if total stem number increases

Table 2 Logistic model for colonisation of monospecific plots between 1992 and 2002

Number of plots	Model P	Parameters in the model	Parameter P	β
376	<0.001	Constant	0.022	3.671
		Treeseed	0.008	−0.001
		Altitude	0.005	−0.004

β is the coefficient for each of the parameters

provided for a climatic basis of the observed changes. Alternatively, the observed increase in recruitment of juniper and the rapid colonisation of juniper woodlands by other tree species with a lower tolerance to browsing has been interpreted as a consequence of the reduction in density of domestic herbivores on the local scale (DeSoto et al. 2010). Nevertheless, we did not obtain any statistical relationship between the colonisation rate and livestock abundance in our data set. The absence of detailed records on free-ranging livestock and the different scales between forest inventory data (a few square metres) and livestock density data (tenths of square kilometres) severely limited our ability to consistently compare forest composition and extent of herbivore impact. Thus, the causal force behind this process could not be ascertained.

In spite of the conservative proxy used for propagule availability, the colonisation of *J. thurifera* woodlands by oaks and pines was related to the proximity of mature trees of these species. This result is in agreement with the role of dispersal limitation in structuring plant communities (Gómez-Aparicio et al. 2009) and its potential to modulate the response of forest species to global change (Pacala and Hurtt 1993). The importance of limited dispersal in community organisation can be exacerbated in fragmented landscapes such as those characterising Mediterranean areas, where the frequency of long-distance dispersal events has a major influence on the probability of plant colonisation and its persistence in habitat patches (Zavala and Zea 2004; Montoya et al. 2008). On the other hand, a higher colonisation rate was observed in plots located at lower altitude, which may be related to the relative abundance of *J. thurifera* stands at the top of plateaus. In these positions, juniper woodlands can persist as monospecific stands for longer periods, because dispersal of other tree species that are more abundant in lower-altitude areas is complicated due to gravimetric constraints and the behaviour of dispersers. However, although propagule availability can modulate the pace of the colonisation process, it cannot be considered a cause of the colonisation process.

Interestingly, less-competitive Spanish juniper is expanding into other forested environments, mainly pine and oak forests, albeit at a slower pace (0.6% year^{-1}). According to our model, this would lead to a large range increase (over 30%) over the course of the present century. The arrival of juniper propagules to forested areas is not a novel phenomenon. In spite of significant predispersive mortality (Montesinos et al. 2010), this species possesses a high colonising capacity at larger distances, due to its dispersal by different thrush species (Santos et al. 1999). Thus, the effective establishment of *J. thurifera* currently seen may be a consequence of the easing of preexisting limiting factors, probably related to traditional forestry-management practices. Moreover, it is important to note that our estimates of future changes in *J. thurifera* woodland composition may be conservative, because we have only considered the expansion of juniper into previously forested areas, overlooking colonisation of abandoned fields, which is actually occurring at a similar pace (Pueyo and Alados 2007; Olano et al. 2009a).

Our results provide evidence on how rapid changes in community composition and species range are occurring over large areas, even in the centre of the species range, and not only at the boundary of its range. Changes in juniper woodland composition in central Spain, due to oak and pine colonisation, are occurring across a large area, corresponding to 25% of the world range of juniper, which will increase the rarity of the currently dominating

woodland type, the monospecific *J. thurifera* woodland. Conservation of this priority habitat (Davies et al. 2004) should incorporate compositional changes as part of the dynamics of this ecosystem (DeSoto et al. 2010). This process is occurring simultaneously with a spread of Spanish juniper into surrounding forested areas and abandoned fields, which significantly increases its actual range. Consequently, disruption of the borders between currently existing forest types and an overall increase in tree species α-diversity are occurring simultaneously. Our results do not preclude the impact of climate change in this process, but suggest that factors additional to climate should

be considered to understand and anticipate forthcoming changes in Mediterranean forest (Linares et al. 2009).

Appendix

Fig. 4 Distribution of *J. thurifera* plots in 1992 (*black dots*) and neighbouring plots occupied by *Pinus* (*grey triangles*) or *Quercus* (*white quadrates*) species

● Juniperus thurifera
▲ Pinus
□ Quercus
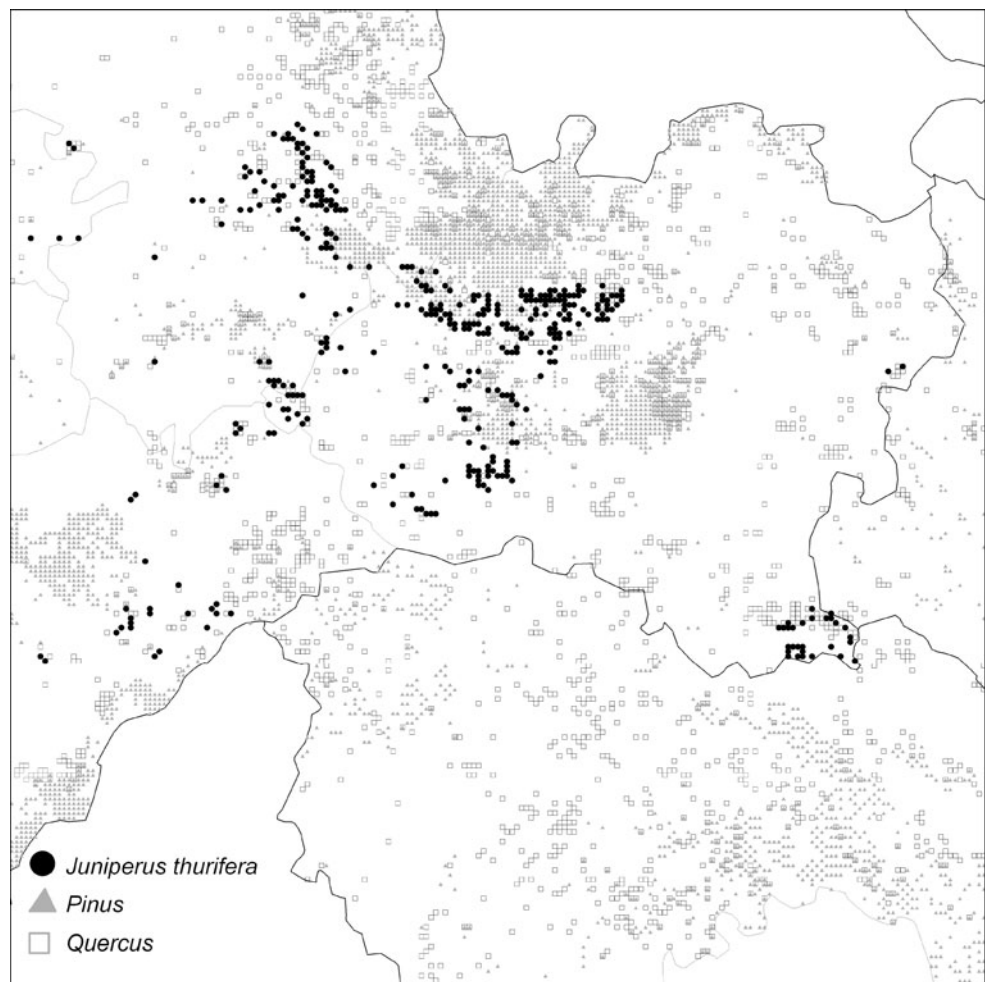
References

Anderson BJ, Akcakaya HR, Fordham DA, Martinez-Meyer E, Thuiller W, Brook BW (2009) Dynamics of range margins for metapopulations under climate change. Proc R Soc Lond B 276:1415–1420

Blanco E, Casado MA, Costa M et al. (1997) Los Bosques Ibéricos: Una interpretación geobotánica. Ed. Planeta, Madrid

Brommer JE (2004) The range margin of northern birds shifts poleward. Ann Zool Fenn 41:391–397

Camarero JJ, Olano JM, Parras A (2010) Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. New Phytol 185:471–480

Caswell H (1989) Matrix population models. Sinauer Associates, Sunderland

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

Davies CE, Moss D, Hill MO (2004) EUNIS habitat classification revised 2004. European Topic Centre on Nature Protection and Biodiversity, Paris

DeSoto L, Olano JM, Rozas V, De la Cruz M (2010) Release of Juniperus thurifera woodlands from herbivore-mediated arrested succession in Spain. Appl Veg Sci 13:15–25

Gaston KJ (2003) The structure and dynamics of geographic ranges. Oxford University Press, New York

Gauquelin T, Bertaudiere V, Montes N, Badri W, Asmode JF (1999) Endangered stands of thuriferous juniper in the western Mediterranean basin: ecological status, conservation and management. Biodivers Conserv 8:1479–1498

Gellrich M, Baur P, Koch B, Zimmermann NE (2007) Agricultural land abandonment and natural forest re-growth in the Swiss mountains: a spatially explicit economic analysis. Agr Ecosyst Environ 118:93–108

Gómez-Aparicio L, Zavala MA, Bonet FJ, Zamora R (2009) Are pine plantations useful restoration tools of Mediterranean forests? An assessment along gradients of climatic conditions, stand density and distance to seed sources. Ecol Appl 19:2124–2141

Gorczynski L (1920) Sur le calcul du degré du continentalisme et son application dans la climatologie. Geografiska Annaler 2:324–331

Hosmer DW, Lemeshaw S (2000) Applied logistic regression, 2nd edn. Wiley, New York, 392 p

Jump A, Mátyas C, Peñuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species. Trends Ecol Evol 24:694–701

Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam

Linares JC, Camarero JJ, Carreira JA (2009) Interacting effects of changes in climate and forest cover on mortality and growth of the southernmost European fir forests. Glob Ecol Biogeogr 18:485–497

Magurran AE (1989) Diversidad ecológica y su medición. Ed. Vedrá, Barcelona

Matesanz S, Escudero A, Valladares F (2009) Influence of three global change drivers on a Mediterranean shrub. Ecology 90:2609–2621

Mazzoleni S, Di Pasquale G, Di Martino P, Rego F, Mulligan M (2004) Recent dynamics of Mediterranean vegetation and landscape. Wiley, Chichester

Ministerio de Medio Ambiente (2003) Tercer Inventario Forestal Nacional, Madrid

Montesinos D, García-Fayos P, Verdú M (2010) Relictual distribution reaches the top: elevation constrains fertility and leaf longevity in Juniperus thurifera. Acta Oecol 36:120–125

Montoya D, Zavala MA, Rodríguez MA, Purves D (2008) Animal vs wind dispersal and the robustness of tree species to deforestation. Science 320:1502–1504

Olano JM, 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. For Ecol Manage 255:506–512

Olano JM, Altelarrea JM, Rozas V, Sanz D (2009a) 50 años de cambios de usos en el LIC Sierra de Cabrejas (Soria). Actas del V Congreso Forestal Español, Ávila (in press)

Olano JM, Laskurain NA, Escudero A, De la Cruz M (2009b) Why and where adult trees die in a secondary temperate forest? The role of neighbourhood. Ann For Sci 66:105

Pacala SW, Hurtt GC (1993) Terrestrial vegetation and climate change: integrating models and experiments. In: Kareiva PM, Kingsolver JG, Huey RB (eds) Biotic interactions and global change. Sinauer Associates Inc., Sunderland, pp 57–74

Peinado M, Rivas-Martínez S (1987) La vegetación de España. Servicio de Publicaciones Universidad Alcalá de Henares, Madrid

Pueyo Y, Alados CL (2007) Effects of fragmentation, abiotic factors and land use on vegetation recovery in a semi-arid Mediterranean area. Basic Appl Ecol 8:158–170

Purves D (2009) The demography of range boundaries versus range cores in eastern US tree species. Proc R Soc Lond B 276:1477–1484

Rietkerk M, Dekker SC, de Ruiter PC, van de Koppel J (2004) Self-organized patchiness and catastrophic shifts in ecosystems. Science 305:1926–1929

Rivas-Martínez S (1987) Memoria del mapa de series de vegetación de España. Ministerio de Agricultura, Pesca y Alimentación, Madrid

Rozas V, Olano JM, 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. Ann For Sci 65:809

Rozas V, DeSoto L, Olano JM (2009) Sex-specific, age-dependent sensitivity of tree-ring growth to climate in the dioecious tree Juniperus thurifera. New Phytol 182:687–697

Sánchez-Palomares O, Sánchez-Serrano F, Carretero MP (1999) Modelos y cartografía de estimaciones climáticas termopluviométricas para la España peninsular. INIA, col. Fuera de Serie, Madrid

Santos T, Tellería JL, Virgos E (1999) Dispersal of Spanish Juniper Juniperus thurifera by birds and mammals in a fragmented landscape. Ecography 22:193–204

Sanz-Elorza M, Dana ED, González A, Sobrino E (2003) Changes in the high mountain vegetation of the central Iberian peninsula as probable sign of global warming. Ann Bot 92:273–280

Svenning JC, Skov F (2004) Limited filling of the potential range in European tree species. Ecol Lett 7:565–573

ter Braak CJF (1990) Update notes. CANOCO version 3.1. Microcomputer Power, Ithaca

ter Braak CJF, Smilauer P (1997) Canoco for windows version 4.0. Centre for Biometry, Wageningen

Urbieta IR, Zavala MA, Marañón T (2008) Human and non-human determinants of forest composition in southern Spain: evidence of shifts towards cork oak dominance due to last century management. J Biogeogr 35:1688–1700

Wilson RJ, Gutiérrez D, Gutiérrez J, Monserrat VJ (2007) An elevational shift in butterfly species richness and composition accompanying recent climate change. Global Change Biol 13:1873–1887

Zavala MA, Zea E (2004) Mechanisms maintaining biodiversity in Mediterranean pine-oak forests: insights from a spatial simulation model. Plant Ecol 171:197–207