

# Repercussions of Simulated Climate Change on the Diversity of Woody-Recruit Bank in a Mediterranean-type Ecosystem

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## ABSTRACT

Extreme climatic events have the potential to affect plant communities around the world, and especially in the Mediterranean basin, where the frequency of milder and drier summers is expected to be altered under a global-change scenario. We experimentally investigated the effect of three contrasting climatic scenarios on the diversity and abundance of the natural woody-recruit bank among three characteristic habitats in a Mediterranean-type ecosystem: forest, shrubland, and bare soil. The climatic scenarios were dry summers (30% summer rainfall reduction), wet summers (simulating summer storms), and current climatic conditions (control). Seedling emergence and survival after the first summer was recorded during 4 consecutive years. The wet summer boosted

abundance and diversity at emergence and summer survival, rendering the highest Shannon  $H'$  index. By contrast, the dry summer had no effect on emergence, although survival tended to decline. Nonetheless, the habitat had a key role, bare soil showing almost null recruitment whatever the climatic scenario, and forest keeping the highest diversity in all of them. Our results show that recruit-bank density and diversity depends heavily on extreme climatic events. Community dynamics will depend not only on increased drought but also on the balance between dry and wet years.

**Key words:** abundance; climatic variability; diversity; drought; extreme events; recruitment.

## INTRODUCTION

Climatic variability is a prominent feature in most ecosystems worldwide (Henderson-Sellers and Robinson 1991). A major source of this variability

is the temporal pattern of rainfall, which can vary across years and/or seasons. Under a global-change scenario, drier years are predicted for the coming decades in large areas of the planet, as well as a reduction in the frequency of mild ones (Houghton and others 2001). Nonetheless, occasional rainy years will still persist in many areas within a context of increased aridity (Esteban-Parra and others 1998; Rodrigo 2002), although the yearly variability of these favorable conditions for plant recruitment is expected to intensify (Christensen and others 2007; Giorgi and Lionello 2008). Thus, the understanding of the effect of extreme climatic

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events under a global-change scenario, both greater aridity and fewer mild years, is crucial for the accurate forecast of future plant-community dynamics.

Consequences of extreme climatic events have been detected at different scales from the community to the species level. The outcomes should be expressed as forest die-back (Allen and Breshears 1998; Breshears and others 2005), species loss (Thomas and others 2004; Thuiller and others 2005), or growth reduction (Ogaya and others 2003) in the case of extreme drought, or as higher growth and survival for individuals (Valladares and Sánchez-Gómez 2006; Squeo and others 2007; Gómez-Aparicio and others 2008) and higher community recruitment (Castro and others 2005; Mendoza and others 2009a) in the case of extremely rainy conditions. This may induce significant shifts in diversity patterns within communities (Tilman 1998; Chapin and others 2001). In fact, the ecological effects of extreme events, either drier or milder, have been identified as one of the main gaps in the knowledge of community ecology (Agrawal and others 2007; Jentsch and Beierkuhnlein 2008).

Under the current context of global change, it is predicted that arid, semiarid, and Mediterranean ecosystems will be among the most affected by strong anomalies in water pulses (Christensen and others 2007; Giorgi and Lionello 2008). In the case of Mediterranean ecosystems, dry summers are the rule, although exceptionally rainy summers occur with great irregularity (Henderson-Sellers and Robinson 1991; Esteban-Parra and others 1998). These rare wet summers may represent the only window of opportunity for recruitment (*sensu* Eriksson and Fröberg 1996) of some long-lived woody species, because their establishment is otherwise hampered by drought (for example, Traveset and others 2003; Gómez-Aparicio and others 2005; Lázaro and others 2006; Urbieto and others 2008).

The present study examines the impact of contrasting rare events (rainy summers versus very dry summers) for the diversity and abundance of the bank of woody recruits of Mediterranean mountain forests. These southern European forests are composed of plants with different ecological requirements and biogeographical origins (Blanca and others 1998; Mendoza and others 2009a), so that differences in recruitment under current and forthcoming variable water regimes can influence future forest composition. Knowledge of the recruit-bank dynamics under contrasting climatic scenarios is critical to forecast future replacement of

adults. Because events of adult mortality due to climate change may occur in a short time span (Bigler and others 2006; Bréda and others 2006; Allen and others 2010), the recruit bank may be used as an indicator of future community composition and abundance (Allen and Breshears 1998). Furthermore, seedlings are the only vital stage capable of colonizing new areas, and their response to climatic scenarios is therefore critical to understanding community dynamics for the coming decades.

Our experimental approach simulated three contrasting climatic scenarios (drier, milder, and current rainfall pattern) under field conditions across the three principal habitats comprising Mediterranean mountains: open areas, shrubland, and forest. Rainfall scenarios were selected according to maximum historical records on the study area and from predictions of increased aridity by the A-2 scenario of the IPCC (IPCC 2007). Abundance and species richness of the natural woody-seedling bank were monitored at emergence from 2006 to 2009 and survival was monitored for up to three growing seasons. Recruit bank dynamics reveal the potential for future replacement of adults (Hampe and Arroyo 2002; Castro and others 2005) and are expected to be particularly sensitive to between-year climatic variability and consequently to directional climate change (Weltzin and McPherson 2000; Jump and others 2007). Thus, the establishment of new recruits in a population has often been used to monitor the effects of climate change on plant communities (Lewis-Smith 1994; Sternberg and others 1999; Kullman 2002; Lloret and others 2009). Overall, we seek to understand the effect of contrasting potential rainfall scenarios using the recruit bank as an ecological indicator of the community's ability to maintain its composition in a Mediterranean-type ecosystem. Three specific questions were posed: (1) What are the effects of the strong climatic events on the abundance and diversity of the natural recruit bank at emergence and after the first summer? (2) Are these effects consistent over the different habitat structures of the ecosystem? (3) Are these effects consistent over the successive years?

## MATERIALS AND METHODS

### Study Area

The present study was conducted in La Cortijuela area, within the limits of Sierra Nevada National Park (1650 m.a.s.l.; 37°05'N, 3°28'W, Granada, SE Spain). This mountain area has a continental

Mediterranean climate, with cold winters and hot dry summers. Rainfall is  $828 \text{ mm y}^{-1}$  (mean 1990–2009), concentrated mostly during spring and autumn. Mean temperatures of the coldest (January) and hottest (July) months are  $3.5$  and  $21.6^\circ\text{C}$ , respectively. The vegetation in the area is composed of patches under different management, with a predominance of pine plantations, shrublands, open areas, and patches of native forest (see Matías and others 2009 for more details). The experiment was conducted inside a natural  $12.4 \text{ ha}$  fenced area for ungulate enclosure since 1986. The dominant tree species inside the fenced area are *Pinus sylvestris* L., *Pinus nigra* Arnold., and *Quercus ilex* L., with other accompanying trees such as *Acer opalus* Mill. and *Sorbus aria* L. The predominant shrubs are fleshy fruited, such as *Crataegus monogyna* Jacq., *Berberis vulgaris* L., *Amelanchier ovalis* Medik. and *Prunus ramburii* Boiss., or dry fruited such as *Salvia lavandulifolia* Vahl. and *Cytisus scoparius* L.

## Experimental Design

A fully factorial field experiment was performed by crossing two main factors: climatic scenario and habitat, each with three levels, to test the effect on woody-seedling establishment. For the climatic scenario treatment, three different levels were selected. (1) “Dry summer” was based on the SRES A-2 model by the Intergovernmental Panel on Climate Change (IPCC 2007), where a reduction in summer rainfall of 30% is predicted for Mediterranean areas. For this treatment, we built rain exclusion shelters (Yahdjian and Sala 2002) formed by a  $2 \times 2 \text{ m}$  metal frame supporting V-shaped clear methacrylate bands without UV filters (Barlocast®; Faberplast S.L., Madrid), covering 35% of the surface, and intercepting the same percentage of natural water supply by rain. A ditch was excavated 20 cm deep along the entire shelter to intercept runoff water. Rainout shelters were placed from April to September, simulating drier and longer summers. (2) “Sporadic rainy summer” (irrigation) was intended to simulate the sporadic summer storms characteristic of Mediterranean mountains. We placed  $2 \times 2 \text{ m}$  squares on the soil with a water-addition system composed of four sprinklers at the corners. Each week from mid-June to the end of September, we added a water quantity of  $12 \text{ mm m}^{-2}$ , simulating a summer storm. If a natural storm occurred in a week, the irrigation pulse was not added. The total water added during the summer was 180 mm, equivalent to the mean summer rainfall of the five mildest summers of the 1902–2006 series in the study area; (3) “Current

climatic conditions” involved  $2 \times 2 \text{ m}$  squares exposed to natural rainy conditions during experiment development. Hereafter, these climatic scenarios will be referred to as *dry*, *wet*, and *control* scenarios, respectively. For the habitat factor, we selected the three principal habitats in Mediterranean mountains differing in plant coverage and representing different successional states: (1) open, areas of bare soil or covered with sparse herbaceous vegetation, representing the lowest canopy cover; (2) shrubland, composed of the dominant shrubs in the study area, principally *Crataegus monogyna*, *Prunus ramburii*, and *Genista speciosa*, representing the mid canopy cover; and (3) forest, formed by a mixed woodland of *Pinus sylvestris*, *Pinus nigra*, and *Quercus ilex*, and represents the densest canopy cover. All habitats are adjacent to each other and presented a similar soil texture (Matías and others 2011), although they differed in seed dispersal (Mendoza and others 2009b). In each of the three habitats, we placed 24 plots of  $2 \times 2 \text{ m}$ , and randomly assigned eight of them to each of the three simulated climatic scenarios, giving a total of 72 plots (3 climatic scenarios  $\times$  3 habitats  $\times$  8 replicates). In all study plots, soil–water content was measured monthly by the time-domain reflectometry method (TDR-100, Spectrum Technologies Inc., Plainfield, IL) integrating the values of the top 20 cm of soil. Study plots were sampled by two perpendicular transects crossing on the center of the plot, recording the volumetric water content every 0.5 m with a portable TDR, performing a total of nine measures per plot. Precipitation data during experiment development under the different scenarios are shown on Table 1.

## Seedling Monitoring

The number of seedlings of all woody species that emerged and survived each year was monitored from 2006 to 2009 in eight permanent sampling quadrats of  $400 \text{ cm}^2$  ( $20 \times 20 \text{ cm}$ ) in each study plot. All seeds were naturally dispersed by birds, wind, or ballistically, and came from nearby adult vegetation (Mendoza and others 2009b). The simulation of climatic scenarios started in late spring 2007, so that 2006 seedling monitoring was performed to identify any possible pre-treatment variability between experimental plots. Emergence was recorded in the spring (May) of each year by marking each individual (identified to species level) with a permanent colored tag (2006 to 2009 cohorts, hereafter). Survival was recorded for all individuals at the end of the growing season (September of each year). Thus, post-treatment

**Table 1.** Precipitation (in  $l\ m^{-2}$ ) from April to September under the Different Climatic Scenario Simulations during the Pre-treatment Year (2006), during Experiment Development (2007–2009), and Mean Value ( $\pm$ SE) of the Last 20 years (1990–2009 series)

Scenario	2006	2007	2008	2009	Mean 1990–2009
Dry	224.5	237.6	243.4	113.8	
Control	224.5	365.5	374.5	175.1	264.2 $\pm$ 24.2
Wet	224.5	545.5	554.5	355.1	

seedling survival was monitored up to three growing seasons for the 2007 cohort, two growing seasons for the 2008 cohort, and one growing season for the 2009 cohort. To avoid any border effect, a buffer area 0.4 m wide was kept in all the plots.

## Data Analysis

Soil volumetric water content was analyzed among habitats and among climatic scenarios by a repeated-measures ANOVA to assess the efficiency of rainfall control. For the analysis of the effect of treatments on seedling-bank diversity and its impact on community recruitment, we considered three complementary approaches. First, abundance and species richness were calculated for each year at both emergence and first-summer survival times, pooling the data of the eight quadrats per plot. The first summer is the most critical period for the establishment of seedlings of the woody community in the study system (Castro and others 2005; Mendoza and others 2009a), and thus we considered it an appropriate time to estimate treatment impact on diversity. These analyses were performed independently for pre-treatment (2006) and post-treatment (2007 to 2009) cohorts with factorial ANOVAs. We used climatic scenario and habitat as predictor variables for the pre-treatment model, and climatic scenario, habitat, and cohort for the post-treatment model. Differences in climatic scenarios among years or habitats were tested by a Bonferroni-Dunn post hoc test. We further calculated the Shannon  $H'$  evenness index as an integrative estimator of diversity (Magurran 2004). Second, we estimated changes in rank abundance patterns to explore changes in the diversity of the recruit bank among different years. For this, we performed a repeated-measures ANOVA, with cohort as within-subject factor, climatic scenario as the between-subject factor, and species-rank abundances as the response variables, pooling the data of the three habitats (Lloret and others 2004). Third, we explored longer lasting consequences of the different climatic scenarios on diversity and recruitment by analyzing the survival curves of the

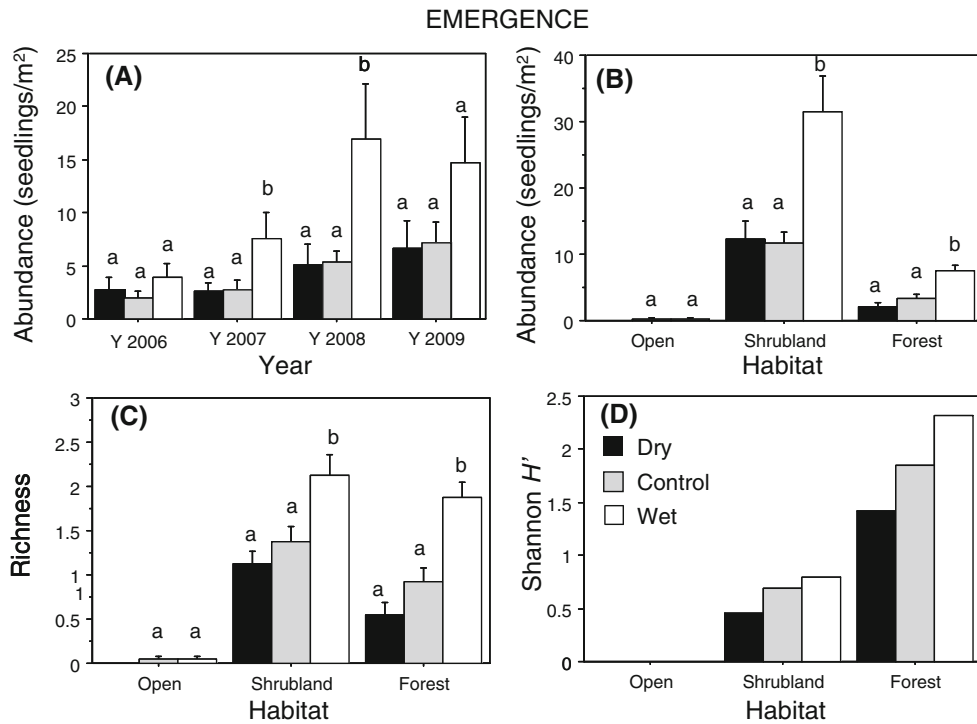
2007 and 2008 cohorts until the end of the experiment (after three and two growing seasons, respectively). The Log-Rank Chi-square statistic was used to test homogeneity of the survival curves across climatic scenarios (Kalbfleisch and Prentice 1980), pooling the data of the three habitats. The Shannon  $H'$  evenness index was calculated using the program EstimateS Win 7.5.0 (Colwell 2005). All other analyses were performed following the JMP v 7.0 package procedures (SAS Institute Inc., 2007). Values are given throughout this paper as mean  $\pm$  standard error.

## RESULTS

Soil volumetric water content significantly differed among habitats ( $F_{2,715} = 499.7$ ,  $P < 0.0001$ ; forest 15.1%  $\pm$  0.18, shrubland 14.6%  $\pm$  0.17, open 12.4%  $\pm$  0.15), and among climatic scenarios ( $F_{2,715} = 1214.7$ ,  $P < 0.0001$ ; wet summer 16.4%  $\pm$  0.16, control 13.8%  $\pm$  0.18, dry summer 11.9%  $\pm$  0.15), which supported the idea that the rainfall manipulations exerted a strong effect on soil-moisture availability.

A total of 599 seedlings emerged during the course of the experiment (ESM Appendix 1). The species richness is a representative portion of the woody community in the study area, as we tagged 15 seedling species versus 16 seed species caught in seed traps at the same study location (Mendoza and others 2009b). There was high heterogeneity among habitats, both in abundance and species richness. Overall, shrubland was the habitat from which the highest number of individuals emerged (77% of the total), followed by forest (22%) and open (almost 1%; Figure 1B).

For the 2006 cohort, there were differences in abundance among habitats at both emergence and first summer survival, but there were no differences among climatic scenarios (Table 2). Thus, we can assume that differences among scenarios in the following years were due to the treatments. For 2007 to 2009 cohorts (those subjected to treatments applications), the differences among habitats and climatic scenarios were significant for seedling



**Figure 1.** Mean values per plot for seedling-bank abundance (expressed as seedlings/m<sup>2</sup>) at emergence under the different climatic scenarios: dry summer (black bars), control (gray bars), and wet summer (white bars) during the four study years, pooling habitats (A) and in the three habitats pooling years (B). C and D represent the mean species richness per plot by habitat, and the Shannon H' evenness index under the different climatic scenarios, respectively, at emergence. Different letters denote significant differences (P < 0.05) among scenarios within the same year or habitat (Bonferroni-Dunn post-hoc test). Note that climatic-scenario simulations were not applied during 2006. Error bars represents SE.

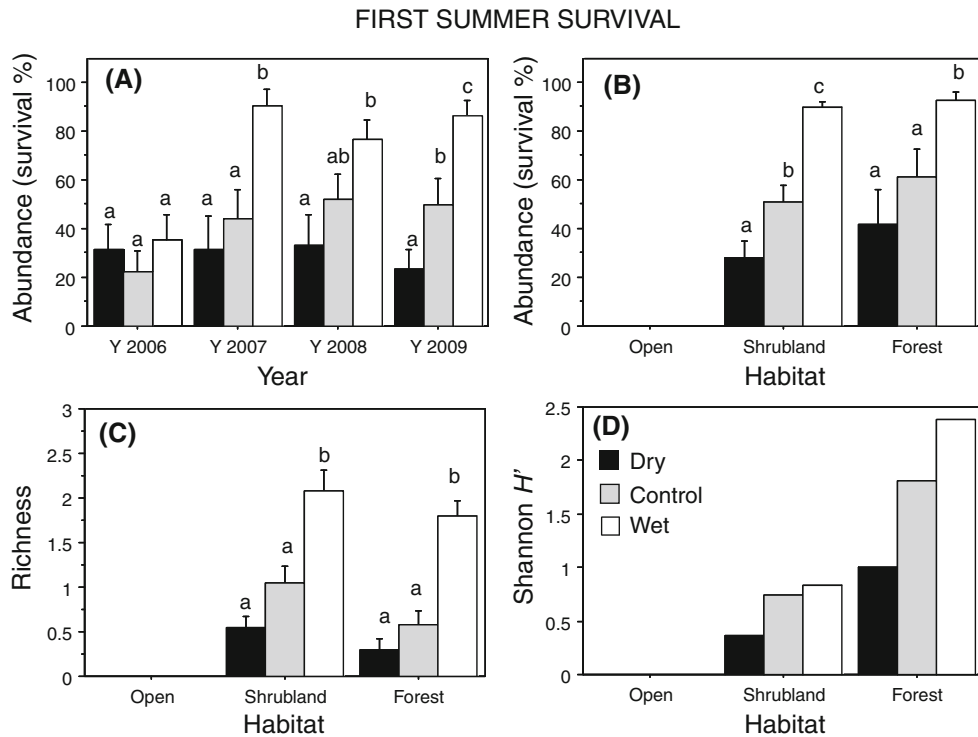
**Table 2.** Results of the ANOVA Test for Seedling Abundance at Emergence and Survival after the First Summer as Dependent Variables, and Habitat, Climatic Scenario, and Cohort of Emergence as Predictors during the Pre-treatment Year (2006) and during the Experiment (Treatment Years: 2007 to 2009)

Factor	DF	Pre-treatment year				Treatment years			
		Abundance		Survival		Abundance		Survival	
		F	P	F	P	F	P	F	P
Habitat (H)	2	5.84	<b>0.004</b>	11.65	<b>&lt;0.0001</b>	68.61	<b>&lt;0.0001</b>	16.76	<b>&lt;0.0001</b>
Scenario (S)	2	0.89	0.42	0.92	0.41	16.34	<b>&lt;0.0001</b>	8.16	<b>0.0005</b>
Cohort (C)	2	–	–	–	–	6.25	<b>0.0024</b>	0.06	0.94
H × S	4	1.12	0.36	0.48	0.75	8.51	<b>&lt;0.0001</b>	1.44	0.23
H × C	4	–	–	–	–	5.58	<b>0.0003</b>	1.27	0.29
S × C	4	–	–	–	–	0.97	0.42	0.10	0.98
H × S × C	8	–	–	–	–	0.84	0.57	0.61	0.77

Significant factors and interactions are in bold.

abundance at emergence and for survival percentage after the first summer (Table 2). Cohort and the interaction between habitat and climatic scenario significantly differed only for abundance. This inter-annual variability in abundance was not detected in survival, establishing a similar proportion

of seedlings during the three study years. Among climatic scenarios, the wet-summer scenario increased seedling abundance (Figure 1A, B) but, more importantly, increased seedling's survival probabilities (Figure 2A, B), in all cases showing higher abundance and survival. By contrast, the



**Figure 2.** Mean seedling survival per plot after the first summer under the different climatic scenarios: dry summer (*black bars*), control (*gray bars*), and wet summer (*white bars*) during the four study years, pooling habitats (**A**) and in the three habitats pooling years (**B**). **C** represents the mean species richness per plot by habitat established after the first summer; and **D** represents the Shannon  $H'$  evenness index under the different climatic scenarios after the first summer. Different letters denote significant differences ( $P < 0.05$ ) among scenarios within the same year (Bonferroni-Dunn post-hoc test). Note that climatic scenarios simulations were not applied during 2006. Error bars represent SE.

dry-summer scenario had no effect on the seedling-bank abundance, although survival consistently tended to decline, its effect being significant only for the 2009 cohort (Figure 2A). Among habitats, although shrubland was the habitat with the highest abundance (Figure 1B), forest was the habitat with the highest survival (72% in forest vs. 57% in shrubland, and 0% in open; Figure 2B). Open was not only the habitat with lowest abundance, but also had zero survival.

Mean species richness significantly differed among habitats and among climatic scenarios, both for abundance at emergence (scenario:  $F = 25.0$ ,  $P < 0.0001$ ; habitat:  $F = 91.4$ ,  $P < 0.0001$ ) and survival percentage after the first summer (scenario:  $F = 41.4$ ,  $P < 0.0001$ ; habitat:  $F = 58.9$ ,  $P < 0.0001$ ). Among scenarios, the same pattern appeared as in the case of abundance, with higher richness under the wet summer and a trend towards reduction under the dry-summer scenario (Figures 1C, 2C). Although the mean richness per plot was highest in shrubland (Figure 2C), in all cases forest was the habitat with highest total species richness (14 out of 15

species), followed by shrubland with 9 species, and open with 2. This pattern was reinforced by the Shannon  $H'$  evenness index, being higher in forest and under the wet-summer scenario at emergence and after the first summer (Figures 1D, 2D).

No significant inter-annual differences appeared in the rank-abundance pattern within climatic scenarios at either emergence ( $F_{2,41} = 2.25$ ,  $P = 0.12$ ) or after the first summer ( $F_{2,39} = 1.64$ ,  $P = 0.21$ ; Figure 3). A similar set of species emerged and survived under each climatic scenario during the 3 years in which treatments were applied.

Long-lasting effects of simulated climatic scenarios persisted through the successive years. The results from the survival analysis with the 2007 and 2008 cohorts until the end of the experiment showed strong differences between climatic scenarios in the survival curves over time (2007 cohort:  $\chi^2 = 44.90$ ,  $P < 0.0001$ ; 2008 cohort:  $\chi^2 = 42.92$ ,  $P < 0.0001$ ; Figure 4). Seedlings growing under the wet-summer scenario were more likely to survive from emergence onwards, whereas seedlings growing under the dry summer

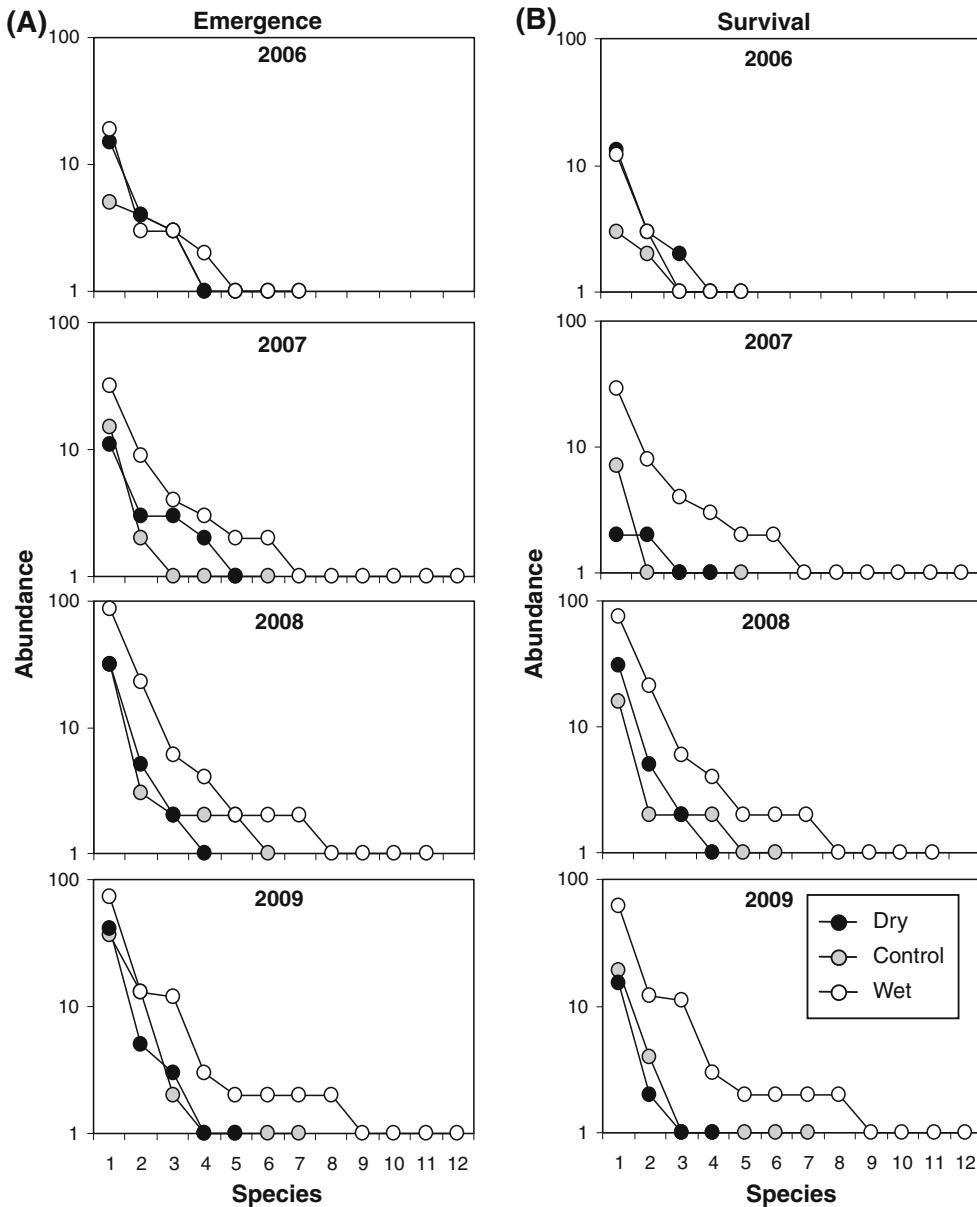


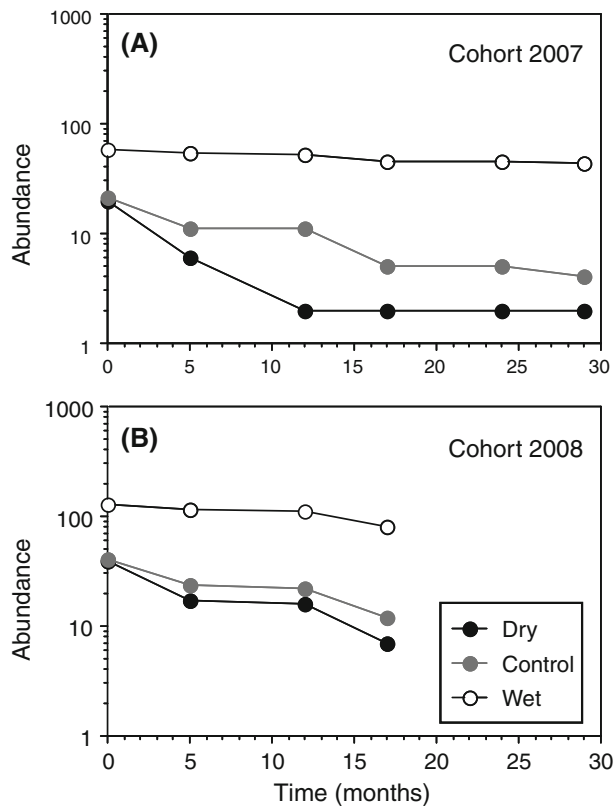
Figure 3. Rank/abundance plot under the different climatic scenarios: dry summer (black dot), wet summer (white dot), and current climatic conditions (control, gray dot) during the 2006–2009 period. **A** represents number of individuals and species emerged, whereas **B** represents the number of individuals and species surviving after the first summer.

scenario had lower survival than those in the control treatment.

### DISCUSSION

The results show that different climatic scenarios exert a strong impact on the diversity and abundance of the natural woody-recruit bank. The community growing under the wet scenario had the highest species richness and was also the most diverse of the different habitats. Thus, the results indicate that: (1) exceptional rainy summers have a strong influence on community structure (Holmgren and others 2006a; Mendoza and others 2009a), and (2) increased aridity may intensify the

current stressful conditions for community regeneration. The less abundant and diverse recruit bank, together with the lower survival probability of recruits under a drier scenario, might have as an ultimate consequence a progressive species loss in successive years. According to Lloret and others (2004), species loss due to climatic alterations is related to species abundance, that is, less abundant species being more prone to disappear under drier conditions, thereby strengthening the dominance. By contrast, the wet-summer scenario strongly boosted survival and richness of established recruits in a significant way in shrubland and forest habitats. Only during the mildest years can new individuals from the most drought-sensitive species



**Figure 4.** Seedling survival (logarithmic scale) of the 2007 (**A**), and 2008 (**B**) cohorts under the dry (*black dots*), control (*gray dots*), and wet (*white dots*) summer scenarios. Seedlings were monitored from emergence to the end September 2009. Data from the three habitats are pooled.

recruit and express the qualitative and quantitative potential recruitment of the community (Mendoza and others 2009a). The effect also persisted in the survival over successive years, given that seedlings growing under the wet-summer scenario survived in high proportions during successive years. This pattern was demographically consistent over the 3 years in which climatic simulations were applied, clearly demonstrating that wet summers act as long-lasting windows of opportunity for recruitment in Mediterranean ecosystems, especially for mid-to-long lived species as those from this study. In fact, previous studies have shown that seedling establishment during relatively rare favorable years is quite common around the world, for example, *Pinus ponderosa* in Colorado (League and Veblen 2006), *Picea schrenkiana* in north-western China (Wang and others 2006), *Prosopis* spp. in South America (Holmgren and others 2006b), or *Juniperus communis* (García and others 1999) and *Buxus balearica* (Lázaro and others 2006) in the Mediterranean Basin. The present work highlights the

long-term consequences for recruitment of both wetter and drier summers across a habitat degradation framework, a long-lasting response similar to that found by Holmgren and others (2006b) in semiarid ecosystems as a consequence of El Niño Southern Oscillation.

The benefits of a wet summer not only varied according to the species but also proved to be habitat specific (Holmgren and Scheffer 2001; Holmgren and others 2006a);—that is, seedling recruitment in forest was higher than for other habitats. Forest was the habitat that maintained the most diverse recruit bank even during periods of extreme dryness, whereas shrubland reached the maximum abundance, and open was by far the habitat with the lowest abundance and species richness at emergence (less than 1% of total seedlings and only 2 species). These differences are related initially to differential seed production and dispersal (Mendoza and others 2009b; Matías and others 2010; Zamora and others 2010) and subsequently to post-dispersal seed predation (Gómez 2004; Matías and others 2009) among habitats. Besides these natural differences, the effect of the climatic scenarios was modulated by the habitat effect. In this way, the strong seed limitation in the open areas (Mendoza and others 2009b), together with the severe establishment limitation as a consequence of the null survival probability, occluded any signal of the different climatic scenarios in this habitat. By contrast, the intensity of the climatic scenarios effect on shrubland and forest showed a contrasting pattern: the overall differences across climatic scenarios in abundance and survival were more evident in shrubland, whereas the denser canopy in forest had ameliorated these differences (Kitzberger and others 2000; Bey 2003; Pyke and Andelman 2007). However, differences across climatic scenarios in richness and diversity were highest in forest, presumably due to the higher seed input (Mendoza and others 2009b), which allowed the expression of the highest recruitment potential under the wet scenario. Thus, although the effect of the climatic scenarios was consistent across habitats, its intensity was modulated by specific habitat characteristics.

The results of the present study indicate that the predicted lower frequency of wet summers in the Mediterranean region (Christensen and others 2007; Giorgi and Lionello 2008) may have far-reaching consequences for forest dynamics. An unusual wet summer has a quantitative impact on Mediterranean communities, as the number of recruits increases in most species. Also, a wet summer offers a qualitative effect, being the only window



for recruitment for those species with higher water requirements, such as those species with a boreo-alpine origin at the southern limit of their distribution area (Hampe and Petit 2005; Mendoza and others 2009a) and thereby enables a diverse recruit bank, consisting of Mediterranean and boreo-alpine species. If mild summers become less frequent in coming decades, and drier summers become the norm as expected by the forecasting models (Houghton and others 2001; Giorgi and Lionello 2008), a shift in community structure involving diversity loss would be expected. With drier summers, a healthy and diverse recruit bank able to compensate for tree mortality would be less likely to persist, and thus the woody community may be prone to drastic changes in composition and dominance pattern.

In conclusion, our results clearly indicate that woody-recruit bank density and diversity depend heavily on extreme climatic events. On the one hand, the expected reduction in summer rainfall implies greater difficulties for regeneration and forest expansion, especially critical for boreo-alpine species, which would lose their window of opportunity for recruitment. On the other hand, the expected greater frequency and intensity of extremely dry periods would reduce the abundance and diversity of seedlings and saplings in the recruit bank, especially in open areas. Overall, although sporadic wet summers can greatly enhance seedling emergence and survival, and express the potential recruitment of the community, the predicted drier summers would hamper community recruitment. This pattern is consistent among cohorts and the different habitats in the community, even in forest, the most diverse habitat. For this reason, the impact of climate change on the diversity and dynamics of forest communities will depend not only on the expected increase in aridity (Giorgi and Lionello 2008), but more importantly, on the reduced frequency of wet years. For the coming decades, both constraints may converge in an overall reduction of forest diversity and an increased dominance of the most drought-tolerant species.

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