Linking stochasticity to determinism of woody plant recruitment in a mosaic landscape: A spatially explicit approach

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Abstract

Here, we investigate small-scale spatial variation of environmental factors potentially influencing woody-plant establishment for 3 years (2004, 2005 and 2006) along a heterogeneous landscape. Environmental variables of over 2883 potential microsites were sampled in different landscape units with a spatially explicit design, and seeds of four tree species were sown at the different microsites. We used spatial-analysis techniques to quantify spatial heterogeneity of the environment surrounding the seeds, and to relate seedling and sapling survival to the spatial structure of environmental factors studied. Most environmental variables showed aggregated spatial patterns among landscape units. However, survival showed random spatial patterns in most of the cases, although it may depend on year-to-year variation of precipitation. Thus, spatial patterns of survival were random under both wet and dry conditions, while aggregated patterns emerged under intermediate conditions. Aggregated survival, if detected, was better explained by the environmental variables studied as plant age increased. In addition, the spatial consistency found across demographic stages, represents hotspots of recruitment, for which direct identification would be critical for restoration activities. Our results showed a balance between stochasticity at early stages and environmental determinism at later stages, showing, behind the idiosyncratic character of plant recruitment, stronger general rules at sapling stages.

Zusammenfassung

Über drei Jahre hinweg (2004, 2005 und 2006) untersuchten wir die räumliche Variation der Umweltfaktoren auf kleinen Skalen, die möglicherweise die Etablierung von holzigen Pflanzen in einer heterogenen Landschaft beeinflusst. Die Umweltvariablen von über 2833 potenziellen Mikrostandorten wurden mit einem explizit räumlichen Design in unterschiedlichen Landschaftseinheiten erfasst und die Samen von vier Baumarten an den verschiedenen Mikrostandorten ausgesät. Wir nutzten räumliche Analysetechniken um die räumliche Heterogenität der Umwelt in der direkten Umgebung der Samen zu erfassen und um die Keimling- und Schössling-Überlebensraten in Beziehung zu der räumlichen Struktur der untersuchten Umweltfaktoren zu setzen. Die meisten der Umweltvariablen zeigten ein gehäuftes räumliches Muster in den Landschaftseinheiten. Die Überlebensraten zeigten jedoch in den meisten dieser Fälle zufällige räumliche Muster, obwohl dies von dem von Jahr zu Jahr variierenden Niederschlag abhängen könnte. Daher waren die räumlichen Muster der Überlebensrate sowohl unter trockenen

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wie auch feuchten Bedingungen zufällig, während die gehäuften Muster bei mittelmäßigen Bedingungen auftauchten. Wenn aggregiertes Überleben festgestellt wurde, konnte dieses besser durch die erfassten Umweltvariablen erklärt werden, wenn das Pflanzenalter zunahm. Darüber hinaus repräsentierte die räumliche Durchgängigkeit, die über die demographischen Stadien hinweg gefunden wurde, Hotspots der Rekrutierung. Deren direkte Identifizierung könnte für Naturschutzaktivitäten wichtig sein. Unsere Ergebnisse zeigen eine Balance zwischen der Zufälligkeit in frühen Stadien und der Bestimmung durch die Umwelt in den späteren Stadien, und sie zeigen, neben dem spezifischen Charakter der Pflanzenrekrutierung, strengere allgemeine Regeln im Schösslingsstadium.

Introduction

Because plants are sessile organisms, their fate is determined by site characteristics (Silvertown 1981). For long-lived plants, successful establishment is often restricted to a temporal and/or spatial window of favourable conditions, such as gaps produced by a tree fall, or an unusually rainy year in a variable environment. Because early recruitment is the most variable and least predictable demographic stage, it is critical to define the biophysical characteristics determining seedling-establishment success (the safe site concept; Harper, Clatworthy, McNaughton, & Sagar 1961). The scale of the safe site was traditionally emphasized by the "microsite" or "microhabitat" terminology. However, little is known concerning the role of spatial heterogeneity on plant recruitment at a small scale. This role is crucial since several studies have shown that abiotic factors vary in space, even within a few meters or even centimetres (Lechowicz & Bell 1991). Consequently, the dynamic of safe sites changes in both space and time as a result of abiotic and biotic factors (Urbanska 1997), although some general rules behind such idiosyncratic recruitment have been described for seeds and seedlings (Hampe, García-Castaño, Schupp, & Jordano 2008). Nevertheless, we are not aware of studies explicitly considering spatio-temporal components over further stages in recruitment. Therefore, new analytical approaches are needed in order to disentangle the demographic responses from the spatial variability linked to ecological factors. Two basic components can be considered as a means of defining the ecological variation associated with spatial heterogeneity (Borcard, Legendre, & Drapeau 1992): (1) the spatial component, which acts as a synthetic variable for the underlying processes that govern the spatial pattern, and (2) the environmental component, which is the fraction of the variation that can be explained by environmental descriptors independent of any spatial structure. The combination of these two components (space and environment) can determine the probabilities of recruitment under a broad sample of ecological conditions. Thus, recent work has demonstrated the importance of incorporating the spatial component in research on plant-regeneration dynamics (Beckage & Clark 2003), although there are few studies that analysed explicitly the spatial component of plant survival (but see Maestre, Cortina,

Bautista, Bellot, & Vallejo 2003; Messaoud & Houle 2006). Furthermore, it remains unknown to what extent the spatial and temporal variation in recruitment dynamics interact in heterogeneous, real landscapes, and which of these components has greater effects on regeneration patterns.

This paper examines whether the spatial survival pattern of Mediterranean woody seedlings and saplings was related to environmental spatio-temporal patterns at the microsite scale in three major landscape units of a Mediterranean mountain region (Sierra Nevada National Park, SE Spain): native forest, pine reforestation stand and shrubland (Matías et al. 2009). In each landscape unit, we conducted a multivariate characterization of ca. 1000 microsites approximately 1 m apart. In these microsites, seeds of four tree species were sown, rather than planted, to create more realistic conditions. Sowings were done in three different seasons, allowing us to assess demographic responses to temporal variability of precipitation over three years and to identify microsites with higher probabilities of long-term survival. The observed spatial survival patterns were related to inter-annual variability in spring and summer precipitation. We hypothesised that the small-scale survival pattern underlies larger-scale variations such that (Fig. 1): (a) relatively wet summer conditions will
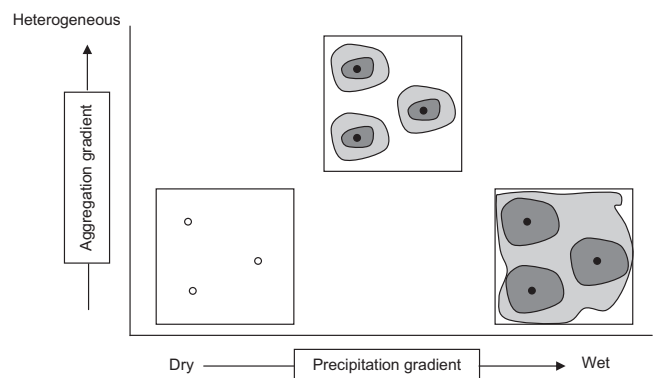

Fig. 1. Conceptual scheme showing our working hypothesis on the relationship between spatial pattern of survival and precipitation. The grey scale, from white to black, indicates survival probability from low to high. The spatial pattern of survival will be regular or random when summer conditions are extremely dry or wet. Under intermediate precipitation, aggregated spatial patterns will emerge.

result in high survival along the space, due to high microsite availability, and no aggregated survival will emerge; (b) on the contrary, relatively dry summer conditions will result in low survival along the space and, again, there will be no aggregated survival due to unsuitability of microsites; (c) aggregated spatial patterns might emerged only under intermediate climatic conditions, since the spatial structure of environmental variables will influence the spatial survival pattern.

Specifically, our main questions were: (1) What is the small-scale spatial pattern of environmental variables across landscape units? (2) What is the small-scale spatial pattern of seedling and sapling survival? (3) Does the spatio-temporal pattern of survival relate to small-scale environmental heterogeneity and rainfall? (4) To what extent are the suitable and unsuitable sites of recruitment predictable across years? (5) Are the results potentially applicable for restoration and reforestation programs?

Materials and methods

Study sites

The study was conducted in Sierra Nevada National Park, surrounding the Trevenque Peak area (Granada Province, SE Spain), during 2004, 2005, and 2006. The climate is of the Mediterranean mountain type, with hot, dry summers and cold, snowy winters, and high rainfall (879 mm year^{-1}, average 1990–2006), which is heaviest in autumn and spring. The bedrock is calcareous and the predominant soils are regosols and cambisols (see Castro, Zamora, Hódar, & Gómez 2004 for more information concerning the area). This protected area (1600–1900 m a.s.l.) is a mosaic landscape composed of three main units: shrubland, reforestation stand, and native forest (see Appendix A: Fig. 1). The native forest (37°04′54″N, 3°28′17″W, 1680 m a.s.l.) is mainly composed of *Pinus sylvestris* ssp. *nevadense* Christ. mixed with other trees such as *Sorbus aria* L. Crantz., *Quercus ilex* L. ssp. *ballota* (Desf.) Samp. or *Acer opalus* ssp. *granatense* (Boiss.) Font Quer & Roth., and a dense shrubby understory composed of different fleshy-fruited shrub species. The reforestation stand (planted around 1950) (37°04′33″N, 3°28′18″W, 1790 m a.s.l.) contains *Pinus sylvestris* L. (ca. 70% in the studied plot) and *Pinus nigra* Arnold., with a total density of 521 individuals ha^{-1}. The shrubland (37°04′50″N, 3°27′50″W, 1825 m a.s.l.) is a post-fire area (burnt in 1983) dominated by the pioneer shrubs *Salvia lavandulifolia* Vahl. and *Erinacea anthyllis* Link.

Sampling design

In each of the three landscape units, a 31 m × 31 m plot was established in a representative area. In each 31 m × 31 m plot, 961 sampling points (hereafter points) were established using a 1 m × 1 m sampling grid. Plots were fenced to avoid trampling by cattle and wild ungulates. To achieve a spatially explicit design, X and Y coordinates of each point were determined using a Total Station (model DTM-332, Nikon, Tokyo, Japan). At each point, environmental variables were measured in a circular plot 0.30 m in diameter, following the "plant's eye-view" approach, which is based on measurements of habitat structure immediately surrounding the sampling point (Quero, Gómez-Aparicio, Zamora, & Maestre 2008). The following variables were measured: average soil compaction, depth of the maximum soil-compaction value, light availability, soil moisture, depth of the litter layer, cover of herbaceous species, stone and moss cover, woody debris cover, shrub cover, and percentage of micro-slope, a soil-surface micro-topography parameter. Soil compaction was measured using a Penetrologger penetrometer (Eijkelcamp, Giesbeek, Netherlands). This device provides a 60 cm profile describing the variation of soil compaction with depth (every 1 cm) at each point. From these profiles, two variables relevant for rooting capacity and seedling establishment (Gómez-Aparicio, Valladares, Zamora, & Quero 2005) were determined: (1) the average compaction over the profile and (2) the depth of maximum compaction. (3) Light availability (hereafter, GSF) was quantified with hemispherical photography. Photographs were taken at each sampling point using a standard procedure (see Puerta-Piñero, Gómez, & Valladares 2007 for a complete description of the method). Global site factor (GSF) is a continuous variable ranging from 1 (open sky) to 0 (complete cover interception). (4) For the three study years, we measured soil moisture (volumetric water content, VWC) in the first 20 cm of depth (with a TDR mod 100; Spectrum Technologies, Inc., Plainfield, IL, USA) at the middle of spring and after summer (before autumn rains). (5) Depth of the litter layer was measured by inserting a metal ruler down to the soil surface. Different percentages of cover, (6) herbaceous, (7) stone and moss, (8) woody debris and (9) shrub, were visually estimated. (10) Micro-topography was measured using the Total Station (see above), which determined at each point the relative altitude (relative Z coordinate) with respect to the lowest point in each landscape unit. Percentage of micro-slope was calculated at each point, taking into account relative Z of surrounding points. This parameter was determined using ArcGIS v9 (ESRI, Redlands, CA, USA).

Sowings

In January 2004, 2005, and 2006, seeds of four tree species were sown in each 31 m × 31 m plot: *Sorbus aria*, *Quercus ilex* ssp. *ballota*, *Acer opalus* ssp. *granatense* and *Pinus sylvestris* ssp. *nevadensis* (hereafter, *S. aria*, *Q. ilex*, *A. opalus*, and *P. sylvestris*, respectively). These tree species are major components of the study site (see above and Castro et al. 2004). Seeds were sown in a spatially homogeneous sub-sample of 300 sampling points. In each year, each species was sown at different sampling points. Within sampling points, seeds were separated enough to avoid intra- and inter-specific competition among seedlings. We sowed one acorn of *Q. ilex*

per point, whereas 3 seeds per point were sown for the rest of species due to lower seed viability (García-Fayos 2001). Seeds were buried at ca. 3 cm. During the three years, emergence and survival was monitored in spring and after summer, respectively. Evidence of seed predation was recorded in each spring season, being marginal for the native forest and the reforestation stand.

Data analysis

Quantifying the spatial pattern of environmental variables and seedling survival

We used different indices produced by SADIE (spatial analysis by distance indices, Perry 1998): the index of aggregation (I_a) provides information on the overall spatial pattern of each environmental variable. The spatial pattern is aggregated if $I_a > 1$, random if I_a is close to one, and regular if $I_a < 1$. The index of clustering (v) measures the degree of clustering of the data into patches (areas of high values of the target variable) and gaps (areas of low values); v is a continuous variable, thus data can be contoured by kriging in a two-dimensional map, showing their spatial distribution. Points within patches have values of $v \geq 1.5$, whereas those within gaps have values of $v \leq -1.5$ (Perry & Dixon 2002).

Spatial covariation of survival per species across years was studied with the SADIE overall association index (χ), which measures whether two variables are spatially associated, dissociated or not related. Indeed, χ is the correlation coefficient between the values of v of two variables (Perry & Dixon 2002). Since sowings within species were not done at the same sampling points, v values for all sampling points were interpolated using ordinary block kriging (Maestre & Cortina 2002). The local association index (χ) reveals local characteristics of spatial association between two variables undiscovered by the analysis of their overall association (Anselin 1995). Positive values of χ indicate the presence of coincidences of patches and gaps in both variables, while negative values indicate the presence of a patch in one variable and a gap in the other (Perry & Dixon 2002). Similar to v, χ is a continuous variable that can be mapped and contoured for graphic display.

For environmental variables, we performed a separate SADIE analysis per variable and landscape unit; continuous variables were categorized according to Maestre and Quero (2008). For seedling survival, a SADIE analysis was made for each species, cohort, and landscape unit. Over the three study years, seedling survival was highly variable (Fig. 2); therefore, we analysed only the cases with more than 30 sampling points with emerged individuals. SADIE analysis was made using SadieShell v.1.3. To draw either the spatial pattern or spatial covariation of studied variables, we produced v and χ maps with SURFER v 8.0 (Golden Software, Golden, CO, USA).

Relating spatial pattern of survival to small-scale environmental heterogeneity

When spatial pattern of survival was aggregated, we performed a binomial logistic regression in combination with a variance-partition method (Borcard et al. 1992). Binomial logistic regressions modelled the spatial pattern of plant survival as a function of the environmental variables measured (Hosmer & Lemeshow 1989), and the variance-partition method employs R-squares of the binomial logistic regressions to evaluate the importance of environmental variables with respect to the spatial aggregation of survival, and their relative importance with respect to spatially structured biotic and abiotic factors not considered in the study (see Maestre et al. 2003 for further details). This approach provides a partitioning of seedling survival into four fractions of variation: (a) survival explained by environmental variables independent of any spatial structure (fraction *a*), (b) survival explained by the spatial structure of environmental variables (fraction *b*), (c) survival explained by the spatial structure independent of any environmental variables (fraction *c*), and (d) survival explained by neither environmental nor spatial variables (fraction *d*). We transformed continuous data to meet normality and to achieve a more stable solution (Norŭsis 1997). Before the analyses, we checked for colinearity of environmental variables by performing multiple linear regressions separately for each environmental variable, where the variable in question was the dependent variable, and the remaining environmental variables used as independent variables. We calculated the variance inflation factor (VIF) among the different variables as an indicator for colinearity. The VIF was in all cases lower than 7, indicating lack of colinearity among environmental variables (Chatterjee & Price 1991). Both logistic and multiple linear regressions were performed with SPSS v14.0 (SPSS Inc, Chicago, IL, USA).

Results

Precipitation patterns

Comparing the three sowing dates, 2004 and 2006 were wetter than 2005. Accumulated precipitation in 2004 was 460 and 44 mm in spring and summer, respectively. In 2005, accumulated precipitation was 56 and 8 mm in spring and summer, respectively. In 2006, accumulated precipitation was 165 and 18 mm in spring and summer, respectively (see Appendix A: Fig. 2).

Spatial pattern of environmental variables

SADIE analysis showed an aggregated spatial pattern for most of the environmental variables studied ($I_a > 1$) across landscape units (Table 1). Mean aggregation indices were higher in the native forest and reforestation stand than in the shrubland ($P < 0.05$). Light availability in the native forest
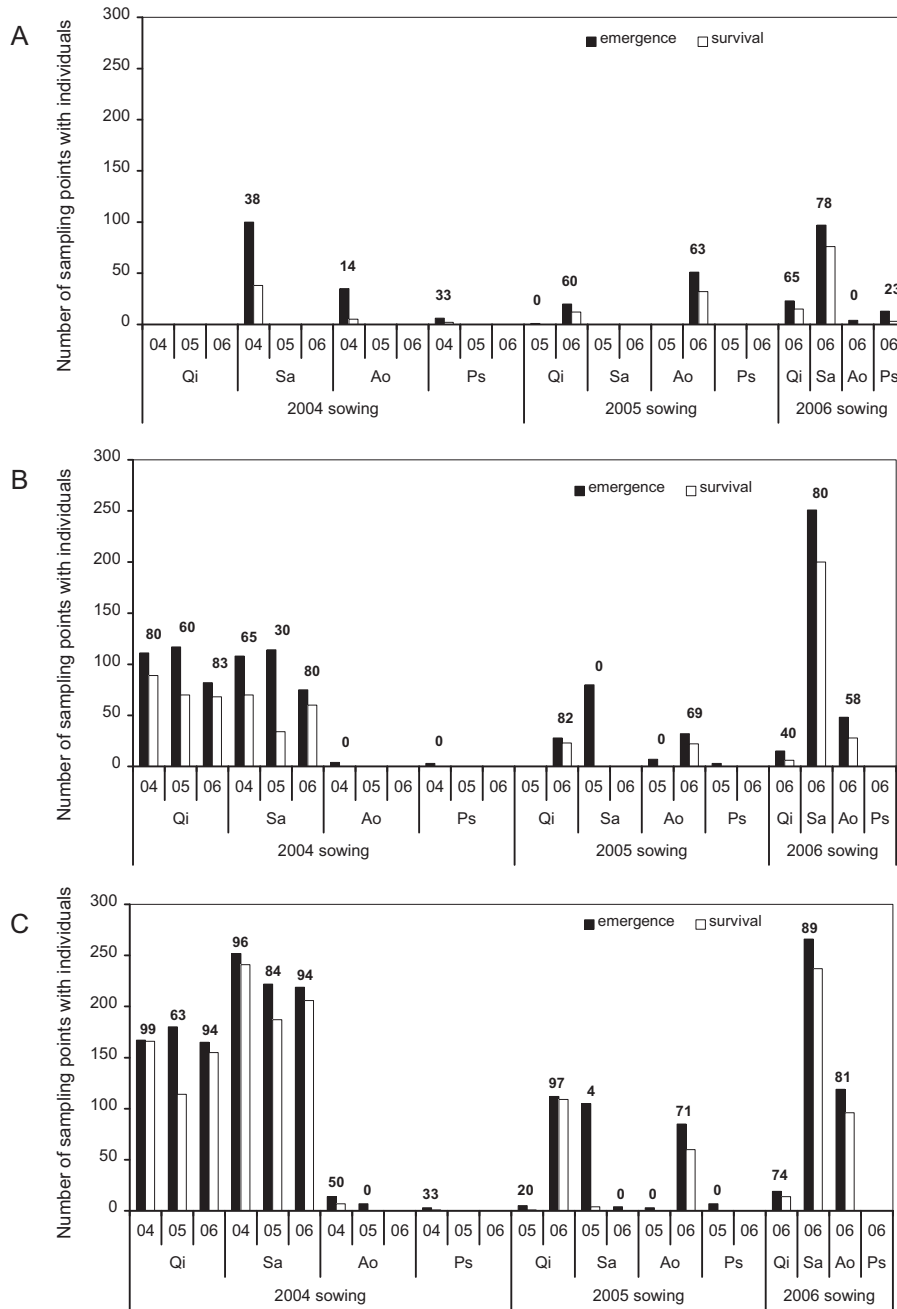
Fig. 2. Number of sampling points with individuals of the studied species in each landscape unit. (A) Shrubland, (B) Native forest, and (C) Reforestation stand. Years (2004, 2005 and 2006) indicate the censuses in each sowing year, emergence in spring and survival after summer. Numbers above the columns indicate survival percentage in each case, calculated as sampling points with emerged plants/sampling points with plant survived after the summer. Qi (*Quercus ilex* ssp. *ballota*); Sa (*Sorbus aria*); Ao (*Acer opalus* ssp. *granatense*); Ps (*Pinus sylvestris* ssp. *nevadensis*).

had a higher I_a value in comparison to the reforestation and shrubland sites (Table 1 and Appendix A: Fig. 3). Temporal variation of soil moisture spatial patterns were found: in the "wet" year (2004), soil moisture heterogeneity at the native forest and reforestation sites increased from spring to the end of the summer; the same trend was observed in the reforestation and shrubland sites during the "dry" year (2005) (Table 1 and Appendix A: Fig. 4).

Plant performance

Following the spring rains, the highest emergence rates for all species were found in 2004, except at the shrubland site (Fig. 2A) at which plant establishment from seed may have been impeded by stony ground, minimal tree cover and a high rate of seed predation of *Q. ilex*. Likewise, emergence in the "dry" year (2005) was lower than in 2004 and 2006

Table 1. Aggregation index-values (I_a) and level of significance ($*P<0.05$) describing the spatial pattern of environmental variables studied in three different landscape units. If $I_a > 1$, the spatial pattern is aggregated; when I_a is close to unity, the pattern is random, and regular, if $I_a < 1$. GSF: global site factor (relative units, see M&M section); % VWC, percentage of volumetric water content. Mean ± SD, and minimum and maximum values are also shown ($n = 961$ for each habitat type).

Variable	Unit		Native forest	Reforestation	Shrubland
Average soil compaction	MPa	I_a	**10.7***	**7.1***	**5.6***
		Mean ± SD	2.56 ± 0.89	2.04 ± 0.77	1.28 ± 0.67
		Min–Max	0.18–5.05	0.12–4.26	0.11–3.80
Depth of the maximum soil compaction value	cm	I_a	**2.7***	**2.3***	**2.1***
		Mean ± SD	36.8 ± 12.3	31.5 ± 13.9	22.2 ± 9.6
		Min–Max	4.0–53.0	4.0–54.0	3.0–53.0
Light availability (GSF)	%/100	I_a	**6.2***	**2.6***	**1.7***
		Mean ± SD	0.15 ± 0.05	0.13 ± 0.04	0.76 ± 0.16
		Min–Max	0.02–0.33	0.02–0.25	0.11–0.95
Soil moisture spring 04	%VWC	I_a	**3.7***	**3.1***	**1.6***
		Mean ± SD	35.3 ± 5.9	32.9 ± 6.1	19.3 ± 4.3
		Min–Max	16.0–62.0	8.0–51.0	7.0–36.0
Soil moisture summer 04	%VWC	I_a	**5.2***	**3.8***	**1.3***
		Mean ± SD	9.23 ± 2.46	11.1 ± 2.8	5.7 ± 1.7
		Min–Max	3.0–21.0	3.0–25.0	4.0–20.0
Soil moisture spring 05	%VWC	I_a	**2.9***	**2.8***	**1.5***
		Mean ± SD	7.93 ± 2.03	11.30 ± 2.90	8.06 ± 1.80
		Min–Max	2–13	1–19	4–16
Soil moisture summer 05	%VWC	I_a	**2.5***	**3.3***	**3.1***
		Mean ± SD	4.58 ± 1.30	5.47 ± 1.81	3.98 ± 0.95
		Min–Max	1–10	1–12	2–11
Soil moisture spring 06	%VWC	I_a	**3.1***	**6.1***	**1.9***
		Mean ± SD	24.5 ± 4.7	24.5 ± 5.3	21.6 ± 4.5
		Min–Max	7–43	8–41	11–38
Soil moisture summer 06	%VWC	I_a	**2.7***	**5.3***	**2.3***
		Mean ± SD	5.48 ± 1.51	6.23 ± 2.20	4.22 ± 1.02
		Min–Max	1–12	1–13	2–10
Depth of the litter layer	mm	I_a	**3.9***	**6.9***	**1.6***
		Mean ± SD	53.7 ± 26.2	52.8 ± 28.5	17.7 ± 4.2
		Min–Max	0–170	10–190	0–100
Cover of herbaceous species	%	I_a	**2.8***	**4.3***	**5.2***
		Mean ± SD	19 ± 25	5 ± 10	8 ± 13
		Min–Max	0–100	0–80	0–95
Stone and moss cover	%	I_a	0.9	**1.9***	**1.7***
		Mean ± SD	0.2 ± 1.4	1 ± 7	8 ± 13
		Min–Max	0–35	0–80	0–95
Woody debris cover	%	I_a	**2.3***	**2.6***	**1.9***
		Mean ± SD	16 ± 13	14 ± 10	1 ± 4
		Min–Max	0–100	0–60	0–75
Shrub cover	%	I_a	**3.1***	**1.3***	**2.4***
		Mean ± SD	8 ± 14	4 ± 10	31 ± 29
		Min–Max	0–90	0–85	0–100
Micro slope	%	I_a	**7.1***	**9.5***	**3.8***
		Mean ± SD	28.2 ± 8.1	19.2 ± 5.8	21.8 ± 7.7
		Min–Max	8.6–49	0.5–37.3	2.6–58.2

(Fig. 2). *P. sylvestris* had low or null emergence in the native forest and the reforestation stand sites during the three study years (Fig. 2B and C). Similar to emergence, survival after summer varied among years; survival was lower after the dry summer (2005) in comparison to after wetter summers (2004 and 2006).

Spatial survival patterns

When sample size was suitable for analyses of spatial survival patterns, evidence of aggregated survival was found in 3 out 23 cases, being *S. aria* the only species with survival aggregation (Table 2). In the remaining cases, I_a was

Table 2. SADIE aggregation indices (I_a) of survival for the different surveys. Significance level according to a permutation test is indicated by an asterisk (*$P < 0.05$; **$P < 0.01$). Spatial survival pattern is aggregated if I_a is significant and positive. I_a values lower than 1 show a regular spatial pattern and I_a values close to 1 and not significant indicate a random spatial pattern. For *P. sylvestris*, SADIE analysis was not performed due to low sample size ($n < 30$).

Habitat type and sowing year	Species and survey								
	Quercus ilex			*Sorbus aria*			*Acer opalus*		
	2004	2005	2006	2004	2005	2006	2004	2005	2006
Native forest									
2004	1.3	0.9	1.0	1.1	1.0	**1.5***	×	×	×
2005		×	×	†	×			×	1.1
2006			×			**1.4***			1.2
Reforestation stand									
2004	†	0.9	1.0	1.1	**1.6****	0.9	×	×	×
2005		×	1.2		0.9	×		×	1.2
2006			×			1.0			1.0
Shrubland									
2004	×	×	×	1.2	×	×	1.1	×	×
2005		×	×		×	×			×
2006			×			1.2			1.1

(×) SADIE analysis was not performed because sample size was too small ($n < 30$).
(†) SADIE analysis was not performed because of high (>99%) or low (0%) survival rates (see Fig. 2).

close to 1 and non-significant, indicating random patterns of survival within the plots. These results depended on sowing year: after the wettest summer (2004), no species had a spatially aggregated pattern of seedling survival in the native forest and reforestation stands. This was likely due to high rates of seedling survival at most of the survey points. After the driest 2005 year, there was only one case in which 2-year-old saplings exhibited aggregated survival (*S. aria* in the reforestation stand, Table 2); these individuals most likely survived the harsh 2005 summer because their larger root systems allowed them to obtain enough soil moisture to survive the summer. On the contrary, after the milder summer of 2006, we found aggregated spatial patterns for *S. aria* seedlings and 3-year-old saplings (Table 2). Maps with clustering indices revealed patches and gaps of survival in these cases (Fig. 3). Indeed, spatial covariation analysis of survival showed an overall spatial association between 2006 *S. aria* seedlings and *S. aria* 3-year-old saplings in native forest ($\chi = 0.32$, $P < 0.001$). The map of χ-values (Fig. 4) revealed patches of spatial association of survival, suggesting that 2006 *S. aria* seedlings survived in the same areas as three-year-old saplings of *S. aria*.

Variation partitioning of aggregated spatial patterns of survival

The total variation explained was lowest for one-year-old *S. aria* seedlings in the native forest (14%), followed by 2-year-old *S. aria* saplings in the reforestation stand (23%) and 3-year-old *S. Aria* saplings in native forest (52%), suggesting an increase over time in the variation explained by the spatial structure and the environmental variables studied (Fig. 5). The fraction of variation explained by environmental variables that was independent of any spatial structure (fraction *a*) was highest for the three-year-old saplings in the native forest. Fraction b, which represents the spatial structure of the environmental variables, ranged from 0 to 10%, suggesting either a moderate or a null relationship between spatial pattern of survival and the spatial structure of environmental variables. Variation explained by the spatial structure independent of any environmental variables (fraction *c*) was low for seedlings (3%) and moderate in two- and three-year-old saplings (13 and 19%, respectively). The amount of unexplained variation (fraction *d*) was quite high in the three cases studied, especially at the earlier stages.

Discussion

We examined whether spatial and temporal variation in environmental variables was crucial for woody-plant establishment in Mediterranean mountain ecosystems. Our sowing experiment showed that seedling emergence and plant survival varied among the studied landscape units, and that a strong random component was linked to spatial patterns of early survival. However, when aggregated patterns were revealed in *S. aria*, spatial consistency of survival patches was shown to persist over years, and this survival aggregation was better explained by the heterogeneity of environmental variables as plants grew older.
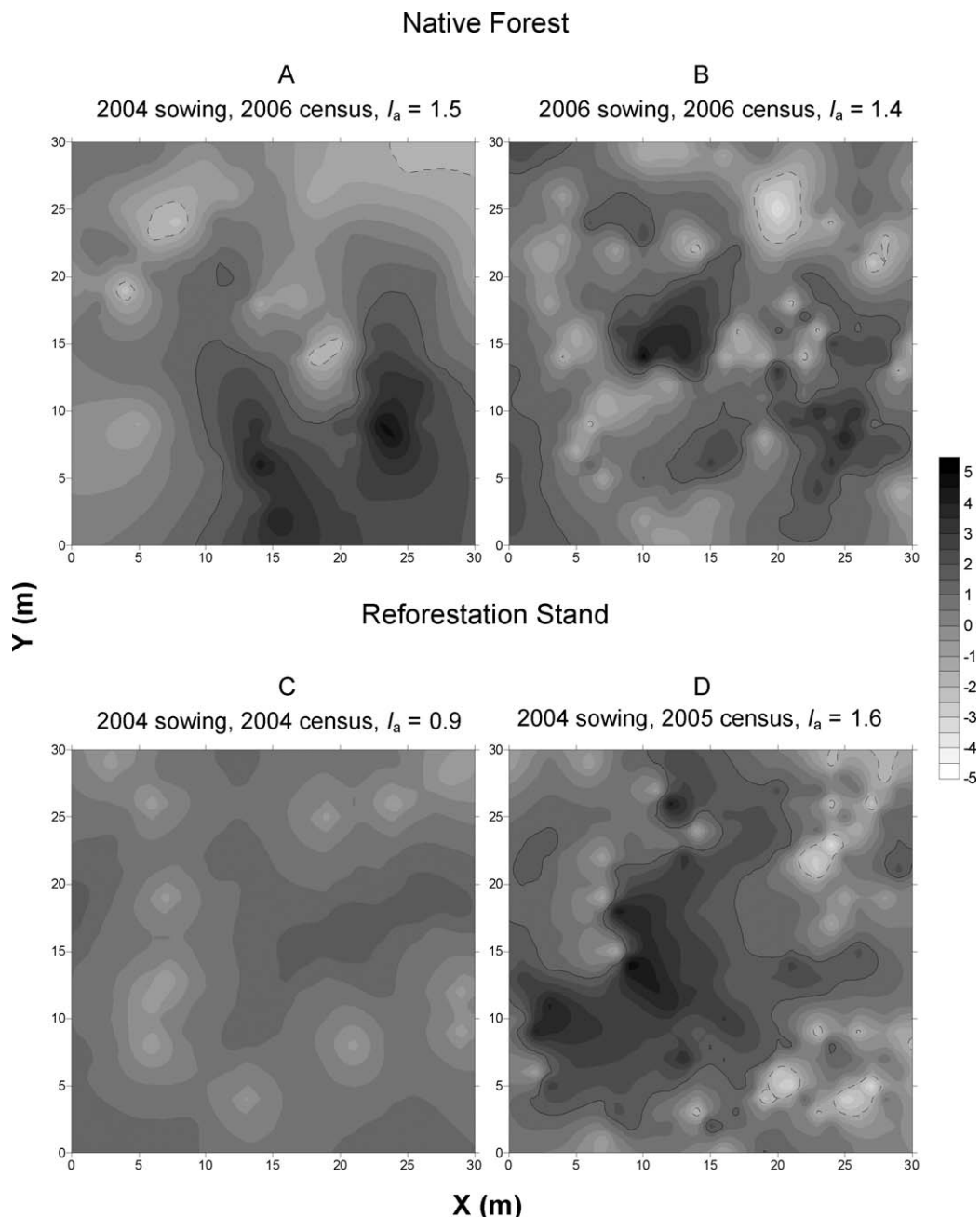
Native Forest

Fig. 3. Maps of SADIE clustering indices (ν) of survival for *Sorbus aria* in native forest and reforestation stands. Dark areas delimited by solid black lines indicate survival patches ($\nu > 1.5$) and light areas delimited by dashed black lines indicate gaps of mortality ($\nu < -1.5$). For brevity, only the three cases with survival heterogeneity (see Table 2) plus one example of regular spatial pattern (subfigure C) is shown.

Spatial heterogeneity of environmental variables and spatial patterns of survival

The spatial-analysis methods used in this study showed that fine-scale spatial aggregations of environmental variables are the general pattern (Table 1, see also Gallardo, Rodríguez-Saucedo, Covelo, & Fernandez-Alés 2000; Maestre et al. 2003; Valladares & Guzmán 2006). Furthermore, the present study shows that small-scale spatial heterogeneity varies with landscape unit. Thus, the shrubland site had the lowest aggregation indices, indicating a reduced microsite range attributable to low structural complexity such as shrub patches and open interspaces (Gómez-Aparicio, Valladares, et al. 2005). In contrast, the native forest and the reforestation sites were characterized by higher structural complexity (e.g., trees, shrubs, woody debris, and small gaps) that resulted in a broader, more continuous spectrum of microsites.
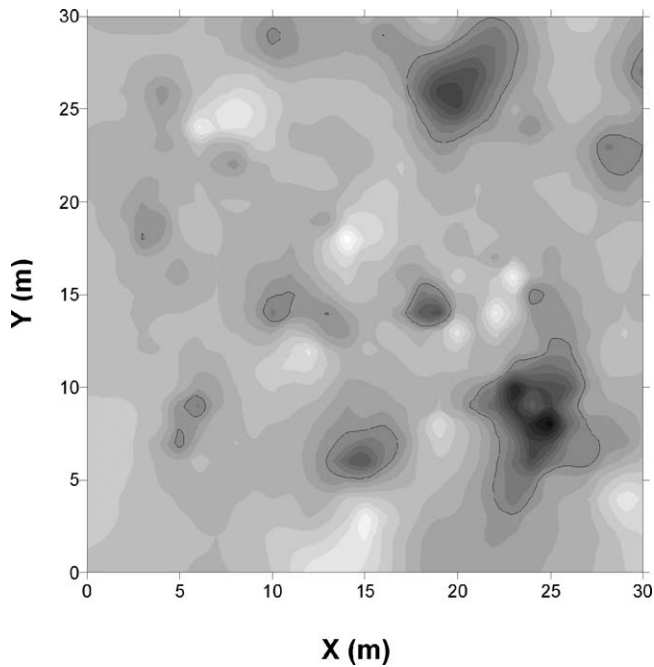
Fig. 4. Map of SADIE local association indices (χ) between 2006 seedlings and 3-year-old saplings of *Sorbus aria* in native forest. Dark and light areas indicate association and dissociation areas of both cohorts, respectively, being delimited by solid black lines where significant ($P < 0.05$).

As opposed to fine-scale patterns of environmental variables, fine-scale patterns of survival are not the norm in this study (Table 2), suggesting that the spatial patterns of environment do not translate into spatial survival patterns (Gómez-Aparicio, Valladares, et al. 2005). Hence, the detected environmental variability may not have biological relevance for recruits. On the other hand, some environmental components such as precipitation can play an important role on plant establishment beyond the microenvironment, by reducing plant responses to fine-scale environmental heterogeneity and, therefore, the probability of aggregated spatial patterns. Indeed, rainfall temporal patterns during the three study years appeared to cause highly variable survival, rang-
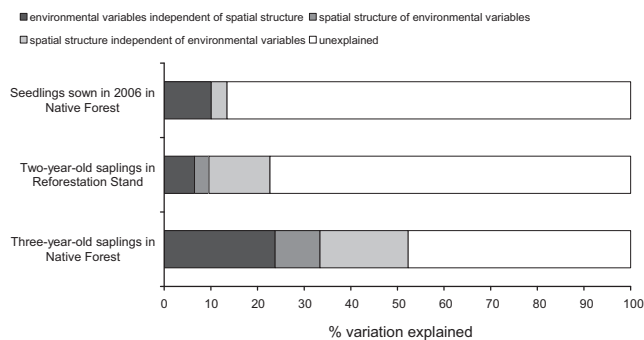

Fig. 5. Summary of variation partitioning of survival for *Sorbus aria* in native forest and reforestation stands. The fractions of variation explained by three factors are shown in grey scale.

ing from about 100% after the wet summer of 2004 to 0% after the dry summer of 2005. The importance of year-to-year variability of precipitation on plant establishment have been demonstrated in other studies (see Gómez-Aparicio, Gómez, & Zamora 2005 for *Acer opalus* or Castro et al. 2004 for *Pinus sylvestris*).

When survival aggregation was detected in *S. Aria*, the variation-partitioning method explained a moderate percentage of this spatial pattern, though the percentage explained increased with plant age. Nevertheless, the unexplained fraction was relatively high in all cases. Similar results have been reported in other studies (Borcard et al. 1992; Maestre et al. 2003). Thus, this fraction should be the consequence of other factors not included in the study (Maestre et al. 2003), which may be biotic, such as allelopathic substance of neighbour plants (Escudero, Albert, Pita, & Pérez-García 2000), seed size (Westoby, Leishman, & Lord 1996), physiological status (Gómez-Aparicio, Valladares, & Zamora 2006), and even genetic variability. The fraction explaining spatial structure regardless of environmental variables was relatively important in two-year-old saplings, suggesting some contagious biological processes that have no environmental component or no relation to the environmental variables measured (Maestre et al. 2003). In the native forest, a great part of variation was explained by environmental variables, suggesting an overlap between spatial pattern of survival and spatial structure of the environmental variables measured.

In short, the variation-partitioning analysis showed that survival aggregation in *S. aria* was partially controlled by the environmental variables studied, mainly in the case of 3-year-old saplings, indicating a stronger non-random filtering by environmental variables as the saplings' age increased. In this way, along the recruitment process, there is a combination of stochasticity at early stages and environmental determinism at further stages. Our study is the first experimental, spatially explicit approach that demonstrates this dual nature of recruitment.

Spatio-temporal pattern of plant establishment: ecological significance and implications for practice

The hypothesis of the influence of precipitation variability on spatial patterns is supported by *S. aria,* the only species suitable for making robust demographic spatial analyses in our study. For this species, spatial pattern of survival was random when summer conditions were dry (2005) or wet (2004). On the contrary, under intermediate climatic conditions, an aggregated spatial pattern emerged. Thus, along a precipitation gradient, high mortality of *S. aria* was found everywhere after the dry summer, while an aggregated spatial pattern of survival was found in the summer with moderate precipitation. On the other end of the precipitation gradient, a rainy summer resulted in high survival, which is interpreted as every point in the space was above the critical threshold

of soil moisture for *S. aria* survival. As a complementary result, patches of different ages of *S. aria* were spatially coincident across years (Fig. 4). These patches could represent hotspots with a high prospect of success, for early plant recruitment (Hampe et al. 2008) or for later demographic stages (this study). Hotspots for recruitment can be considered the interface between regeneration and restoration ecology (*sensu* Urbanska 1997) and therefore, identification of hotspots becomes critical for restoration activities. However, in spite of the observed spatial consistency in *S. aria*, the other evaluated species showed random patterns of survival (Table 2), probably due to the low sample size reached after summer for these species.

In short, our spatial explicit approach demonstrated that environmental variables exerted a strong, non-random filter on woody plant regeneration as plant's age increased. In view of this result, it is essential, before sowing or planting, to develop environmental indicators and new analytical tools to differentiate, easily and accurately, between microsites where saplings survival probability is higher, and microsites with high probability of recruitment failure. In the context of climatic variability, and given that resources invested in restoration are always limited, special care must be dedicated to identify general rules behind the stochasticity of early recruitment.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae. 2010.11.007.

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