



# Uncoupled spatiotemporal patterns of seed dispersal and regeneration in Pyrenean silver fir populations



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## ABSTRACT

Silver fir (*Abies alba*) reaches its southwestern distribution limit (rear edge) in the Pyrenees, where it forms highly fragmented populations threatened by drought-induced die-off. Therefore, we need a better knowledge of regeneration patterns and processes (seed production and dispersal, regeneration niche) of such rear-edge stands to assist their long-term conservation. Seed rain patterns were studied in two structurally contrasting sites: an even-aged pure stand (Las Eras) and an uneven-aged mixed silver fir-beech (*Fagus sylvatica*) stand (Gamüeta) over 8 and 12 years, respectively. Seed production experienced a greater synchrony in years of high seed production than when crops were low, suggesting masting behavior in both sites. Seed inverse modeling methods resulted in dispersal curves differing between sites, with estimates of mean dispersal distances of 9.9 and 21.5 m for the pure and mixed stands, respectively. Long-term sampling of seed dispersal and production was complemented with an analysis of silver fir regeneration niche. Seed and seedling patterns were spatially uncoupled, emphasizing the relevance of microsite filtering of regeneration. Understorey light environment was the main factor explaining seedling emergence and mortality. Our study provides a mechanistic basis and a methodological approach for understanding the colonization ability of Pyrenean rear-edge silver fir stands and similar tree populations.

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## 1. Introduction

Forest dynamics depend largely on tree regeneration which is influenced by biotic and abiotic factors acting at different spatial and temporal scales (Clark et al., 1998a). Seed production and dispersal, germination and seedling establishment are among the main processes determining successful tree recruitment (Dovčičak et al., 2003). Constraints acting on tree regeneration include low amount of viable seeds, restricted spatial extent of seed dispersal and reduced availability of suitable microsites for seedling establishment (regeneration niche *sensu* Grubb, 1977). At an individual level, seed production is directly related to tree size (Greene and Johnson, 1994). However, there are other factors affecting seed production at wide spatiotemporal scales (stand, decades) such as

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stand density, tree-to-tree competition or climatic conditions triggering reproductive events or prolonging seed dormancy (Greene et al., 2002; Debain et al., 2003, 2007; van Mantgem et al., 2006).

Seed production often fluctuates from year to year, especially in the case of masting tree species, in which there is a synchronous production of many seeds at irregular intervals in the same population (Silvertown, 1980; Herrera et al., 1998). Some of the causes of masting are related to climatic variability, resource matching, success in pollination and predator satiation (Janzen, 1971; Kelly, 1994; Kelly and Sork, 2002). Besides seed fecundity, seed dispersal patterns are a critical component in the spatial variation of tree recruitment (Ribbens et al., 1994; Nathan and Muller-Landau, 2000). Seed density almost invariably declines leptokurtically with distance to the parent tree, so the offspring are clustered near the source and extended distribution tails usually represent rare long-distance dispersal events (Clark et al., 1998b; Stoyan and Wagner, 2001).

Some microsites are more suitable for seed germination and seedling survival than others, and that suitability depends on microtopography, canopy cover, understory type or presence of decayed wood (Beckage et al., 2000; Dovčiak et al., 2003). Therefore, the regeneration niche concept is central because it defines the requirements for a high chance of success in the replacement of mature trees (Grubb, 1977). The regeneration niche includes multiple interacting filters of tree recruitment such as canopy cover in temperate forests (Runkle, 1981) or soil water availability in drought-prone Mediterranean forests (Marañón et al., 2004). Habitat requirements of recruits also change throughout the different regeneration stages since young seedlings may heavily depend on water availability while older saplings require more light (Dovčiak et al., 2003). Further, interactions between adults and seedlings of other tree species constitute a complex balance between competition and facilitation, depending on factors such as abiotic stress or tree density (Callaway and Walker, 1997). Successful recruitment might be also expected to be higher at some distance of parental trees where predator pressure decreases as seed and seedling density do (Janzen, 1970). Therefore, the importance of seed dispersal or selective recruitment in specific microsites may be differently magnified by factors acting sequentially on seed germination and seedling establishment.

Here we assess the importance of seed production and dispersal as related to seedling establishment for the regeneration of Pyrenean silver fir (*Abies alba*) forests. To get a deeper insight on regeneration processes of these forests is very relevant because they constitute the south westernmost limit (rear-edge) of the species distribution area in Europe. Rear-edge populations, which frequently gather rare ecotypes and genotypes, are typically restricted to specific drought-prone habitats as compared with more central localities (Hampe and Petit, 2005). Therefore, studying the regeneration of rear-edge populations is of great interest because they portray ecological scenarios which may develop in more northern core areas under warmer or drier conditions (Castro et al., 2004). Besides, western Pyrenean silver fir forests are experiencing drought-induced die-off processes and they are also highly fragmented due to their past historical use for logging, both threatening their persistence and regeneration (Camarero et al., 2011). In addition, bioclimatic envelope models predict significant reductions of the Pyrenean silver-fir area due to intensified warming at the end of the 21st century (Serra-Diaz et al., 2012). Hence, the study of regeneration of rear-edge Pyrenean silver fir forests is crucial to assess their ability to recruit, migrate and colonize new territories in a warmer and drier climatic scenario.

Our aim is to characterize the spatio-temporal patterns of seed production, seed dispersal and seedling establishment of silver fir in two Pyrenean forests with contrasting structure and composition. Our specific objectives are: (i) to analyze the temporal variation of seed production in Pyrenean silver fir and its relation to regional climatic conditions, (ii) to determine the spatial patterns of seed dispersal and characterize seed dispersal curves, and (iii) to relate the spatial patterns of seedling establishment with environmental (canopy openness, substrate) and biotic variables (seed deposition, basal area) with the aim of describing the species' regeneration niche.

## 2. Materials and methods

### 2.1. Study species and site

Silver fir (*A. alba* Mill.) is one of the tree species with larger biomass and height (up to 40 m) in the Spanish Pyrenees, where its distribution area reaches the southwestern limit (Fig. 1). There, this species dominates subalpine and montane forests, mainly on

northern and northwestern slopes of mesic and humid sites with fresh and deep soils (Blanco et al., 1997). Most Pyrenean silver fir forests were subjected to selective logging up to the late 1950s when their exploitation for timber greatly decreased (Camarero et al., 2011).

Silver fir is a monoecious and shade-tolerant conifer (Ruiz de la Torre, 2006). It regenerates from seeds that are winged and dispersed by wind from upright cones (Ruiz de la Torre, 2006). Cones ripen from September to October, and they are located in the upper third of the crown from where seeds are released until May. Silver fir bears fruit every year although it is known that seed production varies greatly between years and in mast years the seeds may present higher germination potential than in years of low crop amount (Ruiz de la Torre, 2006). Seeds produce a resin with high monoterpene content, which constitutes up to about 20% of the fresh mass of seeds (Čermák, 1987). This resin is related to seed predators deterrence, defenses against pathogens, protection of the embryo from drying, and the deep physiological dormancy experienced by silver fir seeds, which usually germinate in spring under wet conditions (Kolotelo, 1998).

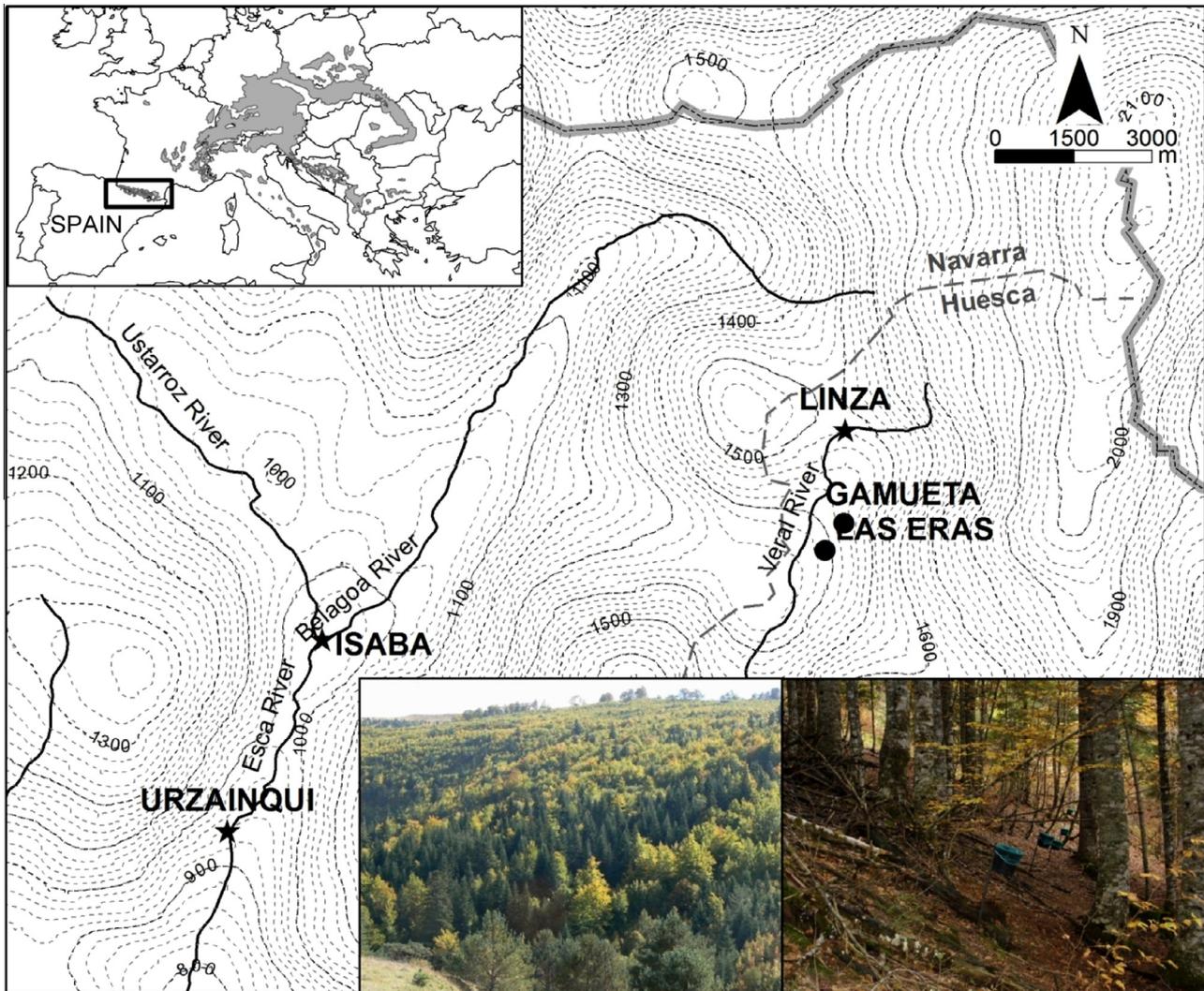
The study was conducted on the upper part of Ansó Valley (Parque Natural de los Valles Occidentales, western Aragón, Spain; Fig. 1), where beech (*Fagus sylvatica* L.) or Scots pine (*Pinus sylvestris* L.) can coexist with silver fir. Other less abundant species in these forests are *Sorbus aucuparia* L., *Sorbus aria* (L.) Crantz, and *Betula alba* L. We studied two structurally different sites located in Gamueta (42°53' 55"N, 0°47'59"W, elevation 1395–1415 m a.s.l.) and Las Eras (42°52'40"N, 0°48'18"W, elevation 1320–1350 m a.s.l.) (Fig. 1). Gamueta is a mature and mixed silver fir-beech forest, while Las Eras is a young and pure silver-fir forest with higher tree density than Gamueta (see Table 1 for a list of characteristics of each stand). The soils of both study sites are basic and derived from marls and limestones.

The climate in the study area is temperate and subjected to oceanic influence (wet winter and spring seasons) with a high rainfall amount distributed throughout the year, and fog and snow are frequent in winter. Mean temperature is 8.5 °C, with December (1.9 °C) and August (15.8 °C) being the coldest and warmest months, respectively. Total annual rainfall is 1843 mm, and July and August are the driest months. Ground may be covered by snow from November until March, and average wind speed during the dispersal season (September–May) is 2.07 m s<sup>-1</sup>.

### 2.2. Adult location and seed shadows

Two 900-m<sup>2</sup> square plots (30 m × 30 m) were established in each stand. The first plot (Gamueta) was set in fall 2001, whereas the second one (Las Eras) was set in fall 2005. We measured the location (coordinates *x*, *y*) and size (diameter at breast height – dbh–, total height) of all adult trees (dbh > 20 cm, individuals over 1.3 m in height) and seedlings (individuals with height < 0.5 m) located within the plots, as well as within a buffer zone 10-m wide surrounding the plots.

At the beginning of the study we placed 36 seed traps in each plot following a regular 5-m grid (Fig. 2). Traps were cylindrical containers of 0.014 m<sup>2</sup> circular collecting surface coated with fine mesh bags and placed 0.5 m above the ground. Seeds were monthly or bimonthly collected from traps during the dispersal season (September–May) until fall 2012, resulting in 12 and 8 years of seed rain estimates in Gamueta and Las Eras, respectively. We grouped seeds depending on whether they were collected in autumn (September–November) or in winter–spring (December–May) to determine when the most seed fall occurs. Then, seed density (seeds m<sup>-2</sup>) was calculated on annual or seasonal basis considering the amount of seeds collected in each trap. We determined the number of predated seeds collected within



**Fig. 1.** Location of silver fir study sites (circles) and meteorological stations (stars). The left upper inset shows the European distribution of *A. alba* (upper left corner), whereas the lower pictures show images of Las Eras (landscape) and Gamueta (seed traps).

**Table 1**

Characteristics of the study plots. Variables refer to *A. alba* excepting canopy openness, which consider all trees present in the stand. Values are means  $\pm$  SD.

Site	Slope ( $^{\circ}$ )	Aspect	Basal area ( $\text{m}^2 \text{ha}^{-1}$ )	Density ( $\text{ind ha}^{-1}$ )	Diameter at 1,3 m (cm)	Height (m)	Age (years) <sup>b</sup>	Canopy openness (%) <sup>c</sup>
Gamueta	23	N	54.6 <sup>a</sup>	333	35.7 $\pm$ 28.9	18.1 $\pm$ 9.2	176 $\pm$ 45	6.0 $\pm$ 0.2a
Las Eras	15	NW-N	42.0	856	22.7 $\pm$ 10.6	13.1 $\pm$ 4.9	60 $\pm$ 12	7.4 $\pm$ 0.3b

<sup>a</sup> *F. sylvatica* basal area in this plot is  $6.1 \text{ m}^2 \text{ha}^{-1}$ .

<sup>b</sup> Age was estimated by taking cores at the base of the thickest trees (J.J. Camarero, unpublished results).

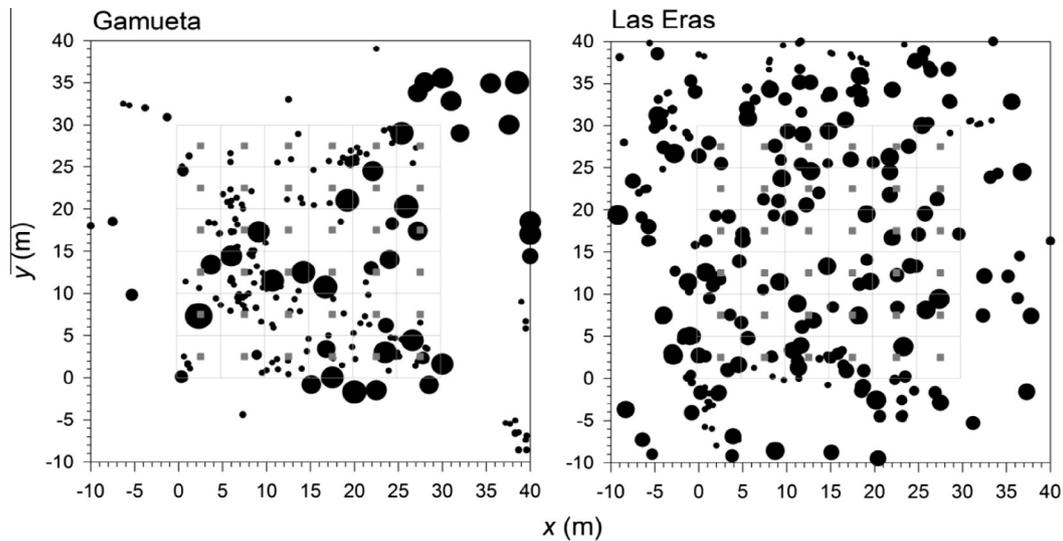
<sup>c</sup> Different letters indicate significant differences ( $P < 0.01$ ) based on a 1-way ANOVA.

traps by placing open rectangular bags containing 10 seeds near each of the seed traps and visiting them every month in autumn and spring, i.e. when they were not covered by snow (Paluch, 2011). Bags were 20-cm tall and 15-cm wide and they were made of nylon mesh. We found no evidence of seed predation by rodents and birds.

### 2.3. Seedling emergence and microsite variables

To assess changes in seedling emergence among years we counted emerged 1- and 2-year-old seedlings tagged and located within four  $625\text{-cm}^2$  square subplots located around each seed trap. First, an initial seedling count was performed in both study

sites, where every seedling located within the  $900\text{-m}^2$  plot was recorded (see Section 2.2). Second, annual censuses were performed within the subplots. Third, seasonal seedling censuses were also done in late spring or early summer (May–June) and in fall (September–October) during some years (2004 and 2005 in Gamueta, and 2005 in Las Eras). Seedling counts were transformed into density data by dividing the number of seedlings counted by the considered area:  $900\text{-m}^2$  in the first census, and  $9\text{-m}^2$  ( $625\text{-cm}^2 \times 4$  subplots  $\times$  36 traps) in other censuses. Seedling emergence data were related to spatial patterns of seed density of the previous fall and winter using the Spearman correlation coefficient to evaluate whether production and seed dispersal limit seed germination. The significance of this test was calculated



**Fig. 2.** Location of fixed seed traps (gray squares) and *A. alba* individuals (black points) in the two study sites. The point size is proportional to the diameter at 1.3 m of each individual. The regular 5-m grid used to arrange seed traps (gray squares) is also shown (negative coordinates correspond to individuals located in the buffer zone, i.e. outside the trap area).

taking into account the possible existence of spatial autocorrelation in the seed data by applying the Dutilleul (1993) method, which corrects the significance level considering the amount of spatial autocorrelation present in the compared datasets.

Environmental (substrate, canopy openness) and biotic variables (basal area, density) were quantified to characterize the regeneration niche of silver fir at the microsite scale, this scale being defined at 1-m<sup>2</sup> spatial resolution. We did this only in Gamueta site, where a high number of seedlings established in 2002, and because it was structurally more heterogeneous than the site Las Eras. We sampled following a regular 1-m<sup>2</sup> grid covering the whole plot. We chose the following variables to characterize the microsite: coverage of different kinds of substrate (bare ground, rock, moss, wood, needle and leaf litter), fir and beech cover, and density of beech stems. We estimated canopy openness at 1 m height using a densiometer (Stumpf, 2008). We obtained these estimates at noon of cloudy days in early autumn, when beech leaves were still on the trees.

In addition, we quantified stand-level canopy openness in both study sites as an integrative estimate of the radiation received by the regeneration strata. Canopy openness is the fraction of sky seen through multiple layers of tree canopies above a certain point (Boivin et al., 2011). We took hemispherical pictures at the location of each seed trap at a height of 1.3 m with a Nikon Coolpix 900 digital camera to which a fisheye lens was coupled. Pictures were taken in June 2008 on cloudy days with homogeneous light conditions. Canopy openness (%) was determined following Canham et al. (1999). Images were transformed according to a defined threshold, so that all the “shading” elements (trunks, branches and leaves) were set to black and the background to white. Canopy openness was defined as the ratio of the surface occupied by white pixels (sky area visible through the crown) to the total surface of the two-dimensional projected silhouette of the crown.

#### 2.4. Spatio-temporal seed deposition patterns

To analyze the spatial autocorrelation of seasonal seed fall patterns in both study sites we used Moran spatial correlograms (Legendre and Legendre, 1998). The Moran's  $I$  coefficient is analogous to Pearson's  $r$  and it usually ranges between  $-1$  and  $+1$ , with negative and positive values corresponding to negative

and positive spatial autocorrelation, respectively (the value of  $I = 0$  indicates the lack of spatial autocorrelation). We considered distance intervals of 5 m (distances between traps), thus seven distance classes ( $k$ ) were obtained. The correlograms were considered to be globally significant ( $P$ ) when any of the tested distance classes showed  $P < 0.007$ , where  $P$  is equal to  $P/k$  (Legendre and Legendre, 1998).

Inter-annual variability in seed production was assessed using the coefficient of variation (temporal CV) of annual mean values (Herrera et al., 1998; Koenig et al., 2003). To estimate the degree of synchrony in seed production among trees, which is a feature of masting species, we also calculated the coefficient variation over the 36 seed traps (spatial CV) for every year of study. It has been postulated that seed crop would be spatially more variable in years of low synchrony among trees (or in years when only a few trees reproduced) thus leading to a higher CV (Mencuccini et al., 1995). Spatial CVs were correlated using the Pearson correlation coefficient to mean seed density for every year to test if dispersal was less (more) spatially homogeneous dispersion in years of low (high) seed production. Temporal autocorrelation was assessed by relating seed production between consecutive years and the significance of this test was corrected for the presence of spatial autocorrelation using Dutilleul (1993) method. Lastly, to determine whether seed production was driven by inter-annual climate variability seed data were related to monthly and seasonal climatic variables (mean temperature, total precipitation) for the previous summer (JJA), fall (SON) and winter (DJF) and the following spring (MAM). Climate data were taken from the weather station located in Linza at ca. 1.5 km from the study sites (42°53'55"N, 0°47'58"W, 1340 m a.s.l., period 2001–2012), and interpolated with data from nearby stations (Isaba, 42°51'52"N, 0°55'24"W, 843 m a.s.l.; Urzainqui, 42°49'53"N, 0°56'48"W, 722 m a.s.l.; located at 10.5 and 13.5 km from the study sites, respectively; see Fig. 1).

#### 2.5. Modeling seed production and dispersal

Seed production and dispersal were modeled using the inverse modeling methods proposed by Ribbens et al. (1994). Seed density in each seed trap was assumed to be a function of the distribution of distances to adults, tree fecundity, and the form of a dispersal

kernel (Ribbens et al., 1994; Clark et al., 1999; Uriarte et al., 2005; Canham and Uriarte, 2006). Tree fecundity ( $P_j$ ) was included as a function of adult tree size (dbh,  $w_j$ ) (Ribbens et al., 1994; Greene and Johnson, 1994):

$$P_j = \exp\{\beta_j + \alpha_t + \gamma \ln(w_j)\} \quad (1)$$

where  $\alpha_t$  is the fecundity parameter,  $\gamma$  is the allometric fecundity exponent, and  $\beta_j$  is a random deviation in seed production for each tree, assumed to follow a normal distribution.

Dispersal was considered to be an isotropic process characterized by a dispersal kernel function, a probability density function of the location of seed deposition per unit area as a function of the distance from its source (Ribbens et al., 1994). We used a log-normal kernel, appropriate to model seed dispersal of anemochorous species (Stoyan and Wagner, 2001; Greene and Calogeropoulos, 2002; Greene et al., 2004; Martínez et al., 2011). The log-normal distribution is defined by the shape ( $S_t$ ) and scale ( $L_t$ ) parameters, which depend on the distance to the source tree ( $x_{ij}$ ):

$$F(x_{ij}, L_t, S_t) = \{(2\pi)^{1.5} S_t^2\}^{-1} \exp\{-[\ln(x/L)]^2 / (2S_t^2)\} \quad (2)$$

Seed density data recorded during the sampling period were summed to estimate cumulative seed dispersal at each location. The expected seed density on seed traps was assumed to follow a Poisson distribution (as in Ribbens et al., 1994; Clark et al., 1999; Martínez and González-Taboada, 2009). The model was fitted using Markov Chain Monte Carlo (MCMC) methods; Gibbs' sampling for fecundity parameters and adaptive Metropolis–Hastings steps for the parameters of the distribution kernel (Clark et al., 1999). A total of 10,000 Monte Carlo steps were run and the final 5000 steps were thinned with a lag of 5 steps to avoid serial autocorrelation. The resulting 1000 steps were used to summarize the parameters and to propagate the uncertainty in parameter estimation to the shapes of the kernel functions and the estimates of the distribution of dispersal distances. We computed a Pearson correlation coefficient between the observed and the expected values to estimate the goodness of fit of the model (Sagnard et al., 2007; Martínez and González-Taboada, 2009).

## 2.6. Seed release experiment

During an autumn morning, filled silver-fir seeds were released ( $n = 56$ ) from a 20-m tall tower under moderate wind speeds ( $0.5\text{--}4 \text{ m s}^{-1}$ ) (see more details in Camarero et al., 2005). This height was selected because it was close to 0.75 times the mean height ( $\pm$ SE) of mature individuals ( $27.7 \pm 1.6 \text{ m}$ ), which is a proxy of seed dispersal distance (Greene and Calogeropoulos, 2002). We noted the horizontal distance travelled by each seed released.

## 2.7. Seedling mortality rates

The seedling censuses allowed us to estimate intra-annual mortality rate for both age classes considering the mean interval duration between seasonal samplings (113 days). Seedling mortality rate ( $m$ ) was estimated by using the formulation proposed by Sheil et al. (1995):

$$m = 1 - (N_t/N_0)^{1/t} \quad (3)$$

where  $N_0$  and  $N_t$  are seedlings counts at the beginning and end of the measurement interval ( $t$ , in years). Mortality rate was calculated for two time intervals and only if  $N_0 \geq 10$  seedlings.

## 2.8. Statistical characterization of the regeneration niche

To evaluate the associations between seedling density and predictor microsite variables a multivariate general linear model was

adjusted. Microsite variables were normalized using either angular or logarithmic transformations, and then standardized to allow comparisons among regression coefficients. Variables with a variance inflation factor higher than 3 were considered collinear and dropped from the model to avoid redundancy (Fox and Monette, 1992). Since seedling count had far more zeros than what would be expected for a Poisson distribution ( $\chi^2 = 29.60$ ,  $P < 0.001$ ), zero-inflated models were used to relate the number of emerged seedlings and microsite variables (Zeileis et al., 2008). The probability of having a false zero was estimated using a logistic regression whose only parameter was an intercept, and a likelihood ratio test was employed to determine which distribution to use for the count process. Model selection was based on second-order AIC (AICc) and all models that differed less than 2 points of the lowest AICc value were averaged to obtain model-averaged coefficients and probabilities (Burnham and Anderson, 2002). The *MuMIn*, *pscl* and *lmtree* packages of the R statistical software (R Development Core Team, 2013) were employed.

## 3. Results

### 3.1. Spatio-temporal patterns of seed dispersal

Annual seed production in the pure silver-fir stand located at Las Eras was greater than that observed in the mixed Gamueta forest (Table 2 and Fig. 3), with mean densities of 268 and 71 seeds  $\text{m}^{-2}$ , respectively. Seed patterns showed significant spatial structure for some study years, and those patterns were characterized by significant positive spatial autocorrelation at short distances (0–10 m). Aggregated seed deposition patterns at small scales were usually associated to high seed production (e.g., 2009–2010 in Gamueta and 2011–2012 in Las Eras) and to low spatial variability among traps (low spatial CV values). We found a statistically significant negative relationship between seed production and the spatial CV in both sites (Gamueta,  $r = -0.70$ ,  $P = 0.012$ ; Las Eras,  $r = -0.83$ ,  $P = 0.010$ ).

Seed production was quite variable along time in both sites (Fig. 3), with temporal CV values being lower in Gamueta (54%) than in Las Eras (73%) for the common period 2005–2012. In addition, seed production in 2009–2010 was significantly correlated to the following year, in both forests (Gamueta,  $r = 0.45$ ,  $P = 0.008$ ; Las Eras,  $r = 0.47$ ,  $P = 0.016$ ), which indicates the presence of positive temporal autocorrelation in seed production. Seed production data showed a significant positive relationship with March temperature ( $r = 0.59$ ,  $P = 0.04$ ) and a negative one with August precipitation ( $r = -0.62$ ,  $P = 0.03$ ). In Gamueta, the annual number of established one-year-old seedlings was positively related to precipitation of the previous fall ( $r = 0.77$ ,  $P = 0.04$ ) and winter ( $r = 0.88$ ,  $P = 0.004$ ).

### 3.2. Seed dispersal curves

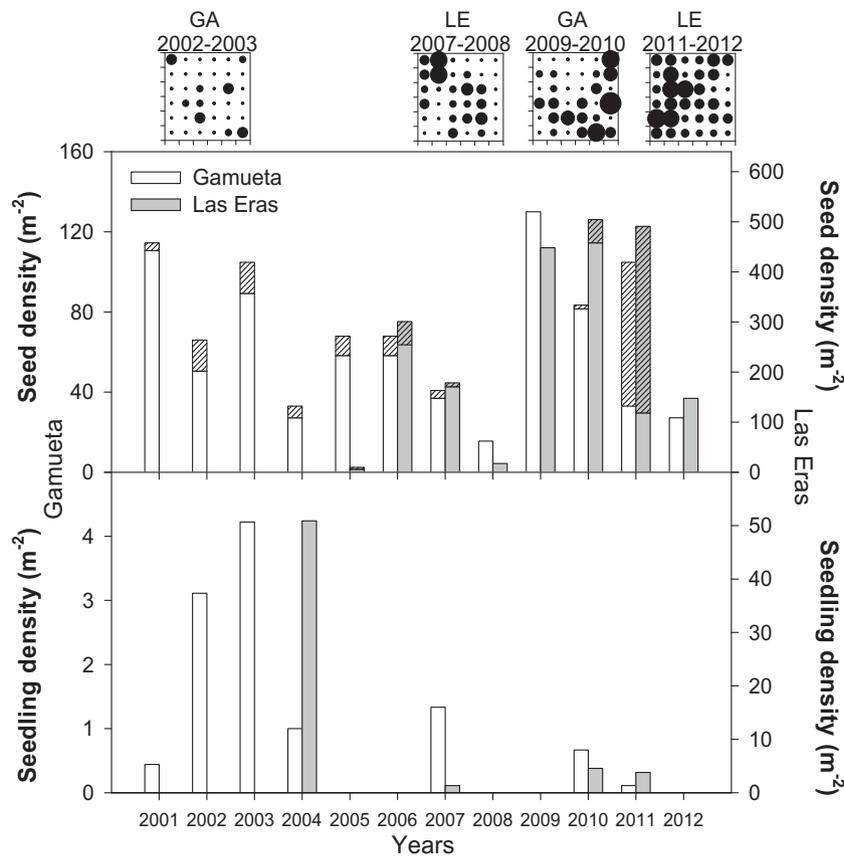
Seed production and dispersal models provided a good fit to cumulated dispersal estimated in both Gamueta and Las Eras (product-moment correlation  $r$  of greater than 0.50, Table 3). The shape of the kernel differed between the two study sites as higher values of  $S$  and  $L$  parameters in Gamueta determined a higher probability of seed deposition at greater distances in this location (Fig. 4). Indeed, estimated mean seed dispersal distances ( $d$ ) were higher in Gamueta (21.6 m) than in Las Eras (9.9 m). The standard seed production ( $\alpha$ ) and the allometric fecundity exponent ( $\gamma$ ) reflected the observed variation in seed production. A positive allometric scaling was found in the selected models, indicating a proportionally greater importance of larger individuals in seed production. In Gamueta the scaling parameter was lower than in Las

**Table 2**

Changes in seed density and related statistics (CV, coefficient of variation) observed in the two study sites (Gamqueta, Las Eras). Data correspond to the fall and winter seasons. The overall spatial autocorrelation was based on the significance of Moran spatial correlograms of seed density (the distance classes at which the maximum spatial autocorrelation was observed is indicated between brackets).

Dispersal season (years)	Gamqueta			Las Eras		
	Mean $\pm$ SE (seeds $m^{-2}$ )	Spatial CV (%)	Spatial autocorrelation (distance class)	Mean $\pm$ SE (seeds $m^{-2}$ )	Spatial CV (%)	Spatial autocorrelation (distance class)
2001–2002	114 $\pm$ 15	76.00	No	–	–	–
2002–2003	66 $\pm$ 12	107.21	Negative (25–30 m)	–	–	–
2003–2004	105 $\pm$ 16	93.55	No	–	–	–
2004–2005	33 $\pm$ 8	138.50	No	–	–	–
2005–2006	68 $\pm$ 11	97.76	No	10 $\pm$ 4	252.53	No
2006–2007	69 $\pm$ 11	94.58	No	301 $\pm$ 26	52.03	No
2007–2008	41 $\pm$ 10	172.75	No	179 $\pm$ 22	70.90	Positive (0–5 m)
2008–2009 <sup>a</sup>	16 $\pm$ 5	190.74	No	17 $\pm$ 6	222.68	No
2009–2010 <sup>a</sup>	130 $\pm$ 19	89.13	Positive (5–10 m)	448 $\pm$ 39	52.47	Negative (20–25 m)
2010–2011	83 $\pm$ 13	93.48	No	505 $\pm$ 45	53.07	Negative (20–25 m)
2011–2012	105 $\pm$ 11	60.68	Negative (25–30 m)	491 $\pm$ 31	37.64	Positive (5–10 m)
2012–2013 <sup>a</sup>	27 $\pm$ 16	354.59	No	147 $\pm$ 21	83.80	No

<sup>a</sup> There was only seed data during the fall season.



**Fig. 3.** Annual seed (top graph) and one-year-old seedling densities (bottom graph) registered in the Gamqueta (GA, white bars) and Las Eras (LE, gray bars) study sites. In the case of seed density, the empty portion bars correspond to seeds collected during fall, while the scratched portion of bars represent seeds collected from winter up to spring. Note the difference in the scales of seed and seedling densities observed between Gamqueta and Las Eras. The upper plots display the spatial patterns of seed density in traps for selected dispersal seasons characterized by contrasting seed production and spatial patterns of seed fall (see Tables 2 and 4), in which the point size is proportional to the number of seeds collected.

Eras probably because of the dominance of older and bigger trees in the first site, which could indicate a senescence-related decreased reproduction. The estimated mean seed dispersal distances partially agree with the distances observed in the seed-release experiment since 65% of released seeds dispersed between 8 and 16 m (Fig. 4). Mean weight ( $\pm$ SE) and area of released seeds were  $84.12 \pm 2.98$  mg and  $2.49 \pm 0.05$  cm<sup>2</sup>, respectively.

### 3.3. Regeneration niche

No significant correlations were found between seed density from the previous fall and winter and one-year-old seedlings density of the following year (Table 4). Seedling mortality rates were higher in Gamqueta (58% in 2003–2004, 68% in 2004–2005) than in Las Eras (45% in 2005–2006, 34% in 2011–2012). Seasonal mor-

**Table 3**

Estimated parameters fitted to the silver fir seed dispersed densities for each study location during 2001–2011 (Gamueta) and 2005–2011 (Las Eras) periods. For each parameter, 90% credible intervals are presented along with the median value.

Parameters	Gamueta	Las Eras
$\alpha$	4.76 (3.66, 9.27)	2.12 (0.92, 5.77)
$\beta$	0.17 (0.13, 0.21)	0.11 (0.09, 0.14)
$\gamma$	1.30 (0.12, 3.32)	2.15 (1.01, 2.52)
$L$	12.95 (7.32, 26.20)	8.58 (6.38, 12.58)
$S$	1.0163 (0.5886, 1.2888)	0.5174 (0.3487, 0.7433)
$\sigma$	0.1650 (0.1354, 0.2028)	0.0708 (0.0599, 0.0823)
$\tau$	0.1649 (0.1358, 0.1988)	0.0704 (0.0614, 0.0812)
$r$	0.53 (0.47, 0.58)	0.53 (0.42, 0.60)
$d$ (m)	21.55 (8.94, 58.17)	9.89 (7.97, 16.98)

The  $\alpha$  statistic is the fecundity parameter,  $\beta$  is the random deviation on seed production for each tree and  $\gamma$  is the allometric fecundity exponent.  $S$  and  $L$  are the shape and the scale parameters, and  $\sigma$  and  $\tau$  are the variance parameters for residuals and for random effects in fecundity, respectively.  $r$  is the Pearson correlation coefficient obtained from the correlation between observed and predicted seed density values. The parameter  $d$  is the mean seed displacement distance.

tality rates presented a similar pattern as in the previous case, and they were higher in Gamueta (92% and 51% for 1- and 2-year-old seedlings, respectively) than in Las Eras (63% and 32% for 1- and 2-year-old seedlings, respectively).

Differences in seedling mortality between the two forests coincided with their diverse canopy openness values (Table 1), which was significantly higher in Las Eras ( $F = 14.39$ ,  $P < 0.01$ ). This fact suggests that seedling recruitment is less successful in areas with

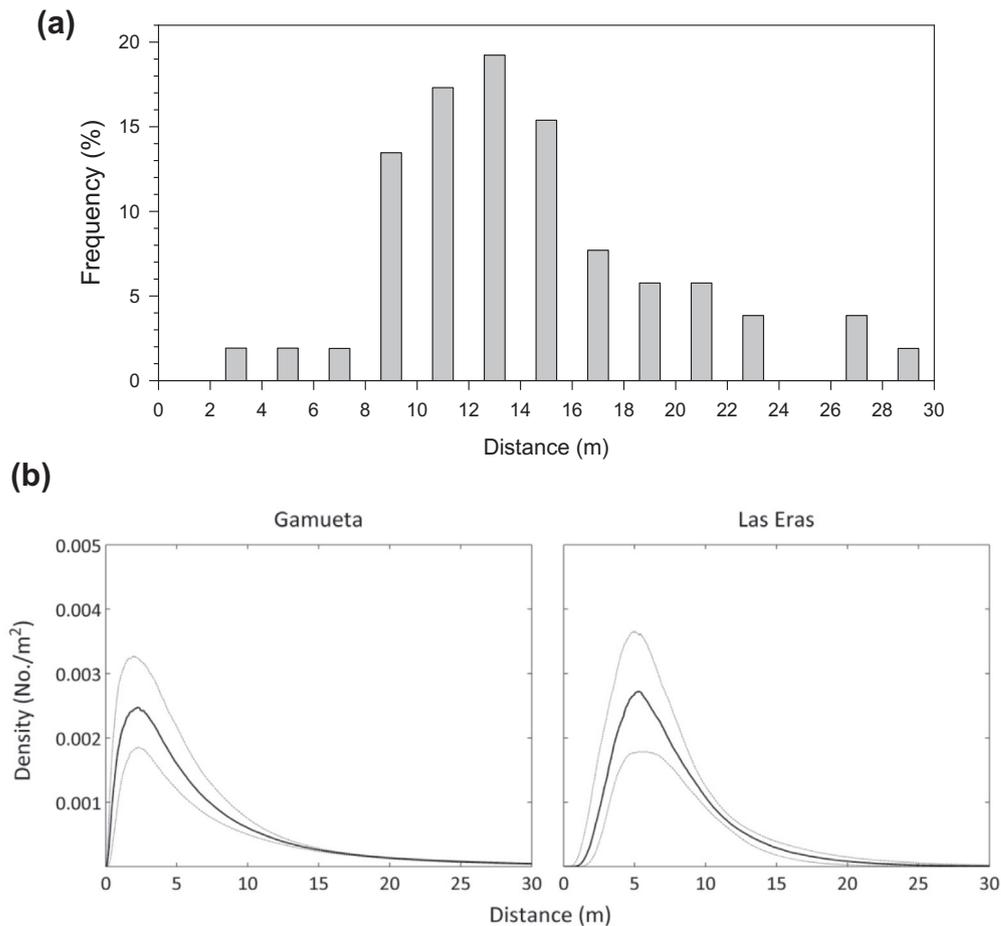
low canopy openness. In fact, overstory cover was the main factor compromising silver fir recruitment in Gamueta (Table 5). Beech stem density was also positively and significantly related to silver-fir seedling establishment.

## 4. Discussion

### 4.1. Interpretation of spatiotemporal seed patterns

The spatial patterns of seed rain intensity and seedling density were spatially uncoupled, even after masting events, as has been observed in North American balsam fir stands (Duchesneau and Morin, 1999). This suggests the existence of diverse filters differently acting on regeneration processes. The spatial and temporal patterns of seed fall and production in the two Pyrenean silver-fir forests varied markedly among years, as have been reported in other European forests of the same species (Paluch, 2011). This spatiotemporal variability suggests a masting behavior for silver fir throughout the species distribution range in Europe. However, the temporal CVs were not exceptionally high if compared with the CV range (80–120%) reported by Kelly (1994) for 42 masting species. Nevertheless, CV values are not enough to identify masting because within-population synchrony should be also demonstrated.

Positive spatial autocorrelation of seed fall patterns at short distances reported in years of high seed production, coupled with negative correlation between seed density and its spatial variability (estimated by spatial CVs), pointed out spatial synchrony in



**Fig. 4.** Comparison of the frequency of seed-dispersal distances of silver fir observed in the seed release experiment (a) and the dispersal curves (seeds m<sup>-2</sup>) fitted through inverse modeling (b). The curves show the best fitted kernels based on seed shadows calculated in Gamueta (left, data for the period 2001–2011) and Las Eras (right, data for the period 2005–2011). Uncertainty in the estimated kernel parameters was projected to determine the credible intervals (gray lines) (see Section 2.5).

**Table 4**

Seedling density (1- and 2-year-old recruits) observed around each seed trap and related statistics (CV, coefficient of variation). The third column of each site shows the association (Spearman correlation coefficients) between density of 1- and 2-year-old seedlings (recorded in late summer) and the amount of seeds collected in fall-winter 1 or 2 years before, respectively. The significance value of the Spearman coefficients was corrected by taking into account the presence of spatial autocorrelation.

Year	Gamueta			Las Eras		
	Mean density $\pm$ SE (seedlings $m^{-2}$ )	CV (%)	Seed–seedling correlation ( <i>P</i> )	Mean density $\pm$ SE (seedlings $m^{-2}$ )	CV (%)	Seed–seedling correlation ( <i>P</i> )
<i>One-year-old seedlings</i>						
2001	0.14 <sup>a</sup>	–	–	–	–	–
2002	0.11 $\pm$ 0.01	58.47	0.02 (0.63)	–	–	–
2003	0.78 $\pm$ 0.17	134.36	–0.08 (0.35)	–	–	–
2004	1.06 $\pm$ 0.24	139.50	–0.05 (0.57)	–	–	–
2005	0.25 $\pm$ 0.10	241.42	0.26 (0.06)	12.72 $\pm$ 1.80	84.74	–
2006	–	–	–	–	–	–
2008	0.33 $\pm$ 0.10	175.66	0.04 (0.14)	0.33 $\pm$ 0.10	177.37	0.16 (0.27)
2011	0.17 $\pm$ 0.06	226.78	0.21 (0.76)	1.14 $\pm$ 0.23	123.23	0.04 (0.31)
2012	0.03 $\pm$ 0.03	600.00	0.53 (0.59)	0.94 $\pm$ 0.21	134.63	–0.27 (0.11)
<i>Two-years old seedlings</i>						
2001	–	–	–	–	–	–
2002	–	–	–	–	–	–
2003	0.83 $\pm$ 0.19	139.06	–0.17 (0.21)	–	–	–
2004	1.14 $\pm$ 0.21	111.37	0.02 (0.74)	–	–	–
2005	0.25 $\pm$ 0.10	241.42	–0.02 (0.55)	1.31 $\pm$ 0.27	124.30	–
2006	–	–	–	12.72 $\pm$ 1.80	84.74	–
2008	0.44 $\pm$ 0.14	189.74	0.17 (0.57)	0.53 $\pm$ 0.15	174.21	–0.12 (0.67)
2011	0.11 $\pm$ 0.07	358.57	0.06 (0.54)	1.28 $\pm$ 0.35	164.13	–0.13 (0.17)
2012	0.06 $\pm$ 0.04	418.16	0.18 (0.80)	0.75 $\pm$ 0.18	144.93	–0.11 (0.57)

<sup>a</sup> Seedling sampling was conducted in the whole plot. Therefore this data is not a mean value calculated for all traps but the sum of all seedlings expressed as number  $m^{-2}$ .

**Table 5**

Effect of microhabitat characteristics based on a multivariate model of the number of *A. alba* seedlings established in Gamueta. Model-averaged coefficients from the negative binomial count distribution are shown.

Variables	Coefficients	Standard error	<i>P</i>
Canopy openness	0.3112	0.1103	0.0048
Beech density	0.2835	0.1151	0.0138
Beech basal area	–0.1185	0.1202	0.3240
Leaf litter	–0.0417	0.1105	0.7060
Wood and branches	–0.0390	0.1150	0.7335

fruiting among tree individuals in those high production years. In masting species, few trees in a population usually seed in non-masting years thus originating a seed rain that is spatially very heterogeneous. During mast years, most trees produce seeds and this should generate a less spatially variable seed rain (Houle, 1999; Sork et al., 1993). Thus, the inter-annual pattern of seed rain spatial variability may reflect within-population synchrony in some way. However, these results should be carefully interpreted since accurate conclusions about masting must arise from individual level studies (Herrera, 1998), which are logistically unfeasible for trees taller than 30 m and dominant in many mountain and temperate forests.

Although the limited duration of the study impeded assessing periodicity in seed production since long duration studies (possibly longer than 20 years) are required, other studies have reported seed mast years in silver fir occurring at a 2–4 years interval (Cremer et al., 2012). Otherwise, temporal restrictions were evaluated by means of correlations between seed fall data of consecutive years. Positive temporal autocorrelation between two consecutive years of high crop production, reported here and by Paluch (2011) in Poland, which contradicts other studies (Houle, 1998), may be interpreted as the absence of functional (carbohydrate storage) or anatomical (flowering buds) constraints on mast seed production.

The temporal consistency on seed production was linked to the presence of seed-fall spatial foci. It is remarkable that the seed fall patterns were heterogeneous even in relatively homogeneous even-aged stands such as Las Eras. Usually, the number of fallen

seeds in silver-fir forests is positively associated to local stand density because in dense patches trees may produce more seeds and dense canopies allow effective trapping of seeds and promote local dispersal by reducing wind turbulence (Paluch, 2011). It could be also possible that sites with abundant seed fall are occupied by dominant trees showing recurrent fruiting, i.e. good seed producers (Paluch and Jastrzebski, 2013). Therefore, local variability in tree density or in fruiting may explain the spatial variability in seed availability. Finally, secondary dispersal or post-dispersal predation are not plausible explanations for the seed patterns observed since traps were placed at the same height in even slopes and predation pressure was negligible.

Silver fir seed production is enhanced by previous warm spring conditions which may induce a better development of reproductive buds or promote pollination. On the other hand, dry conditions at the time of cone ripening also favor seed production, as has been found in other North American fir species (Houle, 1999). Therefore, seed production in silver fir responds to climatic cues which could indicate selective advantages through an enhanced inter-annual variation in seed production (Kelly and Sork, 2002). Future studies should check if variable seed production corresponds to changing levels of seed viability, which seems to be the case in similar rear-edge silver fir populations (Restoux, 2009).

#### 4.2. Seed dispersal depends on the stand type

Seed dispersal curves were characterized following an inverse modeling approach and using a log-normal kernel. Greene and Johnson (1989) also argued that dispersal by wind can be well-approximated by a log-normal function, since long-term horizontal wind speed is assumed to be log-normally distributed. This kernel is also in agreement with mechanistic approaches simulating seed dispersal (Nathan et al., 2002; Tackenberg, 2003).

Overall, dispersal is mainly driven by the height of reproducing trees releasing the seeds (Okubo and Levin, 1989). Accordingly, the greater mean seed dispersal distance estimated for the mixed stand (Gamueta) may be interpreted in relation to its greater structural heterogeneity, i.e. older and bigger trees of different ages dominate that population, whereas younger and smaller even-aged

individuals prevailed in the pure stand (Las Eras). So tree height differences between and within stands might explain changes in dispersal curves such as the maximum dispersal distance (Dovčiak et al., 2008). Only 5% of released seeds travelled distances similar to that estimated for the mature mixed stand, while 14% of released seeds reached distances similar to that estimated for the young pure stand. This suggests that release experiment must be combined with inverse models to fully account for the effect of stand structure (e.g., tree height, basal area, tree locations, stand density and composition) on seed dispersal.

Compared to most other wind-dispersed temperate conifers, silver fir produces relatively large seeds. Therefore, seed dispersal has been assumed to be restricted to relatively short distances (Cremer et al., 2012). Consistently, mean dispersal distances for silver fir presented here are similar to those estimated in previous studies for this species (6–11 m, Paluch, 2011; 13–19 m, Sagnard et al., 2007; 20–50 m, Kohlermann, 1950; Korpel and Vins, 1965; Restoux, 2009) and lower than for other coniferous species with smaller seeds (Ribbens et al., 1994; Greene et al., 2004). However, the strongly overlapping seed shadows in the study stands could result in underestimation of the effects of long-distance dispersal (Paluch, 2011). Moreover, Cremer et al. (2012) used genetic markers of seeds and mother trees and suggested that silver-fir seed dispersal distances estimated through inverse modeling may underestimate actual distances due to the existence of more complex dispersal mechanisms than are readily assumed such as long-range dispersal at moderate or high wind speeds. Reducing the allometric exponent ( $\gamma$ ), which links fertility of trees with their sizes (dbh), decreases the relative importance of the larger trees on the global seed production. The lower value found in Gamueta may be consequence of a senescence-related reduction in seed production, given the dominance of older individuals at this site, while in Las Eras almost all trees are similar and medium sized (Fig. 2). Comparable dynamics have been described in similar Pyrenean silver fir forests (Gil Pelegrín et al., 1989).

#### 4.3. A complex regeneration niche for silver fir

Several authors have found that silver fir avoids microsites with high levels of radiation under too open canopies (Diaci, 2002; Paluch, 2005; Rozenbergar et al., 2007), so silver fir recruitment is restricted to moderately open understory or small gaps (Grassi and Bagnaresi, 2001; Stancioiu and O'Hara, 2006; Ameztegui and Coll, 2011). Spatial heterogeneity in light intensity may produce areas prone to maintain high seedling densities, triggered by past masting events, giving place to seedling banks (Szewczyk and Szewczyk, 2010). This study was conducted in rather closed stands, which are characteristic of silver-fir dominated forests of the Pyrenees. In such conditions, a positive effect of canopy openness over seedling establishment was detected (Table 5). This may reflect the need of some radiation to maintain positive carbon balance by photosynthetic activity for assure survival and seedling growth once seed reserves run out (Kobe et al., 1995). Canopy openness seems to have a significant influence not only on the development of silver fir seedlings and juveniles, but also on establishment of young recruits at least when understory conditions are not too dark (Aunós et al., 2003, 2007; Grassi et al., 2004). The light demand in early stages of silver-fir regeneration could be also related to the canopy cover of conspecific adults individuals, which compete more for light resources as they grow and reach canopy. Further research could evaluate if tall and thin canopies constitute a particular feature of Pyrenean silver-fir ecotypes. At later life stages, some authors observed no associations with canopy openness and regeneration, i.e. between the density of fir saplings and light conditions (Dobrowolska, 1998).

In the mixed-stand, silver fir seedling emergence was related to dense patches of beech sprouts (Table 5). Similar results have been reported by silver fir by Dobrowolska (1998) or by Simard et al. (2003) for Canadian fir forests. In both cases a greater survival of fir seedlings was observed under some tree species. This is consistent with the radiation dependence of seedlings establishment and survival since canopy openness and density of beech sprout showed a negative correlation between them, i.e. typically thin stems and sparse foliage beech sprout patches does not represent shady microsites, in contrast they might provide some others advantages to seedling development. The positive effect of beech cover at intermediate or low forest layers on seedling establishment could be attributable to its deciduous character. Higher light penetration is accompanied by warmer forest floor temperatures and an earlier snowmelt in late winter, which hastens germination, having early-emerging seedlings typically increased survival (Simard et al., 2003). Note that beech basal area, representing the presence of dominant and big trees and shady conditions, was negatively albeit weakly related to seedling establishment (Stancioiu and O'Hara, 2006).

Nevertheless, silver fir regeneration does not only depend on light conditions (Rozenbergar et al., 2007). Several studies have demonstrated that recruitment success in coniferous forests is strongly influenced by the types of substrate available (e.g., Simard et al., 1998; Mori et al., 2004). We did not observe significant effects of substrate type on silver-fir recruitment despite the relative abundance of coarse woody debris in both sites. This might be because moisture-retention capacity, which is very relevant for seedling germination, is usually adequate at the time of germination following snow-melt irrespective of substrate type (Duchesneau and Morin, 1999; Mori et al., 2004). The analyses of climate-seedling associations support this idea since wet conditions in fall and winter, usually accompanied by snow in the latter season, provide a long-term water reserve to the soil which may favor seed germination in spring. Further, the relatively large seed size of fir species may make seedlings less dependent on substrate conditions (Knapp and Smith, 1982). In contrast, other conifers including fir show preferential establishment on 'nurse logs' (Gray and Spies, 1997; Takahashi et al., 2000; Parent et al., 2003) or thin moss mats (e.g. Knapp and Smith, 1982). Regeneration on nurse logs allows avoiding ground vegetation competition, long lasting snow cover and low soil temperatures. However, silver fir seedlings in the study sites were neither related to coarse woody debris nor to moss patches (results not presented). This may be due to the abundance of open microsites, despite ground vegetation was more dense in the mixed Gamueta stand, and the relatively mild conditions of the study area where snowpack has usually disappeared in early spring.

#### 4.4. Uncoupled patterns of seed dispersal and seedling recruitment

Secondary dispersal could also explain the seed-seedling spatial uncoupling since silver-fir seeds may disperse over large distances across the snow cover or after rainfall events (Cremer et al., 2012). High slopes in the Gamueta site could facilitate dragging of seeds after fall and winter rainfalls leading to its accumulation in concave microsites and depressions where branches and leaf litter pile or where the upper soil horizons favor seedling establishment (Paluch, 2005). We observed that fallen logs and thick branches lying perpendicular to the maximum slope often promote accumulation of litter and organic matter as well as silver fir seeds. Seed dormancy might also uncouple seeds and seedlings spatial patterns as well. Silver-fir seeds require winter dormancy which prevents early germination and seedling mortality caused by low temperatures, and also adequate moisture conditions in spring (Kolotelo, 1998). Germination is also enhanced by wet conditions in spring because the high monoterpene content of the seed

resin impedes germination under dry conditions. Moreover, other factors may be influencing the seedling emergence pattern such as preferential predation of seedlings and saplings in some sites (Diaci, 2002; Rozenbergar et al., 2007; Simard et al., 2003), or a low proportion of viable seeds (Paluch, 2011; Cremer et al., 2012; Sagnard et al., 2007).

## 5. Conclusions

Current seed production and recruitment assure the persistence of western Pyrenean silver fir populations, at least in areas not presenting severe die-off. A high annual variation in seed production was found. Forest structure drives seed dispersal distances. Silver fir regeneration was found to be mainly determined by microsite conditions (climate, light availability, substrate) thus uncoupling the spatial seed dispersal and seedling emergence patterns. The importance of this filter (regeneration niche) may increase as populations get closer to their southern or xeric distribution limits (rear-edge forests), where ecological conditions are harsher for tree regeneration than in the core area. In these conditions, the regeneration niche is expected to be as a stronger bottleneck of silver-fir regeneration than seed production and fall patterns.

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