



# A seeding experiment for testing tree-community recruitment under variable environments: Implications for forest regeneration and conservation in Mediterranean habitats

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## ABSTRACT

As a result of historical and ecological factors, woody-plant communities are composed of species with different biogeographic origins that presumably diverge in their ability to recruit under variable environments. The aim of this study is to evaluate the conservation implications of the differences in recruitment of six tree species of different biogeographical origin coexisting in a Mediterranean mountain forest. Under field conditions, we experimentally sowed a total of 16,650 seeds belonging to two Mediterranean (*Quercus ilex* and *Q. pyrenaica*), two Sub-Mediterranean (*Acer opalus* subsp. *granatense* and *Sorbus aria*), and two boreo-alpine (*Pinus sylvestris* and *Taxus baccata*) species. We selected the three most common successional scenarios where seeds are dispersed (woodland, shrubland, and open areas), and half of the seeds were irrigated simulating a rainy summer in terms of Mediterranean ecosystems. Seedling survival was strongly affected by the type of habitat as well as irrigation. The recruitment of the six species was possible only in wooded areas under wet conditions (20–60%). In shrubland, only Mediterranean and Sub-Mediterranean species recruited in typical dry years (10–50%), but irrigation increased their survival (25–65%) and allowed *P. sylvestris* to recruit (32%). Open areas constituted the most adverse scenario for seedling recruitment, especially for non-watered seedlings (0% for boreo-alpine species, 1–24% for the rest). Overall, the benefit of a wet summer was more critical for the recruitment of boreo-alpine species (*P. sylvestris* and *T. baccata*) than for the rest, although a rainy summer is also necessary for the recruitment of *A. granatense* and *S. aria* in shrubland habitats. Our experimental results indicate that the maintenance of current species composition in Mediterranean mountain forests is critically dependent on the periodic, scattered occurrence of wet summers. From a conservation standpoint, the predictions of less rainy summers and greater aridity in the future imply a change in the relative abundance of species in the mature forest, with Mediterranean species becoming dominant and boreo-alpine species becoming even rarer and, consequently, a serious threat for the persistence of boreo-alpine species at their southern distribution limit.

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## 1. Introduction

The species composition of a plant community is the result of both historical and ecological factors (Archibold, 1994; Davis and Scholtz, 2001; Herzog and Kessler, 2006; Ricklefs, 2006; Qian et al., 2007). Historically, contemporary assemblages of woody species represent mixtures of taxa with disparate biogeographical origin that also span broad geological ages (Herrera, 1992; Carrión et al., 2003; Thompson, 2005; Ricklefs, 2006). Ecologically, each environment may filter a different combination of species, with

consequences for composition and relative abundance of species in local assemblages (George and Bazzaz, 1999a,b). Since fast changes in ecological conditions are predicted due to global change, it is critical for plant community conservationists to understand differences in recruitment between species coexisting in current assemblages.

Due to its latitudinal position, the Mediterranean Basin has been a source and sink of species during glacial and inter-glacial periods of the Quaternary (Herrera, 1992; Carrión et al., 2003; Blondel and Aronson, 1999; Thompson, 2005; de Heredia et al., 2007). As a result, current communities are composed of species with disparate biogeographical origin. Particularly, Mediterranean mountain ranges in the southern Iberian Peninsula acted as refuges for boreo-alpine species such as *Pinus sylvestris* var. *nevadensis* H. Christ. or *Taxus baccata* L. after the last glacial period (Tittensor, 1980; Boratynski, 1991; Sinclair et al., 1999; Blanca et al., 1998;

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de Heredia et al., 2007). These populations represent the southern limit of the distribution area and, under a Mediterranean climate, boreo-alpine species face environmental constraints that differ from those of their main, northern distribution area (García et al., 2000; Castro et al., 2004; Hampe and Petit, 2005).

Human activities have been altering natural habitats and the spatial distribution of species in the Mediterranean Basin for thousands of years (Blondel and Aronson, 1999; Thompson, 2005; Blondel, 2006). Current Mediterranean landscapes are mosaics of patches with different size, degree of human management (Blondel and Aronson, 1999; Thompson, 2005). As consequence, there are an array of successional scenarios differing in major environmental factors (light availability, soil moisture, nutrients) which can determine species composition and coexistence. Most of these factors can fluctuate inter-annually due to variation in climatic conditions, thus altering the quality of the habitat for recruitment (e.g. Greenlee and Callaway, 1996; Tielbörger and Kadmon, 2000; Ibáñez and Schupp, 2001; Gómez-Aparicio et al., 2005, 2008). Summer dryness dominates the Mediterranean climate and represents the main constraint for seedling establishment (Castro et al., 2005a; Giménez-Benavides et al., 2007). However, some scattered years have rainy summers, especially in mountain areas (Rodó and Comín, 2001; Gómez-Aparicio et al., 2005). Therefore, these two different climatic scenarios (the infrequent wet vs. the typical dry summers) are assumed to influence seedling recruitment variably depending on the species. Wet summers are expected to be more crucial for the recruitment of boreo-alpine species, because normally they need such rare events of rainfall to have a window of opportunity for seedling recruitment (*sensu* Eriksson and Fröberg, 1996). Contrarily, species with Mediterranean or Sub-Mediterranean origin are assumed to be more adapted to drought stress (Pigott and Pigott, 1993; Rodà et al., 1999).

The aim of this study is to evaluate the impact of different climatic and successional scenarios on the recruitment of six tree species of disparate biogeographical origin coexisting in a Mediterranean forest. For this, we conducted a direct seed-sowing experiment in the three most abundant habitats where seeds are dispersed. These habitats are equivalent to the most common successional scenarios and they differ in radiation and soil moisture. We also included a watering treatment that simulated a mild summer in terms of Mediterranean ecosystems (Rodó and Comín, 2001), in order to represent two potential climatic scenarios (rare wet summer vs. typical dry summer). To our knowledge, this is the first field seeding experiment that includes the main tree species appearing in a given Mediterranean community, i.e. mountain forests of southern Iberian Peninsula. This deals with the critical issue of understanding the potential filtering of species with disparate origin composing forest communities and, hence, the prediction of the possible forest composition in the future under the scenario of increasing aridity projected for all the subtropics, including the Mediterranean Basin (Christensen et al., 2007; Seager et al., 2007).

## 2. Materials and methods

### 2.1. Study site and species

The field experiment was carried out from 2003 to 2005 in the Sierra Nevada National Park (S Spain). The study site is an area of 12.4 ha fenced against large mammals (37°05'N and 3°28'W, 1600 m a.s.l.). The dominant bedrock is limestone, giving rise to basic loamy soils. The climate is mountain Mediterranean with the precipitation concentrated between late autumn and winter (usually snow) and a severe summer drought (June–August). Mean precipitation is 840 mm (1991–2005; data from a climatic station

located at the study site). Average cumulative rainfall of summer is 48 mm (1902–2005; data from a meteorological station placed in the city of Granada and correlated with data from the meteorological station of the study area;  $R^2 = 0.73$ ;  $P < 0.0001$ ). The 1902–2005 series includes 8 years with summer rainfall at least twice the average ( $\geq 96$  mm), which may be considered wet summers in terms of the Mediterranean climate (Gómez-Aparicio et al., 2005). Rainfall during the years of experiment was 975 mm (14 mm in summer) in 2003, 770 mm (28 mm in summer) in 2004, and 394 mm (8 mm in summer) in 2005, this last year being the driest year of the 1991–2005 series.

The study species were *Quercus ilex* L., *Quercus pyrenaica* Willd., *Acer opalus* subsp. *granatense* (Boiss.) Font Quer and Rothm. (hereafter *A. granatense*), *Sorbus aria* L., *P. sylvestris* var. *nevadensis* Christ, and *T. baccata* L., which are the main species that compose the tree canopy of natural stands in the study area. They diverge in their biogeographical distribution (Castroviejo et al., 1986; Blanca et al., 2002): *T. baccata* and *P. sylvestris* have Euro-Siberian distribution; the two *Quercus* spp. have a typical Mediterranean distribution (Rodà et al., 1999); *A. granatense* appears in the southern Iberian Peninsula, North Africa, and Mallorca, normally in ravines and shady areas (Blanca et al., 2002); and the distribution of *S. aria* ranges from Europe, Asia, Macaronesia, to North Africa, appearing in southern Iberian Peninsula in shady ravines and north-facing slopes (Castroviejo et al., 1986). In terms of their ecological requirements, *Quercus* spp. are Mediterranean, *A. granatense* and *S. aria* are Sub-Mediterranean, and *P. sylvestris* and *T. baccata* are boreo-alpine species (Blanco et al., 2005).

The vegetation in the study area is a fine mosaic composed of woodland fragments intermingled with shrublands and open areas, as a result of the degradation of former native forests of *P. sylvestris*. The dominant tree species in the area are *P. sylvestris*, followed by *Q. ilex*, while the other four are less abundant. Shrubland is composed of several woody species, such as *Genista cinerea* (Vill.) DC., *Crataegus monogyna* Jacq., *Prunus ramburii* Boiss., *Thymus mastichina* L., and *Salvia lavandulifolia* Vahl. (Molero-Mesa et al., 1992; Junta de Andalucía, 2001).

### 2.2. Field methods and experimental design

To simulate the two climatic scenarios appearing in Mediterranean mountain ecosystems, i.e. typical dry summers vs. scattered wet summers, we performed a sowing experiment for the six study species, using two levels of water addition. We collected seeds and acorns during the fruiting season (autumn) from different parent trees in the study area. We removed the pulp of fleshy fruits, moved the seeds, and stored them, together with acorns, at 2–4 °C until used. Before the sowing, seed or fruit viability was tested using standard procedures, rejecting the clearly aborted or predated seeds (García-Fayos et al., 2001). Standard seed germination rates were known from previous works in the study area (Gómez, 2004; Gómez-Aparicio, 2004; Castro et al., 2005b) and were consistent with the data from our experimental results (see after). For simplicity, we refer hereafter to all propagules as seeds.

Sowing was performed in the three habitats that represent the main landscape units of the mosaic area, where seedling emergence occurs naturally (Castro et al., 2005a; Mendoza et al., 2009): (1) open areas, gaps of bare ground or covered by sparse herbaceous vegetation; (2) shrubland, under the canopy of the most abundant shrubs in the study site; (3) woodland, under pine canopy. The sowing experiment was replicated in 2003 and 2004 (called hereafter 2003 trial and 2004 trial; Table 1). The sampling design was haphazardly stratified for each habitat type and sowing stations were our experimental replicates, each one spaced at least 3 m of the others. Each sowing station was composed from a set of randomly arranged wire cages (in order to prevent seed predation)

**Table 1**

Scheme of the experimental design. We selected 3 types of habitat (open, shrubland, and woodland). The total number of sampling stations per habitat was 60 for the 2003 experimental trial and 30 for the 2004 trial. Within each habitat, half of the sampling stations were irrigated and the other half were kept as control. *T. baccata* was not sown in 2004 trial. The number of seeds per sampling station was adjusted to seed size.

Habitat	Watering	N sowing stations		Species sowed		
		2003 trial	2004 trial	2003 trial	2004 trial	N seeds (per sowing station)
Open	Control	30	15	<i>Q. ilex</i>	<i>Q. ilex</i>	5
	Watered	30	15	<i>Q. pyrenaica</i>	<i>Q. pyrenaica</i>	5
Shrubland	Control	30	15	<i>A. granatense</i>	<i>A. granatense</i>	15
	Watered	30	15	<i>S. aria</i>	<i>S. aria</i>	15
Woodland	Control	30	15	<i>P. sylvestris</i>	<i>P. sylvestris</i>	15
	Watered	30	15	<i>T. baccata</i>		10

with the sown seeds of each species. All species were sown in January in 2003 and in 2004 except *T. baccata*, which was sown only in 2003 because the lack of emergence of this species in 2003 discouraged us from repeating sowings in 2004. A total of 11,700 seeds were sown in 2003 trial and 4950 in 2004 trial (Table 1).

For each experiment trial, half of the sowing stations were randomly assigned to an irrigation treatment and the other half to control. Water was applied only during the year of sowing (first-growing season), thus simulating a scattered episode of “rainy summer”. The surface area irrigated (30 × 30 cm) was greater than the area of the sowing station in order to avoid border effects. Irrigation consisted of adding ca. 2 l of water at each application time (equivalent to 22 mm; see (Castro et al., 2005a) for a similar procedure). The total amount of water added approximates the amount from the torrential summer storms that characterize wet summers in Mediterranean systems (Castro et al., 2005a; Gómez-Aparicio et al., 2005).

### 2.3. Characterization of the abiotic environment

The spatial variability of light was explored with hemispherical digital photography (Rich, 1990). Pictures were taken in each of the 180 sowing stations using the standard procedure (see Puerta-Piñero et al. (2007) for a complete description of the methods). The images were analysed using Hemiview canopy-analysis software version 2.1 (1999, delta-T Devices Ltd., Cambridge, UK), from which we derived a value of Global Site Factor (GSF) per image (Rich, 1990). Values of GSF range from 1 (open sky) to 0 (complete obstruction).

The spatial variability of the percentage of volumetric soil-water content (VWC%) of the top soil (12 cm depth) was monitored with a Theta-Probe sensor (Delta-T Devices Ltd., Cambridge, UK). Two measurements were taken 3–5 days after irrigation in half of the sowing stations every 14 days in 2003, and every 30 days in 2004, making a total of 13 measurements for the entire study.

### 2.4. Seedling monitoring

Seedling emergence (percentage of seeds emerged from the sown seeds), survival (percentage of seedlings surviving from the emerged seeds), and cause of mortality were monitored for two growing seasons in each experimental trial; i.e. until September 2004 for seedlings that emerged in 2003, and until September 2005 for seedlings that emerged in 2004. Seedling monitoring was performed weekly in 2003 and fortnightly in 2004. Weeds were carefully removed in order to avoid competition.

### 2.5. Data analysis

Differences in GSF between the three habitats were compared with a one-way ANOVA. Volumetric soil-water content was compared between habitat types and irrigation treatment using a repeated-measures ANOVA. Analyses of emergence and survival

were performed using a logistic model with emergence/survival rate (proportion of the number of emerged seedlings to the total number of sown seeds, or proportion of the number of surviving seedlings to the total number of emerged seedlings) as the response variable, binomial probability distribution, and logit link function (Quinn and Keough, 2002; Bravo-Oviedo et al., 2006). Analyses were separated for each species and year of emergence. In the case of emergence, we cannot guarantee that seed viability was similar among species at the time of sowing, precluding among species comparisons. Values are given throughout this paper with mean ± standard error. All analyses were made using JMP v. 7.0 (SAS Institute Inc., 2007) and R 2.6.0. (R Development Core Team, 2007).

## 3. Results

### 3.1. Abiotic environment

The GSF values significantly differed between habitat types ( $F_{2,179} = 326.99$ ;  $P < 0.0001$ ;  $R^2 = 0.79$ ). Open was the type of habitat with the highest radiation values ( $0.83 \pm 0.01$ ), followed by shrubland ( $0.57 \pm 0.03$ ), and lastly by woodland ( $0.23 \pm 0.03$ ).

The summer mean values of volumetric water content (% VWC) were significantly higher for watered sowing stations than for control in all the habitats (Tables 2 and 3). The percent VWC in 2004 was higher than in 2003 for all habitats and watering treatments (Table 2), reflecting that the summer of 2003 was drier than that of 2004.

### 3.2. Seedling emergence

All species except *T. baccata* registered emergence the same year of sowing (Table 4). First-year emergence of seedlings for 2003 trial was  $28.8 \pm 0.8\%$  for the 2003 trial and  $33.6 \pm 1.3\%$  for 2004 trial (Table 4). Habitat type was the best factor explaining first-year emergence in all cases, although the pattern was not consistent among species and years (Tables 4 and 5). Watering significantly increased emergence only for seedlings of *Q. ilex* and *S. aria* sown in 2003, and of *P. sylvestris* sown in 2004 (Tables 4 and 5).

Seedlings of *A. granatense* and *S. aria* had second-year emergence, i.e. also emerged the year after sowing (Table 4). As in the case of first-year emergence, habitat was the best explaining factor (Table 5). Only second-year emergence of *S. aria* in 2005 was significantly increased by watering. Meanwhile, the emergence pattern of *T. baccata* was unique, because it emerged only the year after sowing, i.e. in 2004. Watering was the best explaining factor for the emergence of *T. baccata*, as 85% of emerged seedlings had been irrigated the year before (Tables 4 and 5).

### 3.3. First summer seedling survival

The total percentage of seedlings that survived the first summer was 50.8% for seedlings that emerged in 2003 and 56.1% for those



**Table 5**

Summary of the logistic model for first-year and second-year emergence under different habitats and irrigation levels. Analyses were separated for each species and year of emergence. Habitats are open, shrubland, and woodland. Irrigation levels are control and water supplementation. Emergence rate was calculated as the proportion of emerged seedlings to the total number of sown seeds per cage. The degrees of freedom for all models were 2 for habitat (*H*) effect, 1 for watering (*W*) and 2 for *H* × *W*. Significant *p* values are shown in bold.

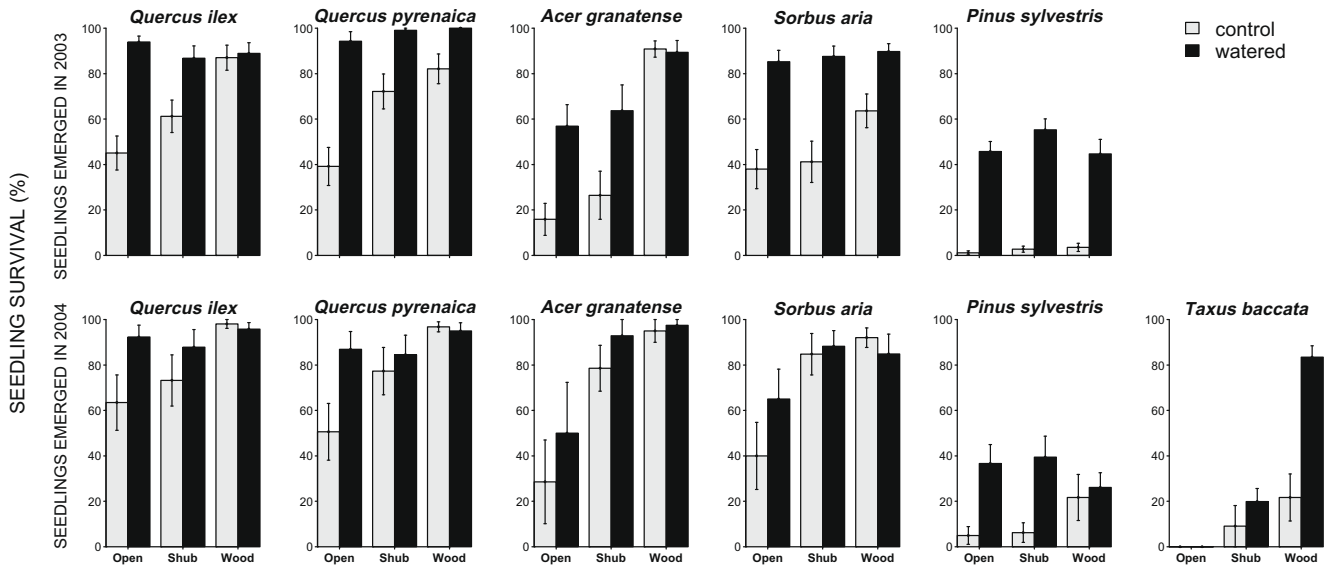
Species	Year of sowing	2003				2004			
		2003		2004		2004		2005	
		Effects	X <sup>2</sup>	<i>p</i>	X <sup>2</sup>	<i>p</i>	X <sup>2</sup>	<i>p</i>	X <sup>2</sup>
<i>Q. ilex</i>	Habitat ( <i>H</i> )	11.359	<b>0.0034</b>			7.489	<b>0.0237</b>		
	Watering ( <i>W</i> )	4.176	<b>0.041</b>			2.170	0.1407		
	<i>H</i> × <i>W</i>	0.161	0.9228			1.129	0.5687		
<i>Q. pyrenaica</i>	Habitat ( <i>H</i> )	5.103	0.078			10.017	<b>0.0067</b>		
	Watering ( <i>W</i> )	2.137	0.1438			0.388	0.5336		
	<i>H</i> × <i>W</i>	5.757	0.0562			4.613	0.0996		
<i>A. granatense</i>	Habitat ( <i>H</i> )	1.177	0.5551	7.251	<b>0.0266</b>	12.051	<b>0.0024</b>	34.314	<b>&lt;0.0001</b>
	Watering ( <i>W</i> )	0.001	0.9719	0.036	0.8505	1.131	0.2875	0.000	0.9994
	<i>H</i> × <i>W</i>	2.212	0.3308	1.168	0.5578	0.160	0.9232	0.928	0.6287
<i>S. aria</i>	Habitat ( <i>H</i> )	50.039	<b>&lt;0.0001</b>	14.005	<b>0.0009</b>	37.594	<b>&lt;0.0001</b>	46.172	<b>&lt;0.0001</b>
	Watering ( <i>W</i> )	5.374	<b>0.0204</b>	6.251	<b>0.0124</b>	1.189	0.2756	2.494	0.1143
	<i>H</i> × <i>W</i>	4.197	0.1227	2.083	0.3529	0.286	0.8669	24.802	<b>&lt;0.0001</b>
<i>P. sylvestris</i>	Habitat ( <i>H</i> )	183.499	<b>&lt;0.0001</b>			26.833	<b>&lt;0.0001</b>		
	Watering ( <i>W</i> )	1.203	0.2727			6.576	<b>0.0103</b>		
	<i>H</i> × <i>W</i>	1.629	0.4429			36.824	<b>&lt;0.0001</b>		
<i>T. baccata</i>	Habitat ( <i>H</i> )			29.881	<b>&lt;0.0001</b>				
	Watering ( <i>W</i> )			234.041	<b>&lt;0.0001</b>				
	<i>H</i> × <i>W</i>			9.791	<b>0.0075</b>				

**Table 6**

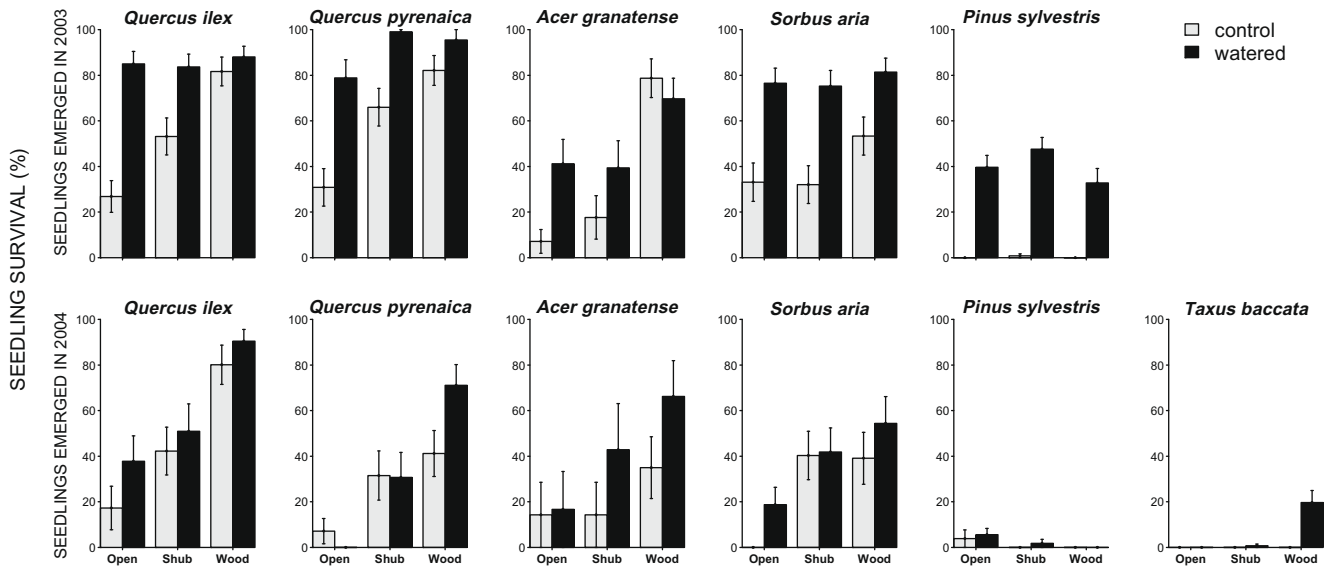
Summary of the logistic model for survival after first and second summer under different habitats and irrigation levels. Analyses were separated for each species and year of emergence. Habitats are open, shrubland, and woodland. Irrigation levels are control and water supplementation. Degrees of freedom of the models were 2 for habitat (*H*) effect, 1 for watering (*W*), and 2 for *H* × *W* for all species except for *T. baccata* (*H* = 1; *W* = 1; *H* × *W* = 1). Models for second summer survival for *P. sylvestris* emerged in 2004 and for *T. baccata* were not performed because the number of surviving seedlings was too low. Significant *p* values are shown in bold.

Species	Year of emergence	2003				2004			
		First summer		Second summer		First summer		Second summer	
		Effects	X <sup>2</sup>	<i>p</i>	X <sup>2</sup>	<i>p</i>	X <sup>2</sup>	<i>p</i>	X <sup>2</sup>
<i>Q. ilex</i>	Habitat ( <i>H</i> )	10.111	<b>0.0064</b>	17.523	<b>0.0002</b>	7.257	<b>0.0266</b>	54.774	<b>&lt;0.0001</b>
	Watering ( <i>W</i> )	29.827	<b>&lt;0.0001</b>	50.342	<b>&lt;0.0001</b>	1.453	0.2281	2.045	0.1527
	<i>H</i> × <i>W</i>	18.116	<b>0.0001</b>	20.257	<b>&lt;0.0001</b>	5.348	0.069	3.262	0.1957
<i>Q. pyrenaica</i>	Habitat ( <i>H</i> )	7.296	<b>0.026</b>	19.787	<b>&lt;0.0001</b>	17.463	<b>0.0002</b>	59.104	<b>0.011</b>
	Watering ( <i>W</i> )	54.757	<b>&lt;0.0001</b>	43.913	<b>&lt;0.0001</b>	3.240	0.0719	1.631	0.0963
	<i>H</i> × <i>W</i>	0.440	0.8027	4.012	0.1346	4.992	0.0824	14.038	0.6547
<i>A. granatense</i>	Habitat ( <i>H</i> )	70.361	<b>&lt;0.0001</b>	66.668	<b>&lt;0.0001</b>	15.986	<b>0.0003</b>	9.011	<b>0.011</b>
	Watering ( <i>W</i> )	20.108	<b>&lt;0.0001</b>	19.006	<b>&lt;0.0001</b>	0.517	0.4719	2.766	0.0963
	<i>H</i> × <i>W</i>	7.511	<b>0.023</b>	16.898	<b>0.0002</b>	0.691	0.7077	0.847	0.6547
<i>S. aria</i>	Habitat ( <i>H</i> )	14.959	<b>0.0006</b>	18.686	<b>&lt;0.0001</b>	24.891	<b>&lt;0.0001</b>	38.440	<b>&lt;0.0001</b>
	Watering ( <i>W</i> )	59.725	<b>&lt;0.0001</b>	54.329	<b>&lt;0.0001</b>	1.604	0.2053	9.960	<b>0.0016</b>
	<i>H</i> × <i>W</i>	1.172	0.5566	0.576	0.7497	6.652	<b>0.0359</b>	10.664	<b>0.0048</b>
<i>P. sylvestris</i>	Habitat ( <i>H</i> )	5.884	0.0528	6.669	<b>0.0356</b>	1.125	0.5699		
	Watering ( <i>W</i> )	460.756	<b>&lt;0.0001</b>	465.923	<b>&lt;0.0001</b>	43.112	<b>&lt;0.0001</b>		
	<i>H</i> × <i>W</i>	7.917	<b>0.0191</b>	3.990	0.136	8.248	<b>0.0162</b>		
<i>T. baccata</i>	Habitat ( <i>H</i> )	25.086	<b>&lt;0.0001</b>						
	Watering ( <i>W</i> )	19.639	<b>&lt;0.0001</b>						
	<i>H</i> × <i>W</i>	0.929	0.3352						





**Fig. 1.** First summer seedling survival (percentages) for the six species studied in different habitats and irrigation levels. Habitats are open, shrubland (shrub), and woodland (wood). Irrigation levels are control (grey bars) and water supplementation (black bars). Data of each experimental trial are shown. First summer survival is calculated as the number of seedlings surviving the first summer divided by the number of emerged seedlings.

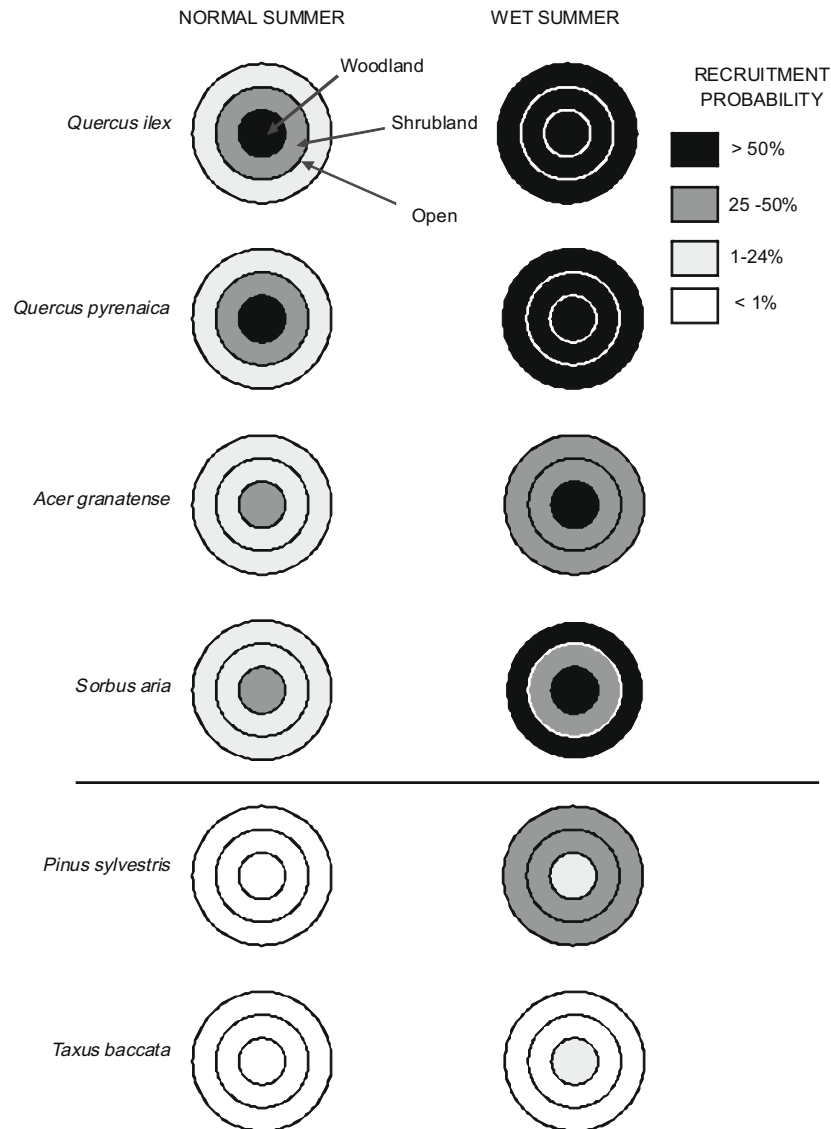


**Fig. 2.** Second summer seedling survival (percentages) for the six species studied in different habitats and irrigation levels. Habitats are open, shrubland (shrub) and woodland (wood). Irrigation levels are control (grey bars) and water supplementation (black bars). Data of each experimental trial are shown. Second summer survival is calculated as the number of seedlings surviving the second summer divided by the number of emerged seedlings.

In relation to seedling emergence, habitat type was more influential than watering, surely because the irrigation treatment started after the onset of the emergence (see (Castro et al., 2005a) for similar results). Only for *T. baccata* did emergence occur exclusively 1 year after sowing, due to physiological dormancy of seeds (Thomas and Polwart, 2003), and mostly for seeds that had been irrigated the year before. Water addition also increased seedling survival for all species, although the effect was greater in 2003 than in 2004, presumably because the former year had been drier than latter (as reflected by the higher percentage of soil-water content found in control plots in 2004). However, in both experimental trials, the benefit of a wet summer was more critical for boreo-alpine species than for the rest. In particular, *T. baccata* was strongly dependent on wet summers, given that is the only species which

needed two episodes of wet summer, one for emergence and another for survival.

Related to the habitat type, drought alleviation boosted seedling survival far more in open than in shrubland and, especially, in woodland (following an inverse gradient of light availability in the understory). These chosen habitats for the experiment represent the three most common successional stages in Mediterranean ecosystems: late-successional (woodland), mid-successional (shrubland), and pioneer (open). Woodland was the habitat that most boosted seedling recruitment, because all species were able to recruit when the summer was wet, and all species except *T. baccata* also recruited when the summer was typically dry (Fig. 3). Shading in woodland reduced seedling mortality presumably due to a combination of higher soil moisture, lower photochemical



**Fig. 3.** Schematic diagram showing the recruitment probabilities under each different ecological scenario. Concentric circles represent a different successional scenario: the one inside is woodland, the intermediate shrubland, and the outer one shows open. Circles are shadowed according to the recruitment probability: less than 1%, between 1% and 24%, between 25% and 50%, and more than 50%.

damage, higher relative humidity, and lower soil temperature (Castro et al., 2002, 2004; Gómez-Aparicio et al., 2004). Shrubland increased seedling emergence and survival in an intermediate way thanks to the amelioration of environmental conditions (Callaway, 1995; Gómez-Aparicio et al., 2004, 2008; Mendoza et al., 2009), but the effect depended on the species. When the summer was typically dry, boreo-alpine species were not able to recruit in shrubland, in contrast to Mediterranean species such as *Q. ilex*, *Q. pyrenaica*, and *S. aria*. However, when the summer was wet, recruitment in shrubland was possible for *P. sylvestris*, while Mediterranean and Sub-Mediterranean species significantly increased survival (Fig. 3). Lastly, open was the most adverse scenario for seedling recruitment, given that the establishment of all species was constrained in dry summers. Water stress and photo inhibition due to full sunlight in open areas may represent a strong limitation for seedling establishment (Gómez-Aparicio et al., 2005, 2006; Castro-Díez et al., 2006; Quero et al., 2006), and only wet summers increased the recruitment probabilities in open for Mediterranean and Sub-Mediterranean species, but not for boreo-alpine species.

Regarding forest regeneration implications, our experimental results indicate that the maintenance of the current species composition in forests is critically dependent on wet summers, given that they are the only conditions under which all species can recruit. Also, rainy summers magnify colonization to shrublands (for all species except *T. baccata*), the habitats that typically surround native forests, and at last allow the expansion of realized niches of tree species (Bruno et al., 2003; Baumeister and Callaway, 2006; Valiente-Banuet et al., 2006; Valiente-Banuet and Verdú, 2007). Forest expansion into the most pioneer habitats, open areas, would be restricted to the most drought-tolerant species, such as *Q. ilex*, *Q. pyrenaica* and *S. aria*, and mainly in a wet summer.

#### 4.1. Lessons for conservation under a global change scenario

Our study provides the first experimental results demonstrating that boreo-alpine species are more constrained in seedling recruitment than are the Mediterranean or Sub-Mediterranean ones, with important implications for the conservation of species composition under a scenario of global change (Lloret et al., 2004). As more arid-

ity is projected for Mediterranean ecosystems, rainy summers will become less frequent in the future (Moreno, 2005; IPCC, 2007). Therefore, the woody taxa most dependent on summer rainfall are threatened to be less abundant or even to disappear, because they will undergo severe limitations for emergence (i.e. *T. baccata*) and survival (*T. baccata* and *P. sylvestris*; Fig. 3). This constitutes an extra threat for these boreo-alpine species appearing at the southern limit of their distribution area, as they are already endangered (IUCN, 1994; Blanca et al., 1998).

The results of this study also show that the coexistence of species would be restricted to the most favourable scenarios for all species, i.e. woodlands. This reinforces the conservation value of woodlands, because they are the types of habitats where a diverse pool of seedlings can be maintained. Woodlands appear to be good habitats for the early stages of plants, but the possibility also exists that in later stages the scarcity of light may have negative consequences for sapling growth, especially for the more light-demanding species, such a *Pinus* sp. and *Quercus* sp. (Espelta et al., 1995; Castro et al., 2005a; Gómez-Aparicio et al., 2006), thus hampering forest regeneration. In this sense, the lower light limitation in shrublands implies the potential of these areas for forest expansion even under typically dry summers, particularly for *Q. ilex* and *Q. pyrenaica*. However, the necessity of a rainy summer for forest expansion for the rest of tree species (*A. granatense*, *S. aria*, *P. sylvestris*, and *T. baccata*) constitutes a strong limitation for the recuperation of the current forest diversity in this secondary-successional habitat.

In conclusion, conservation strategies should take into account the weak recruitment of boreo-alpine species under typically dry summers of Mediterranean as well as their critical dependence on rare wet summers and on specific habitats (i.e. woodlands) for successful recruitment. This represents a threat for the maintenance of current species composition in southern Mediterranean mountain forests, a change in the relative abundance of species (with Mediterranean species becoming dominant and boreo-alpine species becoming even rarer), and a stronger reduction in the distribution area of tree species (in particular, boreo-alpine species), as climatic change brings steadily more severe aridity.

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