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

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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 a 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 colonization 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 colonization; Markovian models.

Introduction

Understanding the mechanisms underpinning geographical ranges is a key issue in ecology and biogeography (Gaston 2003). Species' ranges of distribution are largely driven by environmental correlates but also by population interactions and seed dispersal (e.g. Pacala and Hurtt, 1993). Under the current global change scenario, 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 centered on shifts of species ranges along altitudinal gradients (Jump et al. 2009). Moreover, the widespread land-use change 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 shaped ecosystem structure and function for ages (e.g. Urbieto et al. 2008), and the transition from a traditional labor-intensive self-consumption driven agriculture to an industrialized market-oriented agriculture has involved profound changes in land-use patterns (Gellrich et al. 2007). Production has been intensified in the most fertile spots, whereas vast areas of marginal lands have been neglected. Hence, formerly productive areas in mountain regions –both by 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 global change drivers 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 ecosystem spatial configuration and on historical effects determining demographic thresholds in community dynamics (Rietkerk et al. 2004). Concretely, there is growing evidence of the dramatic role of dispersal syndromes and local seed pools in current forest community reorganization (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 interest has been

given, however, to the effects of global change across a significant fraction of the species' range (Purves 2009). This research line 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 activities 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 scarcely-populated mountain regions of the central Iberian Peninsula (Blanco et al. 1997). In the last 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 fire wood or construction (Gauquelin et al. 1999; Olano et al. 2008, Rozas et al. 2008). Recently, a process of densification and colonization 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 hypothesize that changes in *J. thurifera* woodland structure may be a widespread phenomena 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 Castilla y León in Spain. We focused on Castilla y León region because it encompasses 34% of *J. thurifera* world range and includes the most representative and extensive areas of formerly managed *J. thurifera* woodland in Spain. Our specific questions were: 1) Is *J. thurifera* woodlands suffering changes in structure and composition? 2) Which is the speed and future direction of these changes? and 3) Which is the role of key potential factors controlling this process, such as climate, livestock density and propagule availability?

Methods

Study species and area

Spanish juniper is a long-lived tree, endemic of the western Mediterranean basin. Its most important populations are located in Spain (95.1% of the world surface) 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, where the understorey is grazed by sheep and goats.

During the last century social transformations have caused a progressive abandonment of these traditional management practices along its European range. Concurrently, juniper woodlands are considered a priority habitat by the European Union Directive 92/43/EEC, EUNIS 9560 (Davies et al. 2004). Our study is focused on Castilla y León Autonomous Region, which hosts 214,000 ha of *J. thurifera* woodland, comprising a 34.2% of its world surface. Most of these woodlands are located at the eastern half of the Region (Fig. 1) at altitudes between 800-1300 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 (see details in 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 dbh between 7.5-12.5 cm were recorded within a 5 m radius; 10 m for 12.5-22.5 cm; 15 m for 22.5-42.5 cm and 25 m for dbh > 42.5 cm. Such sampling schema allows estimating density for 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 ten years may be considered short to study long-lived woody species, however it is long enough to detect changes in this forested ecosystem (Olano et al. 2009b), especially considering 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 of them were included. We discarded those plots whose recorded position in 1992 was not correctly identified in 2002. As a result, data corresponding to 659 plots were included in the analyses. In each plot UTM coordinates, municipality and tree density per species were considered. A digital terrain elevation model with 10 m of resolution was used to obtain physiographic information such as altitude, slope and aspect for every plot. Climatic data 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 (Gorzynski 1920) and the Mediterraneity Index-Im3 (Rivas-Martínez 1987).

In order to assess the potential effects of livestock density on tree establishment we used the Agrarian Census from the Spanish National Statistics Institute (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, since 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. Although, the effect of livestock in *J. thurifera* growth is immediate, restricting primary and secondary growth (Olano et al. 2008; DeSoto et al. 2010). Its effect on forest composition shows a temporal lag, since trees need several years to reach minimal sampling size. So, 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 one adult pine (pineseed), one adult oak (oakseed) or both one pine and one oak (treeseed). Based on the UTM coordinates of the SFI plots, the nearest neighbourhood distances between the sampling points was calculated with the Hawth Tool extension of Arc GIS 9.2. Using the source *Juniperus*, the average of the three nearest distances to plots with pines, oaks and the set pines+oaks were calculated. Obviously, since source trees would also be present in the space between sampling plots, our parameter provides a very conservative estimate of the available seed source.

Data analysis

The plots were classified in four classes according to the dominance of *J. thurifera*: a) Monospecific plots; b) Plots with at least two tree species, with *J. thurifera* representing more than 10% of the stems, hereafter Mixed plots; c) Plots with *J. thurifera* comprising less than 10% of the stems, hereafter Occasional plots; 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.

In order to ascertain future changes in stand 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* stands using a Markovian model comprising the 21th century. 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 constitutes an approximation to actual future trends in the composition and extent of *J. thurifera* woodlands in Castilla y León. Since the estimation of the parameters for the model is sensitive to the numbers of non-occupied plots (*i.e.* potentially available habitat), three numbers of non-occupied plots (500, 1000 and 2000) were arbitrarily established, in order to evaluate the effect of this parameters on the results.

If plot colonization by other tree species is occurring due to a change in climatic conditions, recently colonized 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 since both species show different climatic preferences, whereas pine species were not tested due to the smaller number of plots colonized 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 any of both sampling dates. A dummy parameter indicating presence or absence of *Q. ilex* or *Q. faginea* in 1992 was used as 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). These analyses were conducted using CANOCO for Windows v. 4.0 (ter Braak and Smilauer 1997).

A logistic model (Legendre and Legendre, 1998) was used in order to determine which factors provided a better prediction of tree colonization 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: pine seed, oak seed and tree seed. Variables were included in the model by the Wald forward stepwise selection. Cut-off value for inclusion in the model was 0.05, and 0.1 to exclude a previously included variable. Overall model significance was evaluated using log likelihood ratio (Hosmer and Lemeshaw 2000). Additionally, 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 statistics that 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 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 reduced 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); since all these plots still presented *J. thurifera* individuals in 2002, this decline (18 % of the plots, 2.21% plots y^{-1}) is explained by the colonization by other tree species. The transition matrix showed an increase of the number of mixed plots at the expense of monospecific plots (Fig. 2), with the incorporation of 39 newly colonized plots. Markovian models predict very similar results in spite of the colonizing threshold (Fig. 3). The number of

monospecific plots will be surpassed by that of mixed plots as soon as 2012 and by occasional plots in 2042, becoming increasingly rare. *J. thurifera* will increase significantly its occupied area in the three scenarios, from 33 to 44%.

This increase in species richness and diversity is related to the rapid colonization by oaks (*Q. ilex* and *Q. faginea*) and to a lesser extent by pines (*P. pinaster* Ait., *P. sylvestris* L. and *P. nigra* Arnold) (Tab. 1). The number of pine individuals increased substantially from 13.63% for *P. nigra* to 52.42% for *P. sylvestris*. Plot colonization was faster than species recruitment in *Q. faginea* and *P. nigra*, thus leading to a decrease in mean stem density per occupied plot. Contrarily, the other tree species 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 the colonized plots and the previously occupied ones for *Q. ilex* ($F = 0.169$, $P = 0.199$) or *Q. faginea* ($F = 0.72$, $P = 0.419$). A satisfactory logistic model was achieved (Table 2) including two parameters, distance to seed source (treeseed) and altitude. Colonization was slower in areas far from available seed source (*Quercus* or *Pinus*) or at higher altitudes. ROC curve showed that the logistic model reasonably predicted colonization ($C = 0.683$, $P < 0.001$).

Discussion

As we hypothesized previously, the composition of juniper woodlands is changing along all the studied area. Oaks and pines are colonizing monospecific stands at a rapid pace (2.21% year⁻¹), simultaneously with a sharp increase in juniper stem density (1.31% year⁻¹). Although in 1992 most Juniper plots were monospecific, the Markovian models consistently predict that *J. thurifera* monospecific stands will become extremely rare during the 21th century.

Monospecificity of *J. thurifera* woodlands has been traditionally attributed to environmental constraints such as harsh continental climate and shallow soils that would limit the performance of other tree species (Peinado and Rivas-Martínez 1987). The colonization of juniper woodlands by species such as oaks and

249 pines might be interpreted as a result of an improvement of climatic conditions, as has already been
250 reported for other plant species in the Iberian Peninsula (Sanz-Elorza et al. 2003). However, since climate
251 factors were excluded by the logistic model as drivers for plot changes, nor colonized plots differ in their
252 climatic conditions from those previously occupied by *Q. ilex* and *Q. faginea*, no support was provided to
253 a climatic basis in the observed changes. Alternatively, the observed increase in recruitment of juniper,
254 and the rapid colonization of juniper woodlands by other tree species with a lower tolerance to browsing,
255 has been interpreted as a consequence of the reduction of density of domestic herbivores at local scale
256 (DeSoto et al. 2010). Nevertheless, we did not obtained any statistical relationship between colonization
257 rate and livestock abundance in our data set. The absence of detailed free-ranging livestock records and
258 the different scales between forest inventory data (a few square meters) and livestock density data (tenths
259 of square kilometres) severely limit our ability to consistently compare forest composition and herbivory
260 rates. Thus, the causal force behind this process could not be ascertained.

261
262 In spite of the conservative proxy used for propagule availability, the colonization of *J. thurifera*
263 woodlands by oaks and pines was related to the proximity of mature trees of these species. This result is
264 in agreement with the role of dispersal limitation in structuring plant communities (Gómez-Aparicio et al.
265 2009) and its potential to modulate the response of forest species to global change (Pacala and Hurtt
266 1993). The importance of limited dispersal in community organization can be exacerbated in fragmented
267 landscapes such as those characterizing Mediterranean areas, where the frequency of long-distance
268 dispersal events has a major influence on the probability of plant colonization and its persistence in
269 habitat patches (Zavala and Zea 2004; Montoya et al. 2008). On the other hand, a higher colonization rate
270 was observed in plots located at lower altitude which may be related to the relative abundance of *J.*
271 *thurifera* stands at the top of plateaus. In these positions juniper woodlands can persist as monospecific
272 stands for longer periods since dispersal of other tree species more abundant in lower areas is complicated
273 due to gravimetric constraints and dispersers' behavior. However, although propagule availability can
274 modulate the pace of the colonization process, it can not be considered as a cause for the colonization
275 process.

276
277 Interestingly, less-competitive Spanish juniper is expanding into other forested environments, mainly pine
278 and oak forests, albeit at a slower pace ($0.6\% \text{ year}^{-1}$). According to our model, this would lead to a large

range increase (over 30%) during the present century. The arrival of juniper propagules to forested areas is not a novel phenomenon. In spite of a large pre-dispersive mortality (Montesinos et al. 2010), this species possess a high colonizing capacity at larger distances, due to its dispersal by different thrush species (Santos et al. 1999). Thus, the effective establishment of *J. thurifera* occurring nowadays may be a consequence of the release of pre-existing limiting factors, probably related to traditional forestry management practices. Moreover, it is important to note that our estimates of future changes in Juniper woodland composition may be conservative, since we only considered the expansion of juniper into previously forested areas, thus overlooking the colonization of abandoned fields, which is actually occurring at 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 colonization, occur over a large area corresponding to 25% of juniper worldwide range, 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 increases significantly its actual range. Consequently, both a disruption of the borders between currently existing forest types and an overall increase of tree species α -diversity are occurring simultaneously. Our results do not preclude the impact of climatic change in this process, but remarks that additional factors different from climate should be considered to understand and anticipate forthcoming changes in Mediterranean forest (Linares et al. 2009).

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Table 1: Number of occupied plots, stems and stem density per occupied plot in 1992, and percentage of change per tree species between 1992 and 2002. Note that density is based on the number of occupied plots, so it can decrease even if total stem number increases.

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

Table 2: Logistic model for colonization of monospecific stands between 1992 and 2002. β is the coefficient for each of the parameters

Number of stands	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

Figure 1: Study area and sampling sites location, showing the four categories recognized for changes in *J. thurifera* plots distribution and composition in the period 1992-2002. Pure and mixed plots in 1992 and 2002 are differentiated of plots that changed since pure to mixed, and new colonized stands by *J. thurifera*, in this period. Solid line corresponds to the limit of Castilla y León region. Names and dashed lines correspond to Castilla y León provinces.

Figure 2: Transition matrix among the different plot classes in *J. thurifera* woodlands in Castilla y León, Spain, in the period 1992-2002. Numbers in the boxes indicate the number of stands in each state in 1992 and 2002. Arrows show the probability of transition, in percentage, of the 1992 plots. The exception is the transition from absent to occasional *J. thurifera* plots, which shows the absolute number of plots.

Appendix 1. Distribution of *Juniperus thurifera* plots in 1992 (black dots) and neighboring plots occupied by *Pinus* (grey triangles) or *Quercus* (white quadrates) species.