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Spatial patterns of trees and juveniles in a laurel forest of Tenerife, Canary Islands

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Abstract

Spatial patterns are important characteristics of the forest and they can reveal such things as successional status and ecological characteristics of the species. We tested the hypothesis that spatial distribution will be different, depending on whether the species is intolerant or tolerant to shade. We assessed the spatial distribution of trees (> 4 cm dbh) and juveniles in eight laurel forest plots. A univariate spatial analysis (performed with Ripley's K_1) showed that all tree species have significant aggregation at short distances (2 m). Nevertheless, two groups of species could be differentiated: *Erica scoparia*, *Myrica faya* and *Ilex canariensis* showed a tendency for aggregation at large distances (larger than 6 m) while *L. azorica* and *Prunus lusitanica* showed aggregation only at shorter distances. Ripley's Bivariate $K_{1,2}$ analyses showed no significant differences in the spatial distribution of analyzed species pairs from a null model. Only *Laurus azorica* had a sufficient sample size for analysis of juvenile distribution. A univariate analysis revealed that *L. azorica* seedlings (stems < 50 cm high) were clumped in some plots up to 5 m, but this was not consistent. Saplings (stems > 50 cm high and < 4 cm dbh) did not show strong clumping even at short distances. *L. azorica* saplings had no significant aggregation with, nor repulsion from, adults of the same or different species. Spatial patterns of the species should be considered in the development of restoration plans of the laurel forest 90% of which has disappeared or been intensively disturbed on Tenerife Island.

Introduction

Spatial patterns of trees are important characteristics of forests (Vacek and Lepš 1996) and can be used for analyzing canopy replacement (Horn 1975; Woods 1979; Busing 1996), regeneration (Condit et al. 1992; Norton 1991), changes in forest dynamics after disturbance (Alekseev and Zherebtsov 1995; Vacek and Lepš 1996) and biological relationships between tree species such as competition (Hatton 1989; Duncan 1991), dispersion (Collins and Klahr 1991), or adult-juvenile relationship (He et al. 1997). Also, the spatial distribution of trees can be important for the management of natural areas (Moeur 1993).

Tree spatial distributions change with the successional stage of the forest (Greig-Smith 1952). Ecological processes can be inferred from the spatial distribution, for example, localized density-dependent mortality can result in a regular distribution of trees (Lepš and Kindlman 1987; Chapin et al. 1989). Because of this, sometimes a more complete understanding of spatial distribution of trees can be obtained in a temporal monitoring of their distribution (Lepš 1990).

Tenerife's evergreen laurel forest has been extensively exploited since the arrival of the Europeans in the 15th century (Parsons 1981). Today, only 10% of the forest remains, which has been formally protected since 1988, currently experiencing fewer human disturbances and no area reduction. No data is available about the precise forest age, but aerial photographs from 1952 show the forest in its current state, in terms of both extent and physiognomy, showing no remarkable alterations. In the 1940s, there was still some illegal, small-scale forest exploitation due to its protection schedule and public character. Presently programs concerning laurel forest restoration are being developed with a low success rate, mainly due to a lack of information about characteristics of this particular ecosystem and its dynamics (Arévalo 1998). The purpose of this paper is to test the hypothesis that the ecological characteristics of the species, such as its tolerance to germinate in shade conditions or not, will affect its spatial distribution. We also will describe the spatial distribution of the most abundant sapling and seedling species of the laurel forest, *Laurus azorica* (Arévalo (1998); Arévalo and Fernández-Palacios (1998); Fernández-Palacios & Arévalo 1998), and interpret our results in light of laurel forest dynamics. These results could provide some useful information for the development of restoration plans and recommendations for plantations.

Material and methods

Study site

The study was conducted in Anaga Natural Park in the northeast corner of Tenerife (28°19′ N, 16°34′ W), Canary Islands. The park encompasses a 7 to 8 million year-old basaltic massif (Ancochea et al. 1990), covering some 130 km^2 and representing 7% of Tenerife's area. We selected two stations in the park as representing the best conserved laurel-forest remnants of Anaga: "El Moquinal" on the windward slope and "Monte de Aguirre" on the leeward slope. We chose approximately 300 ha of the best conserved forest in each station.

Annual precipitation of the park reaches 900 mm, but can be twice this amount if fog drip is considered (Kämmer 1974). The mean annual temperature is close to 15 °C with minimal annual and daily fluctuations. There are no frost events. Study site soils have been classified in the order Entisol, suborder Orthens (Fernández-Caldas et al. 1985).

The canopy height of Anaga's laurel-forest varies between 10 and 20 m, depending on slope. Maximal heights are found at the ravine bed's floor, decreasing progressively towards the ravine bed's borders. Dominant species include *Laurus azorica*, *Erica scoparia*, *Erica arborea*, *Ilex canariensis*, *Prunus lusitanica*, *Myrica faya* and *Viburnum tinus*. *Viburnum tinus* is a short understory tree which occasionally reaches the canopy, but it was not considered a canopy tree in this study.

The species of the forest can be classified as shade tolerant or shade intolerant, depending on different characteristics (Whitmore 1989). We used available information from the literature to differentiate these groups of species. Although physiological information would be the most accurate information to categorize the groups, there is no such information available for the canopy species of the laurel forest. However, other information related to ecological characteristics of the species such as germination rate in a greenhouse seed bank (Arévalo and Fernández-Palacios 2000), germination in natural conditions, asexual regeneration, foliar area, and seed size for almost all of the species are useful for placing species into groups.

Species that can't germinate in a close forest canopy (Whitmore 1989) and/or display asexual regeneration by sucker or basal sprouts (Fernández-Palacios & Arévalo 1998) are considered shade intolerant. Other characteristics of shade-intolerant species are a large seed production and small seed size, in opposition to shade tolerant species (Swaine and Whitmore 1988). A higher persistence in the seed bank and a dominance in germination in the seed bank are characteristics of shade-intolerant species (Arévalo and Fernández-Palacios 2000). We used such ecological characteristics to differentiate between the two groups (Table 2).

Data collection

In June and July of 1996, we randomly located four 625 m^2 square plots (25 × 25 m) in each of two sites with different altitudes and aspects. Plots 1 to 4 were in El Moquinal and plots 5 to 8 in Aguirre (Table 1). We defined trees as stems $\geqslant$ 4 cm dbh (independent of its origin, sexual or asexual), saplings as stems < 50 cm tall and < 4 cm dbh with a sexual origin and seedlings as stems < 50 cm tall. We considered basal sprouts as sapling-sized stems of asexual origin (connections with parent stems were apparent) and dbh < 4 cm. Basal sprouts were not considered in the spatial analysis since their aggregated distribution could obscure the spatial distribution of saplings. Previous studies recommended these classes in concordance with the physiognomy of this forest (Fernández-Palacios & Arévalo 1998). We mapped all trees (using a reference point in the plot and mapping all the trees with respect to that point), seedlings and saplings in

Table 1. General biotic and abiotic information of the plots. Plots 1 to 4 were at the Moquinal site and 5 to 8 at the Aguirre site.

	Abiotic characteristics			Biotic characteristics				
	Altitude (m)	Aspect	Slope (°)	Canopy Cover (%)	Understory Cover (%)	Basal Area (m^2/ha)	Saplings (stems/m^2)	Suckers (stems/m^2)
Plot								
1	770	N	20	100	15	34.40	0.10	0.25
2	705	NW	35	95	5	43.16	0.02	0.15
3	785	NW	20	100	10	37.04	0.04	0.36
4	755	NW	17	100	15	40.93	0.10	0.49
5	965	S	30	95	5	54.04	0.19	0.13
6	925	S	10	100	10	45.93	0.21	0.09
7	945	S	30	95	5	46.82	0.08	0.14
8	910	S	30	95	15	44.29	0.16	0.36

Table 2. Characteristics of the most abundant species of the plots.

Species	Germination % in seed bank^{+}	Delay time of germination (months)	Leaf area* (cm^2)	Seed diameter* (mm)
Erica arborea	27.1	Up to 11 months	0.01	0.08
Erica scoparia	69.0	Up to 11 months	0.05	0.10
Myrica faya	1.7	Up to 9 months	22.70	4.69
Ilex canariensis	0	–	13.60	4.00
Laurus azorica	1.1	Up to 2 months	25.90	10.22
Prunus lusitanica	0	–	30.70	9.00
Viburnum tinus	1.1	Up to 6 months	81.20	4.75

(+) Values obtained from Arévalo and Fernández-Palacios (2000).
(*) Mean values of the leaf area (for leaf of the understory 0–5 m) and seed diameter (Ceballos and Ortuño 1974; Delgado 2000)

the plots (with 0.05 m precision) using Cartesian coordinate systems. In the square plot, each stem had an *x* and a *y* value, depending on its distance to the reference point (one of the corners of the plot). A buffer of two meters around each plot was also considered in the analysis, and all the trees in that buffer were counted so that one of spatial analysis could be used to relate juvenile distribution to adults. A detailed summary of tree density, basal area and sapling and seedling density of the plots can be found in Arévalo (1998).

Spatial analysis

We studied the spatial distributions of all canopy tree species with more than ten stems per plot using Ripley's univariate $K_1(t)$ function modified by Szwagrzyk (1992), which determines the consistency of the empirical distribution of distances among individuals with the Poisson distribution (Szwagrzyk and Czerwczak 1993), and is given by the equation:

$$K_1(t) = \frac{\nu(A)}{n^2} \sum_{x \in A} \sum_{y \in A \cup B} 1_{(0t]}(d(xy))$$

where: *n*=the number of trees in the plot; *v(A)* = the area of the inner circle of the plot analyzed; *t* = the distance between trees; *x,y* = the points of the Euclidian distance of the points x and y. The K_1(t) function is transformed into a function L_1(t) as follow:

$$L_1(t) = \left(\frac{k_1(t)}{\pi}\right)^{0.5}$$

The buffer zones were included to solve the problem of edges effects (Ripley 1977). To detect departure from complete spatial randomness (CSR), constant approximate 5% confidence intervals were established.

Also, we used the bivariate Ripley's $K_{1,2}(t)$ function in the analysis, which compares the expected number with the observed number of individuals of

Table 3. a) Trees density individuals/ha, b) seedlings/100m^2, c) saplings/100m^2 and d) basal sprouts/100 m^2 by species and plots. The category "Other species" is composed of the species: *Apollonias barbujana, Ilex perado, Persea indica, Picconia excelsa, Rhamnus glandulosa and Teline canariensis.*

a)

Density	Moquinal Site Plots						Aguirre Site Plots					
Species	1	2	3	4	Mean	std	5	6	7	8	Mean	std
Erica arborea	256	–	32	–	72.0	107.0	16	48	32	528	156.0	215.1
Erica scoparia	–	–	16	64	20.0	26.2	3.728	1.568	1.088	16	1,600.0	1351.0
Ilex canariensis	1.200	432	1.232	912	944.0	321.8	400	528	480	384	448.0	59.8
Laurus azorica	688	544	720	544	624.0	81.8	1.136	704	864	1.264	992.0	220.3
Myrica faya	144	208	80	160	148.0	46.8	1.216	512	400	256	596.0	369.3
Prunus lusitanica	1.264	960	2.256	1.296	1,444.0	487.0	–	–	–	16	4.0	7.9
Other species	352	–	64	192	152.0	135.6	96	48	192	112	112.0	52.8

b)

Seedlings/100 m^2	Moquinal Site Plots						Aguirre Site Plots					
Species	1	2	3	4	Mean	std	5	6	7	8	Mean	std
Erica arborea	–	–	–	–	–	–	–	–	–	–	–	–
Erica scoparia	–	–	–	–	–	–	0.16	0.16	–	–	0.08	0.08
Ilex canariensis	0.32	–	0.80	0.48	0.40	0.29	0.16	–	0.16	0.16	0.12	0.07
Laurus azorica	5.60	12.16	5.44	15.36	9.64	4.27	16.64	24.64	4.80	79.52	42.20	24.43
Myrica faya	–	0.16	0.16	0.16	0.12	0.07	0.32	–	–	–	0.08	0.14
Prunus lusitanica	0.64	4.96	5.92	10.24	5.44	3.41	–	–	–	1.12	0.28	0.48
Other species	0.80	0.48	–	6.56	1.96	2.67	1.60	30.08	3.36	5.60	10.16	11.59

c)

Saplings/100 m^2	Moquinal Site Plots						Aguirre Site Plots					
Species	1	2	3	4	Mean	std	5	6	7	8	Mean	std
Erica arborea	–	–	–	–	–	–	–	–	–	–	–	–
Erica scoparia	–	–	–	–	–	–	0.32	–	0.32	–	0.16	0.16
Ilex canariensis	–	–	0.32	0.32	0.16	0.16	0.16	–	0.32	–	0.12	0.13
Laurus azorica	6.08	1.76	3.36	7.68	4.72	2.30	14.72	17.60	5.12	11.36	12.20	4.65
Myrica faya	0.16	–	–	–	0.04	0.07	0.48	–	0.16	–	0.16	0.20
Prunus lusitanica	0.80	–	0.64	0.48	0.48	0.30	0.32	0.16	0.32	0.64	0.36	0.17
Other species	3.20	–	–	1.12	1.08	1.31	3.20	3.04	1.28	2.88	2.60	0.77

d)

Basal sprouts/100 m^2	Moquinal Site Plots						Aguirre Site Plots					
Species	1	2	3	4	Mean	Std	5	6	7	8	Mean	Std
Erica arborea	–	–	–	–	–	–	–	–	–	–	–	–
Erica scoparia	–	–	–	–	–	–	2.56	0.64	0.80	–	1.00	0.95
Ilex canariensis	2.08	2.08	4.32	8.96	4.36	2.81	2.88	2.56	2.88	1.28	2.40	0.66
Laurus azorica	11.20	4.32	5.12	10.08	7.68	3.00	9.28	4.80	9.60	23.04	11.68	6.83
Myrica faya	–	1.44	–	0.96	0.60	0.62	3.68	3.68	1.28	3.04	2.92	0.98
Prunus lusitanica	12.00	7.36	26.88	29.12	18.84	9.34	–	–	–	0.48	0.12	0.21
Other species	1.28	–	0.32	1.44	0.76	0.61	–	–	0.80	0.64	0.36	0.36

other species within a distance t (Ripley 1977). As each of the analyzed plots was divided into an inner circle (A) and a buffer zone (B), the spatial relationship between different tree species was analyzed using the function:

$$\tilde{K}_{12}(t) = \frac{\nu(A)}{n_1 n_2}\sum_x\sum_y 1_{(0t]}d(xy)$$

- n(A) = area of the analyzed plot (inner circle).
- n_1 = number of objects of the first type (species).
- n_2 = number of objects of the second type (species).
- x = objects of the first type (first component).
- y = objects of the second type (second component).

We applied the formula of $L_1(t)$ (Salonen et al. 1992) to transform the values of K_{12}. Second order spatial analysis offers the possibility of detecting patterns at multiple scales. Also the bivariate test is conducted differently than the univariate, with a random toroidal shift of the entire date set (intact) rather than individual trees being given random coordinates (univariate test).

These analyses are effective in detecting spatial relationships between points on a map (Bailey and Gatrell 1995) and are recommended when information of multiple neighbor (e.g. closest regenerative stems to every tree) distances are available (Busing 1996). The null hypotheses are that 1) tree stems are not regular or clumped for $K_1(t)$ and that 2) the distributions of species are spatially independent of each other for $K_{1,2}(t)$. We calculated the values at each meter until 10 m. Because we did not run the analyses when there were less than ten stems (a lower number of stems is not enough to reveal consistent patterns in the spatial distribution) of the species in the plot, the number of plots in which we ran the analyses differs among species.

Spatial distributions of seedlings and saplings of *Laurus azorica* were analyzed with the modified univariate $K_1(t)$ function. For a graphical representation we transformed $K_1(t)$ to W_k The indicator W_k (for details see Szwagrzyk 1990) was used to estimated departure of the trees' distribution from CSR.

$$W_k = \frac{\max\limits_t (L_1(t) - t)}{S} \times \mathrm{sign}(L_1(t) - t)$$

- $\max\limits_t (L_1(t) - t)$ = maximal deviation of the $L_1(t)$ function from CSR;
- S = width of the confidence interval;

$$\begin{cases} \mathrm{sign}(L_1(t) - t) = -1.0, & \text{if} \quad L_1(t) - t < 0 \\ \mathrm{sign}(L_1(t) - t) = -1.0, & \text{if} \quad L_1(t) - t \geqslant 0 \end{cases}$$

Values of $W_k < -1$ indicated a regular distribution and values > 1 indicated a clumped distribution of the trees. The use of W_k allowed us to offer a graphical representation of the results. This transformation allowed us to graphically visualize the pattern across multiple scales. When the spatial distribution of stems at the given distance did not differ from a random distribution (a Monte Carlo test with 200 iterations of randomly generated *x, y* coordinates), the value of the curve at that distance is zero. When significant aggregation was detected, the values of the curve were positive and higher than 1 (the value increased depending on the differences between the expected value and observed value). Negative values < – 1 indicated significant repulsion at the given distance.

We used the dispersion statistic of Hamill and Wright (1986) to determine scarcity or overabundance of *Laurus azorica* saplings or seedlings in the vicinity of adults of the same or different species. The test of Hamill and Wright (1986) was specifically designed to analyze the dispersion of juvenile plants relative to conspecific adults, and we used it instead of a K(t) function. The function F(s) of Hamill and Wright represents that under the random hypothesis the probability that a juvenile will be less than or equal to a given distance from its nearest adult neighbor is equal to the proportion of the total area that is within that distance of any adult. So, the function F(s) represents the cumulative distribution function of juvenile-to-nearest-adult distances under the random hypothesis.

The basis of this statistic is a null model of spatial distribution of sapling stems with respect to adults. The null hypothesis is that juveniles are located randomly with respect to the adults. This could be tested with the Kolmogorov-Smirnov test, comparing the maximum difference between the observed and null hypothesis with a critical value based on the number of distances used in calculating the observed distribution (number of juveniles in the data set) (Hamill and Wright 1986). One of the advantages of these methods is that it can relate the juveniles inside the plot with trees in a buffer area surrounding the plot. This aspect is important for analyzing species dispersion (Hamill and Wright 1986).

We performed the Kolmogorov-Smirnov test among the saplings and seedlings of *Laurus azorica* and the different species of trees to evaluate whether the avoidance of these adults was a general pattern or just simply avoidance of large trees. Greater juvenile to nearest-adult distances than expected indicates “relatively clumped” at the given distance. “Relatively over-dispersed” is indicated when there are less juvenile-to-nearest-adult distances than expected.

Nomenclature

For the denomination of the species included in our analysis we followed Hansen and Sunding (1985).

Results

We classified species as shade intolerant or shade tolerant by their ecological characteristics. The large leaf area, large seed size, short delay germination time in greenhouse seed banks and low germination percentage in greehouse seed banks (Table 2), together with the ability to germinate under a close canopy or the presence of asexual sprouts characterized *Laurus azorica*, *Prunus lusitanica* and *Viburnum tinus* as shade tolerant species, and *Erica arborea*, *Erica scoparia* and *Myrica faya* as shade intolerant. *Ilex canariensis* can be considered an intermediate species due to the intermediate nature of its characteristics.

The canopy of El Moquinal plots is dominated by *Prunus lusitanica* and *Ilex canariensis*, and Aguirre plots by *Myrica faya*, *Erica scoparia* and *Laurus azorica* . Seedlings and saplings of *L. azorica* dominate the regeneration in all the plots. Basal sprouts of *P. lusitanica* and *L. azorica* dominate in El Moquinal and basal sprouts of *L. azorica* dominated in Aguirre.

The univariate spatial analyses revealed significant clumping for species at different distances (Table 4). Although the minimum number of stems required to run the analysis did not allow analysis of species in all plots, a few consistent patterns were obtained. All species showed significant aggregation at short distances, but two groups could be differentiated: shade-intolerant showed significant aggregation at all distances in the majority of the plots calculated (especially *Erica scoparia*) and shade tolerant species (*Launis azorica* and *Prunus lusitanica*) only showed significant aggregation at distances less than 2 m. All trees included in the analyses reproduce asexually (primarily by basal sprouts), and consequently all the species are aggregated at short distances.

Table 4. Results of Ripley’s univariate $K_1(t)$ function analysis for species with a density per plot higher than 10. No significant regular distribution has been detected in any of the plots. Data in the table indicate number of plots that showed significant ($p < 0.01$) aggregation at the given distance. Value 0 indicates that not any of the plot analysed at that distance showed any spatial distribution different from a completed spatial randomness.

		Distance (m)									
Species	N°. plots(*)	1	2	3	4	5	6	7	8	9	10
Erica scoparia	3	3	3	3	3	3	3	3	3	3	2
Ilex canariensis	8	8	8	7	5	3	3	2	2	2	2
Myrica faya	5	5	5	5	4	1	1	1	1	0	0
Laurus azorica	8	8	4	2	1	0	0	0	0	0	0
Prunus lusitanica	4	4	3	0	0	0	0	0	0	0	0

[*] Number of plots where the analysis was developed. The rest of the plots did not have enough data to satisfactorily run the analysis.

The spatial relationships between different tree species using the bivariate Ripley’s K_{12} or K_{21} showed no significant differences in the spatial distribution of analyzed species pairs and random distributions for all of the analyzed distances (in these analyses we used the same species used in the univariate analyses with all possible combinations of pairs; (Tables 5 and 6)).

Figure 1 shows the W_k transformation of the univariate Ripley’s $K_1(t)$ for *Laurus azorica* seedlings and saplings. Figure1a indicates no significant aggregation ($W_k > 1$) at any of the plots at any of the distances, and Figure 1b shows that seedlings in all the Aguirre plots are significantly aggregated at distances up to 5 meters (except for plot 5). Values of $W_k > 0.333$ and $W_k < 1$ are considered intermediate between CSR and clumped (Szwagrzyk and Czerwczak 1993). This is indicating that seedlings are intermediate clumped in all the plots (except for plot 1). For saplings (Figures 1c and 1d), the significant clumped distribution was not detected at almost any distance, just intermediate clumped distribution for all the plots except plots 5 and 7. The spatial aggregation found in Aguirre for seedlings was not as evident for saplings (just plot 8 showed aggregation at 1 meter, Figure 1d). No over-dispersion ($W_k < 1$) at any of the analyzed distances was found for seedling or saplings at either site.

The results of the statistic of Hamill and Wright (1986) are shown in (Table 5) for seedlings and (Table 6) for saplings. Although we found some signifi-

Table 5. Results of the Hamill and Wright (1986) analysis of the spatial distribution of seedlings of *Laurus azorica* with respect to adult individuals.(*)

		Distance (m)									
Species	N° of plots	1	2	3	4	5	6	7	8	9	10
Erica arborea	2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Erica scoparia	3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Ilex canariensis	8	0, − 1	+1,0	0,0	+1,0	+1,0	0,0	0,0	0,0	0,0	0,0
Myrica faya	7	0,0	0,0	0, − 3	0, − 2	0, − 2	0, − 1	0, − 1	0, − 1	0, − 1	0, − 1
Laurus azorica	8	0, − 1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Prunus lusitanica	4	0,0	0,0	0, − 1	0, − 1	0,0	0,0	0,0	0,0	0,0	0,0
Viburnum tinus	1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0

* At each distance is indicated the number of plots in which the seedlings showed significant overabundancy (with a positive sign) and the number of plots in which the seedlings showed significant scarcity (with a negative sign).

Table 6. Results of the Hamill and Wright (1986) analysis of the spatial distribution of saplings of *Laurus azorica* with respect to adult individuals.(*)

		Distance (m)									
Species	N° of plots	1	2	3	4	5	6	7	8	9	10
Erica arborea	2	0,0	0,0	0,0	0, − 1	0, − 1	0, − 1	0, − 1	0,0	0,0	0,0
Erica scoparia	3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Ilex canariensis	8	0,0	0,0	+1,0	+1,0	+1,0	0, − 1	0,0	0,0	0,0	0,0
Myrica faya	7	0,0	0,0	0,0	0,0	0, − 1	+1,0	0,0	0,0	0,0	0,0
Laurus azorica	8	0,0	0, − 1	0, − 1	0, − 1	0,0	0,0	0,0	0,0	0,0	0,0
Prunus lusitanica	4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Viburnum tinus	1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0

∗ At each distance is indicated the number of plots in which the seedlings showed significant overabundancy (with a positive sign) and the number of plots in which the seedlings showed significant scarcity (with a negative sign).

cant overabundance or scarcity in the plots analyzed, no consistent trends in the spatial distribution of seedlings and saplings with respect to the adults could be identified.

Discussion

The univariate spatial analysis of trees revealed the existence of two different groups: 1) *Laurus azorica* and *Prunus lusitanica*, which showed aggregation at short (<3 m) distances and 2) *Erica scoparia*, *Ilex canariensis*, and *Myrica faya*, which tended to show aggregation at larger distances. Following Table 2, we could relate both groups of species detected in the spatial analysis to shade tolerant and shade intolerant species.

Shade-intolerant species can be characterized by the dependence of their seed germination on direct sun light (*Myrica faya*) and by the preference of the species (*Erica arborea* and *Erica scoparia*) for transitional habitat between laurel forest and pine forest or mountain peaks lashed by winds. The high affinity of these species for these specific habitats results in a clumped spatial distribution. The effect of seed predators, herbivores, or pathogens is not documented, but since these factors should lead to overdispersion (Augspurger 1983; Clark and Clark 1984), our results suggest that they play a minor role. We suggest that the ability of saplings to reach the canopy is not affected directly by the proximity of adults of the same or different species as much as by other factors (e.g., space, light, physiology of species) as can be extrapolated from the lack of significant spatial relationships among species. Asexual regeneration plays an important role in the spatial distribution of the trees determinating the important aggregation found in all the plots for all the species.

A significant clumped spatial distribution of seedlings was only evident at the Aguirre site, and was almost non-existent for the saplings at both sites (just intermediate distribution between clumped and CRS).

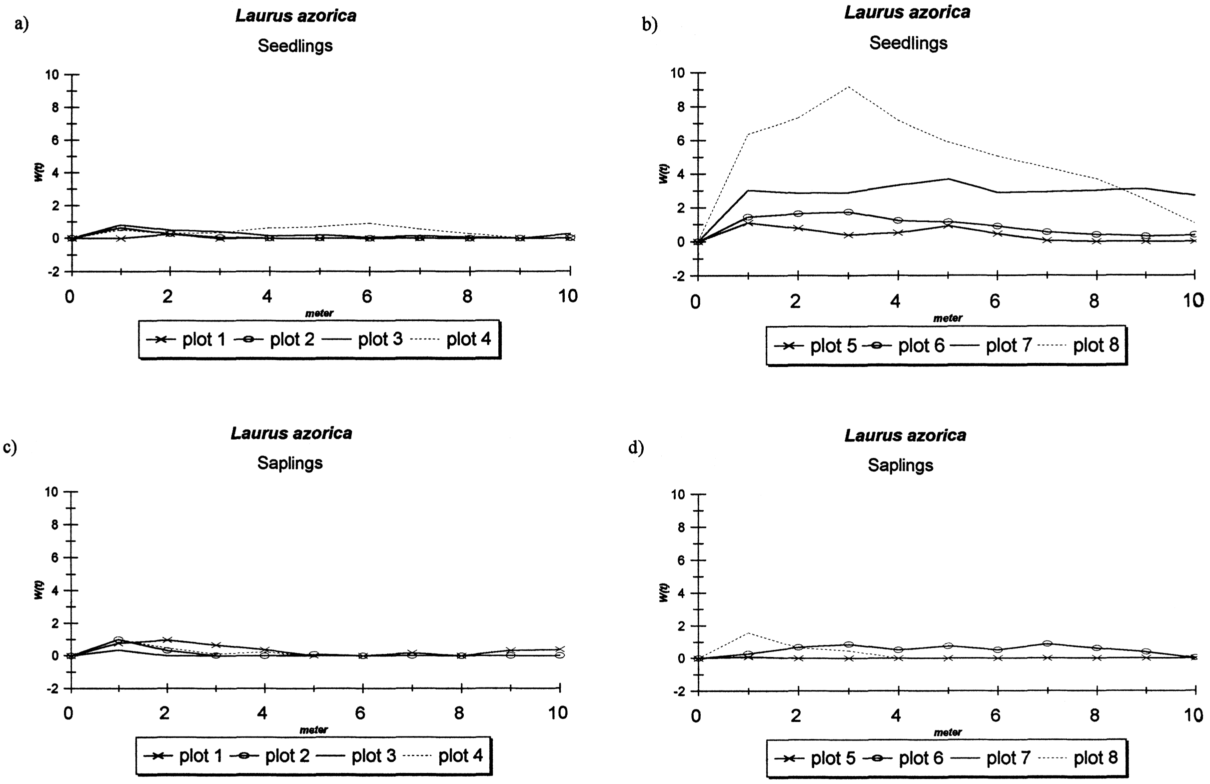

Figure 1. Values of the W_k index for seedlings and saplings of *Laurus azorica* in El Moquinal (1 to 4) and Aguirre plots (5 to 8). The index was calculated every meter until 10 m. (notice the different scale in graph b). When W_k is > 1, it is indicating significant clumped distribution, when it is < 1 and > 0.333 it is indicating an intermediate situation between clumped and complete spatial randomness. When $W_k < -1$ it is indicating significant aggregated distribution, when it is > -1 and < -0.333 it is indicating an intermediate situation between aggregated and complete spatial randomness.

We suggest that microsite characteristics are more important in the spatial distribution of seedlings and saplings. However, the change from significantly clumped to significantly regular spatial distributions with increasing age of stems has been reported in different studies (Greig-Smith 1952; Whipple 1980; Good and Whipple 1982). Significant regular stem distributions have been related to later successional stages (Oliver and Larson 1990). The high rate of asexual regeneration by basal sprouts (Arévalo 1998) is responsible for the aggregated distribution of trees at short distances in the laurel forest. For this reason, the regular distribution found in other late-successional forests are not likely to occur in the laurel forest.

No data are available about the age of the forest, but we assume that it is at least a few generations old. Although illegal human disturbances occurred up to 50 years ago, creating some earlier successional patches in the forest, these were minor and did not affect the study sites. This assumption is supported by the lack of government exploitation reports from this area in the last three centuries.

Disturbances (natural and anthropogenic) have been identified as another determining factor of the clumped spatial distribution of species (Akashi 1996; Busing 1998). Natural disturbances such as big gaps are uncommon in this forest, with less than 0.22% of the canopy of the forest in gap phase due to the short size of the gaps opened (Arévalo and Fernández-Palacios 1998). Other disturbances such as landslides, insect outbreaks or hurricanes have not been reported this century (Arévalo 1998).

Our results indicate that after the transition from seedlings to saplings, stems remain aggregated at local scales in favorable microsites (such as areas with less canopy cover and flat areas). Environmental micro-heterogeneity has been recognized as an important factor in determining the spatial distribution of regeneration (Manabe and Yamamoto 1997). The aggregation is maintained also in trees at short distances, but in this case, due to the high rate of asexual regeneration.

Differences between spatial distributions of species should be considered in plantations and reforestation programs of the laurel forest to follow the natural forest distribution and also in the development of management programs (Moeur 1993). In order to understand the dynamics of the laurel forest more completely, and due to the dependence of the spatial distribution on the successional stage (Lepš 1990), we recognize the necessity of a long-term study with representative permanent plots (van der Maarel 1993).

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