

1 **Disruption of *Juniperus thurifera* woodland structure along its northwestern**  
2 **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<sup>-1</sup>) and tree diversity increased due to rapid colonisation by oaks and pines (2.21% occupied plots year<sup>-1</sup>). In addition, the presence of juniper increased in other types of forests at a moderate rate (0.6% y<sup>-1</sup>). 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.

41 **Introduction**

42

43 Understanding the mechanisms underpinning geographical ranges is a key issue in ecology and  
44 biogeography (Gaston 2003). Species' ranges of distribution are largely driven by environmental  
45 correlates but also by population interactions and seed dispersal (e.g. Pacala and Hurtt, 1993). Under the  
46 current global change scenario, major shifts in species distribution may become the rule. In fact, range  
47 variations due to climatic conditions have already been described (Brommer 2004; Wilson et al. 2007),  
48 although data in relation to plants are scarcer and mainly centered on shifts of species ranges along  
49 altitudinal gradients (Jump et al. 2009). Moreover, the widespread land-use change may be leading to  
50 additional sources of variation such as habitat fragmentation or reduced habitat quality (Matesanz et al.  
51 2009).

52

53 In Mediterranean countries, human activities have shaped ecosystem structure and function for ages (e.g.  
54 Urbieta et al. 2008), and the transition from a traditional labor-intensive self-consumption driven  
55 agriculture to an industrialized market-oriented agriculture has involved profound changes in land-use  
56 patterns (Gellrich et al. 2007). Production has been intensified in the most fertile spots, whereas vast areas  
57 of marginal lands have been neglected. Hence, formerly productive areas in mountain regions –both by  
58 traditional agriculture or by free ranging livestock– are experiencing landscape changes and undergoing  
59 secondary succession due to recent changes in land use (Mazzoleni et al. 2004, Chauchard et al. 2007).

60

61 The interaction between successional reactivation and other global change drivers may involve the onset  
62 of novel vegetation trajectories. Currently dominant species may be replaced by other taxa from the  
63 regional species pool, which could lead to a new equilibrium state of the ecosystem *sensu* Rietkerk et al.  
64 (2004). These phenomena are contingent on the ecosystem spatial configuration and on historical effects  
65 determining demographic thresholds in community dynamics (Rietkerk et al. 2004). Concretely, there is  
66 growing evidence of the dramatic role of dispersal syndromes and local seed pools in current forest  
67 community reorganization (Montoya et al. 2008).

68

69 Most of the studies describing potential changes in species distributions in response to global change are  
70 focused on the margins of their distribution range (Anderson et al. 2009). Much less interest has been

71 given, however, to the effects of global change across a significant fraction of the species' range (Purves  
72 2009). This research line is particularly exciting given that plant species usually do not cover their  
73 potential climatically-defined range, and its actual distribution is normally defined by other factors such  
74 as human activities or the availability of seed sources (Svenning and Skov 2004).

75

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

92

## 93 **Methods**

94

### 95 *Study species and area*

96

97 Spanish juniper is a long-lived tree, endemic of the western Mediterranean basin. Its most important  
98 populations are located in Spain (95.1% of the world surface) and Morocco (4.8%) with isolated  
99 populations in Argelia, Italy and France (Blanco et al. 1997). It forms open woodlands that have been  
100 traditionally managed in a wood-pasture system, where the understorey is grazed by sheep and goats.

101 During the last century social transformations have caused a progressive abandonment of these traditional  
102 management practices along its European range. Concurrently, juniper woodlands are considered a  
103 priority habitat by the European Union Directive 92/43/EEC, EUNIS 9560 (Davies et al. 2004). Our study  
104 is focused on Castilla y León Autonomous Region, which hosts 214,000 ha of *J. thurifera* woodland,  
105 comprising a 34.2% of its world surface. Most of these woodlands are located at the eastern half of the  
106 Region (Fig. 1) at altitudes between 800-1300 m under Mediterranean continental climate, on shallow and  
107 stony soils.

108

#### 109 *Data collection*

110 The Spanish Forest Inventory (SFI) consists of a systematic recording of permanent plots distributed over  
111 a grid of 1×1 km on forested areas (see details in Ministerio de Medio Ambiente, 2003). In every plot, all  
112 trees were recorded according to both their diameter at breast height (dbh, measured at 1.3 m above  
113 ground) and their distance to the centre of the plot: trees showing dbh between 7.5-12.5 cm were recorded  
114 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  
115 sampling schema allows estimating density for every species in the plot. In the study area, the Second  
116 Forest Inventory (2-SFI) and the Third Forest Inventory (3-SFI) were accomplished in 1992 and 2002,  
117 respectively. A time-span of ten years may be considered short to study long-lived woody species,  
118 however it is long enough to detect changes in this forested ecosystem (Olano et al. 2009b), especially  
119 considering the large sample size of study plots and the wide study area considered in this work..

120

121 Plots sampled in both inventories and containing *J. thurifera* individuals in at least one of them were  
122 included. We discarded those plots whose recorded position in 1992 was not correctly identified in 2002.  
123 As a result, data corresponding to 659 plots were included in the analyses. In each plot UTM coordinates,  
124 municipality and tree density per species were considered. A digital terrain elevation model with 10 m of  
125 resolution was used to obtain physiographic information such as altitude, slope and aspect for every plot.  
126 Climatic data were obtained by using estclima, a multiple regression model based on meteorological  
127 station data (Sánchez-Palomares et al. 1999) that provides monthly averages for temperature and  
128 precipitation with a geographical resolution of 1×1 km. For subsequent analysis we selected a reduced  
129 group of informative climatic parameters: mean July and December temperatures, total spring rainfall, the

130 Gorezynski Continentality Index (Gorzynski 1920) and the Mediterraneity Index-Im3 (Rivas-Martínez  
131 1987).

132

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

142

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

150

151

152 *Data analysis*

153

154 The plots were classified in four classes according to the dominance of *J. thurifera*: a) Monospecific  
155 plots; b) Plots with at least two tree species, with *J. thurifera* representing more than 10% of the stems,  
156 hereafter Mixed plots; c) Plots with *J. thurifera* comprising less than 10% of the stems, hereafter  
157 Occasional plots; d) Plots without *J. thurifera*.

158

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

163

164 In order to ascertain future changes in stand composition we calculated a transition matrix (Caswell 1989)  
165 describing the probability of transition between the different *J. thurifera* woodland classes. This matrix  
166 was used to predict the future composition of *J. thurifera* stands using a Markovian model comprising the  
167 21th century. Number of plots in each class in time t+1 was obtained by multiplying plots in each class in  
168 time t by the transition matrix. We assumed that regeneration and mortality rates of the different tree  
169 species during the next century would be similar to those recorded during the study period, so that this  
170 prediction constitutes an approximation to actual future trends in the composition and extent of *J.*  
171 *thurifera* woodlands in Castilla y León. Since the estimation of the parameters for the model is sensitive  
172 to the numbers of non-occupied plots (*i.e.* potentially available habitat), three numbers of non-occupied  
173 plots (500, 1000 and 2000) were arbitrarily established, in order to evaluate the effect of this parameters  
174 on the results.

175

176 If plot colonization by other tree species is occurring due to a change in climatic conditions, recently  
177 colonized plots will show differences in their climatic conditions from previously occupied plots. This  
178 hypothesis was tested via Redundancy Analysis (RDA) (Legendre and Legendre, 1998). This test was  
179 performed separately for *Quercus ilex* L. and *Q. faginea* Lam since both species show different climatic  
180 preferences, whereas pine species were not tested due to the smaller number of plots colonized by these  
181 species. A data set for each species was created, including the previously mentioned climatic variables  
182 and all the plots where the species had been present at any of both sampling dates. A dummy parameter  
183 indicating presence or absence of *Q. ilex* or *Q. faginea* in 1992 was used as constraining matrix for each  
184 data set. This dummy parameter was randomly assigned by a Monte Carlo permutation test with 999  
185 randomisations to determine whether there were differences in multivariate climatic space between  
186 groups. The canonical eigenvalue was used to build the *F*-ratio statistic (ter Braak 1990). These analyses  
187 were conducted using CANOCO for Windows v. 4.0 (ter Braak and Smilauer 1997).

188

189 A logistic model (Legendre and Legendre, 1998) was used in order to determine which factors provided a  
190 better prediction of tree colonization in the monospecific plots in 2-SFI. Four groups of variables were  
191 considered: 1) Climatic variables affecting *J. thurifera* growth (Rozas et al. 2009, Camarero et al. 2010):  
192 July and December temperatures, spring rainfall, Gorezynski Continentality Index and Mediterraneity  
193 Index. 2) Physiographic variables: altitude, slope and aspect. 3) Variables related to land use: population  
194 in 1999/(population in 1961+1), goats+sheep number in 1999/(goats+sheep number in 1982+1). And 4)  
195 variables related to seed source distance: pineseed, oakseed and treeseed. Variables were included in the  
196 model by the Wald forward stepwise selection. Cut-off value for inclusion in the model was 0.05, and 0.1  
197 to exclude a previously included variable. Overall model significance was evaluated using log likelihood  
198 ratio (Hosmer and Lemeshaw 2000). Additionally, Receiver Operating Characteristic (ROC) curve was  
199 employed to test the validity of the logistic regressions. ROC curves provide an evaluation of the model  
200 sensitivity (rate of true positives) and specificity (rate of false positives). The validity is estimated by the  
201 C statistics that measures the area under the curve and compares it with the null hypothesis (Hosmer and  
202 Lemeshaw 2000).

203

## 204 **Results**

205

206 The number of plots including *J. thurifera* increased 6.1% (0.6% plots  $y^{-1}$ ) between 1992 and 2002. Most  
207 plots were monospecific (62.7% in 1992; 48.5% in 2002) with a smaller percentage of mixed plots  
208 (30.3% in 1992; 38.5% in 2002) and a reduced number of occasional plots (6.9% in 1992; 13% in 2002).  
209 The richness of tree species per plot increased during the study period (1.47 in 1992; 1.71 in 2002;  $Z = -$   
210 11.648,  $P < 0.0001$ ), even after excluding monospecific plots ( $Z = -6.468$ ,  $P < 0.0001$ ). The same pattern  
211 holds for tree diversity (0.199 in 1992; 0.317 in 2002;  $Z = -10.404$ ,  $P < 0.0001$ ), even after excluding  
212 monospecific plots ( $Z = -4.132$ ,  $P < 0.0001$ ).

213

214 The number of monospecific plots declined from 389 to 319 (Fig. 2); since all these plots still presented *J.*  
215 *thurifera* individuals in 2002, this decline (18 % of the plots, 2.21% plots  $y^{-1}$ ) is explained by the  
216 colonization by other tree species. The transition matrix showed an increase of the number of mixed plots  
217 at the expense of monospecific plots (Fig. 2), with the incorporation of 39 newly colonized plots.  
218 Markovian models predict very similar results in spite of the colonizing threshold (Fig. 3). The number of



219 monospecific plots will be surpassed by that of mixed plots as soon as 2012 and by occasional plots in  
220 2042, becoming increasingly rare. *J. thurifera* will increase significantly its occupied area in the three  
221 scenarios, from 33 to 44%.

222

223 This increase in species richness and diversity is related to the rapid colonization by oaks (*Q. ilex* and *Q.*  
224 *faginea*) and to a lesser extent by pines (*P. pinaster* Ait., *P. sylvestris* L. and *P. nigra* Arnold) (Tab. 1).  
225 The number of pine individuals increased substantially from 13.63% for *P. nigra* to 52.42% for *P.*  
226 *sylvestris*. Plot colonization was faster than species recruitment in *Q. faginea* and *P. nigra*, thus leading to  
227 a decrease in mean stem density per occupied plot. Contrarily, the other tree species increased their  
228 densities. *J. thurifera* showed a relevant increase in total tree number and density per occupied plot from  
229 197 stems ha<sup>-1</sup> in 1992 to 220 in 2002 ( $Z = -7.110$ ,  $P < 0.001$ ).

230

231 Climatic parameters did not differ between the colonized plots and the previously occupied ones for *Q.*  
232 *ilex* ( $F = 0.169$ ,  $P = 0.199$ ) or *Q. faginea* ( $F = 0.72$ ,  $P = 0.419$ ). A satisfactory logistic model was  
233 achieved (Table 2) including two parameters, distance to seed source (treeseed) and altitude. Colonization  
234 was slower in areas far from available seed source (*Quercus* or *Pinus*) or at higher altitudes. ROC curve  
235 showed that the logistic model reasonably predicted colonization ( $C = 0.683$ ,  $P < 0.001$ ).

236

237

## 238 **Discussion**

239

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

245

246 Monospecificity of *J. thurifera* woodlands has been traditionally attributed to environmental constraints  
247 such as harsh continental climate and shallow soils that would limit the performance of other tree species  
248 (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% year<sup>-1</sup>). According to our model, this would lead to a large

279 range increase (over 30%) during the present century. The arrival of juniper propagules to forested areas  
280 is not a novel phenomenon. In spite of a large pre-dispersive mortality (Montesinos et al. 2010), this  
281 species possess a high colonizing capacity at larger distances, due to its dispersal by different thrush  
282 species (Santos et al. 1999). Thus, the effective establishment of *J. thurifera* occurring nowadays may be  
283 a consequence of the release of pre-existing limiting factors, probably related to traditional forestry  
284 management practices. Moreover, it is important to note that our estimates of future changes in Juniper  
285 woodland composition may be conservative, since we only considered the expansion of juniper into  
286 previously forested areas, thus overlooking the colonization of abandoned fields, which is actually  
287 occurring at similar pace (Pueyo and Alados 2007, Olano et al. 2009a).

288

289 Our results provide evidence on how rapid changes in community composition and species range are  
290 occurring over large areas, even in the centre of the species range, and not only at the boundary of its  
291 range. Changes in juniper woodland composition in central Spain, due to oak and pine colonization, occur  
292 over a large area corresponding to 25% of juniper worldwide range, which will increase the rarity of the  
293 currently dominating woodland type, the monospecific *J. thurifera* woodland. Conservation of this  
294 priority habitat (Davies et al. 2004) should incorporate compositional changes as part of the dynamics of  
295 this ecosystem (DeSoto et al. 2010). This process is occurring simultaneously with a spread of Spanish  
296 juniper into surrounding forested areas and abandoned fields, which increases significantly its actual  
297 range. Consequently, both a disruption of the borders between currently existing forest types and an  
298 overall increase of tree species  $\alpha$ -diversity are occurring simultaneously. Our results do not preclude the  
299 impact of climatic change in this process, but remarks that additional factors different from climate  
300 should be considered to understand and anticipate forthcoming changes in Mediterranean forest (Linares  
301 et al. 2009).

302

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

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|                            | <i>Plots in 1992</i> | <i>Change (%)<br/>1992-2002</i> | <i>Total<br/>stem number</i> | <i>Change (%)<br/>1992-2002</i> | <i>Density in 1992<br/>(stems ha<sup>-1</sup>)</i> | <i>Change (%)<br/>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%                         |



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412 **Table 2:** Logistic model for colonization of monospecific stands between 1992 and

413 2002.  $\beta$  is the coefficient for each of the parameters

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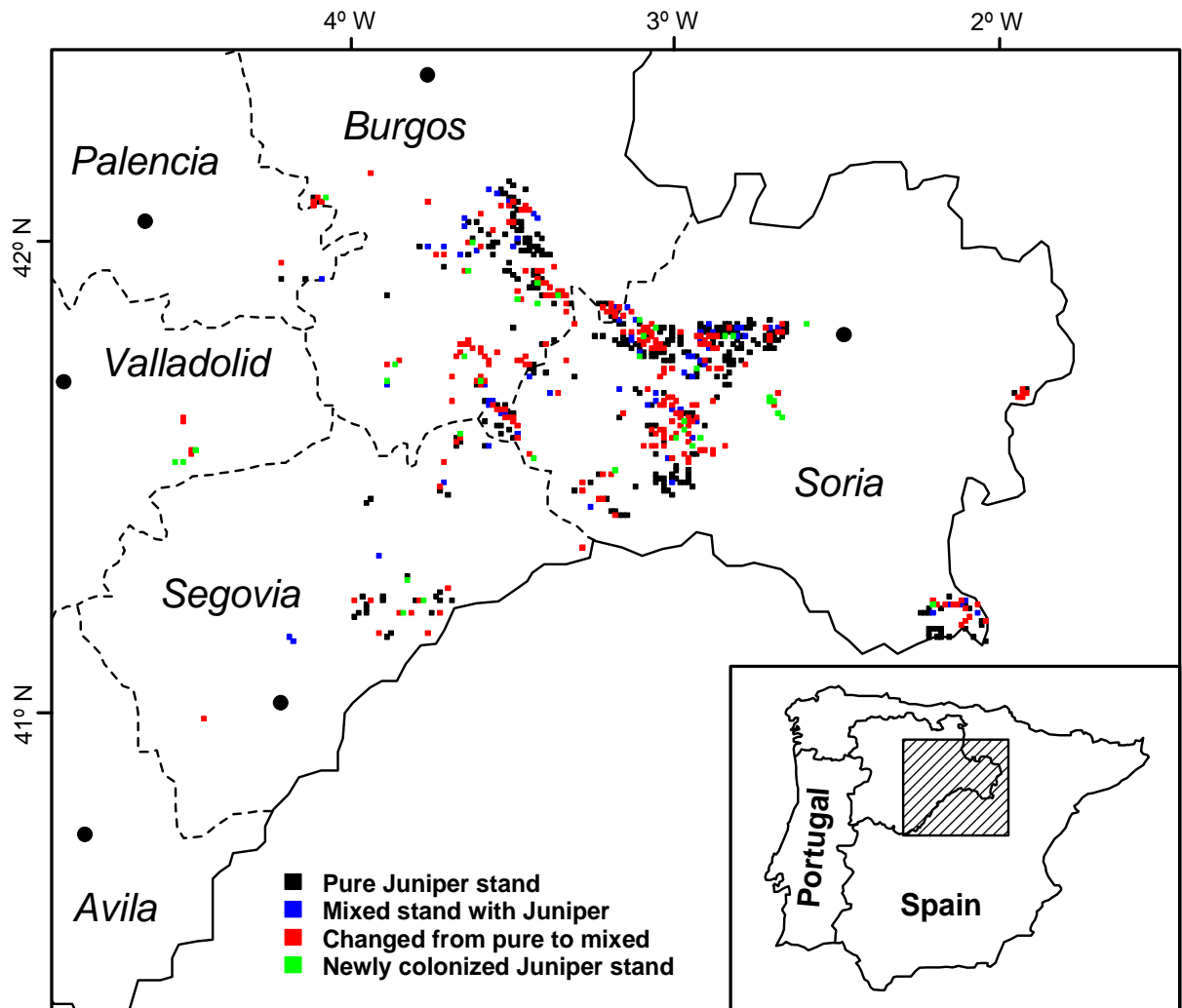
| Number of stands | Model $P$ | Parameters in the model | Parameter $P$ | $\beta$ |
|------------------|-----------|-------------------------|---------------|---------|
| 376              | <0.001    | Constant                | 0.022         | 3.671   |
|                  |           | Treeseed                | 0.008         | -0.001  |
|                  |           | Altitude                | 0.005         | -0.004  |

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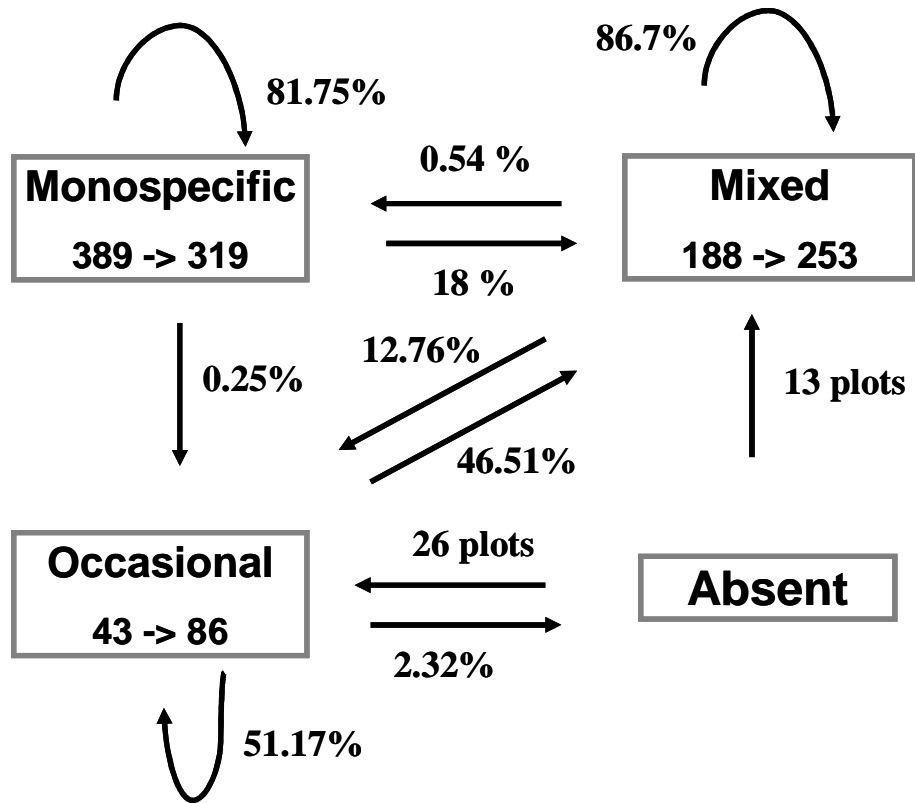
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418 **Figure 1:** Study area and sampling sites location, showing the four categories  
419 recognized for changes in *J. thurifera* plots distribution and composition in the period  
420 1992-2002. Pure and mixed plots in 1992 and 2002 are differentiated of plots that  
421 changed since pure to mixed, and new colonized stands by *J. thurifera*, in this period.  
422 Solid line corresponds to the limit of Castilla y León region. Names and dashed lines  
423 correspond to Castilla y León provinces.  
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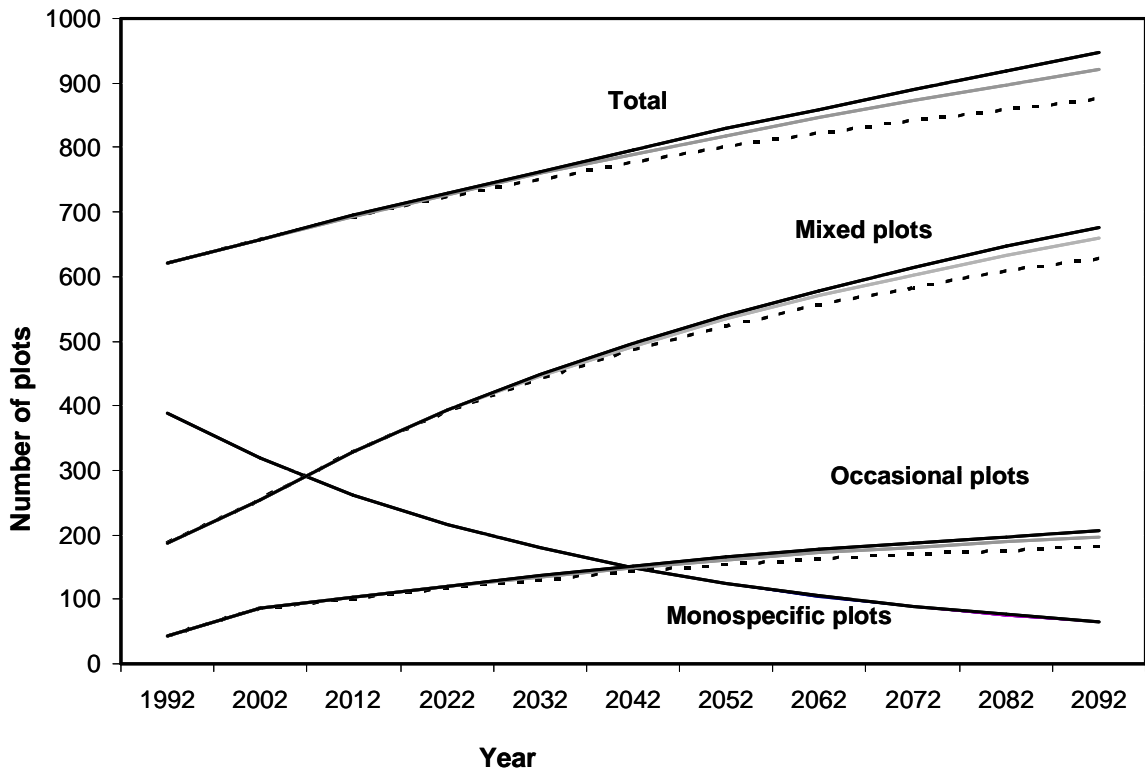


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426 **Figure 2:** Transition matrix among the different plot classes in *J. thurifera* woodlands  
 427 in Castilla y León, Spain, in the period 1992-2002. Numbers in the boxes indicate the  
 428 number of stands in each state in 1992 and 2002. Arrows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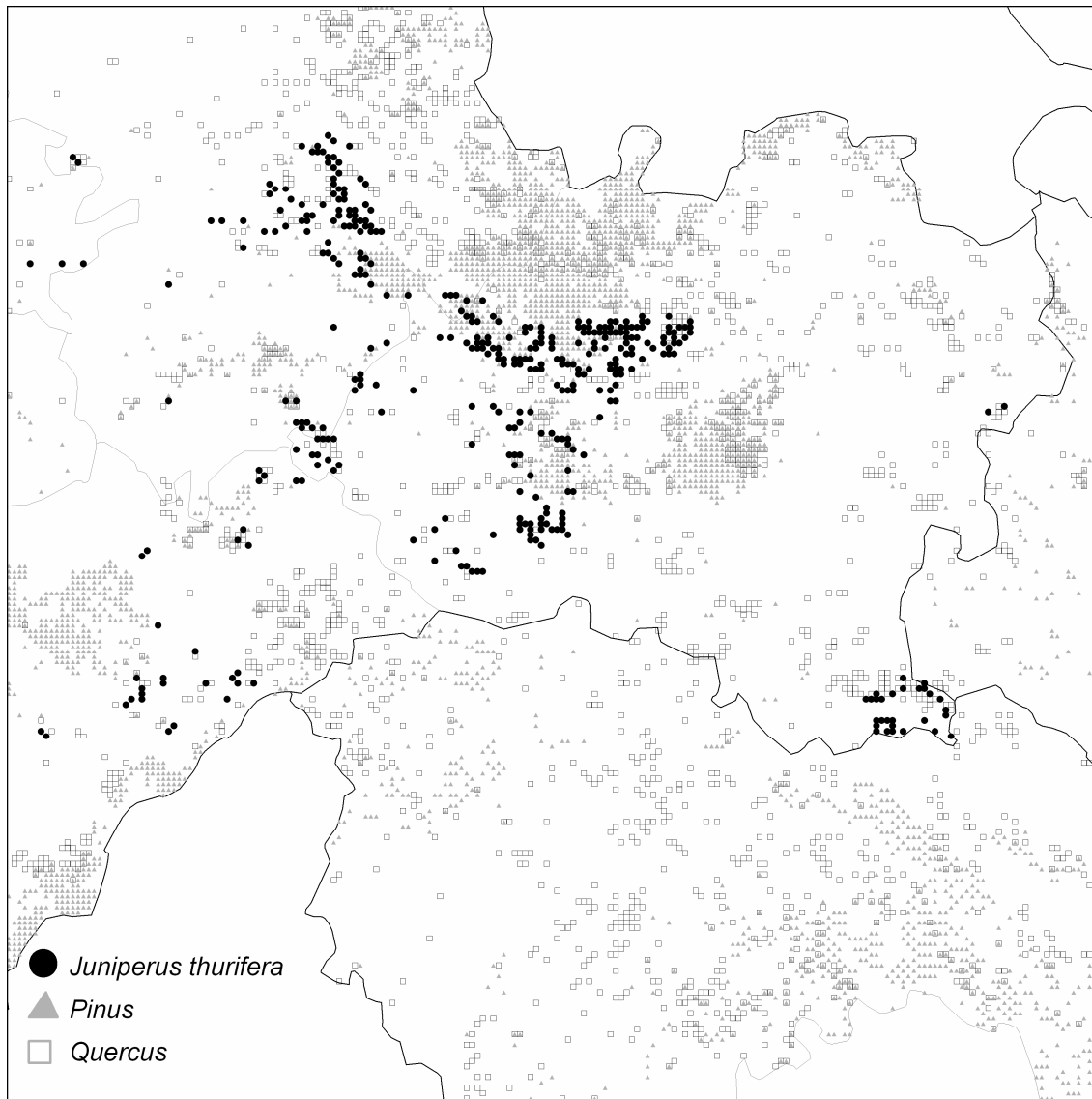


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Appendix 1. Distribution of *Juniperus thurifera* plots in 1992 (black dots) and neighboring plots occupied by *Pinus* (grey triangles) or *Quercus* (white quadrates) species.



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