

Regeneration of Mediterranean *Pinus sylvestris* under two alternative shelterwood systems within a multiscale framework

Ignacio Barbeito, Valerie LeMay, Rafael Calama, and Isabel Cañellas

Abstract: The inability to obtain sufficient numbers of naturally regenerated trees following partial harvests of some Mediterranean Basin managed forests has prompted the need to critically assess common silvicultural practices. In this study, we examined Scots pine (*Pinus sylvestris* L.) regeneration patterns under two shelterwood systems using a multiscale framework. The uniform shelterwood (US) system includes heavier and less frequent timber extractions than the group shelterwood (GS) system. Removal of competing vegetation to expose mineral soil (soil preparation) is sometimes used for US but is not commonly needed in GS. A generalized linear model was used to predict regeneration density for each shelterwood system using environmental variables at microsite- and forest-level scales, medium-scale overstory tree characteristics, and spatial metrics that represent a range of spatial scales. Although US had a higher mean regeneration density, GS had a wider range of regeneration ages. The results derived from this study suggest that ground-level disturbance to break up the herb or organic layer may be required for regeneration establishment. This may occur during repeated partial harvests; otherwise, soil preparation may be required. Overall, this multiscale framework approach resulted in improved predictions and a better understanding of regeneration processes.

Résumé : L'incapacité à obtenir un nombre suffisant d'arbres naturellement régénérés à la suite de coupes partielles appliquées à certaines forêts aménagées du bassin méditerranéen a suscité le besoin de procéder à une évaluation sérieuse des pratiques sylvicoles courantes. Cette étude se penche sur les patrons de régénération de pin sylvestre (*Pinus sylvestris* L.) engendrés par deux systèmes de coupe progressive en utilisant un cadre d'analyse multi-échelle. Le système de coupe progressive uniforme (CPU) prévoit des coupes plus intensives et moins fréquentes que le système de coupe progressive par groupes (CPG). L'élimination de la végétation concurrente dans le but d'exposer le sol minéral (préparation de terrain) est parfois utilisée avec la CPU mais n'est généralement pas nécessaire avec la CPG. Un modèle linéaire généralisé a été utilisé pour prévoir la densité de régénération de chaque système de coupe progressive à l'aide de variables environnementales à l'échelle du microsite et de la forêt, des caractéristiques des arbres de l'étage dominant à une échelle intermédiaire et de mesures spatiales représentant une gamme d'échelles spatiales. Bien que la densité moyenne de la régénération ait été plus élevée avec la CPU, la gamme d'âge de la régénération établie à la suite d'une CPG était plus étendue. Les résultats tirés de cette étude indiquent que la perturbation du sol pour briser la couche de matière organique ou d'herbacées peut être requise pour favoriser l'établissement de la régénération. Une telle perturbation du sol peut se produire sans mesures particulières lors de récoltes partielles répétées mais, dans les autres cas, une préparation de terrain peut être nécessaire. Globalement, ce cadre d'analyse multi-échelle a permis d'améliorer nos prévisions et notre compréhension des processus de régénération.

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Introduction

Scots pine (*Pinus sylvestris* L.) mountain forests of the Iberian Peninsula represent the southernmost distribution of this typical boreal species (Castro et al. 2004). In these Mediterranean Basin forests, the duration of summer droughts is particularly important for regeneration. For some species, the combination of seed production and fa-

vourable climatic conditions for seedling establishment occurs only every 20–40 years (González-Martínez and Bravo 2001). Great spatial and temporal variability of regeneration patterns has been shown for Scots pine in this region, depending on climatic variability and seed availability (Montes and Cañellas 2007).

Harvest of overstory trees is the main disturbance regulating regeneration in most managed Mediterranean forests.

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I. Barbeito.¹ Departamento Sistemas y Recursos Forestales, CIFOR-INIA, Ctra. Coruña, km 7.5, Madrid 28040, Spain; WSL Institute for Snow and Avalanche Research SLF, Flüelastrasse 11, CH-7260 Davos, Switzerland.

V. LeMay. Department of Forest Resources Management, University of British Columbia, 2045-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada.

R. Calama and I. Cañellas. Departamento Sistemas y Recursos Forestales, CIFOR-INIA, Ctra. Coruña, km 7.5, Madrid 28040, Spain.

¹Corresponding author (e-mail: barbeito@slf.ch).

Gaps created by partial harvest result in increased availability of light and other resources for understory trees and other plants. At the same time, increased evaporation may occur, resulting in moisture stress (Aussenac 2000). Recently, recurrent and severe summer drought episodes (González-Hidalgo et al. 2001) have caused levels of regeneration that are insufficient for providing desired future forest products, and common silvicultural practices have been called into question (e.g., Aussenac 2000). Since future climate scenarios predict more frequent droughts and warmer temperatures (Intergovernmental Panel on Climate Change 2007), there is a greater need to find silvicultural systems that might mitigate drought impacts on regeneration. Other contributors to regeneration failures include forage by herbivores (Zamora et al. 2001). Regeneration periods longer than those used in common silvicultural systems may be needed to achieve regeneration success (Bravo and Díaz-Balteiro 2004).

A number of empirical studies have been published on post-harvest regeneration of coniferous species in boreal forests of northern Europe (e.g., Valkonen et al. 2002; Eerikäinen et al. 2007), although almost all examined processes only at a single spatial scale and for areas of 1 ha or less. Empirical regeneration studies in moisture-limited sites, such as those common in the Mediterranean region, have mainly focused on post-fire recruitment (Pausas et al. 2004; Fyllas et al. 2008) with few studies on post-harvest regeneration. However, Gómez-Aparicio (2008) used a multiscale framework to study whether recruitment dynamics for a Mediterranean wind-dispersed species were related to coarse-scale site characteristics only or if smaller-scale site characteristics were important.

If natural regeneration is to be used to provide an acceptable level of regeneration after harvest, the effects of management practices at multiple spatial scales need to be understood, including the interactions of small-scale neighbourhood processes with coarser-scale disturbances (Fortin and Melles 2009). Some processes affecting the spatiotemporal regeneration patterns operate at the local scale, including the production of viable seeds (Juntunen and Neuvonen 2006) and seed dispersal (Clark et al. 1998). However, both anthropogenic (e.g., tree harvest, soil preparation) and natural perturbations (e.g., windthrow, epidemic insect and pathogen attacks, seed and seedling predation) can act at larger scales (Fajardo and McIntire 2007). The spatial distribution of regeneration can be used as a surrogate for unmeasured influential variables and processes and to generate new hypotheses about the variables responsible for the processes that generated the patterns (McIntire 2004). To reveal the spatial structures of an ecological data set at any scale based on sample data, spatial-filtering methods based on eigenfunction analyses have been used (Borcard and Legendre 2002; Griffith 2003). Spatial variability can then be explained by adding spatial predictors to models (Griffith 2003).

In this study, we explored the spatial distribution of naturally regenerated Scots pine for two common shelterwood systems in central Spain using a multiscale framework. We focused on the first stage of regeneration when regenerated trees are part of the understory and are under the effects of the overstory (Maltez-Mouro et al. 2009). Our primary ob-

jectives were to (i) examine the differences in stand-level regeneration densities of two stands under different silvicultural systems, (ii) examine the spatial variation in regeneration densities, (iii) examine the relationships between regeneration density and environmental variables at the small and large scales and overstory variables at the medium scale, and (iv) quantify the amount of remaining spatial variability. Our aim was that this study would help managers select strategies that improve conditions for Scots pine natural regeneration in Mediterranean forests, particularly strategies that might be used to mitigate predicted climate changes.

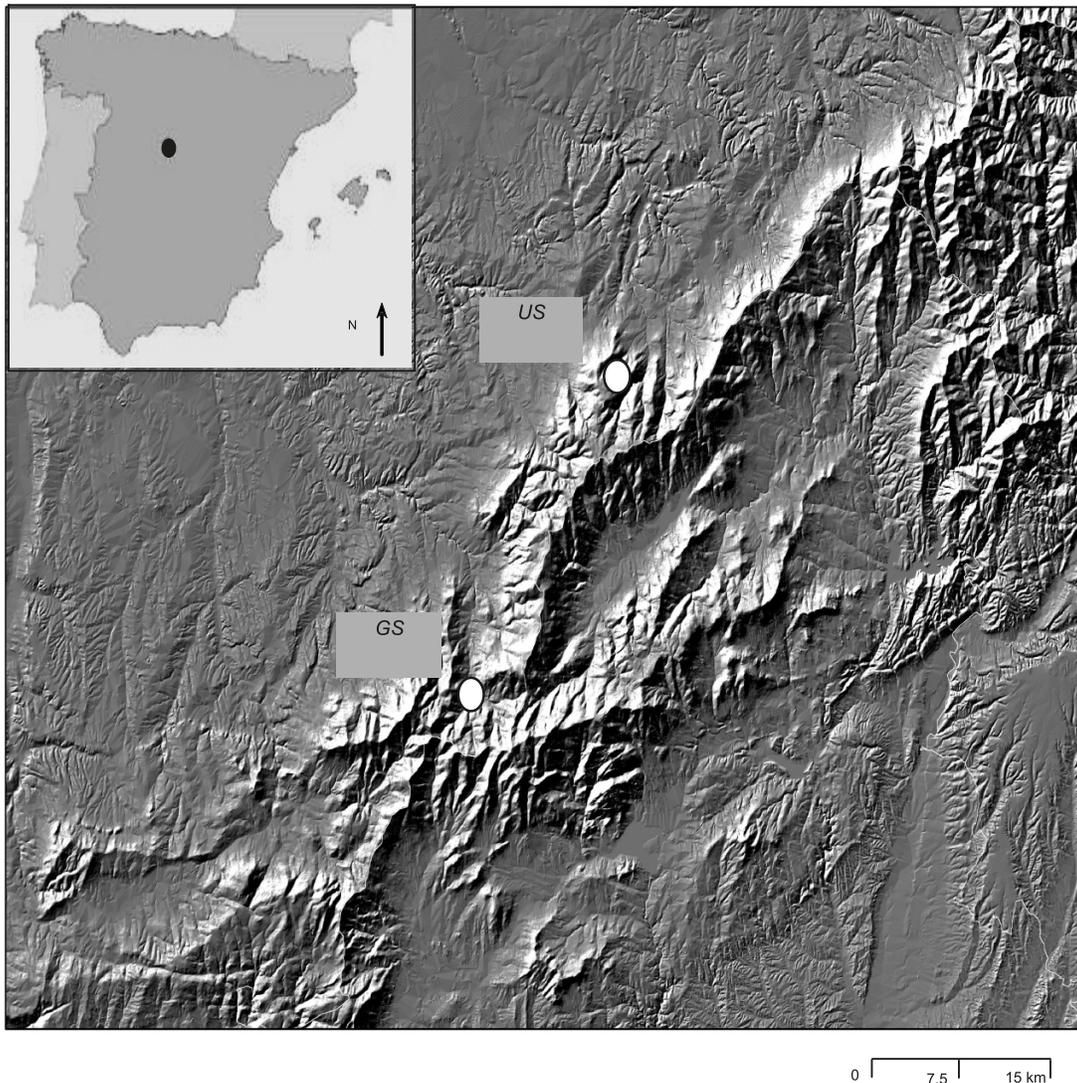
Methods

Study area and silvicultural methods

We sampled regeneration in two managed mountain forests, Navafria and Valsain, located on the north-facing slopes of Sierra de Guadarrama in central Spain (40°49'N, 4°1'W) (Fig. 1). Both forests are located on the north-facing slopes of the mountain range, are pure Scots pine, and have a long history of harvest and management. These forests share similar ecological characteristics with elevation ranging from 1200 to 2200 m above sea level, annual rainfall of about 730 mm, and mean annual temperature around 9.8 °C. The mountains are composed of granite and gneiss. Soils are relatively homogeneous and predominantly humic cambisol soils with leptosol at higher-elevation sites.

These two forests are managed under shelterwood systems that completely rely on the success of natural regeneration. Using these methods, a new stand is established by gradually removing all trees in a series of repeated partial harvests over a period of years, allowing seedlings to become established under the protection of the older trees. In both forests, harvest residues were piled and burned to reduce fire risk and hand-felling with chainsaws was used to minimize the damage to regeneration and retained trees during partial harvests. Of possible shelterwood methods, the uniform shelterwood (US) system used in the Navafria forest is the most widely used regeneration method in Mediterranean forests; however, the group shelterwood (GS) system used in the Valsain forest has been used by managers in even-aged pure Scots pine stands. Stands managed using GS are moderately thinned until they reach 100 years. Trees are then harvested to create small gaps (0.1–0.2 ha). As regeneration appears, subsequent harvests every 4–5 years over a 40-year period are used to widen the gaps where regeneration has successfully established. As a result, natural regeneration establishes progressively under the protection of the older trees until the final harvest at 140 years. Usually, some seed trees are retained in the final harvest (10–25 trees·ha⁻¹). Using US, intensive thinning is applied from age approximately 30 years until 80 years to stimulate crown development and diameter increment. At 80 years, the canopy is opened by removing 20%–30% of the basal area and leaving a density of 200–250 trees·ha⁻¹. Subsequently, additional trees are removed uniformly over the forest area in two or three harvests over a 20-year period leaving a low residual tree density, and remaining trees are finally harvested at 100 years. Since gaps are small using GS, no additional soil preparation is needed, while in US, mechanical

Fig. 1. Geographical location of uniform shelterwood (US) and group shelterwood (GS) forests in central Spain.



soil tilling is often used to eliminate competing vegetation and remove any humus layer after the initial harvest. We selected an area of approximately 40 ha in each of GS and US both at 1 year prior to final harvest. As a result, measured regeneration included the full regeneration periods from the creation of gaps at age 100 to 1 year before final harvest in GS (40 years) and from the opening of the canopy at 80 years to final harvest in US (20 years).

Regeneration sampling

Systematic sampling with 100 m × 100 m spacing was used for GS (45 plots), whereas 150 m × 150 m was used for US (35 plots), since the US stand was more homogeneous. Plots were established at a minimum distance of 50 m from roads and from other harvested areas to avoid edge effects. Since the sampled stands had been fenced, livestock grazing pressure was eliminated and only slight damage from roe deer was observed.

At each grid intersection, a square regeneration plot of 16 m² was established. Trees belonging to the regeneration

cohort were defined as young trees or saplings with a diameter at breast height (DBH) (measured at 1.3 m above ground) less than 7.5 cm and a height greater than 10 cm, as these trees are likely to have survived at least one summer. Mortality of Scots pine seedlings is often very high during the first summer, sometimes reaching 100% (Pardos et al. 2007). We counted the number of regenerated trees and measured the heights (Table 1). As well, the spatial location (i.e., *x,y*-coordinate) of each 16 m² plot centre was recorded. For each stand, we took a random sample of regenerated trees within 0.5 m height intervals from 0.1 m to the recorded maximum height of 3.5 m and measured age by counting the number of rings on cut stems. This information was used to relate age to height of regenerated trees and to obtain the age distribution for each stand.

Environmental variables

In each regeneration plot, we gathered information for four groups of variables. (i) Topographic variables, specifically, elevation, slope, and aspect. These variables represent

Table 1. Characteristics of regeneration and retained adult Scots pine (*Pinus sylvestris*) trees.

Variable	Uniform shelterwood		Group shelterwood	
	Mean	CV (%)	Mean	CV (%)
Regeneration				
Number·m ⁻²	12.7	203.1	2.2	204.5
Height (cm)	40.8	60.3	75.1	131.7
Retained trees				
Number·ha ⁻¹	66.7	51.9	174.9	46.8
DBH (cm)	36.1	20.2	34.6	25
Height (m)	16.3	23.9	22	19.5
Basal area (m ² ·ha ⁻¹)	11.1	29.7	33.4	43.7
IPOT (0–1)	0.11	145.5	0.34	76.5

Note: DBH, diameter at breast height (1.3 m aboveground); IPOT, competition index (influence potential); CV, coefficient of variation.

larger-scale variation. Aspect was converted to an aspect index using aspect index = $\cos(\alpha - 22.5)$, where α is the aspect direction in radians. The aspect index ranges between 1 (northeast-facing slopes) and -1 (southwest-facing slopes) (Pausas et al. 2004). (ii) Light availability. This variable has been shown to be relevant at a small scale (Pardos et al. 2007; Barbeito et al. 2009a). The light availability was measured by taking a digital hemispherical photograph at each plot centre 1.30 m aboveground in overcast conditions. HemiView Canopy Analysis software (Delta-T Devices Ltd.) was used to calculate the global site factor, the proportion of total radiation under a plant relative to that in the open, ranging from 0 (completely closed canopy) to 1 (completely open canopy). (iii) Ground cover features. For each regeneration plot, the cover by herbs, shrubs, stones, and litter was visually estimated to the nearest 10% representing important measures of small-scale site variability. (iv) Topsoil variables. Topsoil variables were identified as being important small-scale site variables for other Mediterranean harvested forests (e.g., Rubio and Escudero 2003). Topsoil was sampled by taking four soil cores (0–15 cm depth) in each plot and aggregating the samples before analysis. The fine soil fraction for the natural soil (<2 mm) was calculated before soil samples were sieved (2 mm) and analyzed for total N (Kjeldahl method), available P (Olsen method), organic C (Walkley and Black method), which was converted to organic matter, colloidal K (atomic absorption), soil pH (in distilled water), and soil moisture percent humidity (gravimetrically). The regeneration plots had wide ranges in topographic, light, soil, and cover attributes (Table 2).

We conducted principal components analysis (Legendre and Legendre 1998) to reduce the number of possible environmental variables. This was followed by factor analysis using a varimax rotation (Kaiser 1958) to provide factors that represent the most important underlying gradients. Factor scores were then considered as possible explanatory variables for estimating regeneration density.

Post-crop retained overstory trees

The retention of an overstory can improve seedbed properties and reduce the frequency of temperature extremes and droughts (Valkonen 2000). However, the density and spatial

pattern of retained overstory trees over time that best meet stated regeneration objectives are often unknown. We assessed overstory stand structure within a 25 m radius from each regeneration plot centre, considering retained seed trees to be those above 22.5 cm DBH; for both forests, there was only a small fraction of trees between 7.5 and 22.5 cm DBH (approximately 5%). For each retained tree, we measured height, DBH, and spatial position (i.e., x,y -coordinates). We used retained tree dimensions (DBH and height), density, and spatial pattern to calculate the influence potential (IPOT) as a measure of overstory competition at each plot centre. IPOT is based on the concept of ecological field theory (Wu et al. 1985) modified to an empirical measure by Kuuluvainen and Pukkala (1989). This was applied as follows:

$$[1] \quad \varnothing_{ij} = \varnothing_{ij}(0) \times \exp(-b_{ij}s_{ij})$$

$$[2] \quad \text{GPOT}_j = \prod_{i=1}^{n_j} (1 - \varnothing_{ij}) \text{ and } \text{IPOT}_j = 1 - \text{GPOT}_j$$

where \varnothing_{ij} is the potential influence of tree i at plot centre j , s_{ij} is the distance from tree i to the plot centre, $\varnothing_{ij}(0)$ is $\text{DBH}_{ij}/(\text{reference diameter})$, DBH_{ij} is the DBH of tree i at plot centre j , b_{ij} is a parameter, and n_j is the number of trees for plot centre j . We chose the maximum DBH in our data, 60 cm, as the reference diameter following Kuuluvainen and Pukkala (1989). The parameter b_{ij} was replaced by a function of the tree height, $b_{ij} = 1/(ah_{ij})$, where h_{ij} is height (metres) of tree i at plot centre j and a is a parameter. We tested alternative values of a from 0 to 1 by 0.1 based on the correlation between regeneration density and IPOT. The value 0.4 recommended by Kuuluvainen and Pukkala (1989) resulted in the highest correlations for both stands. Possible values for IPOT for each plot centre j range from 0 (no competition) to 1 (maximum competition) (for details, see appendix in Siipilehto 2006). This measure of overstory competition was included as an explanatory variable in estimating the regeneration density.

Spatial variables

We used principal coordinates analysis of neighbour ma-

Table 2. Mean and standard deviation values for the topographic, light, soil and cover attributes measured at uniform shelterwood (35 plots) and group shelterwood (45 plots).

Variable	Uniform shelterwood				Group shelterwood			
	Mean	CV(%)	Min.	Max.	Mean	CV(%)	Min.	Max.
Topographic attributes								
Elevation (m)	1680.2	3.6	1569.0	1764.0	1356.2	2.6	1298	1439
Slope (%)	28.6	41.3	5.5	52.7	10.3	47.6	4	22.5
Aspect index (-1 to 1)	0.5	60.0	-0.2	1.0	0.52	50.0	-0.6	1.0
Light attributes								
Global site factor (0-1)	0.7	14.3	0.3	0.9	0.3	33.3	0.1	0.6
Soil attributes								
Moisture (%)	4.2	19.1	2.8	7.4	5.9	28.8	2.5	11.2
Fine texture (<2 mm) (%)	71.6	14.3	37.4	92.8	83.9	11.6	56.4	96.1
pH	4.7	4.3	4.3	5.3	5.3	3.8	4.9	5.8
N (%)	0.4	25.0	0.2	0.5	0.3	33.3	0.1	0.5
C to N ratio	20.9	23.9	12.5	40.5	17.3	11.6	11.5	20.8
P (mg·kg ⁻¹)	11.6	39.7	4.7	24.6	6.4	51.6	2.3	17.5
K (mg·kg ⁻¹)	219.2	24.8	157.1	363.5	291.6	40.5	97.9	582.6
Organic matter (%)	13.1	0.8	7.3	31.6	9.3	26.9	4.3	14.4
Cover attributes								
Shrub (%)	1.2	358.3	0	5.0	16.9	84.1	0	55.0
Herbs (%)	50.1	51.3	3.8	93.8	39.1	44.8	8.8	85
Litter (%)	12.8	90.6	0	46.3	62.1	41.5	10	100
Stoniness (%)	12.9	93.8	0	62.5	2.6	51	0	27.5

trices (PCNM) (Borcard and Legendre 2002) as a tool to represent multiple-scale spatial structures in the response variable of interest (e.g., regeneration density). For this procedure, a matrix of all distances between regeneration plot centres was calculated. Then, PCNM was applied to the distance matrix to yield PCNM vectors that represent all of the spatial scales of our sampling scheme. These vectors were considered as explanatory variables to predict regeneration densities (e.g., García et al. 2009).

Data analysis

We examined the spatial structure of regeneration density using the plot centre spatial coordinates. First, contour plots were obtained to visually represent the spatial variability. Then, Moran's *I* (i.e., spatial autocorrelation statistic) (Legendre and Legendre 1998) was calculated for 10 distance classes using a 100 m class width. A spatial correlogram was obtained by plotting Moran's *I* against the midpoint of each distance class. The hypothesis of no spatial autocorrelation was tested for each distance class using a Bonferroni correction of the significance level (i.e., significance level/number of distance classes was used for each test; Fortin and Dale 2005). Given that environmental heterogeneity and biotic interactions could vary with direction, spatial correlograms were also calculated for each of four cardinal directions as a means of testing for isotropy (Oden and Sokal 1986).

Possible explanatory variables related to regeneration density were examined using generalized linear models (McCullagh and Nelder 1989) and a negative binomial probability density function for each forest. When the response variable is a count of individuals, commonly a Poisson probability distribution is used where the mean is equal to the variance.

However, regeneration is often characterized by variance values exceeding the mean (Table 1). Therefore, a negative binomial distribution is preferred (Venables and Ripley 2002) and has been frequently selected for modelling forest regeneration (e.g., Fyllas et al. 2008).

The overall model to estimate regeneration density was

$$[3] \quad R_{\text{density}} = f(\text{Environment} + \text{IPOT} + \text{Soil Preparation} + \text{Space}) + \text{residual error}$$

where *R*_{density} is the regeneration count for each 16 m² plot, Environment is represented by the two factors extracted for each forest, IPOT represents the competition index of retained adult trees, Soil Preparation is a categorical variable included only in US that indicates soil preparation coded as 1 for soil preparation or 0 for no soil preparation, and Space represents the spatial predictors generated from a PCNM analysis. Thus, the Environment, IPOT, and Soil Preparation variables represent variation based on identified variables, whereas the spatial predictors represent other variables that change with space but were not explicitly measured. Also, the spatial variables allow for investigations at a variety of spatial scales.

The percentage of explained deviance ($100 \times (\text{null deviance} - \text{residual deviance})/\text{null deviance}$) was used as an index of goodness of fit (McCullagh and Nelder 1989). We also used the "decomposition of the variance" approach (Whittaker 1984) to evaluate the relative contribution of the spatial predictors versus other variables. Variance partitioning has been applied to the problem of cross-scale correlations (Mahon et al. 2008) and to separate the contribution of environmental and spatial variables in the explanation of the spatial patterns of species (Urbietta et al. 2008). The ad-

vantages of using this approach is that both the variation that is due to each set of variables and the overlap in contributions can be determined. We calculated the percentage of variation attributable to spatial variables and to the other variables relative to the full model as

$$[4] \quad \begin{aligned} &\text{Variance due to spatial predictors} \\ &\quad = \text{percent deviance (full model)} \\ &\quad - \text{percent deviance (other variables)} \end{aligned}$$

$$[5] \quad \begin{aligned} &\text{Variance due to other predictors} \\ &\quad = \text{percent deviance (full model)} \\ &\quad - \text{percent deviance (spatial variables)} \end{aligned}$$

The percentage of shared variance between these two groups of variables was then calculated as

$$[6] \quad \begin{aligned} &\text{Shared percent deviance} \\ &\quad = \text{percent deviance (full model)} \\ &\quad - \text{percent deviance (spatial predictors)} \\ &\quad - \text{percent deviance (other predictors)} \end{aligned}$$

All calculations, analyses, and graphs were performed using the R environment (R Development Core Team 2008), except for the PCNM analyses, which were conducted using the Spacemaker2 program (Borcard and Legendre 2004).

Results

Regeneration density, distribution, and structure

For the US, 33% of the regeneration plots were soil tilled. More than half of the plots studied had some regeneration (65% in GS and 60.6% in US). Regeneration density was very highly variable, ranging from 0 to 12 individuals·m⁻² in GS (coefficient of variation (CV) = 204.5%) (Table 1) and from 0 to 81 individuals·m⁻² in US (CV = 203.1%) (Table 1), and presented a clearly skewed frequency distribution towards low values in both forests (Fig. 2). The age distribution indicated that regeneration was almost a continual process throughout the whole regeneration period for GS (Fig. 3b), whereas it was concentrated in two specific periods for US (Fig. 3a). Moreover, height differentiation was much greater in GS (CV = 131.7%) than in US (CV = 60.3%).

Spatial autocorrelation analysis of regeneration density indicated global significance at $\alpha = 0.01$ (Bonferroni-corrected test) in both forests and revealed clear differences in spatial structures (Fig. 4). Moran's *I* values at short distances were smaller for GS (0.3) than for US (0.8), showing a greater similarity for neighbouring plots in US. Additionally, the correlogram for GS showed a wide wave shape, suggesting a clumped spatial pattern with a patch size of approximately 300 m and repetition of the spatial pattern (Fortin and Dale 2005). In contrast, the all-directional correlogram for US showed a trend of significant positive values at short distances (<300 m) to negative ones at larger distances (>300 m), indicating that a spatial gradient exists (Fortin and Dale 2005). The directional correlograms supported the observations from the all-directional correlogram and no significant anisotropy was detected for GS or US.

Environmental and competition variables

The IPOT competition indices were higher under the GS system (mean = 0.34) than under the US system (mean = 0.11). This indicates a denser overstorey in GS, which was expected, since more trees were retained (mean = 174.9 trees·ha⁻¹, SD = 81.8) than in US (mean = 66.7 trees·ha⁻¹, SD = 34.6). Also, IPOT values in GS were two times less variable than in US (CV = 76.5% and CV = 145.5%, respectively).

Factor analysis revealed a moderately strong underlying structure of the environmental variables with approximately 50% of the total variance of the environmental variables accounted for by the first two factors in each forest (Table 3). The first underlying gradient (PC_T) represented by the first factor in GS and the second in US could be interpreted as a gradient of erosion where the fine soil fraction decreases as slope increases. Elevation had opposite factor loading signs for GS compared with US, likely as a result of a flat area at the highest elevation in US. Generally, larger factor scores for PC_T were related to higher elevations and steeper slopes with less fine soil, indicating that this factor represents larger-scale processes. The second underlying gradient, PC_S (second factor in GS and first in US), could be interpreted as a gradient of soil nutrients and moisture and, therefore, represents a smaller-scale process. Larger factor scores for PC_S indicated richer soils.

Regeneration models

Initially, PCNM spatial variables were excluded from the generalized linear models to predict pine regeneration. For these models, PC_S was the most important predictor of pine regeneration density in GS, whereas the soil preparation indicator variable and PC_S were the most important variables for US as indicated by the explained deviances (Table 4). Since larger PC_S scores indicate richer soils, regeneration decreased with richer soils for both GS and US. For US, regeneration increased when soil preparation was done to expose more mineral soil. Regeneration density was negatively related to PC_T in GS, indicating that there were fewer regenerated trees on steeper and higher-elevation sites, which tend to have less fine soils. PC_T was not significant ($\alpha = 0.05$) for predicting regeneration in US, possibly because of an interaction with soil preparation and also because PC_T was harder to interpret for US, as noted earlier. The competition index (IPOT) was not significant for GS but had a negative effect on regeneration density for US. However, IPOT is likely related to other variables for both forests and, therefore, coefficients are difficult to interpret.

The full models including spatial predictors from PCNM were then fitted using forward selection methods resulting in retention of four PCNM spatial variables. The full models were able to explain more than 50% of the deviance in regeneration density in both forests (Table 5). The results showed that about half the total deviance was shared between spatial and nonspatial measures for US (49.8%). For GS, the shared deviance was less and the majority of deviance was pure spatial (53.0%). Since soil preparation appeared to be important for US, the pure nonspatial deviance was high (30.6%).

Fig. 2. Frequency distribution of regeneration density in (a) group shelterwood and (b) uniform shelterwood. Note that the x-axes differ in scale.

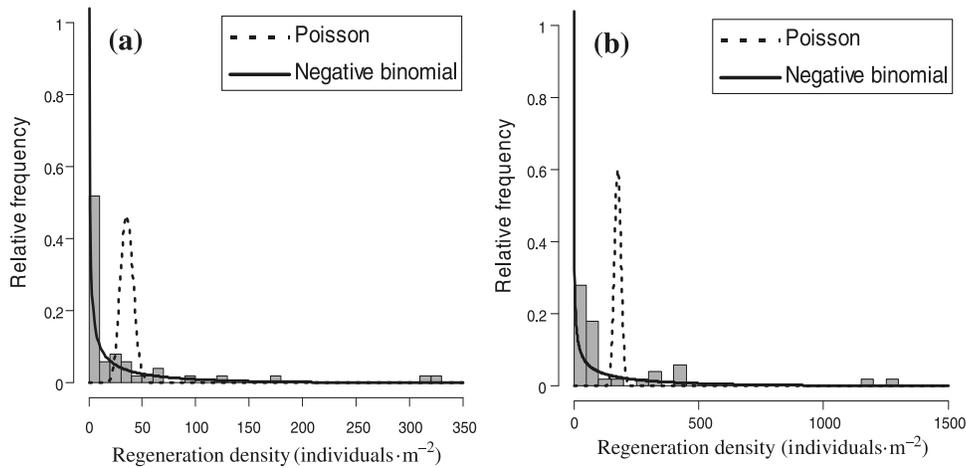
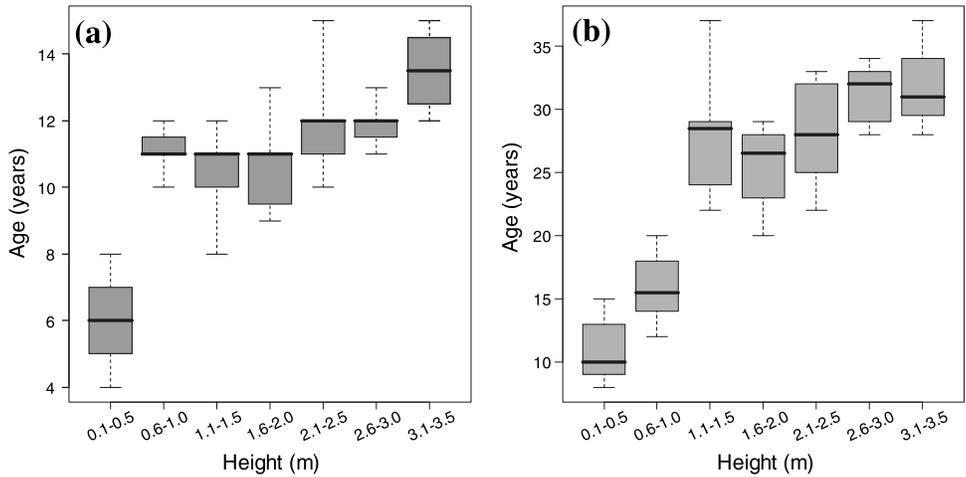


Fig. 3. Age structure of regeneration height classes from 0.1 to 3.5 m (0.5 m interval) for (a) uniform shelterwood and (b) group shelterwood. The box indicates the upper and lower quartiles, the horizontal line indicates the median value, and whiskers indicate the minimum and maximum values.



Discussion

Regeneration density, distribution, and structure

At the stand scale, regeneration density showed high variability and spatially autocorrelated structures for both shelterwood systems. The patchy spatial pattern in GS may reflect the minor smaller-scale overstory removals that allowed seedling establishment in gaps (Oliver and Larson 1996). Along with the long regeneration period (40 years), these effects may explain the nearly continuous age distribution regeneration found in this stand. On the contrary, the gradient pattern found in US may reflect the more homogeneous spatial distribution of residual trees, resulting from heavier thinnings of the overstory in earlier years and continuing with relatively uniform removal of trees before the final removal at 100 years. The concentration of regeneration in areas where organic materials were removed along with the more restricted age distribution suggests that regeneration may have established within the first 2–3 years after preparation, prohibiting subsequent establishment of regenerated trees, as noted by González-Martínez and Bravo (2001).

Factors affecting regeneration

Previous studies at small scales (≤ 0.5 ha) carried out in the same study area revealed a small-scale patchiness of regeneration associated with variations in available light, soil moisture, and microtopography features, with other soil attributes as not significant at that scale (Pardos et al. 2007; Barbeito et al. 2009a). Similarly, the presence of regeneration in moderate light conditions and moister microsites in the early stages has been found in other moisture-limited coniferous forests at a similar scale (Barbeito et al. 2009a; LeMay et al. 2009). For our study, the factor associated with small-scale soil properties was the most important non-spatial variable related to post-harvest Scots pine regeneration for GS. For US, this soil factor was also very important in estimating regeneration, but this was coupled with the soil preparation indicator variable.

The importance of surface soil properties for regeneration establishment in the Mediterranean Basin is widely recognized (e.g., Gómez-Aparicio et al. 2005). The herbaceous layer or a thick organic soil layer constitutes a physical barrier preventing seeds from contacting the mineral soil. Therefore, moderate soil disturbance eliminating these layers

Fig. 4. Spatial patterns of regeneration distribution in (a) uniform shelterwood and (b) group shelterwood. Left: interpolation maps from $n = 45$ points in GS and $n = 35$ points in US in a grid pattern over the sampled study area. High shade intensities indicate large regeneration values. Right: spatial all-directional correlograms with solid circles indicating significant coefficient values of Moran's I after Bonferroni correction. Note that the y-axes differ in scale.

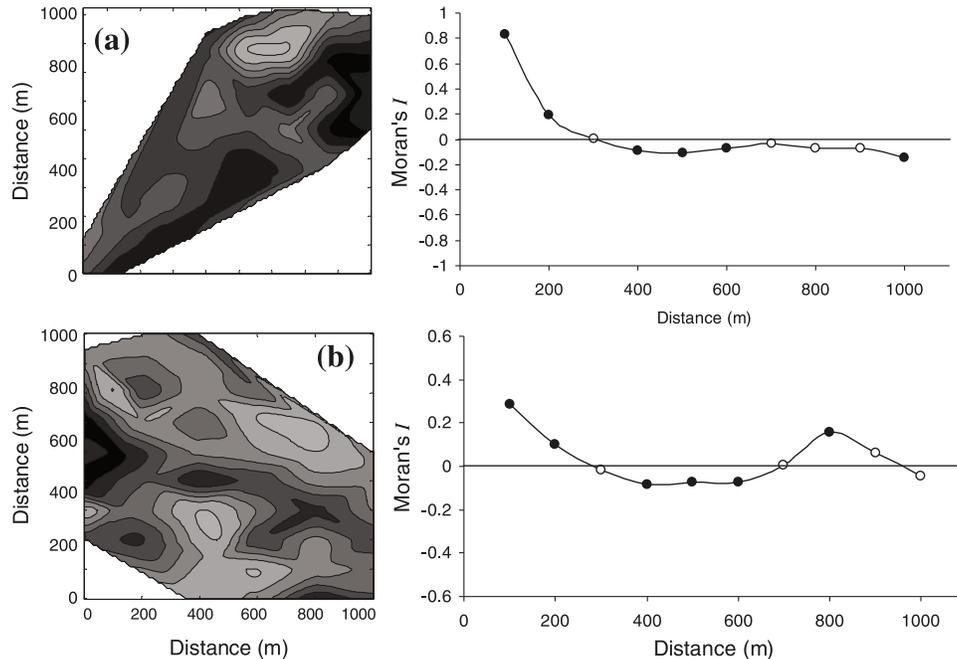


Table 3. Results of factor analysis of the stand environmental variables measured at group shelterwood and uniform shelterwood after varimax rotation.

Environmental variable	Group shelterwood principal components		Uniform shelterwood principal components	
	PC _T (topography)	PC _S (soil)	PC _T (topography)	PC _S (soil)
Elevation	0.76	0.28	-0.92	0.35
Slope	0.65	-0.01	0.73	-0.23
Aspect index	0.26	0.33	0.26	-0.37
Light availability (global site factor)	-0.47	-0.03	0.34	0.06
Soil moisture	-0.23	0.63	0.38	0.68
Fine soil texture	-0.83	-0.09	-0.62	-0.2
pH	0.28	0.14	-0.02	-0.88
N	0.28	0.96	0.15	0.78
C to N ratio	0.40	-0.28	0.51	0.25
P	0.02	0.37	-0.27	0.76
K	-0.08	0.61	0.37	0.29
Shrub cover	0.07	0.35	-0.05	0.17
Herb cover	-0.48	-0.08	-0.03	0.21
Litter cover	0.47	0.11	0.34	0.26
Stoniness	-0.12	0.01	0.35	0.13
% variance explained	31	22	23	27

Note: PC_T, factor explaining the topographical gradient; PC_S, factor explaining the soil condition gradient. Absolute values of factor loadings greater than 0.6 are shown in bold.

can expose mineral soil and result in improved water conductivity (Beland et al. 2000). Our results support this concept, in that soil preparation was associated with higher regeneration in US. Further, previous studies have found higher densities of pine regeneration in mineral soils in boreal forests (e.g., Hille and den Ouden 2004) and Mediterranean forests (Scots pine in the northeast of Spain: González-Martínez and Bravo 2001; Spanish black pine (*Pinus nigra*

Arn. subsp. *salzmannii*) in the east of Spain: del Cerro Barja et al. 2009).

For the GS, the topographical gradient of steeper slopes and stonier soils at higher elevation was associated with less regeneration. These substrates have been found to negatively affect regeneration survival due to a low root-soil contact (Gómez-Aparicio et al. 2005).

The competition index (IPOT) reflects primarily below-

Table 4. Generalized linear model for Scots pine (*Pinus sylvestris*) regeneration density for uniform shelterwood ($n = 35$ plots) and group shelterwood ($n = 45$ plots).

Site	Explanatory variable			
	Factor	Influence	$p > \chi^2 $	Explained deviance (%)
Uniform shelterwood	PC _T	–	0.31	1.6
	PC _S	–	0.043	10.8
	IPOT	–	0.0016	10.1
	Soil preparation	+	<0.001	37.5
Group shelterwood	PC _T	–	0.0012	9.1
	PC _S	–	0.0013	14.4
	IPOT	+	0.091	1.9

Note: PC_T, underlying topographical gradient factor; PC_S, underlying soil condition gradient factor; IPOT, competition index (influence potential) of retained trees based on ecological field theory.

Table 5. Pure spatial and nonspatial (PC_T, PC_S, IPOT, and soil preparation) components and shared component (spatial – nonspatial) explaining variation in Scots pine (*Pinus sylvestris*) regeneration distribution.

Additive components of variation	Uniform shelterwood		Group shelterwood	
	% deviance explained	% total deviance explained	% deviance explained	% total deviance explained
Pure (nonspatial)	17.3	30.6	10.9	18.9
Pure (spatial)	11.0	19.6	30.9	53.0
Shared (Spatial – nonspatial)	28.1	49.8	16.5	28.1
Total	56.4	100	58.3	100

Note: PC_T, underlying topographical gradient factor; PC_S, underlying soil condition gradient factor; IPOT, competition index (influence potential) of retained trees based on ecological field theory. The sum of the deviance explained by the three components and the component explaining the highest percentage of the total deviance are shown in bold.

ground competition for water and nutrients in the case of solitary or grouped retained pines where light interception of retained pine trees is relatively low (Kuuluvainen and Pukkala 1989). As anticipated, increasing residual overstorey measured by increasing IPOT was negatively related to regeneration levels for US. An unexpected result was that the competition index was not significant for predicting regeneration for GS. Since the range of IPOT values was narrower for GS than for US, this may have contributed to this result. At the stand-level scale, the effect of retained trees on the average regeneration density was not significant in most studies of Scots pine regeneration in boreal forests (e.g., Siipilehto 2006). In this study, since the average number of regenerated trees was much lower for GS (35.9 trees·16 m⁻²) with an average IPOT value of 0.11 than for US (202.5 trees·16 m⁻²) with an average IPOT of 0.11, the residual overstorey may have more impact at the stand scale.

Our models explained almost 60% of the deviance in regeneration density in both GS and US. In US, the shared deviance percentage was very high (49.8% of the total explained deviance), probably the result of strong relationships between soil preparation and soil factor variables and spatial predictors, indicating the importance of processes across scales. In contrast, the high percentage of regeneration explained by the pure spatial component in GS suggests that we have not captured important factors that have shaped regeneration spatial patterns. This remaining spatial variation structure could be due to a combination of biotic or abiotic factors that influence regeneration spatial distributions at a large scale, including seed predation (Manson et al. 1998) or animal dispersal (García and Houle 2005). Further, since extractions are much more frequent in GS,

greater disturbances of the soils occurred creating more favourable conditions for germination. This positive impact of partial harvests was observed by Kerr (2000) for Corsican pine (*Pinus nigra* Arn. subsp. *laricio*).

Management implications

Since the stands studied occupy the southernmost distribution of Scots pine and therefore suffer severe summer droughts, managing to reduce competition for scarce water resources is more important than in forests of northern Europe. The results derived from this study suggest that ground-level disturbance to break up the herb or organic layer may be required for regeneration establishment. This may occur during repeated partial harvests; otherwise, soil preparation may be required. If thinning is early and pronounced, increased light can cause a corresponding increase in herbs, creating a physical barrier for regeneration establishment and increasing water competition during summer. Soil preparation reduces competition for resources, particularly for water during summer months, and exposes a better seedbed. Timing soil preparation to coincide with abundant seed production and not with extreme drought is important for regeneration success. Alternatively, if harvest events are less pronounced and spaced over time, regeneration will occur more gradually over time, as evidenced by the diversity of ages in the group shelterwood stand.

This study also indicates that increasing the duration of the regeneration period would increase structural diversity throughout the whole rotation period (Barbeito et al. 2009b), as regeneration cohorts are created over the stand. The relationship between regeneration density and overstorey structure has been found to be critical at smaller scales

where adult trees affected light and soil moisture values (Montes and Cañellas 2007; Barbeito et al. 2009a). In this study, this small-scale variation in regeneration density related to overstorey competition was found for the US stand only, since the GS stand had a limited range for the competition measure. Overall, regeneration strategies need to focus on managing overstorey trees to reduce competition and create gaps (see Barbeito et al. 2009a).

To better understand regeneration dynamics in managed Mediterranean forests, particularly the relationships between ecological factors and regeneration abundance, further studies using a multiscale approach that integrates small scale and stand-level scale (and even forest-level scale) (e.g., García et al. 2009) are needed. The interplay of soil preparation and timing and intensity of removals along with spatial distributions of residual trees could be better assessed through designed experiments for small- and medium-scale processes. However, it is unlikely that designed experiments could be used to investigate relationships at very large spatial scales. Instead, a modelling approach, such as that used in this study, is needed. To improve knowledge of regeneration, long-term monitoring of variables reflecting processes at many scales would be needed to determine how spatial dependence varies over time.

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References

- Aussenac, G. 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Ann. For. Sci.* **57**(3): 287–301. doi:10.1051/forest:2000119.
- Barbeito, I., Fortin, M.-J., Montes, F., and Cañellas, I. 2009a. Response of pine natural regeneration to small-scale spatial variation in a managed Mediterranean mountain forest. *Appl. Veg. Sci.* **12**(4): 488–503. doi:10.1111/j.1654-109X.2009.01043.x.
- Barbeito, I., Cañellas, I., and Montes, F. 2009b. Evaluating the behaviour of vertical structure indices in Scots pine forests. *Ann. For. Sci.* **66**(7): 710. doi:10.1051/forest/2009056.
- Beland, M., Agestam, E., Ekö, M., Gemmel, P., and Nilsson, U. 2000. Scarification and seedfall affects natural regeneration of Scots pine under two shelterwood densities and a clear-cut in southern Sweden. *Scand. J. For. Res.* **15**(2): 247–255. doi:10.1080/028275800750015064.
- Borcard, D., and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol. Model.* **153**(1–2): 51–68. doi:10.1016/S0304-3800(01)00501-4.
- Borcard, D., and Legendre, P. 2004. *Maker2 user's guide*. Département de sciences biologiques, Université de Montréal, Montréal, Qué.
- Bravo, F., and Díaz-Balteiro, L. 2004. Evaluation of new silvicultural alternatives for Scots pine stands in northern Spain. *Ann. For. Sci.* **61**(2): 163–169. doi:10.1051/forest:2004008.
- Castro, J., Zamora, R., Hódar, J.A., and Gómez, J.M. 2004. Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limits: consequence of being in a marginal Mediterranean habitat. *J. Ecol.* **92**(2): 266–277. doi:10.1111/j.0022-0477.2004.00870.x.
- Clark, J.S., Macklin, E., and Wood, L. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecol. Monogr.* **68**(2): 213–235. doi:10.1890/0012-9615(1998)068[0213:SASSOR]2.0.CO;2.
- del Cerro Barja, A., Lucas-Borja, M.E., Martínez García, E., López Serrano, F.R., Andrés Abellán, M., García Morote, F.A., and Navarro López, R. 2009. Influence of stand density and soil treatment on the Spanish Black Pine (*Pinus nigra* Arn. ssp. *Salmannii*) regeneration in Spain. *Investig. Agrar. Sist. Recur. For.* **18**: 167–180.
- Eerikäinen, K., Miina, J., and Valkonen, S. 2007. Models for the regeneration establishment and the development of established seedlings in uneven-aged, Norway spruce dominated forest stands of southern Finland. *For. Ecol. Manag.* **242**(2–3): 444–461. doi:10.1016/j.foreco.2007.01.078.
- Fajardo, A., and McIntire, E.J.B. 2007. Distinguishing microsite and competition processes in tree growth dynamics: an a priori spatial modeling approach. *Am. Nat.* **169**(5): 647–661. doi:10.1086/513492. PMID:17427135.
- Fortin, M.-J., and Dale, M.R.T. 2005. *Spatial analysis. A guide for ecologists*. Cambridge University Press, Cambridge, U.K.
- Fortin, M.-J., and Melles, S.J. 2009. Avian spatial responses to forest spatial heterogeneity at the landscape level: conceptual and statistical challenges. *In* *Real world ecology: large-scale and long-term case studies and method*. Edited by S. Miao, S. Carstenn, and M. Nungesser. Springer, New York. pp. 137–160.
- Fyllas, N.M., Dimitrakopoulos, P.G., and Troumbis, A.Y. 2008. Regeneration dynamics of a mixed Mediterranean pine forest in the absence of fire. *For. Ecol. Manag.* **256**(8): 1552–1559. doi:10.1016/j.foreco.2008.06.046.
- García, D., and Houle, G. 2005. Fine-scale spatial patterns of recruitment in red oak (*Quercus rubra*): what matters most, abiotic or biotic factors? *Ecoscience*, **12**(2): 223–235. doi:10.2980/i1195-6860-12-2-223.1.
- García, D., Rodríguez-Cabal, M., and Amico, G.C. 2009. Seed dispersal by a frugivorous marsupial shapes the spatial scale of a mistletoe population. *J. Ecol.* **97**(2): 217–229. doi:10.1111/j.1365-2745.2008.01470.x.
- Gómez-Aparicio, L. 2008. Spatial patterns of recruitment in Mediterranean plant species: linking the fate of seeds, seedlings and saplings in heterogeneous landscapes at different scales. *J. Ecol.* **96**(6): 1128–1140. doi:10.1111/j.1365-2745.2008.01431.x.
- Gómez-Aparicio, L., Valladares, F., Zamora, R., and Quero, J.L. 2005. Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. *Ecography*, **28**(6): 757–768. doi:10.1111/j.2005.0906-7590.04337.x.
- González-Hidalgo, J.C., De Luis, M., Raventós, J., and Sánchez, J.R. 2001. Spatial distribution of seasonal rainfall trends in a western Mediterranean area. *Int. J. Climatol.* **21**(7): 843–860. doi:10.1002/joc.647.
- González-Martínez, S.C., and Bravo, F. 2001. Density and population structure of the natural regeneration of Scots pine (*Pinus sylvestris* L.) in the High Ebro Basin (Northern Spain). *Ann. For. Sci.* **58**(3): 277–288. doi:10.1051/forest:2001126.
- Griffith, D. 2003. *Spatial autocorrelation and spatial filtering: gaining understanding through theory and scientific visualization*. Springer-Verlag, Berlin, Germany.
- Hille, M., and den Ouden, J. 2004. Improved recruitment and early growth of Scots pine (*Pinus sylvestris* L.) seedlings after fire

- and soil scarification. *Eur. J. For. Res.* **123**(3): 213–218. doi:10.1007/s10342-004-0036-4.
- Intergovernmental Panel on Climate Change. 2007. Climate change 2007. Impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, U.K., and New York.
- Juntunen, V., and Neuvonen, S. 2006. Natural regeneration of Scots pine and Norway spruce close to the timberline in northern Finland. *Silva Fenn.* **40**: 443–458.
- Kaiser, H.F. 1958. The varimax criterion for analytic rotation in factor analysis. *Psychometrika*, **23**(3): 187–200. doi:10.1007/BF02289233.
- Kerr, G. 2000. Natural regeneration of Corsican pine (*Pinus nigra* subsp. *laricio*) in Great Britain. *Forestry*, **73**(5): 479–488. doi:10.1093/forestry/73.5.479.
- Kuuluvainen, T., and Pukkala, T. 1989. Effect of Scots pine seed trees on the density of ground vegetation and tree seedlings. *Silva Fenn.* **36**: 409–422.
- Legendre, P., and Legendre, L. 1998. Numerical ecology. 2nd ed. Elsevier, Amsterdam, The Netherlands.
- LeMay, V., Pommerening, A., and Marshall, P. 2009. Spatio-temporal structure of multi-storied, multi-aged interior Douglas fir (*Pseudotsuga menziesii* var. *glauca*) stands. *J. Ecol.* **97**(5): 1062–1074. doi:10.1111/j.1365-2745.2009.01542.x.
- Mahon, C.L., Martin, K., and LeMay, V. 2008. Do cross-scale correlations confound analysis of nest site selection for chestnut-backed chickadees? *Condor*, **110**(3): 563–568. doi:10.1525/cond.2008.8561.
- Maltez-Mouro, S., García, L.V., and Freitas, H. 2009. Influence of forest structure and environmental variables on recruit survival and performance of two Mediterranean tree species (*Quercus faginea* L. and *Q. suber* Lam.). *Eur. J. For. Res.* **128**: 27–36. doi:10.1007/s10342-008-0236-4.
- Manson, R.H., Ostfeld, R.S., and Canham, C.D. 1998. The effects of tree seed and seedling density on predation rates by rodents in old fields. *Ecoscience*, **5**: 183–190.
- McCullagh, P., and Nelder, J.A. 1989. Generalized linear models. Chapman and Hall, London and New York.
- McIntire, E.J.B. 2004. Understanding natural disturbance boundary formation using spatial data and path analysis. *Ecology*, **85**(7): 1933–1943. doi:10.1890/03-0579.
- Montes, F., and Cañellas, I. 2007. The spatial relationship between the remaining trees from the previous crop and the establishment of saplings in *Pinus sylvestris* stands in Spain. *Appl. Veg. Sci.* **10**(2): 151–160. doi:10.1658/1402-2001(2007)10[151:TSRBPR]2.0.CO;2.
- Oden, N.L., and Sokal, R.R. 1986. Directional autocorrelation: an extension of spatial correlograms to two dimensions. *Syst. Zool.* **35**(4): 608–617. doi:10.2307/2413120.
- Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. Wiley, New York.
- Pardos, M., Montes, F., Aranda, I., and Cañellas, I. 2007. Influence of environmental conditions on germinant survival and diversity of Scots pine (*Pinus sylvestris* L.) in central Spain. *Eur. J. For. Res.* **126**(1): 37–47. doi:10.1007/s10342-005-0090-6.
- Pausas, J.G., Ribeiro, E., and Vallejo, R. 2004. Post-fire regeneration variability of *Pinus halepensis* in the eastern Iberian Peninsula. *For. Ecol. Manag.* **203**(1–3): 251–259. doi:10.1016/j.foreco.2004.07.061.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from www.R-project.org.
- Rubio, A., and Escudero, A. 2003. Clear-cut effects on chestnut forest soil under stressful conditions: lengthening of time-rotation. *For. Ecol. Manag.* **183**(1–3): 195–204. doi:10.1016/S0378-1127(03)00115-4.
- Siipilehto, J. 2006. Height distributions of Scots pine sapling stands affected by retained tree and edge stand competition. *Silva Fenn.* **40**(3): 473–486.
- Urbietta, I.R., Pérez-Ramos, I.M., Zavala, M.A., Marañón, T., and Kobe, R.K. 2008. Soil water content and emergent time control seedling establishment in three co-occurring Mediterranean oak species. *Can. J. For. Res.* **38**(9): 2382–2393. doi:10.1139/X08-089.
- Valkonen, S. 2000. Effect of retained Scots pine trees on regeneration, growth, form and yield of forest stands. *Investig. Agrar. Sist. Recur. For. Fuera Ser. No. 1-2000*.
- Valkonen, S., Ruuska, J., and Siipilehto, J. 2002. Effect of retained trees on the development of young Scots pine stands in southern Finland. *For. Ecol. Manag.* **166**(1–3): 227–243. doi:10.1016/S0378-1127(01)00668-5.
- Venables, W.N., and Ripley, B.D. 2002. Modern applied statistics with S. 4th ed. Springer, New York.
- Whittaker, J. 1984. Model interpretation from the additive elements of the likelihood function. *Appl. Stat.* **33**(1): 52–64. doi:10.2307/2347663.
- Wu, H.-I., Sharpe, P.J.H., Walker, J., and Penridge, L.K. 1985. Ecological field theory: a spatial analysis of resource interference among plants. *Ecol. Model.* **29**(1–4): 215–243. doi:10.1016/0304-3800(85)90054-7.
- Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., and García, D. 2001. Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. *For. Ecol. Manag.* **144**(1–3): 33–42. doi:10.1016/S0378-1127(00)00362-5.