Seed bank spatial pattern in a temperate secondary forest

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Abstract. Seed bank spatial pattern was studied in a secondary forest dominated by *Fagus sylvatica* and *Betula celtiberica* in the Urkiola Natural Park (N Spain). Soil samples were taken every 2 m in a regular grid (196 points) and divided into two fractions (0-3 cm and 3-10 cm deep). The viable seed bank was studied by monitoring seedling emergence for ten months. The effect of different factors on seed bank composition and patterning was analysed using constrained ordination as a hypothesis testing tool. Furthermore, the existence of spatial autocorrelation was evaluated by geostatistical analysis. Seed density was high, 7057 seed.m^{-2}, with a few species dominating. Species composition in the various layers were significantly correlated. The seed bank showed significant spatial structure, which was partially explainable by the spatial structure of the canopy and understorey vegetation. Spatial clumping from 0-8 m was observed in seed bank density and composition, mainly due to the pattern of two abundant taxa *Juncus effusus* and *Ericaceae*. The *Ericaceae* seed bank was related to the spatial distribution of dead stumps of *Erica arborea*. *J. effusus* was not present in the above-ground vegetation, which indicates that its seed bank was formed in the past. As expected, the seed bank of this forest reflects its history, which is characterized by complex man-induced perturbations. The seed bank appears to be structured as a consequence of contrasting driving forces such as canopy structure, understorey composition and structural and microhabitat features.

Keywords: *Betula*; Constrained ordination; *Digitalis*; *Fagus*; Forest regeneration; Hypothesis testing; Temperate forest.

Nomenclature: Aizpuru et al. (1999).

Abbreviations: TVE = Total variance explained.

Introduction

Delayed germination is a trait of many plant species (Leck et al. 1989) in a wide variety of habitats, from tropical forests to deserts (Fenner 1985; Thompson et al. 1997). This characteristic enables plants to persist under circumstances that would be fatal for emerged individuals (Easterling & Ellner 2000). It is to be expected that such a trait will be selected among species living in habitats where environmental conditions change dramatically and in an unpredictable way (Venable & Brown 1988). Building up a seed bank allows plants to dispose of numerous propagules ready to germinate whenever conditions become favourable, even when adult populations are long gone (Warr et al. 1993).

The understorey of successional forests experiences reduced amounts of light and nutrients, due to both above- and below-ground competition (Martens et al. 1997). This can cause serious problems for, or even the disappearance of, many pioneer species. Different perturbations may alter the forest structure (Oliver & Larson 1996), leading to increased light and nutrient levels. This creates temporal windows that enable the recruitment and establishment of pioneer species (Finegan 1984) and consequently the co-existence of species (Nakashizuka 2001). To cope with the stochasticity of perturbations wide dispersal capacity or delayed seed germination (through a persistent seed bank) would be favoured in pioneer plants, enabling them to respond rapidly to these temporal windows (Lorimer 1985).

Many studies have focused on the contribution of seed banks to the regeneration of temperate deciduous forests (Nakagoshi 1985; Pickett & McDonnell 1989; Peterson & Carson 1996). The density and composition of forest seed banks has been the main topic of these studies (see Thompson et al. 1997), while the temporal pattern arising during succession has received less attention (Granström 1982; Rydgren & Hestmark 1997; Grandin & Rydin 1998).

Despite being widely accepted that population processes occur not only in time, but also in space, and that

seed dispersal – which is decisive for recruitment – has a spatial pattern (Nathan & Muller-Landau 2000), there have been few attempts to elucidate the spatial variability of seed banks and search for causes of such patterns (Hyatt 1999; Houle et al. 2001). Furthermore, most of the available pattern studies have been performed at scales at which biological significance is not easy to infer (Bigwood & Inouye 1988). Key questions, such as "what is the relationship between the seed bank and spatial structure of vegetation" remain (Albrecht & Pilgram 1997; Rydgen & Hestmark 1997).

The spatial distribution of seeds has important ecological consequences (Bigwood & Inouye 1988), either through seed predation or density-dependent interactions between seedlings (Inouye 1980). Our knowledge of the factors determining seed banks patterns is scarce. The role of microhabitat heterogeneity – including soil surface variation and light availability, which have been found to be important in the composition and structure of the seed bank (Fenner 1985) – remains unknown.

We have studied the small-scale spatial pattern of the seed bank in a secondary forest in the northern Iberian Peninsula, where *Betula celtiberica* is being replaced by *Fagus sylvatica*. The following questions are addressed: What is the spatial pattern of the local seed bank? Can we detect any significant relationship between the seed bank spatial pattern and above-ground understorey vegetation and tree canopy composition and structure, and with the surface microhabitat heterogeneity? If so, what fraction of seed bank variability may be accounted by the spatial pattern and the other data sets and what is the degree of overlapping?

Material and Methods

Site description

The study site was a 2 ha forest stand located in the Urkiola Natural Park (Basque Country, N Spain, 43° 6' N, 2° 39' W) at 550 m a.s.l. on a steep NE facing slope (inclination 21-38°). Parent material is sandstone and the soil is acidic and very shallow. The area experiences a temperate-oceanic climate with a high annual rainfall of 1655 mm and a mean annual temperature of 11 °C.

According to Herrera et al. (2001) this forest suffered two major incidents during the 20th century. In 1948 most of the *Fagus* trees were felled and *Pinus radiata* planted, these were felled in 1967. Thereafter the stand underwent secondary succession.

In the tree layer, the forest is dominated by *Betula celtiberica*, *Fagus sylvatica*, *Quercus pyrenaica* and *Q. robur*, which account for more than 70% of the total basal area (Herrera et al. 2001).

Sampling

A square plot was selected in the centre of the stand and a 2 m ¥ 2 m grid was laid out, providing 196 grid nodes. The soil seed bank was sampled in January 1999, before any seeds had emerged. Four soil cores (diameter 3 cm) were extracted close to every grid node (one in each of the surrounding grid cells). Before soil extraction, all litter was removed in order to restrict the sample to the persistent seed bank. Every core was divided into two layers (0-3 cm; 3-10 cm). Samples around one grid node were pooled for each layer, resulting in 392 samples. The total soil surface sampled was 0.554 m^2. Soil samples were kept at 4 °C for two months. The viable seed bank was studied by monitoring seedling emergence (ter Heerdt et al. 1996). Soil samples were washed and sieved through a 0.5 cm mesh to retain the coarse fraction. The resulting material was sieved again, through a 0.1 mm mesh to reduce the fine material volume.

The resulting soil samples were put in 10 cm ¥ 10 cm plastic boxes in a greenhouse with constant temperature (20 °C). A sterile substrate of vermiculite and peat (2:1) was mixed with the remaining sample soil in plastic boxes to a depth of 1 cm. Ten cells were filled with the sterile mixture to detect any contamination. As soon as a seedling emerged, it was identified and removed. Unidentified seedlings were grown in individual pots until identification was possible. After 5 mo the soil was regularly crumbled during 3 mo to enhance emergence. Finally, the boxes were watered with a gibberellic acid (GA_3) solution (1000 ppm) and emergence monitored for another 2 mo (12.8% of the seedlings). Counts of seeds per plot were transformed to seed density (seed.m^{-2}).

During June 1999, a floristic inventory was conducted in each grid cell (n =169) and in each 2 m ¥ 2 m square adjacent to the edge of the plot (n = 56). In each cell species cover, bare soil, litter, moss, stone and stump cover were estimated in percentage. For every soil sample at each grid node, the mean cover value of the four adjacent cells was calculated. Trees were identified, mapped and their height and DBH measured throughout the stand. The effect of the tree canopy on soil sampling points was estimated as the influence of neighbouring trees using the influence index of Woods (2000):

$$I_f = S_{(dist<8m)} \, D_n / dist_{n,f} \qquad (1)$$

where D_n is the DBH of an individual neighbouring tree and $dist_{n,f}$ the distance between the neighbouring tree and the grid node. Influence indices were calculated separately for *Fagus* and *Betula* as well as for all tree species pooled.

Statistical analysis

Matrices of seedling counts (log-transformed) at each depth (per species and grid node) were produced. Subsequently, a standardized Mantel test (Legendre & Legendre 1998) was performed to test if seed bank composition differed at the two depths. Significance was tested using a randomization approach with 999 permutations. On the basis of the result ($r_M = 0.40$; $P < 0.001$), the data were merged before further analysis.

The evaluation of the relative importance of environmental conditions (vegetation, microhabitat and canopy structure) was evaluated using constrained ordination techniques (ter Braak 1986), with the location of the sampling sites as a variable. To select the appropriate ordination technique the seed matrix was submitted to Detrended Correspondence Analysis (DCA; ter Braak 1988), with detrending by segments and non-linear rescaling of the axes. Since the length of the extracted gradient was ca. 3 s.d. units, we subsequently conducted Canonical Correspondence Analysis (CCA), following the recommendations of ter Braak (1986).

Several constraining matrices were considered: (1) spatial arrangement, including three variables: X, Y and the interaction term; (2) microhabitat (bare soil, litter, moss, rock and stump cover); (3) understorey vegetation (the most frequent 15 species); (4) canopy (total, *Betula*, *Fagus* and *Ericaceae* cover). The total variation explained (TVE) by each data set was calculated as the sum of all canonical extracted axes using each of these matrices as the constraining data matrix (Borcard et al. 1992). A Monte Carlo permutation test was performed to determine the accuracy of the relationship (999 randomizations) between the two data sets. The sum of all canonical eigenvalues or trace was used to build the *F*-ratio statistic (ter Braak 1990). Only when $P < 0.05$, adjusted for multiple comparisons by the Bonferroni correction (Legendre & Legendre 1998), was the relationship between the two data sets considered significant. If the CCA model was significant, a forward stepwise procedure was carried out to select a reduced model including only significant variables for each matrix. Improvement of the reduced model with each new selected variable was determined by a Monte Carlo permutation test with 999 randomizations.

Variance partitioning with CCA was performed to evaluate the relative importance of these constraints after adjusting the variability of other data sets considered as covariables (Borcard et al. 1992; Legendre & Legendre 1998). This procedure has been called partial CCA (ter Braak 1988). In this case, the question is not only whether correspondence between data sets exists, but what fraction of the seed count information is explained by the covariable data set and how much by the constraining matrix. These analyses were conducted using CANOCO (ter Braak & Šmilauer 1997).

To evaluate the shape of the whole seed bank spatial pattern, a multivariate Mantel correlogram (Legendre & Legendre 1998) was constructed. This technique allows testing for departure from spatial independence, both in its totality and for each distance class. The distance interval was 2 m. To test the significance of each distance class 499 permutations were carried out. The Bonferroni correction was used to account for multiple testing

The spatial structure of the seven most abundant species in the seed bank was also analysed. The existence of any spatial pattern was tested by means of a Moran's I autocorrelation approach. This statistic is related to Pearson's correlation coefficient and can be interpreted in a similar way (Legendre & Legendre 1998). Distance and range were the same as for the Mantel correlograms. Significance was tested for every distance class using a randomization approach with 999 permutations. Moran's I was performed using Rookcase software (Sawada 1999). Finally, interspecific correlations in seed bank densities were tested via pair-wise non-parametric correlations, using Kendall's coefficient of concordance (Sokal & Rohlf 1981). This technique was also used to check for relationships between each species cover and seed bank density. Non-parametric correlations were performed using SPSS v.10.0.

Results

Composition and density of the seed bank

A total of 3911 seedlings belonging to at least 28 taxa emerged in the greenhouse; i.e. a total density of 7057 seed m^{-2} (Table 1). Most of the emerged seedlings (86%) were identified at species level. From the rest, 18% were assigned to a genus (almost all to *Hypericum* spp., either *H. pulchrum* or *H. androsaemum*), 52% to a family, mostly *Ericaceae* (either *Daboecia cantabrica* or *Erica arborea*) and the remaining 261 seedlings were recorded as either dicots or monocots. The surviving seedlings of these categories were classified, but in order to avoid uncertainties with dead material they were treated as synthetic types for further analyses. Seeds had a very uneven density (Table 1). A single species, *Digitalis purpurea*, made up 47% of the seed bank; the eight most frequent species accounted for 92% of the total; 12 taxa were represented by < 5 seed m^{-2}. Seed number in the lower layer was significantly lower than in the upper one ($t = 12.2$; $df = 195$; $P < 0.0005$). On the basis of the values of Kendall's coefficient of concordance between species (corrected for multiple comparisons) we distinguished

Table 1. Above-ground understorey vegetation cover and seed counts per m² at two sampling depths and in total.

Taxa	Seed/m^{-2}			Cover
	0-3 cm	3-10 cm	Total	%
Digitalis purpurea	948	2332	3280	1
Erica arborea	206	413	619	< 1
Daboecia cantabrica	90	368	458	< 1
Ericaceace	119	406	525	
Betula celtiberica	242	150	392	< 1
Juncus effusus	78	258	336	-
Agrostis capillaris	69	164	233	3
Hypericum pulchrum	85	128	213	1
Hypericum androsaemum	42	105	146	2
Hypericum spec.	51	135	186	
Rubus gr. *glandulosus*	51	87	137	16
Stellaria media	23	70	94	-
Luzula multiflora	9	14	23	< 1
Wahlenbergia hederacea	4	18	22	< 1
Carex pilulifera	7	13	20	< 1
Hypericum humifusum	0	13	13	-
Sonchus oleraceus	4	5	9	-
Ulex spec.	2	5	7	< 1
Oxalis acetosella	7	0	7	11
Ranunculus tuberosus	4	2	5	< 1
Juncus cf. *tenuis*	2	4	5	-
Solidago virga-aurea	0	5	5	< 1
Teucrium scorodonia	2	2	4	1
Lysimachia nemorum	4	0	4	< 1
Viola reichenbachiana	2	2	4	< 1
Trifolium spec.	2	0	2	-
Aquilegia vulgaris	0	2	2	-
Veronica officinalis	0	2	2	< 1
Asteraceae	0	2	2	
Poaceae	0	2	2	
Iridaceae	2	0	2	
Dicots	38	90	128	
Monocots	34	123	157	
Unknown	5	11	16	
Lonicera periclymenum				9
Deschampsia flexuosa				9
Pteridium aquilinum				6
Vaccinium myrtillus				6
Blechnum spicant				3
Dryopteris affinis				3
Hedera helix				3
Athyrium filix-femina				2
Holcus mollis				1
Corylus avellana				1
Populus tremula				1
Fagus sylvatica				1
Brachypodium pinnatum				1

Appearing in the above-ground vegetation with a cover < 1%:
Acer pseudoplatanus; *Ajuga reptans*; *Anemone nemorosa*; *Anthoxanthum odoratum*; *Brachypodium sylvaticum*; *Calluna vulgaris*; *Cardamine pratensis*; *Castanea sativa*; *Conopodium majus*; *Crataegus monogyna*; *Dryopteris filix-mas*; *Erica vagans*; *Euphorbia dulcis*; *Frangula alnus*; *Fraxinus excelsior*; *Ilex aquifolium*; *Moehringia trinervia*; *Polygala vulgaris*; *Prunus avium*; *Pyrus* spec.; *Quercus faginea; Quercus ilex; Quercus robur*; *Rosa* spec.; *Tamus communis*; *Veronica chamaedrys*.

two species guilds (Fig. 1), the first formed by *Digitalis purpurea*, *Juncus effusus* and *Agrostis capillaris* and the second by *Betula celtiberica*, Ericaceae, *Hypericum* (in all cases correlations are positive; $P < 0.001$). No relationship between species in different groups was significant.

Only 36% of the species present in above-ground vegetation were present in the seed bank. However, 73% of the species present in the seed bank were also a component of the above-ground vegetation. Non-parametric correlation between above-ground vegetation and seed bank density was significant for *A. capillaris* ($r = 0.195$; $P < 0.001$) and *Hypericum* ($r = 0.166$; $P < 0.002$).

Structure of the seed bank

The Mantel correlogram (Fig. 2) shows a significant spatial pattern for seed bank composition over the first four distance classes ($P < 0.007$). The seed bank seems to be spatially structured in circular patches with diameters of ca. 6-8 m.

To determine which fraction of the total variation of the seed bank matrix was explained by each independent data set, CCAs were conducted (Table 2). The constraining matrices were able to explain significant fractions of variation ranging from 6.3% in the case of microhabitat to 15.7% of the understorey vegetation. To determine what the relevant variables of each of the significant data sets were, several stepwise forward selection approaches were undertaken. Table 3 shows the significantly selected variables and the corresponding falls in the TVE of each reduced model. All variables were significantly selected in the case of the spatial matrix. With respect to the canopy, only total cover and *Betula* cover were selected, bare soil and litter cover in the case of microhabitat and, finally, the cover of five plant species (see Table 3) with respect to vegetation.

To establish whether the fractions of variation explained by each data set were coincident, partial CCAs were performed in which the variation attributable to these data sets (called covariable data sets) was partialled out before adjusting for the remaining information (Fig. 3). Partial models were significant in all the tested cases except for microhabitat and canopy with space as covariable. Therefore, both components were structured following the trends marked by the space matrix. Vegetation explained a relevant fraction of variability after adjusting for space, suggesting the existence of other forming factors that were not spatially structured. Finally, microhabitat, canopy and vegetation presented different levels of overlap, but in all the cases explaining significant non-overlapping fractions of variation.
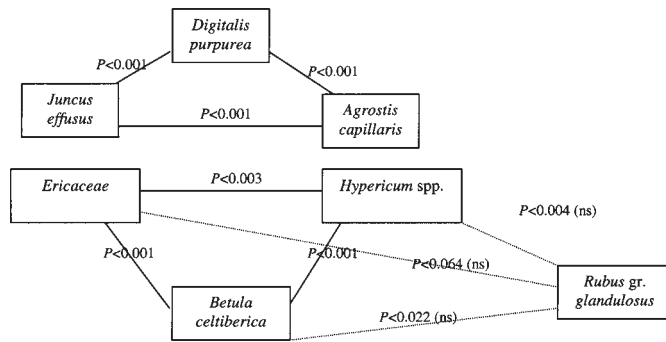
Fig. 1. Kendall's non-parametric correlation among the main species present in the seed bank. All correlations are positive.
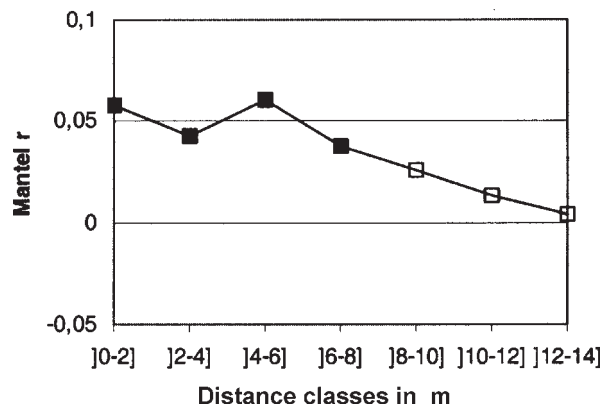

Fig. 2. Mantel correlogram for seed bank composition data. Filled symbols indicate significant correlations significant correlations ($P < 0.05$, after Bonferroni correction for multiple comparisons).
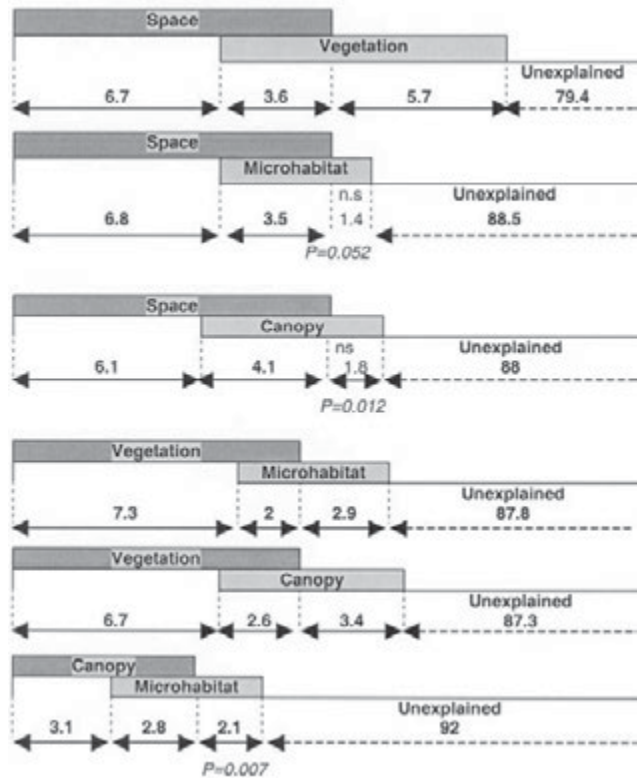

Fig. 3. Partial reduced CCA models in seed count matrix. Horizontal bars show TVE by each data set. Overlapping sections indicate coincident explained variation. n.s. = non-significant, significance level = 0.0001 unless indicated.

Table 2. CCA models using log-transformed seed count data as the main matrix and data sets based on vegetation, microhabitat, canopy and space data as constraining matrices. I_1, I_2, I_3 are the eigenvalues of the corresponding extracted axes. Scons is the sum of all constrained axes, the variation explained by the constraining data set. F_{rat} is the F-ratio statistic and P is the significance level of the reduced model (999 randomizations).

Constraining matrix	I_1	I_2	I_3	Scons	TVE	F_{rat}	P
Vegetation (15 variables)	0.087	0.028	0.020	0.188	15.7	2.210	0.001
Space (3 variables)	0.097	0.020	0.007	0.124	10.3	7.289	0.001
Canopy (4 variables)	0.071	0.010	0.007	0.091	7.6	3.862	0.001
Microhabitat (5 variables)	0.053	0.012	0.006	0.075	6.3	2.513	0.001

Only *Ericaceae* and *J. effusus* had significant spatial structures, as shown in Fig. 4. Moran's I autocorrelation results showed the existence of correlated positive values for the first distance classes, which clearly indicates the existence of circular patches with diameters ca. 6-8 m.

Discussion

Seed bank composition

Two thirds of the species in the seed bank also appeared in the above-ground vegetation. This confirms the general similarity between the species compositions of seed bank and above-ground vegetation (Leckie et al. 2000), although there are also reports to the contrary
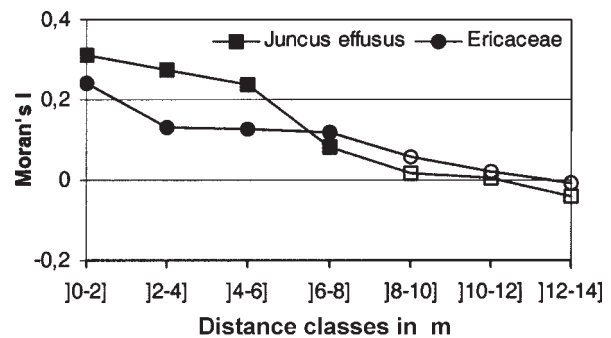

Fig. 4. Moran I correlograms for numbers of seedlings. Only species with significant values are presented. Filled symbols indicate significant correlograms ($P < 0.05$, after Bonferroni correction for multiple comparisons).

Table 3. Results of the stepwise CCA forward selection of significant CCA models (see Table 2). Only significant selected variables are represented. Drop *TVE* expresses the difference between *TVE* of a model including all the variables and the TVE of the reduced model. F_{rat} is the F-ratio statistic and P is the significance level of the reduced model (999 randomizations). Constraining matrices are indicated in the first row. Dryop aff = *Dryopteris affinis*; Hyper and = *Hypericum androsaemum*; Agros cap = *Agrostis capillaris*; Brach pin = *Brachypodium pinnatum*; Hyper pul = *Hypericum pulchrum*.

	Vegetation (15 va)				Canopy (4)				Microhabitat (5)		
		I	F_{rat}	P		I	F_{rat}	P		I	F_{rat}	P
step 1	Dryop aff	0.04	6.54	0.001	Total cover	0.05	6.54	0.001	Bare soil	0.04	6.76	0.001
step 2	Hyper and	0.02	3.63	0.001	Birch cover	0.02	2.87	0.002	Litter cover	0.02	3.08	0.001
step 3	Agros cap	0.02	3.39	0.001							
step 4	Brach pin	0.02	2.91	0.009							
step 5	Hyper pul	0.01	2.37	0.005							

	Reduced model			Reduced model			Reduced model	
	TVE	9.3		TVE	5,9		TVE	4.9
	Drop TVE	6.3		Drop TVE	1,6		Drop TVE	1.9
	F_{rat}	3.864		F_{rat}	6.005		F_{rat}	4.961
	P	0.001		P	0.001		P	0.001

(e.g. Egan & Ungar 2000; Gutiérrez et al. 2000), but in non-forested ecosystems. However, the reverse relationship was not found: nearly two thirds of the species present above-ground did not appear in the seed bank, a result also obtained in similar studies (Rydgren & Hestmark 1997). This indicates that the development of a seed bank is a strategy found in only a small number of forest species. Of the four shrub species that dominate the understorey layer, *Hedera helix*, *Lonicera periclymenum*, *Rubus* gr. *glandulosus* and *Vaccinium myrtillus*, only *Rubus* appeared in the seed bank. *Rubus* is a common component of forest seed banks (Peterson & Carson 1996; Rydgren & Hestmark 1997; Hyatt & Casper 2000). The absence of *H. helix* and *L. periclymenum* (also found by Thompson et al. 1997) was expected. However, the absence of *V. myrtillus* was not expected. This species has often been reported in seed banks, although not always (Thompson et al. 1997). The lack of *V. myrtillus* seeds in the present study may be due to a combination of low survival in soil (Eriksson & Fröborg 1996) and absence of any input into the seed bank due to the very low fruit production in recent years) (pers. obs.). The emergence of *V. myrtillus* has not been detected in a parallel emergence monitoring study either. However, two *Ericaceae*, *Erica arborea* and *Daboecia cantabrica*, with a low presence in the above-ground vegetation, had dense seed banks despite the low fruit production of recent years. Both species are probably declining in this forest since they are not genuine forest shrubs, but species of open forest and heathland. Their seed banks probably originate from earlier stages of succession.

It is commonly argued that shade-tolerant understorey herbs do not appear in forest seed banks. Most of these species rely on clonal growth to expand under the canopy (Grime 1979), although some species of shade-tolerant herbs (*Lysimachia nemorum, Ranunculus tuberosus, Viola reichenbachiana, Veronica officinalis, Carex pilulifera, Oxalis acetosella*) did appear in the seed bank; they were present in very low densities. Furthermore, *Hypericum androsaemum* and *H. pulchrum*, considered natural components of mature forests (Rameau et al. 1989), appeared in important quantities, indicating that for at least for some shade-tolerant plants, seed banks may be a feasible survival strategy.

The non shade-tolerant gap colonizer *Digitalis purpurea* dominates the seed bank. An abundant and extremely long-lasting seed bank is required by this pioneer species due to the absence of an efficient dispersal mechanism.

The relative importance of four wetland species in the seed bank (*Hypericum humifusum, Juncus effusus, J*. cf. *tenuis* and *Wahlenbergia hederacea*) is very interesting. The first three species are currently absent from the forest, even though the seed density of *J. effusus* is very high. Similarly high values have also been cited in other forests (Warr et al. 1994). Persistent seed banks are probably a common trait of wetland species (Rosell & Wells 1999). These species probably appeared during more open stages in the stand, which were present until 30 yr ago (see Herrera et al. 2001), and their seeds may have survived since.

Seed bank studies report changes in composition with depth (McGraw 1987; Rydgren & Hestmark 1997). These have mainly been attributed to historical changes in above-ground vegetation and seed rain regime (McGraw 1987). The present data show a significant correlation in composition with depth. Probably, disturbance most directly affects the composition and density of the local transient seed banks, which are usually closer to the present vegetation (Rydgren & Hestmark 1997), but which were undetected in this study due to litter removal.

Relationship between seed bank composition and above-ground vegetation

Vegetation is thought to exert a large effect on local seed bank composition, both spatially (Hyatt & Casper 2000) and temporally (Bekker et al. 2000). This effect can be direct, via change in seed bank input, or indirect, e.g. by affecting predation (Schupp & Frost 1989) or emergence rates (Hyatt & Casper 2000). Our results show that both tree canopy and understorey vegetation cover account for significant fractions of TVE in seed composition and densities. Three of the five species cover variables included in the reduced understorey model are present in the seed bank (*H. pulchrum*, *H. androsaemum* and *A. capillaris*) and there is a significant relationship between their above-ground cover and seed bank abundance. Their inclusion in the model is probably also influenced by their relationship to the other major seed bank components (see the species guilds in Fig. 1). The only tree species present in the seed bank, *Betula celtiberica*, is also selected in the canopy data set. The other three variables included in these two models (canopy cover, *Dryopteris affinis, Brachypodium pinnatum*) cannot be directly related to seed input and seem to reflect other environmental parameters. Canopy cover can be interpreted in terms of light availability; lower canopy values imply higher biomass production, cover, and therefore seed production by non-shade tolerant pioneers. The interpretation of the effect of the cover of the two species is less obvious, even though they have contrasting requirements in terms of light and soil. Finally, the importance of some soil surface variables in the composition and

structure of the seed bank, such as bare ground and litter cover selected in the last data set (microhabitat), is widely recognized (Fenner 1985).

Spatial structure of seed bank

Seed banks are considered to have a pronounced spatial component (Albrecht & Forster 1996) and our results are in agreement with this statement. Space itself is not an ecological factor but an integration of different concurrent processes (Borcard et al. 1992). The fraction of TVE for each data set presents a relevant spatial arrangement which, in turn, determines a non-significant capability of the microhabitat and canopy data sets to explain seedling variability once space is partialled out. This means that the selected explanatory variables must have an important spatial pattern. Nevertheless, despite the overlap, the vegetation data set is able to significantly explain other fractions of variability. Above-ground herb vegetation has an important spatial pattern linked to that of the seed bank, but it also exerts some control beyond the spatial pattern. Further research is required to evaluate specific hypotheses referring to the relationships between seed bank patterns and understorey composition.

Moreover, there is an important small-scale spatial autocorrelation in seed density. The results show a distribution with patches of 6-8 m in diameter. Although this pattern was representative of the overall species composition, it is mainly due to the much stronger spatial patterns of *Ericaceae* and *Juncus effusus*, which have clumped seed bank distributions conforming to similar patches. To explain this pattern, a non-parametric correlation was sought between seed numbers of *Ericaceae* and dead stumps of *Erica*, using Eq. 1 to estimate their effect. A significant relationship ($r = 0.134$; $P = 0.008$) was found between the stumps and the number of seeds in the bank. This relationship seems to indicate that the existing seed bank pattern for this species is due to an inefficient dispersal mechanism and was probably produced prior to 1985 when most of the *Erica* shrubs were cut down. In the case of *J. effusus,* this relationship cannot be established because neither individuals nor remains were present in the study stand. It seems evident that clumped growth in adult individuals may determine the clumped structures observed in seed banks. It is remarkable that *D. purpurea* and *B. celtiberica* have no pattern, which clearly suggest that these species efficiently occupy all the available space while waiting for a regeneration gap.

In conclusion, seed bank structure is the result of the different life strategies of individual species. These have different patterns and intensities of seed accumulation, both in time and space, and have different ecological significances. The bank includes species with middle to long distance dispersal ability (*Betula*, *Rubus*) which combine (1) spatially homogeneous, medium sized seed banks requiring moderate to large perturbations to give rise to established plants which then persist for long periods; (2) species that take advantage of small and temporal gaps, able to conclude their life cycles in a couple of seasons before the canopy closes, but which make long-term, dense seed banks (*Digitalis*) and (3) open habitat species with long-term seed banks awaiting intense perturbation before germination, e.g. *Juncus, Erica* and even *Hypericum,* a forest species. As a visual example, seed banks, rather than being an underground line where seeds wait for a one-way train to arrive (perturbation), are a complex railway system where trains (regeneration opportunities) arrive with different periodicities and from different directions. The seeds get into these trains at different moments and with different abundancies.

In the context of the actual discussion about seed recruitment limitations in forest communities (Schupp & Fuentes 1995; Clark et al. 1999), a deeper insight into seed bank spatial patterning is required if we are to understand its role in forest dynamics.

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