

## UNDERSTORY FLORISTIC HETEROGENEITY WITHIN A MEDITERRANEAN OAK FOREST: HOW MUCH IS EXPLAINED BY EDAPHIC, SPATIAL AND OVERSTORY COMPONENTS?

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Mouro, Sara, García, L.V., Marañón, T. & Freitas, H. (2005). Understory floristic heterogeneity within a Mediterranean oak forest: how much is explained by edaphic, spatial and overstory components? *Revista Biol. (Lisboa)* **23**: 121-133.

The understory floristic heterogeneity within a well-preserved Mediterranean forest was studied, in the Natural Park of Sudoeste Alentejano e Costa Vicentina (SW Portugal), to investigate if floristic trends were related to the soil chemical parameters, to the spatial component and/or to the overstory sinusia. Three bottom-top hillside and parallel to each other transects were traced, for sequential sampling of floristic, vegetational, edaphic and spatial variables. Multivariate analyses of woody species composition (by DCA), of soil variables (by PCA), and of the edaphic-community relationships (by CCA and pCCA) were performed. Several and particular steps of analysis were performed, for partition of total variation of the species data in: (a) non-spatially structured variation; (b) spatially structured edaphic variation; (c) spatial variation not shared by the soil variables; and (d) unexplained variation. A strong bottom-top gradient of edaphic and understory floristic variation was identified. All the spatial components were important to predict the understory floristic variation and, when those were excluded, soil  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were the best predictors of that variation. We concluded that both the edaphic and spatial parameters, together with the overstory sinusia structure and composition, played a significant role in explaining the understory variation.

Key words: *Quercus faginea*, *Quercus suber*, elevation, topographic gradient, variance partition.

Mouro, Sara, García, L.V., Marañón, T. & Freitas, H. (2005). Heterogeneidade florística do sub-coberto de um bosque de carvalho mediterrânico: Pode ser explicada pela componente edáfica espacial ou pela composição específica da canópia? *Revista Biol. (Lisboa)* **23**: 121-133.

Foi estudada a heterogeneidade florística do sub-coberto de um bosque Mediterrânico em bom estado de conservação, no Parque Natural do Sudoeste Alentejano e Costa Vicentina. O objectivo foi investigar se os gradientes florísticos estão relacionados com parâmetros químicos do solo, espaciais ou da própria estrutura e composição específica da canópia. Os dados florísticos, bem como os dados da comunidade, do solo e espaciais, foram obtidos sequencialmente, ao longo de três transectos paralelos entre si, cada um disposto desde a zona mais baixa até à zona alta da vertente. Foram realizadas análises multivariadas dos dados florísticos (DCA), dos parâmetros químicos do solo (PCA) e dos gradientes espécies-solo (CCA e pCCA). Uma sequência de análises complementares permitiu interpretar a variância florística total do sub-coberto, repartindo-a em: (a) variância não espacialmente estruturada; (b) variância edáfica espacialmente estruturada; (c) variância espacial não partilhada com as variáveis do solo; e (d) variância inexplicada. Foi identificado um forte gradiente florístico do sub-coberto e edáfico, desde a zona baixa até à zona alta da vertente. Os parâmetros espaciais revelaram-se importantes para explicar a heterogeneidade do sub-coberto e, quando esses foram excluídos, a quantidade de  $\text{NH}_4^+$  e  $\text{NO}_3^-$  no solo foram os parâmetros edáficos mais importantes para explicar essa heterogeneidade. Concluiu-se que os parâmetros espaciais e edáficos, bem como a estrutura e a composição específica da canópia, têm um papel essencial para explicar a variância do sub-coberto.

Palavras chave: *Quercus faginea*, *Quercus suber*, elevação, gradiente topográfico, partição da variância.

## INTRODUCTION

The heterogeneity of the forest communities usually has multiple origins, because their spatial structure relates to many different factors that interact and have overlaid effects in space (BORCARD ET AL. 1992). Topography is a main conditioning factor determining the floristic heterogeneity, because the bottom-top gradient of elevation is usually associated to a complex environmental gradient that directly or indirectly affects the spatial patterns of plant species distribution and abundance (e.g. HANBA ET AL. 2000). Nevertheless, the variation in species abundances and forest structure along the

topographic gradient is not uniform, because some sources of spatial heterogeneity are independent of elevation (e.g. ROSS ET AL. 1986; FIGUEROA-RANGEL & OLVERA-VARGAS 2000; GALLARDO 2003).

At the south of Portugal, only small, rare and disperse patches of natural forests remain nowadays, and they persist only in steep slopes. It becomes increasingly important to understand these forest fragments in deep, both for assuring their long-term persistence and to undertake regeneration tasks in degraded forest sites.

In this paper we identify changes in the understory floristic composition and structure, and we determine the relative contribution of edaphic, spatial and community components to explain the identified heterogeneities. We focus on the methodological processes that split between each of those components and therefore allow to better interpretate the overall understory floristic variance

## METHODS

### Study site

The study site is a mixed oak (*Quercus suber* and *Q. faginea*) forest, at a north-faced 32° slope, located in the Natural Park of *Sudoeste Alentejano e Costa Vicentina*, SW Portugal (41° 68' N, 5° 25' E). The climate is of mediterranean-type and the main bedrock is greywacke. The studied forest is well preserved: no records of fire and cut off are known since at least 1956, and management is limited only to the periodic removal of the bark from the biggest cork oak (*Q. suber*) trees.

### Data collection

The studied forest site covered about 400 m along the slope, from the top (70 m elevation) to the bottom (10 m), and is one of the largest and best preserved natural fragments in the region. Three parallel to each other transects were traced, along the slope main variation, i.e. following the bottom-top direction of the hill-side. Each transect was approximately 50 m long and a linear sequence of 4 m spaced samples, for sequential data collection in square plots (4 x 4 m each). The *floristic data* included the number of individuals of each woody species (excluding lianas), per plot. For each individual more than 1.30 m tall, the height, trunk diameter (at breast height, dbh), and the number of trunks (in the case of plants branching from the base) were measured and used to calculate the basal area, used as surrogate of the species overstory biomass. In each plot, as *spatial variables* (designation used hereafter), we measured the spatial X, Y and Z (elevation) coordinates (by EDM - electronic distance measurer - Sokkia SET500). As *community variables* (designation used hereafter), we measured: the slope (using a clinometer), the overstory canopy density (using a spherical densiometer positioned 1m above the ground), the ground-cover percentage of perennial herbaceous plants, moss and litter (by visual direct estimation), and the approximate maximum canopy height.

Topsoil samples (0-10 cm depth) were taken using a corer (2.54 cm diameter) in 6 random positions inside each plot, but then mixed to have one soil sample per plot. Soil samples were kept at approximately 4°C and analysed for 18 physico-chemical parameters, during the next 2 days and following the methods prescribed in Sparks (1996): pH, organic C, organic matter, total N, C/N ratio, exchangeable Ca, Mg, K and Na, exchangeable acidity (EA), effective cationic exchange capacity (CECe), available P, available Zn, Cu, Mn and Fe, B and mineral N content (extracted  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ).

### Data analysis

The *soil heterogeneity*, i.e. the main trends of variation of the soil physico-chemical variables in the plots, was analyzed by principal components analysis (PCA).

The variations in the understory woody species composition and abundance, and their relationships with the edaphic, spatial and community variables, were examined through a sequence of complementary analyses, as proposed by BORCARD ET AL. (1992). 1) The *understory floristic heterogeneity* was analysed by applying detrended correspondence analysis (DCA) on the understory woody species abundance matrix. 2) The *overall soil-understory relationships* were studied by using a stepwise canonical correspondence analysis (CCA, TER BRAAK 1986); the stepwise option allowed that the highly redundant independent variables were not incorporated in the model, which could cause model instability and/or over-estimation of the variance (ØKLAND & EILERTSEN 1994; VANDVIK & BIRKS 2002). 3) The *non-spatially structured understory heterogeneity explained by soil variables* was determined by the partial CCA approach (pCCA; ØKLAND & EILERTSEN 1994), using the best spatial predictors (determined by another pCCA) as covariables. 4) The *spatially structured understory heterogeneity explained by soil variables*, was calculated subtracting the variance explained at step 4 from that of step 3. 5) The *spatial component of the understory heterogeneity that was not shared with soil variables* was obtained after performing a partial CCA, with the edaphic predictors determined at step 4 as covariables, and the spatial variables as predictors. 6) The *unexplained variation* corresponded to the fraction of species variation that was neither explained by the edaphic nor the spatial measured components.

Additionally, the *influence of the overstory on the understory sinusiae* was investigated using the Spearman-rank correlation coefficients (to overtake non-normality) between the variables related to the overstory structure/composition and all the understory/environmental trends previously extracted (using DCA, PCA, CCA, pCCA). Moreover, plots having a significant basal area of only one of the two main oak species (*Q. faginea* and *Q. suber*) were compared for the average values of the edaphic, spatial and community variables, using the Student t-test.

Since repeated tests were carried out (GARCÍA 2004), only contributions having  $p < 0.01$  were considered as significant, while contributions having  $p < 0.05$  (but  $p \geq 0.01$ ) were labeled as marginally significant (ms). All computations and graphical display were made using CANOCO for Windows version 4.02 (TER BRAAK & SMILAUER 1998) and STATISTICA version 6 (STATSOFT, INC. 2001) packages.

## RESULTS

### Soil heterogeneity

The main trend of variation in the soil chemical properties, as reflected by the PCA axis 1 (accounting for 31% of variance), was highly correlated to pH, effective cationic exchange capacity (CEC), concentration of most mineral nutrients and organic matter (OM); therefore, it represented a soil fertility gradient inversely related to the elevation, thus reaching the highest values in the lowest topographic positions (Table 1). The second trend of soil variation, PCA axis 2 (17 % of variance), could be interpreted as a combined gradient of acidity, some micronutrient availability and organic matter decomposition degree. The third principal component (16 % variance) was a combined increment of C/N and nitrate and micronutrient (Zn and Mn) availability. The fourth soil principal component (10% variance) can reveal some ammonium and P oligotrophy, which (unlike the first component) was not paralleled by significant changes in pH or other macro and micronutrients availability, but is positively correlated with K.

### Understory heterogeneity

A total of 21 woody species were found in the studied forest (see Appendix I). Sixteen of those species were considered *understory species*, because their crown was shorter than or covered by other trees; the other five (*Arbutus unedo*, *Erica arborea*, *Quercus coccifera*, *Q. faginea* and *Q. suber*) were named *overstory species*, because each contributed  $> 5\%$  (on average) and together they represented near 97% of the total overstory basal area in the study site.

The results of the DCA on the understory species, *i.e.* excluding the five main overstory species, are shown in Table 2 and Figure 1. At the lowest slope positions (samples labelled with lower numbers), only shade tolerant species, such as *Ruscus aculeatus*, were found, under the canopy dominated by *Q. faginea*. The community closer to the hilltop was characterized by many low-stature shrubs, such as *Genista triacanthos*, *Cistus populifolius* and *Calluna vulgaris*, and by lower soil fertility (shown by PCA1). The second trend of floristic variation (DCA2), was positively correlated with elevation and with the soil PCA; however, it was most strongly correlated with the  $XY^2$  term of spatial data, and therefore not only elevation but all the spatial components – topography – may explain the identified floristic variance.

Table 1. Results of the PCA analysis of the 18 soil chemical variables measured in 25 forest plots of SW Portugal. Only factor loadings with values  $\geq 0.5$  are shown. The coefficient of Spearman rank-correlation between the extracted PCA axes and the Elevation variable is shown; significance values are: \*\*  $p < 0.001$ ; \*  $p < 0.01$ ; ns  $p < 0.05$ ; ns  $p > 0.05$ .

	PCA1	PCA2	PCA3	PCA4
<i>Summary</i>				
Eigenvalues	5.652	3.049	2.843	1.794
% Variance	31.4	16.9	15.8	10.0
pH_KCl	0.50	0.52	-	-
OM	0.55	-0.55	-	-
N	0.62	-	-	-
C/N	-	-0.63	0.58	-
K	0.50	-	-	0.50
Ca	0.81	-	-	-
Mg	0.87	-	-	-
Na	-	-0.53	-	-
EA	-	-0.62	-	-
CEC	0.84	-	-	-
P	0.61	-	-	-0.61
Zn	-	-	0.60	-
Cu	-	0.50	-	-
Mn	-	-0.61	0.57	-
Fe	0.80	-	-	-
B	0.70	-	-	-
NH <sub>4</sub> <sup>+</sup>	0.75	-	-	-0.52
NO <sub>3</sub> <sup>-</sup>	-	-	0.79	-
<i>Spearman's correlation</i>				
Elevation	-0.51*	ns	ns	0.54*

### Soil-understorey relationships

The relationships between the main floristic variability trends and the edaphic variables were examined by stepwise CCA (Table 3). When all soil chemical parameters were considered as potential predictors, the highest significant ( $p < 0.001$ ) model included only two non-redundant environmental variables: NH<sub>4</sub><sup>+</sup> and Zn. In addition to the best predictors, other variables were also correlated with the main species-edaphic trends (see detailed results in Table 3).

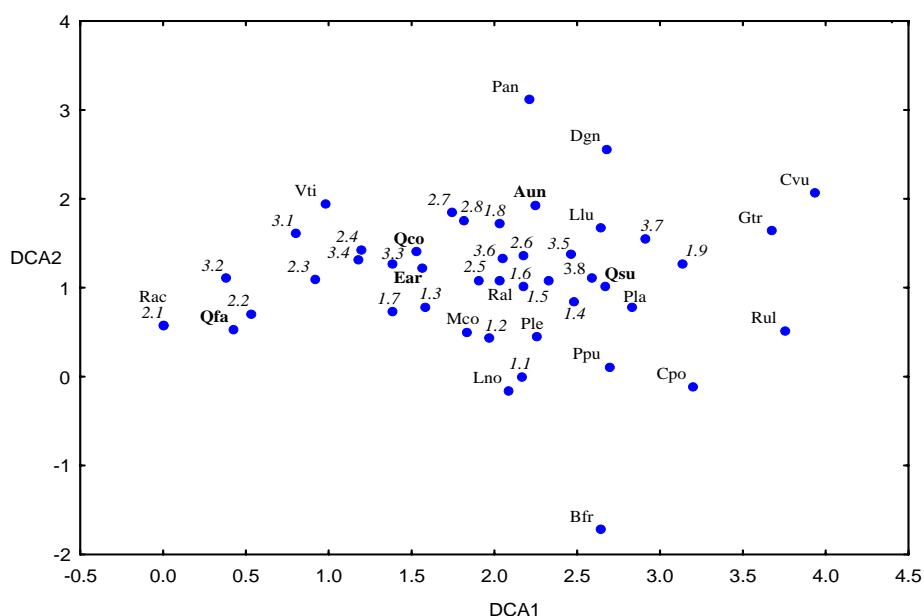


Figure 1. Graphic showing results (scores) of DCA. Analysed data includes the understory species' abundances measured in the 25 plots. The main overstorey species are used as supplementary variables (in bold). *Number.Number* indicates the Transect (1 to 3) and the plot (.1 to .9 - with lower numbers corresponding to lower positions in the slope). See Appendix I for species' labels.

Table 2. Results of the DCA analysis of the abundance of 16 understory woody species. Coefficients of Spearman rank-correlation calculated between the extracted DCA axes and (1) the PCA (on soil parameters) axes, and (2) the spatial variables. Only significant correlations are shown. Significance values are: \*\* p<0.001; \* p<0.01; ms p<0.05; ns p≥0.05. XY<sup>2</sup> – term for the interaction between X's coordinates and the quadratic term of Y's coordinates.

	DCA1	DCA2
<b>Summary</b>		
Eigenvalues	0.361	0.172
Lengths of gradient	3.136	1.842
% variance	<b>26.1</b>	<b>12.3</b>
<i>Spearman's correlations</i>		
PCA1	-0.50 *	ns
PCA4	ns	0.65 **
Elevation	0.64 **	0.63 **
XY <sup>2</sup>	ns	-0.77 **

Table 3. Results of the stepwise CCA analysis for the abundance of 16 understory woody species and the edaphic parameters. The coefficients of Spearman rank-correlation between the extracted CCA axes and: (1) the two significant predictors by stepwise selection, (2) the other edaphic variables, (3) the scores for PCA (on soil parameters) and DCA (on floristic) analyses, and (4) the spatial variables, are shown. Significance values are: \*\*  $p < 0.001$ ; \*  $p < 0.01$ ; ms  $p < 0.05$ ; ns  $p \geq 0.05$ .

	CCA 1	CCA 2
<i>Summary</i>		
Eigenvalues	0.222	0.081
Species-environment correlations	0.804	0.671
Explained variance of species data (%)	16.1	5.8
<i>Predictors' weighted correlations</i>		
NH <sub>4</sub> <sup>+</sup>	-0.57	0.47
Zn	0.66	0.38
<i>Spearman correlation</i>		
	CCAspp 1	CCAspp 2
Mg	0.45 ms	ns
EA	ns	-0.40 ms
P	0.55 *	0.49 *
Zn	-0.65 **	ns
B	0.75 **	ns
NH <sub>4</sub>	0.45 ms	ns
PCA1	0.47 *	ns
PCA3	-0.41 ms	ns
PCA4	ns	-0.54 *
DCA1	-0.99 **	ns
DCA2	ns	-0.84 **
Elevation	-0.59 *	-0.63 **
XY2	ns	0.79 **

### Non-spatially structured understory heterogeneity

This step started by a CCA analysis using only the spatial components, but a pool that includes all the three-dimensional coordinates (X, Y, Z) and their quadratic and cubic terms and interactions, as explanatory variables for the understory floristic gradients. We concluded that elevation (Z) and the product  $XY^2$  (term for the interaction between X's coordinates and the quadratic term of Y's coordinates) were the best spatial predictors for first and second CCA axes, in a highly significant ( $p=0.0001$ ) model. Afterwards, we used those spatial predictors as covariables, in a stepwise partial CCA analysis with the floristic data constrained by the soil data. A significant ( $p=0.005$ ) partial ordination model was obtained, which explained 15.8% of the residual species variance. The results (Table 4) showed that NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup> availability in soil were the two best non-redundant predictors, for explaining forest understory heterogeneity

independently from the spatial component. The comparison of these results with the previously described results of CCA, revealed that Zn was only good predictor of the understory floristic gradients when the spatial structure was not excluded, i.e. Zn has a strong spatial structure. The first pCCA axis was correlated to some soil and community variables, and to floristic and soil-floristic trends previously identified (see details in Table 4).

Table 4. Results of the partial CCA analysis, using the spatial predictors as covariables and the edaphic variables as independent ones. The coefficients of Spearman rank-correlation between the extracted pCCA axes and: (1) the significant predictors by stepwise selection, (2) the other edaphic variables (having, at least,  $p < 0.05$ ), and (3) the scores for PCA (on soil chemistry), DCA (on floristic) and CCA analyses, are shown. Significance values are: \*\*  $p < 0.001$ ; \*  $p < 0.01$ ; ms  $p < 0.05$ ; ns  $p \geq 0.05$ .

	pCCA 1	pCCA 2
<b>pCCA summary</b>		
Eigenvalues	0.168	0.051
Species-environment correlations	0.887	0.725
Explained fraction of the residual species variance (%)	16.0	4.8
<b>Spearman's correlations</b>		
<i>Predictors weighted correlations</i>		
NH <sub>4</sub> <sup>+</sup>	-0.51	0.59
NO <sub>3</sub> <sup>-</sup>	0.71	0.44
<i>Other variables vs. pCCA axes</i>		
	pCCA <sub>spp</sub> 1	pCCA <sub>spp</sub> 2
K	-0.52 *	ns
Zn	0.61 **	ns
Cu	0.41 ms	ns
Mn	ns	ns
B	-0.53 **	ns
NO <sub>3</sub>	0.60 **	ns
PCA3	0.59 *	ns
DCA1	0.65 **	ns
CCA <sub>spp</sub> 1	-0.65 **	ns

#### **Spatially structured understory heterogeneity**

The previous results, allowed us to conclude that the understory heterogeneities explained by soil variables with spatial structure, correspond to (21.9% - 15.8%) 6.1% of the total variation.

### Spatial species variation not shared with the soil variables

Another partial CCA (last line in Table 5), for measuring exclusively the species-spatial relationships – i.e. considering the best edaphic predictors ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) as covariables - showed that 12.6% of the total species variance is after all due to the spatial components and not to the edaphic factors.

### Unexplained variation

Subtracting the species-edaphic variation and the spatial species variance, from the total 100% of species variance shown by DCA, we concluded that 65% of the species variance remained unexplained by the studied edaphic and spatial factors.

Table 5. Summary results of all the performed analyses of the species data, for variance partitioning: 1) unconstrained (DCA/CA); 2) stepwise, selecting the best edaphic predictors; 3) stepwise, selecting the best spatial predictors; 4) stepwise partial CCA, after adjusting by the best spatial set obtained at step 3; and 5) stepwise partial CCA, after adjusting by the best edaphic predictors. For each analysis, the sum of all eigenvalues (trace), the percentage of the community variance explained, the model significance (by Monte Carlo test), and the location of detailed results are shown.

Analysis	Constrained by	Covariables	Predictors	Trace	p (trace)	% of species variance	Results
DCA	-	-	-	1.386	-	100	Table 1, Figure 1
CCA	Soil	-	Zn, $\text{NH}_4^+$	0.304	0.0001	21.9	Table 3
CCA	Coordinates (all)	-	Z, $\text{XY}^2$	0.450	0.0001	32.5	Table 4
pCCA	Soil	Z, $\text{XY}^2$	$\text{NH}_4^+$ , $\text{NO}_3^-$	0.219	0.0050	15.8	Table 6
pCCA	Z, $\text{XY}^2$	$\text{NH}_4^+$ , $\text{NO}_3^-$	$\text{XY}^2$	0.175	0.0010	12.6	

### Overstory-understory relationships

In Table 6 we show the results of Spearman rank-correlations between the axes extracted by the different performed analysis (DCA, CCA and pCCA) - and (1) some relevant community variables, and (2) the basal area of each of the five main overstory species. We concluded that the understory woody sinusiae in the upper slope – i.e. positive direction of DCA1 and opposite direction of CCA1 (see Tables 1 and 3) - were correlated with more light (lower canopy cover and lower maximum canopy height), higher herbaceous ground-cover, less litter ground-cover, and higher species richness (number of species). Besides, these understory sinusiae correlated positively to the lower abundance and basal area of *Q. faginea*, and to higher *Q. suber* abundance and *A. unedo* basal area. The interpretation of some of the main trends in soil chemical properties was further improved: the first PCA component (interpreted as a fertility gradient negatively

related to the elevation) correlated to maximum canopy height, to higher litter ground-cover, and to lower number of species. For the fourth soil chemical trend, we concluded that in the highest topographic positions, where the soil was poorest in ammonium and P (but richest in K), the forest was shorter and accumulated a lower amount of litter, the overstory canopy was more sparse, and the ground-cover of herbaceous vegetation was denser.

Table 6. Results of Spearman rank-correlation between the extracted axes of all the performed analysis (DCA, PCA, CCA, pCCA) and the variables of the community structure and overstory composition. Only values having at least  $p < 0.05$  are shown. Significance values are: \*\*  $p < 0.001$ ; \*  $p < 0.01$ ; ms  $p < 0.05$ ; ns  $p \geq 0.05$ .

	DCA1	PCA1	PCA4	CCAspp 1	pCCAspp 2
Canopy cover	-0.52 *	ns	-0.51*	0.49 *	-
Herbaceous ground-cover	0.77 **	ns	0.53*	-0.76 **	-
Litter ground-cover	-0.69 **	0.41 ms	-0.61	0.68 **	0.40 ms
Max. canopy height	-0.53 *	0.50 *	-0.47 ms	0.50 *	-
Species richness	0.74 **	-0.54 *	ns	-0.78 **	-0.47 *
<i>A. unedo</i> (basal area)	0.43 ms	-	-	0.57 *	-
<i>Q. faginea</i> (abundance)	-0.55 *	-	-	0.53 *	0.44 ms
<i>Q. faginea</i> (basal area)	-0.57 **	-	-	-	-
<i>Q. suber</i> (abundance)	0.47 **	-	-	-0.46 ms	-

There were only three plots where *Q. suber* had a significant contribution (an average of over 30 % of the total basal area) to the overstory biomass while *Q. faginea* was absent. These plots were compared with the three plots having the highest proportion (average of 60 % of the total basal area) of *Q. faginea* while *Q. suber* was absent. The results revealed the influence of the overstory *Quercus* species on the understory sinusiae, by means of conditioning diverse edaphic, spatial and community parameters, at the same time that the mean elevation was not significantly different (Table 7).

## DISCUSSION

From the total understory floristic variance identified, 15.8% could be explained by soil variables, while 12.6% was due to spatial parameters. Although the permutation tests (on trace statistic) demonstrated that soil and spatial variables played a significant role in explaining the understory floristic heterogeneities, 65% remained unexplained. This can be due to a large amount of stochastic variation or to some overlooked factors (BORCARD ET AL. 1992). In fact, the community structure and overstory species, themselves, were shown to condition the forest environment at many levels (e.g. light availability, litter in the soil, etc) and, therefore, to play an important role on the identified heterogeneities of the understory sinusiae.

Table 7. Results of the Student t-test on the studied variables, between plots having a different dominating oak species (*Q. suber* vs. *Q. faginea*) in the overstory. The non-significant correlation with Elevation and Total basal are also shown (italic). Significance values are: \*\* p<0.001; \* p<0.01; ms p<0.05; ns p≥0.05.

Variable	Units	<i>Q. suber</i>		<i>Q. faginea</i>		Significance	
		mean ± SD	mean ± SD	t	p		
Soil P	mg P kg <sup>-1</sup>	2.11 ± 0.45	4.71 ± 1.28	3.79	0.019	ms	
Soil NO <sub>3</sub> <sup>-</sup>	mg N kg <sup>-1</sup>	0.64 ± 0.21	0.0 ± 0.0	-12.59	0.000	**	
Soil Zn	mg kg <sup>-1</sup>	171.7 ± 40.1	37.5 ± 10.9	-6.58	0.003	*	
Canopy cover	%	0.76 ± 0.06	0.92 ± 0.02	4.43	0.011	ms	
Herbaceous ground-cover	%	0.53 ± 0.23	0.15 ± 0.09	-3.02	0.039	ms	
Litter ground-cover	%	0.23 ± 0.12	0.78 ± 0.10	4.91	0.008	*	
XY <sup>2</sup>	-	-	-	6.09	0.004	*	
<i>Elevation</i>	<i>m</i>	<i>90.0 ± 6.3</i>	<i>70.4 ± 13.5</i>	<i>-2.27</i>	<i>0.085</i>	<i>ns</i>	
<i>Total basal area</i>	<i>cm<sup>2</sup></i>	<i>410.20 ± 237.01</i>	<i>484.34 ± 181.54</i>	<i>0.43</i>	<i>0.689</i>	<i>ns</i>	

Results of this observational study suggest that the heterogeneous distribution of distinct dominant canopy species (*Quercus faginea* vs. *Q. suber*) contribute to the understory floristic-environmental variation along the slope. Those species might function as “physical ecosystem engineers”, defined as the organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials (JONES ET AL. 1997).

#### ACKNOWLEDGEMENTS

This work was financially supported by the SFRH / BD / 8322 / 2002 grant to the first author, given by the Portuguese Technology and Science Foundation (FCT), Ministry of Sciences and High Education; T. M. and L. V. G. were supported by the project HETEROMED (REN2002-4041-C02-02). Special thanks go to Ana Mouro, João Luís Mouro, Miguel Porto, Nuno Pires and Sara Dias for assisting in the fieldwork, and Nuno Gomes and associated workers for the EDM loan and field aid.

#### REFERENCES

- BORCARD, D., LEGENDRE, P. & DRAPEAU, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73(3): 1045-1055.
- FIGUEROA-RANGEL, B.L. & OLVERA-VARGAS, M. 2000. Regeneration patterns in relation to canopy species composition and site variables in mixed oak forests in the Sierra de Manantlán Biosphere Reserve, Mexico. *Ecol. Res.* 15: 249-261.
- GALLARDO, A. 2003. Effect of tree canopy on the spatial distribution of soil nutrients in a Mediterranean Dehesa. *Pedobiologia* 47: 117-125.
- GARCÍA, L.V. 2004. Escaping the Bonferroni iron claw in ecological studies. *Oikos* 105: 657-663.
- HANBA, Y. T., NOMA, N. & UMEKI, K. 2000. Relationship between leaf characteristics, tree sizes and species distribution along a slope in a warm temperate forest. *Ecol. Res.* 15: 393-403.

- JONES, C. G., LAWTON, J. H. & SHACHAK, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78 (7): 1946-1957.
- ØKLAND, R.H. & EILERTSEN, O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. *J. Veg. Sci.* 5: 117-126.
- ROSS, M.S., FLANAGAN, L.B. & LA ROI, G.H. 1986. Seasonal and successional changes in light quality and quantity in the understory of boreal forest ecosystem. *Can. J. Bot.* 64: 2792-2799.
- SPARKS, D.L. (ed.) 1996. *Methods of Soil Analysis: Chemical Methods. Part 3.* SSSA, Madison, Wisconsin, US.
- STATSOFT, INC. 2001. *STATISTICA (data analysis software system), version 6.* [www.statsoft.com](http://www.statsoft.com).
- TER BRAAK, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
- TER BRAAK, C. & SMILAUER, P. 1998. *Canoco for Windows, v.4.0.* Center for Biometry Wageningen, Wageningen, NL.
- VANDVIK, V. & BIRKS, H.J.B. 2002. Partitioning floristic variance in Norwegian upland grasslands into within-site and between-site components: Are the patterns determined by environment or by land-use? *Plant Ecol.* 162: 233-245.

### Appendix I

Woody species sampled and abbreviations used in this paper. Some metrics and abundance parameters are shown to describe each species. Nsites = number of samples in which the species occur; Height = mean height (meters); Ntrunks = mean number of trunks at the base; dbh = mean diameter at breast height (millimetres); >130cm = number of individuals more than 130 cm height; <130cm = number of individuals less than 130 cm height; SD = standard deviation.

Spp.	Abbrev.	Nsites	Height ± SD	Ntrunks ± SD	dbh ± SD	>130cm	<130cm
<i>Arbutus unedo</i> L.	Aun	20	3.3 ± 1.3	1.4 ± 0.8	29.6 ± 27.2	46	89
<i>Bupleurum fruticosum</i> L.	Bfr	4	2.5 ± 0.9	1.7 ± 1.2	6.0 ± 3.6	3	9
<i>Calluna vulgaris</i> (L.) Hull	Cvu	7	2.0 ± 0.9	1.7 ± 1.2	7.2 ± 2.9	3	30
<i>Cistus populifolius</i> L.	Cpo	4	2.3 ± 0.9	1.8 ± 1.0	7.0 ± 6.1	4	3
<i>Daphne gnidium</i> L.	Dgn	5	-	-	-	0	9
<i>Erica arborea</i> L.	Ear	25	2.9 ± 0.8	1.7 ± 1.3	24.4 ± 12.3	293	23
<i>Genista triacanthos</i> Brot.	Gtr	8	1.5 ± 0.0	1.0 ± 0.0	1.5 ± 0.7	2	12
<i>Laurus nobilis</i> L.	Lno	2	-	-	-	0	3
<i>Lavandula luisieri</i> (Rozeira) Rivas-Martínez	Llu	4	-	-	-	0	5
<i>Myrtus communis</i> L.	Mco	12	1.9 ± 0.8	1.3 ± 0.5	5.3 ± 4.7	4	37
<i>Phlomis purpurea</i> L.	Ppu	14	1.5 ± 0.0	1.0 ± 0.0	3.5 ± 0.7	2	95
<i>Phillyrea angustifolia</i> L.	Pan	13	2.4 ± 0.8	2.0 ± 1.0	6.7 ± 4.5	7	28
<i>Phillyrea latifolia</i> L.	Pla	4	2.3 ± 1.1	1.0 ± 0.0	16.0 ± 15.6	2	1
<i>Pistacia lentiscus</i> L.	Ple	7	2.1 ± 0.8	1.3 ± 0.5	13.9 ± 10.9	7	8
<i>Quercus coccifera</i> L.	Qco	24	3.2 ± 1.2	3.2 ± 4.3	18.3 ± 13.4	25	185
<i>Quercus faginea</i> Lam.	Qfa	17	4.2 ± 1.7	1.1 ± 0.4	55.4 ± 32.7	35	41
<i>Quercus suber</i> L.	Qsu	14	3.6 ± 1.2	1.0 ± 0.0	53.2 ± 40.8	12	45
<i>Rhamnus alaternus</i> L.	Ral	21	2.2 ± 0.8	1.3 ± 0.6	7.4 ± 5.6	29	106
<i>Rubus ulmifolius</i> Schott	Rul	3	-	-	-	0	3
<i>Ruscus aculeatus</i> L.	Rac	18	-	-	-	0	133
<i>Viburnum tinus</i> L. ssp. <i>tinus</i>	Vti	20	1.9 ± 0.8	1.5 ± 1.0	6.0 ± 1.8	4	170