

Article

Ecological Diversity within Rear-Edge: A Case Study from Mediterranean *Quercus pyrenaica* Willd.

Antonio J. Pérez-Luque ^{1,2,*} , Blas M. Benito ³ , Francisco J. Bonet-García ⁴  and Regino Zamora ^{1,2} 

- ¹ Instituto Interuniversitario de Investigación del Sistema Tierra en Andalucía (CEAMA)—Universidad de Granada, Avda. del Mediterráneo s/n, E-18006 Granada, Spain; rzamora@ugr.es
- ² Grupo de Ecología Terrestre, Departamento de Ecología—Universidad de Granada, Avda. Fuentenueva s/n, E-18071 Granada, Spain
- ³ Department of Ecology & Multidisciplinary—Institute for Environmental Studies “Ramon Margalef”, University of Alicante, Carretera de San Vicente del Raspeig s/n, E-03690 San Vicente del Raspeig, Spain; blasbenito@gmail.com
- ⁴ Departamento de Botánica, Ecología y Fisiología Vegetal—Universidad de Córdoba, Edificio Celestino Mutis, 1º Planta. Campus de Rabanales, E-14014 Córdoba, Spain; fjbonet@uco.es
- * Correspondence: ajperez@ugr.es

Abstract: Understanding the ecology of populations located in the rear edge of their distribution is key to assessing the response of the species to changing environmental conditions. Here, we focus on rear-edge populations of *Quercus pyrenaica* in Sierra Nevada (southern Iberian Peninsula) to analyze their ecological and floristic diversity. We perform multivariate analyses using high-resolution environmental information and forest inventories to determine how environmental variables differ among oak populations, and to identify population groups based on environmental and floristic composition. We find that water availability is a key variable in explaining the distribution of *Q. pyrenaica* and the floristic diversity of their accompanying communities within its rear edge. Three cluster of oak populations were identified based on environmental variables. We found differences among these clusters regarding plant diversity, but not for forest attributes. A remarkable match between the populations clustering derived from analysis of environmental variables and the ordination of the populations according to species composition was found. The diversity of ecological behaviors for *Q. pyrenaica* populations in this rear edge are consistent with the high genetic diversity shown by populations of this oak in the Sierra Nevada. The identification of differences between oak populations within the rear-edge with respect to environmental variables can aid with planning the forest management and restoration actions, particularly considering the importance of some environmental factors in key ecological aspects.

Keywords: rear-edge; oak woodlands; Sierra Nevada (Spain); ecological diversity; floristic diversity



Citation: Pérez-Luque, A.J.; Benito, B.M.; Bonet-García, F.J.; Zamora, R. Ecological Diversity within Rear-Edge: A Case Study from Mediterranean *Quercus pyrenaica* Willd. *Forests* **2021**, *12*, 10. <https://dx.doi.org/10.3390/f12010010>

Received: 27 November 2020

Accepted: 16 December 2020

Published: 23 December 2020

Publisher’s Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2020 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

The study of ecological dynamics within the rear-edge populations is considered essential to establish proper management guidelines under current climate uncertainties [1]. Rear-edge populations are often adapted to local environmental conditions at the limit of the species’ ecological amplitude, and often show a long-term persistence [2]. Local responses to environmental changes may differ from the species mean response [3–6], and such differences may either promote or hamper the survival of edge populations under global change [7]. Furthermore, the heterogeneity in the response to climate change observed across ecological and geographical gradients [8–11], justifies the need to incorporate fine-scale variation of environment variables throughout species ranges to better understand species responses to global change [12,13]. This is particularly important for mountain landscapes, where the topographic complexity may cause a decoupling between the climate and the geographic spaces [14,15].

The environmental heterogeneity (microclimate, geomorphology, topography, etc.) found in mountains allows the existence of a diverse plethora of ecological conditions at very fine spatial scales [16,17], offering an excellent opportunity to study ecological responses to future environmental changes [18–21]. Some tree species, such as *Pinus sylvestris* and *Quercus pyrenaica*, have their rear-edge populations located in mountainous areas of southern Europe. The topographic heterogeneity of such habitats, which act as microclimatic islands within a region of unsuitable climate for the persistence of these species, is likely to have a significant impact on persistence of these populations [22]. In these areas, the climate variation controlled by topography [23,24] is hard to capture, and the fine scale non-climate factors (both biotic and abiotic) can be at least as much relevant for species distribution as climate [25] by modulating the direct effect of regional climate on individuals. Additionally, there are finer scale gradients nested within each mountain range, which reproduce rear, optimum and leading edge conditions making the interpretation of what is currently occurring in the so-called rear edge extremely complex [4,13]. When environmental conditions are homogeneous, similar responses are expected which facilitate future forecast. Conversely, if the environmental conditions are heterogeneous, we expect a variety of responses, which forces us to consider different future scenarios at a very fine spatial scale, since climate change sensitivities could strongly vary at local scales [5,26,27].

Quercus pyrenaica Willd. (Pyrenean oak) is a deciduous Mediterranean tree species widely distributed throughout southwestern France and the Iberian Peninsula reaching their southern limit in mountain areas of northern Morocco [28]. The rear-edge populations of this species are restricted to high-mountain areas where these populations persist as isolated nuclei with ecological conditions very different from those of the main distribution area. *Q. pyrenaica* is considered one of the Mediterranean trees with a higher sensitivity to climate change [29,30]. Several studies analyzed the potential effects of climate change on distribution of this species at different spatio-temporal scales [8,29,31–36] forecasting a decrease in the suitable area of this tree species, particularly in its southern range.

Considering that the conservation strategies for tree species need to take into account the peculiarities of the rear-edge populations [1,2,37], and the high vulnerability to climate change of *Q. pyrenaica* [30], we focus here on the rear-edge populations of this species in the mountains of southern Iberian Peninsula to answer the question: Are the environmental conditions of the rear-edge populations of *Q. pyrenaica* in Sierra Nevada homogeneous? The answer to this question may be useful to analyze how the predicted climate changes would impact the rear-edge population, providing valuable information for the development of efficient forest management and restoration plans. We selected rear-edge populations of *Q. pyrenaica* located in Sierra Nevada (Southern Iberian Peninsula), since peripheral forest tree populations located in mountain areas represent natural laboratories for resolving priority research questions [1]. Particularly, we hypothesize that the rear-edge populations of *Q. pyrenaica* located in mountain areas are representative of different environmental conditions on the local scale due to the strong topographic gradients available at the edge of its range. In this work, we analyze whether these rear-edge populations inhabit similar environmental conditions. We also assess to what extent the environmental variability is matched by the floristic diversity of *Q. pyrenaica* forests. Specifically, the objectives of the work were: (i) to determine the most important environmental variables for the distribution of Pyrenean oak populations in Sierra Nevada; (ii) to identify groups of Pyrenean oak populations based on floristic composition and environmental conditions; and (iii) to unveil whether the rear-edge populations clustering according to environmental variables coincides with their grouping based on their floristic composition.

2. Materials and Methods

2.1. Study Area

The study was conducted in the Sierra Nevada (Andalusia, SE Spain, Figure 1), a mountainous region covering more than 2000 km² with an elevation range of between

860 and 3482 m.a.s.l. The climate is Mediterranean, characterized by cold winters and hot summers, with a pronounced summer drought. The annual average temperature decreases in altitude from 12–16 °C below 1500 m.a.s.l. to 0 °C above 3000 m.a.s.l. Annual precipitation ranges from less than 250 mm in the lowest areas of the mountain range to more than 700 mm in the highest peaks. Winter precipitation is mainly in the form of snow above 2000 m.a.s.l. Additionally, the complex orography causes strong climatic contrasts between south- and north-facing slopes. This mountain range is considered one of the most important biodiversity hotspots in the Mediterranean region [38], hosting 105 endemic plant species for a total of 2353 taxa of vascular plants (33% and 20% of Spanish and European flora, respectively) [39]. Forest cover in Sierra Nevada is dominated by pine plantations (*Pinus halepensis* Mill., *Pinus pinaster* Ait., *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco, and *Pinus sylvestris* L.) covering approximately 37,000 ha. Native forests are mainly dominated by holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) occupying low and medium mountain areas (11,000 ha.), and Pyrenean oak *Quercus pyrenaica* Willd. ranging from 1100 to 2000 m.a.s.l., covering about 3000 ha [40].

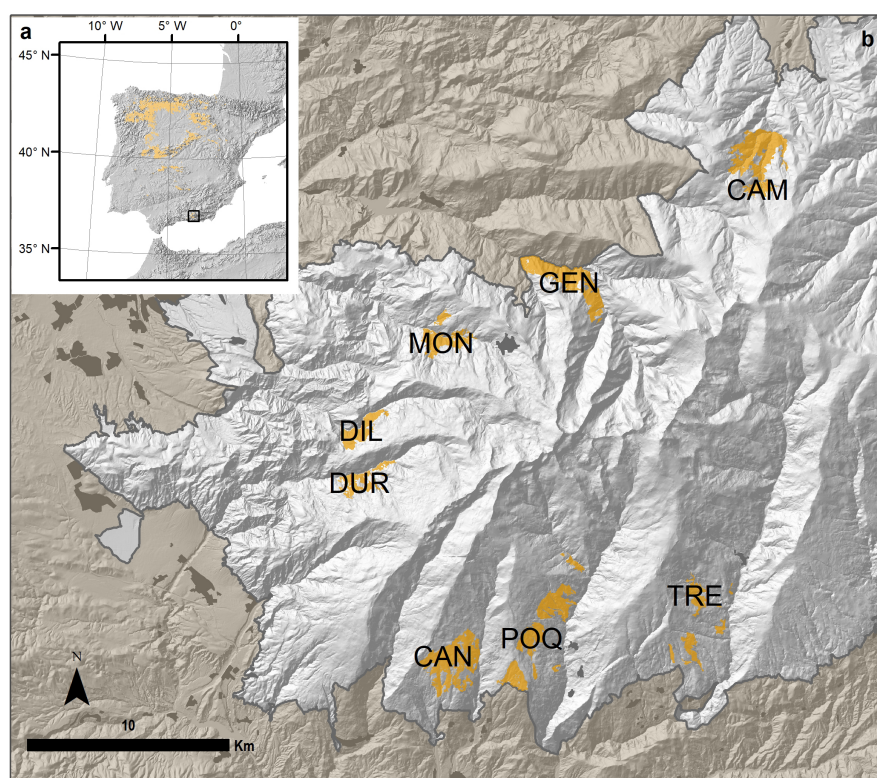


Figure 1. Distribution of *Quercus pyrenaica* forests in the Iberian Peninsula (a) and location of the patches in Sierra Nevada mountain range (b)—the name of each population as in Table 1.

2.2. *Quercus pyrenaica* Forests

Quercus pyrenaica is a deciduous species extending through southwestern France, the Iberian Peninsula, and northern Morocco [28]. The forests of this species reach their southernmost European limit in Andalusian mountains such as Sierra Nevada, where eight populations have been identified (Figure 1a; Table 1) on the basis of their isolated geographic locations in deep valleys separated by distances considerably longer than the average dispersal distances of the seeds by birds such as the Eurasian jay (*Garrulus glandarius*) [41,42]. They are distributed on siliceous soils both in the northwestern and southern slopes of the mountain range and are often associated with major river valleys. These oak woodlands represent a rear edge of their distribution [2], containing high levels of intraspecific genetic diversity [43]. Their conservation status for southern Spain is “Vulnerable”,

and it is expected to suffer from climate change, potentially reducing its suitable habitats in the near future [8,44].

Table 1. Description of the *Quercus pyrenaica* populations in Sierra Nevada. For elevation, minimum, and maximum values are in brackets. The latitude and longitude coordinates referred to the polygon centroid.

Oak Population	Code	River Valley	Municipalities	Elevation (m)	Latitude	Longitude	Area (ha)
El Camarate	CAM	Alhama	Lugros	1740 (1441–2026)	37°10′29.49″ N	3°15′24.33″ W	457.15
Robledal de San Juan	GEN	Genil	Güejar-Sierra	1519 (1189–1899)	37°7′29.63″ N	3°21′54.60″ W	395.00
Loma de la Perdíz	MON	Monachil	Monachil	1780 (1564–1990)	37°5′54.87″ N	3°25′46.65″ W	204.55
Umbría de la Dehesa de Dílar	DIL	Dílar	Dílar	1764 (1478–1960)	37°3′33.61″ N	3°28′29.07″ W	154.07
Loma de Enmedio	DUR	Dúrcal	Dúrcal	1824 (1530–2035)	37°1′58.75″ N	3°28′38.44″ W	137.04
El Robledal de Cáñar	CAN	Chico	Cáñar	1687 (1366–1935)	36°57′28.04″ N	3°25′57.10″ W	436.20
Loma de la Matanza y Loma de Ramón	POQ	Poqueira	Soportújar, Pampaneira, Bubión, Capileira	1740 (1214–1981)	36°57′58.90″ N	3°22′55.12″ W	458.95
Loma de los Lotes	TRE	Trevélez	Pórtugos, Busquístar	1692 (1312–1963)	36°58′37.38″ N	3°17′25.75″ W	197.92

The distribution of *Q. pyrenaica* forests in Sierra Nevada was delimited using the updated version of the forest map of Sierra Nevada on a 1:10,000 scale [40,45]. Black and white orthophotographies from 2001 (0.5-m of spatial resolution) and false color aerial photographs (Color Infrared) from 2005 (1-m resolution) were used to correct errors by detailed photographic interpretation, resulting in a detailed map of oak forests (Figure 1b). Forest patches with at least 50% tree cover of which 75% cover being *Q. pyrenaica* were considered oak patches.

2.3. Environmental Data

For each oak population, we obtained the values of 30 environmental variables selected to represent different direct and indirect gradients important for plant distribution [46,47]: temperature, water availability, topography, solar radiation, and land-use (Table 2). Observed climate data (1960–2010) from 43 meteorological stations 50 km around Sierra Nevada, compiled by Sierra Nevada Global Change Observatory [21], were used as input to compute high resolution (100 × 100 m pixel-size) climate maps [48] based on the mapping method proposed by Ninyerola et al. [49]. Seasonal and annual maps with the averages of direct solar radiation and insolation time were computing using the GIS GRASS module r.sun [50,51]. From a high-resolution digital elevation model (10-m; Department of the Environment, Regional Government of Andalusia), several topographic variables were derived: elevation, slope, aspect, E-W, and N-S gradients, topographic position (difference in elevation between a cell and surrounding cells within a 1000 m radius) [52]. In addition, topographic wetness index and flow accumulation were computed using the r.terraflo module of GRASS GIS. As a surrogate of anthropogenic influence, we computed the frequency of human infrastructures in a 2000 m radius buffer. Finally, for each environmental variable, we extracted the values for all the 100 m size pixels contained within each oak population (Figure 2).

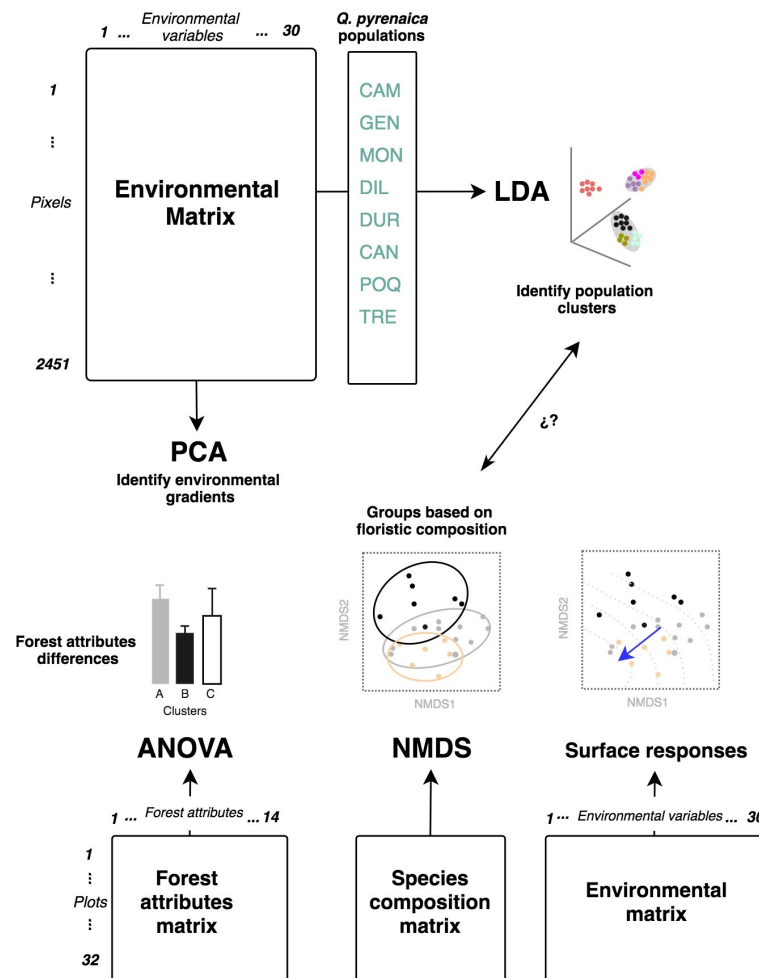


Figure 2. Methodological scheme of the analyses. Using an environmental data matrix, the main environmental gradients that characterize the oak forests at Sierra Nevada were identified using a Principal Component Analysis (PCA). Linear Discriminant Analysis (LDA) was also applied to identify different groups of oak populations. With a matrix of floristic composition, a Non-metric Multidimensional Scaling (NMDS) ordination were applied to visualize patterns of species composition, interpret them according to the environmental factors, and identify groups of oak populations based on similarities between floristic composition. See Materials and Methods for more details.

2.4. Forest Attributes

To characterize oak patches, we selected several stand attributes relating to forest structure, function, and composition from Sierra Nevada Forest Inventory [53] (Table 2). By using this approach, we characterized the plant community both in terms of their species composition, and also regarding their ecological functioning [54,55]. SINFONEVADA forest inventory was carried out during 2004–2005, and it includes an extensive network of plots distributed within the main forest units of the Sierra Nevada mountain range. We selected 32 plots belonging to the deciduous broadleaf forests category. All of them are located within the eight Pyrenean oak populations identified in Sierra Nevada. For each plot (20 × 20 m), all trees with diameter at breast height (dbh) >7.5 cm were tallied by species and dbh. Regeneration, species composition, and abundance were also recorded in two additional subplots (see [53] for a detailed description): a 5-m radius subplot where the seedling abundance of *Q. pyrenaica* was recorded; and a 10-m radius subplot where the species composition and abundance estimated by the Braun–Blanquet cover-abundance scale were measured [56] (see Table S1).

Forest composition (richness) and plant diversity were used as an indicator for overall forest biodiversity. Plant diversity was measured using the Shannon diversity index [57]. The total regeneration was used as a proxy for forest functioning. Finally, as forest structure indicators, we selected the following attributes: the total- and strata- (i.e., tree, shrub, and herbaceous) canopy cover; canopy cover diversity; tree height, tree density, basal area, and volume of adult tree. Canopy covers were computed as the proportion of plot area covered by the whole forest (total) and the different strata considered (tree, shrub, and herbaceous, respectively). Canopy cover diversity was quantified through the Shannon index for the proportion of plot area covered by different vegetation strata (tree, shrub and herbaceous) according to the following equation: $CCd' = \sum_{i=1}^n g_i \cdot \ln g_i$, where g_i is the proportion of strata i of the total plot area and n is the number of strata [58]. Basal area was calculated as the sum of the basal areas of the adult trees assuming a circular cross-section of the trunk. Volume was calculated as the sum of volume ($V = 0.55 \times \text{height} \times \text{diameter}^2$) of all *Q. pyrenaica* adult trees. Additionally, we also extracted the values of the environmental variables for the centroids of the plots, and we added a species-composition matrix for each of the 32 selected plots.

Table 2. Description of environmental variables and forest attributes used in our analysis.

Code	Description	Units
Climate		
precYE	Annual precipitation	mm
precSU	Summer precipitation	mm
precAU	Autumn precipitation	mm
precWI	Winter precipitation	mm
precSP	Spring precipitation	mm
tmaxSU	Summer mean maximum temperature	°C
tmaxAU	Autumn mean maximum temperature	°C
tmaxWI	Winter mean maximum temperature	°C
tmaxSP	Spring mean maximum temperature	°C
tminSU	Summer mean minimum temperature	°C
tminAU	Autumn mean minimum temperature	°C
tminWI	Winter mean minimum temperature	°C
tminSP	Spring mean minimum temperature	°C
Landscape		
human	Anthropogenic influence	cells
Topography		
elev	Elevation	meter
aspect	Aspect	°
slope	Slope	°
tpNS	North-South gradient	%
tpEW	East-West gradient	%
radSU	Summer direct radiation	Wh/m ²
radAU	Autumn direct radiation	Wh/m ²
radWI	Winter direct radiation	Wh/m ²
radSP	Spring direct radiation	Wh/m ²
radhSU	Mean duration of insolation in Summer	hour
radhAU	Mean duration of insolation in Autumn	hour
radhWI	Mean duration of insolation in Winter	hour
radhSP	Mean duration of insolation in Spring	hour
twi	Topographic wetness index	
tpos	Topographic position	meter
flow	Flow accumulation	

Table 2. Cont.

Code	Description	Units
Forest biodiversity		
diver	Plant diversity	
rich	Richness	species number
regTot	Total regeneration	total seedling number
Forest function		
regQp	Pyrenean Oak regeneration	seedling number
regQi	Holm Oak regeneration	seedling number
FCC	Forest canopy cover	%
Forest structure		
FCCTree	Forest canopy cover of Tree	%
FCCShru	Forest canopy cover of Shrub	%
FCCHerb	Forest canopy cover of Herbaceous	%
CCshann	Canopy Cover diversity	
heiTree	Tree Height	m
denTree	Density	trees/ha
BA	Basal area	m ² /ha
vol	Volume	m ³ × ha ⁻¹

2.5. Statistical Analysis

To identify the main environmental gradients that characterize the oak forests at Sierra Nevada, we performed a principal component analysis (PCA) on the standardized variables (Figure 2). Over 75% of the correlations (Spearman's r) among variables were significant ($p < 0.01$). We checked the adequacy of the environmental matrix by applying the Kaiser–Meyer–Olkin test, a measure of sampling adequacy ($KMO = 0.7138$, value greater than 0.5 is considered adequate [59]). The Kaiser–Guttman rule [60], i.e., axes whose eigenvalues are larger than the average of all eigenvalues; and the criterion that any principal component (PC) accounts for at least 10% of the total variance were used to determine the meaningful PCs to be retained for interpretation [61]. The PCA variables with a correlation to the principal components that was higher than 0.7 were selected to describe the environmental gradients indicated by the principal factors. We applied Linear Discriminant analysis (LDA) to determine the environmental variables that best discriminated among Pyrenean oak patches and to identify different groups of populations [61,62].

Then, environmental variables and forest attributes were tested for differences among population groups previously identified. Normality and homoscedasticity were checked using the Shapiro–Wilk test and Levene's test, respectively. If normality and homoscedasticity assumptions were satisfied, we performed ANOVA analysis followed by the Tukey LSD for testing statistical significance. Otherwise, Kruskal–Wallis ANOVA for nonparametric data were conducted followed by manual pairwise comparison using the Mann–Whitney U-test.

Finally, we used a Non-metric Multidimensional Scaling (NMDS) ordination analysis based on Bray–Curtis dissimilarity distance [63] to: (i) visualize patterns of species compositions, (ii) interpret them with respect to the environmental factors (i.e., relate the variability in species composition to environmental variables), and (iii) identify groups of Pyrenean oak populations based on similarities between floristic composition. NMDS involves the reduction of multidimensional similarity data to a low-dimensional ordination in which relative distance indicates relative similarity (i.e., plots with very similar species composition are close and vice versa) [64]. We compared two and three-dimensional solutions based on Kruskal's stress (as a measure of goodness of fit). We also studied the floristic–environment relationships by fitting linear trends on the ordination yielded by the NMDS. For these linear fittings, squared correlation coefficients and empirical p -values were calculated using random permutations ($n = 1000$) of the data [65]. Finally, we fitted non-parametrically smoothed surfaces of continuous environmental variables on the NMDS ordination. The smooth surfaces were fitted using generalized additive models

(GAM) with thin plate splines, using the coefficient of determination (R^2) as goodness-of-fit statistics e.g., [65,66].

All analysis was conducted in R software [67] using the following packages: MASS [68], nFactors [69], and vegan [70]. We also used the packages candisc [71], ellipse [72], ggpubr [73], ggord [74], factoextra [75], and patchwork [76] for visualization.

3. Results

PCA of all measured environmental variables that yielded three significant axes explained 62.11% of the total variance (Table 3). The first PC axis was strong and negatively correlated with radiation and precipitation related variables, and positively with northness gradient and slope (Table 3). Maximum average temperatures showed the strongest negative correlations with the second PC axis. The third PC axis was negatively correlated with minimum average temperatures. The precipitation variables presented weak positive correlation with the third PC axis.

The discriminant analysis yielded three significant functions explaining 97.9% of variance (Table 3). The ordination plot (Figure 3) showed a clear separation of oak populations into three clusters: a single-oak-population (CAM) cluster, namely N in the Figure 3; the second cluster (NW) formed by the GEN, MON, DIL, and DUR oak populations; and the southern cluster (S) composed by the southern oak populations CAN, POQ, and TRE. Southern oak populations were separated out from northern populations along the first LDA axis (Figure 3), which showed slight negatively correlation with autumn rainfall. The second and third LDA axes showed weak correlations with all variables (Table 3).

The three oak clusters showed significant differences for most of the environmental variables analyzed (Table 4). Only winter minimum temperatures ($\chi^2 = 5.35$; p -value = 0.069) and insolation time during summer ($\chi^2 = 0.306$; p -value = 0.306) was similar among the three oak clusters (Table 4). *Post-hoc* analysis showed that, for most of the environmental variables, we found pairwise significant differences between all three of the oak clusters (Table 4).

Forest attributes did not significantly differ among the above described oak clusters except for plant diversity and herbaceous canopy cover (Table 4). The N cluster showed a higher value of Shannon diversity index (2.27 ± 0.17) than the NW cluster (*Mann–Whitney* $U = 22.0$; p -value < 0.01). For stand attributes relating to forest structure, only the herbaceous canopy cover showed significant differences ($\chi^2 = 11.18$; p -value = 0.004; Table 4) between N and NW clusters (*Mann–Whitney* $U = 15.0$; p -value < 0.01). For all other forest structure attributes, despite there being no significant differences, the N cluster showed the lowest values (Table 4). No significant differences were recorded for regeneration variables.

A three-dimensional solution of the NMDS was chosen because its correlation with the original data was higher than for a two-dimensional solution (Linear fit $R^2 = 0.793$ vs. 0.713). Additionally, lower Kruskal's stress value was observed for the three-dimensional solution (Stress = 0.159 vs. 0.226). The NMDS ordination of the forest stands according to their floristic composition was significantly correlated with precipitation variables, elevation, and marginally with winter maximum temperatures (Figure 4; Table 5). The precipitation variables showed highly and negative correlations with NMDS axis 2 (Table 5). The NMDS axis 1 were negatively correlated with elevation ($R^2 = 0.464$) and minimum temperatures, and positively correlated with slope and winter maximum temperatures (Table 5). The NMDS ordinations with fitted vectors and surfaces for significant variables are shown in Figure 5. All of these variables showed a nonlinear significant relationship with the ordination pattern (R^2 values for surfaces were slightly higher than linear R^2 values; Table 5).

Table 3. Results of the principal component and discriminant analysis. The first three axes for PCA and LDA are shown. Loadings and correlations of the environmental variables on the principal component axis are reported. For LDA, canonical correlations of environmental variables with each discriminant function are shown.

Variable	PC1 Load	PC1 cor.	PC2 Load	PC2 cor.	PC3 Load	PC3 cor.	LDA 1	LDA 2	LDA 3
Topography									
twi	−0.022	−0.069	−0.010	−0.024	0.023	0.046	−0.009	0.005	0.018
flow	0.024	0.073	0.011	0.026	−0.008	−0.015	0.004	−0.003	0.005
elev	−0.158	−0.489	−0.016	−0.035	0.142	0.280	0.000	−0.014	0.105
slope	0.222	0.690	−0.068	−0.155	0.157	0.309	0.032	0.034	−0.073
tpos	−0.163	−0.507	−0.019	−0.042	−0.043	−0.085	−0.021	−0.013	0.006
aspect	−0.210	−0.650	−0.012	−0.026	−0.087	−0.172	−0.044	−0.043	0.075
tpEW	0.082	0.255	0.092	0.209	−0.017	−0.033	0.029	0.065	0.044
tpNS	0.238	0.737	0.031	0.070	0.092	0.182	0.076	0.070	−0.070
radWI	−0.270	−0.836	−0.030	−0.067	−0.101	−0.198	−0.071	−0.076	0.081
radSU	−0.276	−0.857	−0.023	−0.051	−0.119	−0.235	−0.067	−0.077	0.084
radSP	−0.287	−0.889	0.031	0.071	−0.152	−0.299	−0.045	−0.059	0.090
radAU	−0.292	−0.906	0.005	0.011	−0.141	−0.279	−0.056	−0.069	0.090
radhWI	−0.286	−0.888	−0.014	−0.032	−0.127	−0.251	−0.073	−0.083	0.098
radhSP	−0.283	−0.878	0.024	0.054	−0.150	−0.295	−0.051	−0.054	0.101
radhSU	−0.138	−0.428	0.111	0.252	−0.105	−0.207	−0.003	0.003	0.061
radhAU	−0.190	−0.590	0.096	0.218	−0.112	−0.220	−0.018	−0.003	0.074
Landscape									
human	−0.143	−0.443	−0.069	−0.156	0.165	0.326	−0.067	0.013	0.107
Climate									
precWI	−0.191	−0.593	−0.178	−0.404	0.301	0.594	−0.081	0.024	−0.076
precSP	−0.178	−0.551	−0.068	−0.153	0.264	0.520	−0.044	0.087	0.074
precSU	−0.226	−0.702	−0.084	−0.190	0.243	0.479	−0.073	0.069	0.092
precAU	−0.223	−0.692	−0.173	−0.391	0.225	0.444	−0.157	−0.043	−0.074
precYE	−0.223	−0.692	−0.145	−0.329	0.274	0.539	−0.092	0.032	−0.001
tminWI	0.042	0.131	−0.342	−0.775	−0.267	−0.525	0.003	−0.001	−0.024
tminSP	0.036	0.110	−0.293	−0.664	−0.311	−0.613	0.007	−0.008	0.001
tminSU	0.022	0.068	−0.189	−0.429	−0.357	−0.705	0.014	−0.011	0.045
tminAU	0.035	0.109	−0.276	−0.625	−0.321	−0.633	0.009	−0.009	0.008
tmaxWI	0.051	0.159	−0.353	−0.800	0.133	0.262	−0.021	0.014	−0.176
tmaxSP	0.063	0.196	−0.355	−0.804	0.091	0.180	−0.009	−0.014	−0.155
tmaxSU	0.056	0.175	−0.396	−0.897	0.015	0.030	−0.010	0.004	−0.120
tmaxAU	0.054	0.166	−0.372	−0.843	0.100	0.196	−0.018	0.011	−0.160
Eigenvalue	9.618		5.130		3.886		150.351	67.162	19.108
Variance	32.061		17.100		12.953		61.780	27.597	7.851
Cumulated variance	32.061		49.161		62.114		61.780	89.378	97.229
Canonical correlation							0.997	0.993	0.975

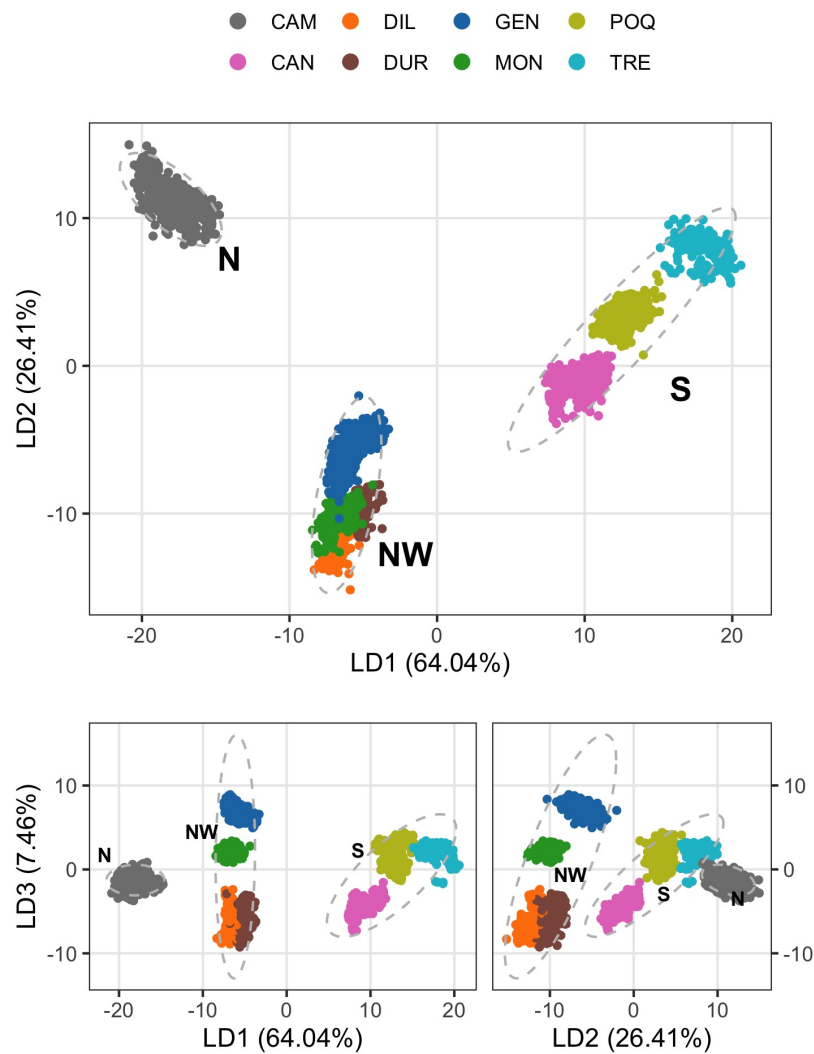


Figure 3. Discriminant analysis ordination of *Quercus pyrenaica* populations. N: northern population group (CAM); NW: northwest population group (GEN, MON, DUR, DIL); and S: southern population group (CAN, POQ, TRE). Population's code as in Table 1. Numbers in brackets expressed explained variance (%) for each discriminant axis.

Table 4. Mean values of environmental variables and forest attributes for the three identified clusters of *Q. pyrenaica* forests derived from the discriminant analysis. The Chi-squared statistics of the nonparametric Kruskal–Wallis test are shown except for those variables analyzed using ANOVA test (fccShru, fccTree and rich). Values within brackets correspond to standard errors. Standard errors are shown in parentheses. Different letters indicate statistically significant differences between clusters' oak populations.

Variable	Statistic	<i>p</i> -Value	d.f.	Group A (N)	Group B (NW)	Group C (S)
Forest attributes						
BA	4.43	0.109	2	0.71 (0.47) a	7.11 (2.00) ab	7.71 (2.78) b
denTree	3.17	0.204	2	61.57 (31.95) a	226.97 (65.10) a	282.47 (86.03) a
fccHerb	11.18	0.004	2	6.50 (0.60) a	2.83 (0.51) b	4.33 (1.12) ab
fcc	4.45	0.108	2	7.50 (0.57) a	8.50 (0.54) a	8.67 (0.99) a
heiTree	1.15	0.563	2	4.19 (1.67) a	6.96 (1.83) a	7.45 (1.76) a
CCShann	2.09	0.352	2	0.85 (0.06) a	0.92 (0.04) a	0.93 (0.04) a
vol	3.63	0.163	2	7.50 (4.92) a	90.05 (29.24) a	76.66 (34.22) a
fccShru	1.96	0.159	2; 29	2.75 (0.86) a	4.50 (0.51) a	5.33 (1.54) a
fccTree	1.41	0.261	2; 29	1.75 (0.62) a	3.33 (0.58) a	2.67 (0.80) a
regTot	0.18	0.913	2	19.38 (6.25) a	47.56 (16.16) a	32.67 (15.82) a
regQi	3.89	0.143	2	5.75 (3.40) a	0.17 (0.09) a	3.50 (2.08) a
regQp	0.39	0.823	2	7.62 (3.21) a	46.39 (16.16) a	29.17 (16.30) a
diver	8.67	0.013	2	2.27 (0.17) a	1.57 (0.13) b	1.83 (0.09) ab
rich	2.95	0.068	2; 29	16.62 (1.95) a	11.72 (1.21) a	14.17 (0.70) a
Environmental						
flow	66.22	0.000	2	345.35 (97.91) a	175.73 (32.95) b	169.57 (21.93) c
twi	60.74	0.000	2	4.90 (0.08) a	5.08 (0.05) b	5.40 (0.05) c
elev	32.38	0.000	2	1740.05 (6.52) a	1669.84 (6.22) b	1710.33 (4.20) c
tpEW	442.28	0.000	2	40.37 (1.47) a	54.36 (0.84) b	28.34 (0.58) c
tpos	201.90	0.000	2	−22.52 (1.73) a	−22.46 (1.64) a	−1.25 (0.75) b
aspect	656.80	0.000	2	160.25 (5.50) a	113.33 (2.33) b	262.06 (3.14) c
slope	568.14	0.000	2	26.10 (0.33) a	29.93 (0.28) b	20.32 (0.25) c
radWI	1301.22	0.000	2	1489.98 (50.78) a	770.18 (31.99) b	3013.85 (25.28) c
radAU	1238.90	0.000	2	5854.49 (40.75) a	5205.08 (30.85) b	6808.90 (17.59) c
radSU	1242.79	0.000	2	3056.60 (59.95) a	2140.28 (41.68) b	4619.39 (26.39) c
radSP	1064.83	0.000	2	6835.85 (29.69) a	6352.91 (25.49) b	7419.43 (14.46) c
radhWI	1565.28	0.000	2	4.77 (0.10) a	2.98 (0.08) b	8.10 (0.05) c
radhAU	125.57	0.000	2	10.44 (0.05) a	10.37 (0.04) a	11.01 (0.03) b
radhSP	1117.91	0.000	2	7.42 (0.06) a	6.47 (0.06) b	9.13 (0.04) c
radhSU	2.36	0.307	2	11.49 (0.05) a	11.37 (0.04) a	11.58 (0.03) a
tpNS	1363.86	0.000	2	62.33 (0.93) a	73.73 (0.66) b	27.76 (0.54) c
dist	2094.16	0.000	2	47.10 (0.04) a	39.52 (0.11) b	25.26 (0.04) c
human	983.67	0.000	2	0.00 (0.00) a	6.95 (0.38) b	19.53 (0.45) c
precYE	1143.00	0.000	2	690.32 (1.66) a	741.43 (1.10) b	778.13 (0.95) c
precWI	926.56	0.000	2	233.38 (0.43) a	246.53 (0.27) b	253.85 (0.28) c
precAU	1703.96	0.000	2	253.82 (0.45) a	267.02 (0.29) b	290.49 (0.35) c
precSP	576.54	0.000	2	135.36 (0.39) a	148.30 (0.32) b	148.28 (0.21) c
precSU	847.35	0.000	2	67.76 (0.39) a	79.57 (0.32) b	85.51 (0.20) c
tmaxWI	184.76	0.000	2	8.22 (0.05) a	9.40 (0.05) b	9.16 (0.04) c
tmaxAU	170.76	0.000	2	16.22 (0.05) a	17.19 (0.05) b	16.97 (0.04) c
tmaxSP	46.60	0.000	2	13.95 (0.04) a	14.35 (0.04) b	14.21 (0.03) c
tmaxSU	87.50	0.000	2	24.93 (0.04) a	25.46 (0.04) b	25.29 (0.03) c
tminWI	5.35	0.069	2	0.45 (0.04) a	0.42 (0.02) a	0.37 (0.02) a
tminAU	28.56	0.000	2	7.15 (0.04) a	6.93 (0.02) b	6.89 (0.02) b
tminSP	18.45	0.000	2	4.55 (0.04) a	4.37 (0.02) b	4.35 (0.02) b
tminSU	80.11	0.000	2	13.13 (0.04) a	12.68 (0.03) b	12.68 (0.03) b

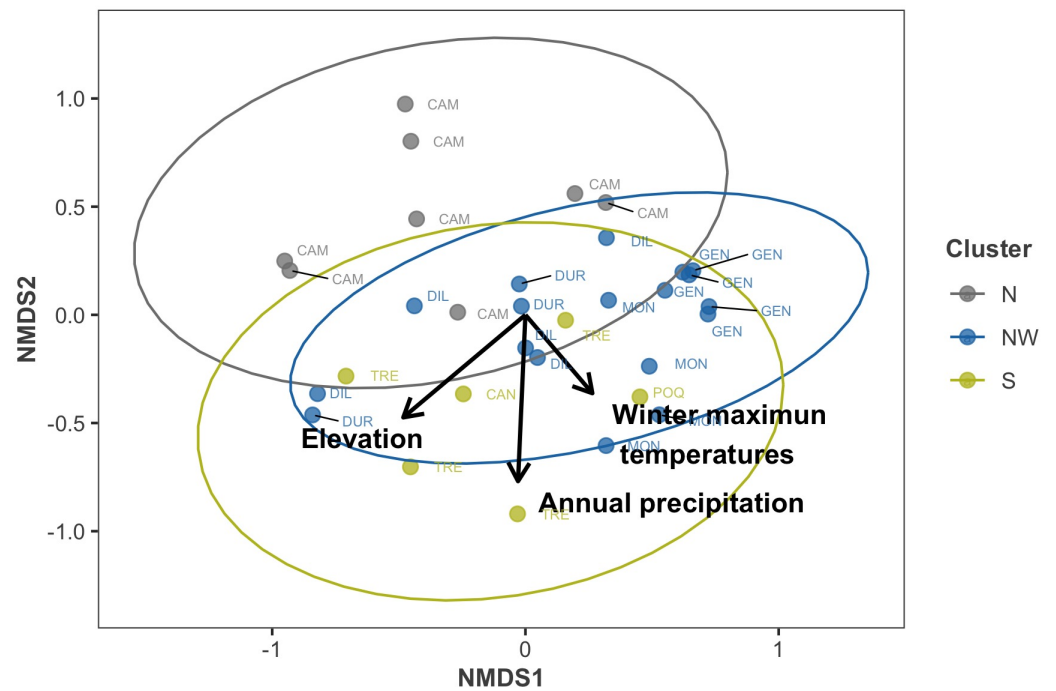


Figure 4. NMDS ordination of the plots. Points represent plot sites displayed according to their similarity in species composition. Proximity in the statistical space indicates plot sites with a similar species composition. Arrows represent vectors of significantly environmental variables explaining the ordination (see Table 5). Each plot was colored according to the three oak-populations’ clusters derived from discriminant analysis. Only two dimensions of the NMDS are illustrated for ease of representation.

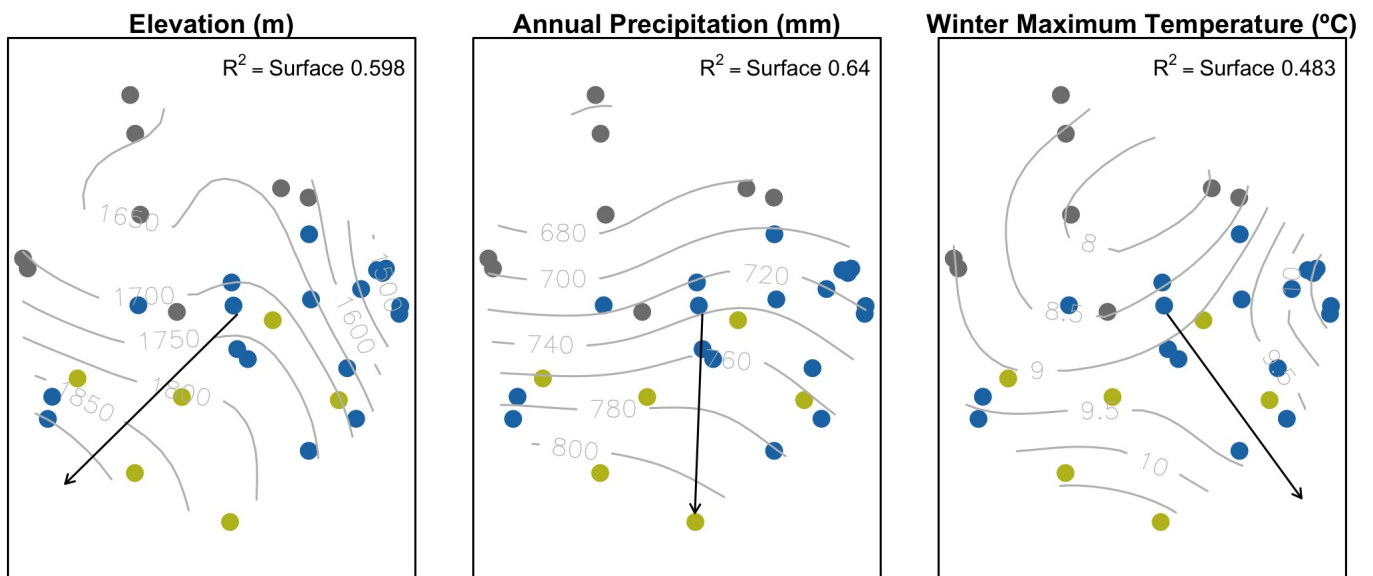


Figure 5. NMDS ordination with fitted environmental vectors and regression surfaces. Length and direction of the arrows indicate the strength and sign of the linear correlation of environmental variable with ordination scores. The surfaces show smooth trends of the relationship between environmental variables and plot scores.

Table 5. Results of the NMDS. Maximum linear correlations (R^2) of the environmental variables (vector) with the NMDS ordination patterns are shown. Significance of the correlations was calculated using 1000 permutations. Nonlinear surface responses using GAM are also shown.

Variable	Vector			Response Surface	
	Vector R^2	Vector p -Value	F	Response Surface R^2	p -Value
Climate					
precWI	0.583	0.001	4.89	0.587	0.000
precSP	0.509	0.001	6.23	0.644	0.000
precSU	0.584	0.001	7.76	0.693	0.000
precAU	0.526	0.001	2.93	0.460	0.000
precYE	0.613	0.001	6.14	0.640	0.000
tminWI	0.071	0.547	0.73	0.175	0.106
tminSP	0.091	0.436	0.63	0.155	0.121
tminSU	0.138	0.223	0.51	0.130	0.140
tminAU	0.101	0.384	0.54	0.137	0.144
tmaxWI	0.234	0.047	3.21	0.483	0.001
tmaxSP	0.112	0.363	0.87	0.202	0.069
tmaxSU	0.206	0.081	1.78	0.341	0.014
tmaxAU	0.225	0.057	2.97	0.463	0.002
Landscape					
human	0.127	0.277	0.14	0.040	0.319
Topography					
twi	0.057	0.649	0.52	0.131	0.133
flow	0.032	0.830	0.00	0.000	0.604
elev	0.464	0.002	5.12	0.598	0.000
slope	0.053	0.631	0.14	0.040	0.293
tpos	0.131	0.261	0.27	0.072	0.232
aspect	0.050	0.696	0.00	0.000	0.646
tpEW	0.050	0.698	0.34	0.090	0.217
tpNS	0.008	0.970	0.31	0.081	0.211
radWI	0.021	0.899	0.12	0.034	0.326
radSU	0.017	0.918	0.00	0.000	0.841
radSP	0.024	0.864	0.00	0.000	0.580
radAU	0.014	0.937	0.00	0.000	0.660
radhWI	0.028	0.837	0.05	0.014	0.384
radhSP	0.038	0.782	0.00	0.000	0.613
radhSU	0.139	0.190	0.01	0.004	0.421
radhAU	0.115	0.280	0.19	0.052	0.274

4. Discussion

4.1. Ecological Diversity within the Rear-Edge

The rear-edge populations of *Quercus pyrenaica* located in mountain areas are not ecologically homogeneous, neither for their environmental conditions nor for their plant species composition. In this study, we find separate groups of *Q. pyrenaica* populations within Sierra Nevada (rear-edge) driven by radiation and rainfall as main discriminant variables (Figure 3). The differences among populations based on environmental variables obtained in our study are in line with differential ecological dynamics reported for *Q. pyrenaica* forests in the Sierra Nevada by other studies. For instance, primary productivity of these forest measured using remote sensing showed a heterogeneous spatial behavior, with oak woodlands of the southern slopes displaying a greater annual vegetation greenness than those from the northern slopes [11,77,78]. In addition, differences have been found in both seasonal dynamics of greenness [77], and in temporal trends for primary productivity in the last few years related with differential snow-cover trends in contrasting slopes [78,79].

Interestingly, our results also showed differences in species diversity among population groups derived from clustering based on environmental variables. These results

are consistent with those provided by Lorite et al. [80], who pointed out that differences observed for the floristic component in the *Q. pyrenaica* populations of Sierra Nevada are related to the microclimatic conditions. Thus, Lorite et al. [80] found that the oak woodlands located in the northern part of the Sierra Nevada showed greater floristic similarity with those located at the center of the *Q. pyrenaica* distribution than those located at southern slopes of Sierra Nevada (geographically closer) [80]. The floristic differences between Sierra Nevada oak populations could also be related to the anthropogenic impact suffered by those populations, since the anthropic disturbances can affect the floristic patterns of the woodlands of this species, as it has been documented for oak woodlands in central Spain [81]. Thus, our results shown that the CAM oak population (N-cluster) showed both the highest plant species diversity and richness (Tables 4 and S1), which may be related to a better conservation status, as this population has been less exposed to intense anthropogenic activity [82]. Conversely, the southern oak populations (CAN, POQ and TRE) showed a poorer floristic composition conditioned by both climate and intense land use [83,84].

We found a remarkable match between the population's clustering derived from the analysis of environmental variables (Figure 3) and the ordination of the populations according to species composition (Figures 4 and 5). These findings suggest a linkage between the heterogeneity of environmental factors and the variability of species composition for these woodlands. The diversity of ecological conditions for *Q. pyrenaica* populations in this rear edge are in line with the high levels of genetic diversity shown by populations of this oak in the Sierra Nevada [43,85,86]. The oak woodland of Sierra Nevada has shown higher values of both genetic diversity and allelic richness than those populations located in Central Spain [85,86]. For Sierra Nevada oak populations, a great genetic differentiation among populations has been reported. [86]. Specifically, Valbuena-Carabaña and Gil [86] found high values of population genetic differentiation between oak stand located in the El Camarate site (CAM population), on the northern slope of Sierra Nevada, and other stands located in the Cádiz site (CAN population), located on the southern slope. The climatic and topographical heterogeneity that exists in the Sierra Nevada offers a great diversity of microhabitats, which has allowed this mountain range to act as a refuge for different species [87–89], including for deciduous *Quercus* species during the last glacial period [90–92]. In fact, there is fossil and genetic evidence for different *Quercus* species that strongly suggests that they survived only in southerly refugia during the last glacial maximum [90,93–95]. The persistence in a refugium suggests a combination of a moderately suitable local environment buffering against the regional climate, and a relative tolerance to climate change, by either pronounced phenotypic plasticity, and/or adaptive capacity [96]. This could be very well the case of *Q. pyrenaica*, a species harboring a high genetic diversity [43], located in a mountain region with a complex topography that could protect local populations against rapid climate shifts and allow species to persist despite regionally unfavorable environments.

4.2. The Importance of Summer Rainfall at the Micro-Habitat Level

The distribution of *Q. pyrenaica* is known to be conditioned by summer drought period with a minimum of 100–150 mm of summer rainfall [97,98]. del Río et al. [99] in a bioclimatic analysis for this species revealed the importance of rainfall and ombrothermic indexes in the separation of temperate and Mediterranean forests [99]. On a more detailed scale, the distribution for this oak is driven by a complex gradient related with temperature, rainfall, and radiation [36,100]. Our study unveils a separation in the environmental space between oak populations at the rear edge related with the spatial pattern of precipitation for this mountain region [101]. Thus, summer and annual rainfall are among the most important factors in explaining the distribution of *Q. pyrenaica* forests in Sierra Nevada (Table 3). The northern and northwestern populations of *Q. pyrenaica* in the Sierra Nevada are located in valley bottoms with northern orientation, where the relative humidity is greater as a result of a lower solar radiation. On the other hand, the populations of the

southern slopes of Sierra Nevada get an extra supply of water from moist air from the neighboring Alborán sea [102]. The differences in water availability among oak populations could affect several ecological processes such as tree-growth [5,11], seedling germination and survival [103–105], and the regeneration of the species [106], mainly due to the key role of water availability in the microsites facilitating the germination and establishment of seedlings.

4.3. Implications for Forecasting and Modeling

The factors controlling species distributions may vary depending on the scale of observation. In large scale areas, the distribution of a species is likely to be controlled by climatic regulators [107], whereas, on local scales, factors related to biological interactions play a relevant role in shaping species distributions [108,109]. At the site level, we found that moisture availability is the environmental factor that better separates the studied oak populations into clearly differentiated clusters. The identification of different population groups based on environmental variables at fine-scale is important when modeling the distribution and forecasting the impact of global change on the species. Our results suggest that incorporating the local adaptations of individual populations into predictive models might help avoid misrepresenting the potential range shift of species under changing climate conditions [7]. This is particularly important for species with rear edges located in mountain ranges, since these areas provide a broad diversity of microhabitats due to climatic and topographical heterogeneity [87]. For instance, some recent works have performed high-resolution models of the distribution of relict trees in Mediterranean southern mountains (e.g., *Abies pinsapo*, *Pinus sylvestris* and *P. nigra*) providing useful information for forest management actions [110].

5. Conclusions: Biodiversity from the Genetics to the Landscape

We identified several groups of oak populations within the rear-edge of the *Q. pyrenaica* forest mainly due to microhabitat conditions. The different clusters of oak populations are supported both by discriminant analysis of environmental variables and by ordination analysis based on the floristic composition in the target populations. Our results show that the diversity in the ecological conditions within these populations results from both the environmental heterogeneity created by the slopes and the contrasting exposures of the valleys they inhabit, and also the anthropic use of these ecosystems e.g., [11,111]. The confluence of these factors generates a multitude of environmental conditions on a fine scale, which are reflected in the distribution, composition, and functioning of the *Quercus pyrenaica* forests. *Quercus pyrenaica* woodlands are highly diverse at all organization levels, from a genetic perspective, i.e., high levels of genetic differentiation within species [43] and differences between populations [86]—to ecosystem-functioning level, i.e., diversity in terms of primary production and growth [78,79], and diversity of resilience to disturbances e.g., [11]. Such ecological heterogeneity is also made evident by the accompanying plant communities, which are very different depending on the oak population considered, such differences being correlated with the differences in environmental conditions among populations.

Mountains such as Sierra Nevada do not only act an elevation gradients along which plant communities are distributed and replaced, in fact, they constitute an ecological mosaic in which other factors besides elevation, e.g., the exposure and the history of human management, create a broad range of responses from the oak woodlands and its very diverse associated vegetation, from genetics to landscape. Understanding the differences that exist between oak populations within the rear edge with respect to environmental variables help us to plan both the forest management and restoration actions, especially taking into account the importance of some environmental factors in key ecological aspects e.g., regeneration and growth [11,104]. Our results also show the importance of the rear-edge mountain areas as a refuge for within-species diversity, and the role of species' southern ranges as hotspots of within-species diversity [112,113]. All of this knowledge

will be important to prioritize the conservation measures, and to design adaptive management actions targeting these populations, in order to maintain their ecological processes and biodiversity.

Supplementary Materials: All the data used in the analyses and the Table S1 (Species present in each population) are available at <https://www.mdpi.com/1999-4907/12/1/10/s1>.

Author Contributions: A.J.P.-L.: Conceptualization, Methodology, Software, Formal analysis, Data curation, Writing—original draft, Writing—review & editing, Visualization; B.M.B.: Methodology, Data curation, Writing—review & editing; F.J.B.-G.: Data curation, Writing—review & editing, Funding acquisition; R.Z.: Writing—review & editing, Funding acquisition. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Acknowledgments: We would like to thank Pablo Reyes-Muñoz and Pablo González-Moreno for the help with climate and forests data preparation. This research work was conducted in the collaborative framework of the “Sierra Nevada Global Change Observatory” monitoring program <http://obsnev.es>. We thank the LIFE-ADAPTAMED (LIFE14 CCA/ES/000612): Protection of key ecosystem services by adaptive management of Climate Change endangered Mediterranean socioecosystems for the funding support, and also the H2020 project European Long-Term Ecosystem and socio-ecological Research Infrastructure (eLTER) for partial funding. B.M.B. acknowledges support from the European Research Council grant agreement No. 647038 (BIODESERT). A.J.P.-L. is grateful for the invaluable support received from his family over the years.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Fady, B.; Aravanopoulos, F.A.; Alizoti, P.; Mátyás, C.; von Wühlisch, G.; Westergren, M.; Belletti, P.; Cvjetkovic, B.; Ducci, F.; Huber, G.; et al. Evolution-based approach needed for the conservation and silviculture of peripheral forest tree populations. *For. Ecol. Manag.* **2016**, *375*, 66–75. [[CrossRef](#)]
2. Hampe, A.; Petit, R.J. Conserving biodiversity under climate change: The rear edge matters. *Ecol. Lett.* **2005**, *8*, 461–467. [[CrossRef](#)] [[PubMed](#)]
3. Castro, J.; Zamora, R.; Hódar, J.A.; Gómez, J.M. Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: Consequences of being in a marginal Mediterranean habitat. *J. Ecol.* **2004**, *92*, 266–277. [[CrossRef](#)]
4. Benavides, R.; Rabasa, S.G.; Granda, E.; Escudero, A.; Hódar, J.A.; Martínez-Vilalta, J.; Rincón, A.M.; Zamora, R.; Valladares, F. Direct and indirect effects of climate on demography and early growth of *Pinus sylvestris* at the rear edge: Changing roles of biotic and abiotic factors. *PLoS ONE* **2013**, *8*, e59824. [[CrossRef](#)]
5. Gea-Izquierdo, G.; Cañellas, I. Local climate forces instability in long-term productivity of a Mediterranean oak along climatic gradients. *Ecosystems* **2014**, *17*, 228–241. [[CrossRef](#)]
6. Matías, L.; Linares, J.C.; Sánchez-Miranda, A.; Jump, A.S. Contrasting growth forecasts across the geographical range of Scots pine due to altitudinal and latitudinal differences in climatic sensitivity. *Glob. Chang. Biol.* **2017**, *23*, 4106–4116. [[CrossRef](#)]
7. Benito-Garzón, M.; Alía, R.; Robson, T.M.; Zavala, M.A. Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Glob. Ecol. Biogeogr.* **2011**, *20*, 766–778. [[CrossRef](#)]
8. Gea-Izquierdo, G.; Fernández-de Uña, L.; Cañellas, I. Growth projections reveal local vulnerability of Mediterranean oaks with rising temperatures. *For. Ecol. Manag.* **2013**, *305*, 282–293. [[CrossRef](#)]
9. Chen, K.; Dorado-Liñán, I.; Akhmetzyanov, L.; Gea-Izquierdo, G.; Zlatanov, T.; Menzel, A. Influence of climate drivers and the North Atlantic Oscillation on beech growth at marginal sites across the Mediterranean. *Clim. Res.* **2015**, *66*, 229–242. [[CrossRef](#)]
10. Dorado-Liñán, I.; Piovesan, G.; Martínez-Sancho, E.; Gea-Izquierdo, G.; Zang, C.; Cañellas, I.; Castagneri, D.; Di Filippo, A.; Gutiérrez, E.; Ewald, J.; et al. Geographical adaptation prevails over species-specific determinism in trees’ vulnerability to climate change at Mediterranean rear-edge forests. *Glob. Chang. Biol.* **2019**, *25*, 1296–1314. [[CrossRef](#)] [[PubMed](#)]
11. Pérez-Luque, A.J.; Gea-Izquierdo, G.; Zamora, R. Land-use legacies and climate change as a double challenge to oak forest resilience: Mismatches of geographical and ecological rear edges. *Ecosystems* **2020**. [[CrossRef](#)]
12. De Frenne, P.; Rodríguez-Sánchez, F.; Coomes, D.A.; Baeten, L.; Verstraeten, G.; Vellend, M.; Bernhardt-Romermann, M.; Brown, C.D.; Brunet, J.; Cornelis, J.; et al. Microclimate moderates plant responses to macroclimate warming. *Proc. Natl. Acad. Sci. USA* **2013**, *110*, 18561–18565. [[CrossRef](#)] [[PubMed](#)]
13. Oldfather, M.F.; Kling, M.M.; Sheth, S.N.; Emery, N.C.; Ackerly, D.D. Range edges in heterogeneous landscapes: Integrating geographic scale and climate complexity into range dynamics. *Glob. Chang. Biol.* **2020**, *26*, 1055–1067. [[CrossRef](#)] [[PubMed](#)]
14. Elsen, P.R.; Tingley, M.W. Global mountain topography and the fate of montane species under climate change. *Nat. Clim. Chang.* **2015**, *5*, 772–776. [[CrossRef](#)]

15. Pironon, S.; Villedas, J.; Morris, W.F.; Doak, D.F.; García, M.B. Do geographic, climatic or historical ranges differentiate the performance of central versus peripheral populations?: The ‘centre-periphery hypothesis’: New perspectives. *Glob. Ecol. Biogeogr.* **2015**, *24*, 611–620. [CrossRef]
16. Hannah, L.; Flint, L.; Syphard, A.D.; Moritz, M.A.; Buckley, L.B.; McCullough, I.M. Fine-grain modeling of species’ response to climate change: holdouts, stepping-stones, and microrefugia. *Trends Ecol. Evol.* **2014**, *29*, 390–397. [CrossRef]
17. Körner, C.; Spehn, E. A Humboldtian view of mountains. *Science* **2019**, *365*, 1061. [CrossRef]
18. Spehn, E.; Korner, C. The “Mountain Laboratory” of Nature—A Largely Unexplored Mine of Information Synthesis of the Book. In *Data Mining for Global Trends in Mountain Biodiversity*; Spehn, E., Korner, C., Eds.; CRC Press: Boca Raton, FL, USA, 2009; pp. 165–169. [CrossRef]
19. Kohler, T.; Wehrli, A.; Jurek, M. (Eds.) *Mountains and Climate Change: A Global Concern*; Sustainable Mountain Development Series; Centre for Development and Environment, Swiss Agency for Development and Cooperation and Geographica Bernensia: Bern, Switzerland, 2014.
20. Payne, D.; Spehn, E.M.; Sneath, M.; Fischer, M. Opportunities for research on mountain biodiversity under global change. *Curr. Opin. Environ. Sustain.* **2017**, *29*, 40–47. [CrossRef]
21. Zamora, R.; Pérez-Luque, A.J.; Bonet, F.J.; Barea-Azcón, J.M.; Aspizua, R.; Sánchez-Gutiérrez, F.J.; Cano-Manuel, F.J.; Ramos-Losada, B.; Henares-Civantos, I. Global Change Impact in the Sierra Nevada Long-Term Ecological Research Site (Southern Spain). *Bull. Ecol. Soc. Am.* **2017**, *98*, 157–164. [CrossRef]
22. Meineri, E.; Hylander, K. Fine-grain, large-domain climate models based on climate station and comprehensive topographic information improve microrefugia detection. *Ecography* **2017**, *40*, 1003–1013. [CrossRef]
23. Franklin, J.; Davis, F.W.; Ikegami, M.; Syphard, A.D.; Flint, L.E.; Flint, A.L.; Hannah, L. Modeling plant species distributions under future climates: How fine scale do climate projections need to be? *Glob. Chang. Biol.* **2013**, *19*, 473–483. [CrossRef] [PubMed]
24. Potter, K.A.; Arthur Woods, H.; Pincebourde, S. Microclimatic challenges in global change biology. *Glob. Chang. Biol.* **2013**, *19*, 2932–2939. [CrossRef] [PubMed]
25. Lo, Y.H.; Blanco, J.A.; Kimmins, J.P.H. A word of caution when planning forest management using projections of tree species range shifts. *For. Chron.* **2010**, *86*, 312–316. [CrossRef]
26. Lindner, M.; Maroschek, M.; Netherer, S.; Kremer, A.; Barbati, A.; Garcia-Gonzalo, J.; Seidl, R.; Delzon, S.; Corona, P.; Kolström, M.; et al. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For. Ecol. Manag.* **2010**, *259*, 698–709. [CrossRef]
27. Tito, R.; Vasconcelos, H.L.; Feeley, K.J. Mountain Ecosystems as Natural Laboratories for Climate Change Experiments. *Front. For. Glob. Chang.* **2020**, *3*, 38. [CrossRef]
28. Franco, A. *Quercus L.* In *Flora Ibérica*; Castroviejo, A., Laínz, M., López-González, G., Montserrat, P., Muñoz-Garmendia, F., Paiva, J., Villar, L., Eds.; Real Jardín Botánico, CSIC: Madrid, Spain, 1990; Volume 2, pp. 15–36.
29. Benito-Garzón, M.; de Dios, R.S.; Ollero, H.S. Effects of climate change on the distribution of Iberian tree species. *Appl. Veg. Sci.* **2008**, *11*, 169–178. [CrossRef]
30. García-Valdés, R.; Zavala, M.A.; Araújo, M.B.; Purves, D.W. Chasing a moving target: Projecting climate change-induced shifts in non-equilibrium tree species distributions. *J. Ecol.* **2013**, *101*, 441–453. [CrossRef]
31. Benito, B.; Lorite, J.; Peñas, J. Simulating potential effects of climatic warming on altitudinal patterns of key species in Mediterranean-alpine ecosystems. *Clim. Chang.* **2011**, *108*, 471–483. [CrossRef]
32. Benito-Garzón, M.; de Dios, R.S.; Ollero, H.S. Predictive modeling of tree species distributions on the Iberian Peninsula during the Last Glacial Maximum and Mid-Holocene. *Ecography* **2007**, *30*, 120–134. [CrossRef]
33. Felicísimo, A. (Ed.) *Impactos, Vulnerabilidad y Adaptación al Cambio Climático de la Biodiversidad Española. 2. Flora y Vegetación*; Oficina Española de Cambio Climático, Ministerio de Medio Ambiente y Medio Rural y Marino: Madrid, Spain, 2011.
34. Ruiz-Benito, P.; Lines, E.R.; Gómez-Aparicio, L.; Zavala, M.A.; Coomes, D.A. Patterns and drivers of tree mortality in Iberian forests: Climatic effects are modified by competition. *PLoS ONE* **2013**, *8*, e56843. [CrossRef]
35. Ruiz-Labourdette, D.; Schmitz, M.F.; Pineda, F.D. Changes in tree species composition in Mediterranean mountains under climate change: Indicators for conservation planning. *Ecol. Indic.* **2013**, *24*, 310–323. [CrossRef]
36. Urbieto, I.R.; García, L.V.; Zavala, M.A.; Marañón, T. Mediterranean pine and oak distribution in southern Spain: Is there a mismatch between regeneration and adult distribution? *J. Veg. Sci.* **2011**, *22*, 18–31. [CrossRef]
37. Rehm, E.M.; Olivas, P.; Stroud, J.; Feeley, K.J. Losing your edge: Climate change and the conservation value of range-edge populations. *Ecol. Evol.* **2015**, *5*, 4315–4326. [CrossRef] [PubMed]
38. Blanca, G.; Cueto, M.; Martínez-Lirola, M.; Molero-Mesa, J. Threatened vascular flora of Sierra Nevada (Southern Spain). *Biol. Conserv.* **1998**, *85*, 269–285. [CrossRef]
39. Lorite, J. An updated checklist of the vascular flora of Sierra Nevada (SE Spain). *Phytotaxa* **2016**, *261*, 1–57. [CrossRef]
40. Pérez-Luque, A.J.; Bonet-García, F.J.; Zamora Rodríguez, R. Map of Ecosystems Types in Sierra Nevada Mountain (Southern Spain). PANGAEA. 2019. Available online: <https://doi.pangaea.de/10.1594/PANGAEA.910176> (accessed on 15 March 2020). [CrossRef]
41. Gómez, J.M. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography* **2003**, *26*, 573–584. [CrossRef]

42. Valbuena-Carabaña, M.; González-Martínez, S.C.; Sork, V.L.; Collada, C.; Soto, A.; Goicoechea, P.G.; Gil, L. Gene flow and hybridisation in a mixed oak forest (*Quercus pyrenaica* Willd. and *Quercus petraea* (Matts.) Liebl.) in central Spain. *Heredity* **2005**, *95*, 457–465. [CrossRef]
43. Valbuena-Carabaña, M.; Gil, L. Genetic resilience in a historically profited root sprouting oak (*Quercus pyrenaica* Willd.) at its southern boundary. *Tree Genet. Genomes* **2013**, *9*, 1129–1142. [CrossRef]
44. Gea-Izquierdo, G.; Nicault, A.; Battipaglia, G.; Dorado-Liñán, I.; Gutiérrez, E.; Ribas, M.; Guiot, J. Risky future for Mediterranean forests unless they undergo extreme carbon fertilization. *Glob. Chang. Biol.* **2017**, *23*, 2915–2927. [CrossRef]
45. CMAOT. Cartografía y Evaluación de la Vegetación y Flora de los Ecosistemas Forestales de Andalucía a Escala de Detalle (1:10,000). Consejería de Medio Ambiente y Ordenación del Territorio: Sevilla, Spain, 2014. Available online: <http://sl.ugr.es/OboY> (accessed on 20 May 2020).
46. Guisan, A.; Zimmermann, N.E. Predictive habitat distribution models in ecology. *Ecol. Model.* **2000**, *135*, 147–186. [CrossRef]
47. Williams, K.J.; Belbin, L.; Austin, M.P.; Stein, J.L.; Ferrier, S. Which environmental variables should I use in my biodiversity model? *Int. J. Geogr. Inf. Sci.* **2012**, *26*, 2009–2047. [CrossRef]
48. Benito, B.M.; Pérez-Pérez, R.; Reyes-Muñoz, P.S. Climate simulations. In *Sierra Nevada Global-Change Observatory: Monitoring Methodologies*; Aspizua, R., Barea-Azcón, J., Bonet, F., Pérez-Luque, A., Zamora, R., Eds.; Consejería de Medio Ambiente: Junta de Andalucía, Spain, 2014; pp. 30–31.
49. Ninyerola, M.; Pons, X.; Roure, J.M. A methodological approach of climatological modeling of air temperature and precipitation through GIS techniques. *Int. J. Climatol.* **2000**, *20*, 1823–1841. [CrossRef]
50. Neteler, M.; Bowman, M.H.; Landa, M.; Metz, M. GRASS GIS: A multi-purpose open source GIS. *Environ. Model. Softw.* **2012**, *31*, 124–130. [CrossRef]
51. Šúri, M.; Hofierka, J. A New GIS-based Solar Radiation Model and Its Application to Photovoltaic Assessments. *Trans. GIS* **2004**, *8*, 175–190. [CrossRef]
52. Guisan, A.; Weiss, S.B.; Weiss, A.D. GLM versus CCA spatial modeling of plant species distribution. *Plant Ecol.* **1999**, *143*, 107–122. [CrossRef]
53. Pérez-Luque, A.J.; Bonet, F.J.; Pérez-Pérez, R.; Aspizua, R.; Lorite, J.; Zamora, R. Sinfonevada: Dataset of floristic diversity in Sierra Nevada forests (SE Spain). *PhytoKeys* **2014**, *35*, 1–15. [CrossRef]
54. McElhinny, C.; Gibbons, P.; Brack, C.; Bauhus, J. Forest and woodland stand structural complexity: Its definition and measurement. *For. Ecol. Manag.* **2005**, *218*, 1–24. [CrossRef]
55. Del Río, M.; Pretzsch, H.; Alberdi, I.; Bielak, K.; Bravo, F.; Brunner, A.; Condés, S.; Ducey, M.J.; Fonseca, T.; von Lüpke, N.; et al. Characterization of the structure, dynamics, and productivity of mixed-species stands: Review and perspectives. *Eur. J. For. Res.* **2016**, *135*, 23–49. [CrossRef]
56. Braun-Blanquet, J. *Pflanzensoziologie: Grundzüge der Vegetationskunde*; Springer: Wien, Austria, 1964.
57. Krebs, C.J. *Ecological Methodology*, 2nd ed.; Benjamin/Cummings: Menlo Park, CA, USA, 1999.
58. Del Río, M.; Montes, F.; Cañellas, I.; Montero, G. Indices of stand structural diversity. *For. Syst.* **2003**, *12*, 159–176. [CrossRef]
59. Dziuban, C.D.; Shirkey, E.C. When is a correlation matrix appropriate for factor analysis? Some decision rules. *Psychol. Bull.* **1974**, *81*, 358–361. [CrossRef]
60. Guttman, L. Some necessary conditions for common-factor analysis. *Psychometrika* **1954**, *19*, 149–161. [CrossRef]
61. Legendre, P.; Legendre, L.F. *Numerical Ecology*; Elsevier: Amsterdam, The Netherlands, 2012; Volume 24.
62. Williams, B.K. Some observations of the use of discriminant analysis in ecology. *Ecology* **1983**, *64*, 1283–1291. [CrossRef]
63. Kruskal, J.B. Nonmetric multidimensional scaling: A numerical method. *Psychometrika* **1964**, *29*, 115–129. [CrossRef]
64. Minchin, P.R. Simulation of multidimensional community patterns: Towards a comprehensive model. *Vegetatio* **1987**, *71*, 145–156. [CrossRef]
65. Oksanen, J. *Multivariate Analysis of Ecological Communities in R: Vegan Tutorial*. 2015. Available online: <https://www.mooreecology.com/uploads/2/4/2/1/24213970/vegantutor.pdf> (accessed on 15 March 2020).
66. Virtanen, R.; Oksanen, J.; Oksanen, L.; Razzhivin, V.Y. Broad-scale vegetation-environment relationships in Eurasian high-latitude areas. *J. Veg. Sci.* **2006**, *17*, 519–528. [CrossRef]
67. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2019. Available online: <https://www.r-project.org/> (accessed on 15 March 2019).
68. Venables, W.N.; Ripley, B.D. *Modern Applied Statistics with S*, 4th ed.; Springer: New York, NY, USA, 2002; ISBN 0-387-95457-0.
69. Raiche, G.; Magis, D. nFactors: Parallel Analysis and Other Non Graphical Solutions to the Cattell Scree Test. R Package Version 2.4.1. 2020. Available online: <https://CRAN.R-project.org/package=nFactors> (accessed on 15 March 2020).
70. Oksanen, J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlenn, D.; Minchin, P.R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; et al. *Vegan: Community Ecology Package*. R Package Version 2.5–6. 2019. Available online: <https://CRAN.R-project.org/package=vegan> (accessed on 15 March 2019).
71. Friendly, M.; Fox, J. Candisc: Visualizing Generalized Canonical Discriminant and Canonical Correlation Analysis. R Package Version 0.8–3. 2020. Available online: <https://CRAN.R-project.org/package=candisc> (accessed on 15 March 2020).
72. Murdoch, D.; Chow, E.D. Ellipse: Functions for Drawing Ellipses and Ellipse-Like Confidence Regions. R Package Version 0.4.2. 2020. Available online: <https://CRAN.R-project.org/package=ellipse> (accessed on 15 March 2020).

73. Kassambara, A. ggpubr: 'ggplot2' Based Publication Ready Plots. R Package Version 0.4.0. 2020. Available online: <https://CRAN.R-project.org/package=ggpubr> (accessed on 15 March 2020).
74. Beck, M.W. ggord: Ordination Plots with ggplot2. R Package Version 1.1.5. 2020. Available online: <https://fawda123.github.io/ggord/> (accessed on 15 March 2020).
75. Kassambara, A.; Mundt, F. factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R Package Version 1.0.7. 2020. Available online: <https://CRAN.R-project.org/package=factoextra> (accessed on 15 March 2020).
76. Pedersen, T.L. Patchwork: The Composer of Plots. R Package Version 1.0.1. 2020. Available online: <https://CRAN.R-project.org/package=patchwork> (accessed on 15 March 2020).
77. Dionisio, M.A.; Alcaraz-Segura, D.; Cabello, J. Satellite-Based Monitoring of Ecosystem Functioning in Protected Areas: Recent Trends in the Oak Forests (*Quercus pyrenaica* Willd.) of Sierra Nevada (Spain). *Int. Perspect. Global Environ. Chang.* **2012**, *355–374*. [[CrossRef](#)]
78. Pérez-Luque, A.; Pérez-Pérez, R.; Bonet-García, F.; Magaña, P. An ontological system based on MODIS images to assess ecosystem functioning of Natura 2000 habitats: A case study for *Quercus pyrenaica* forests. *Int. J. Appl. Earth Obs. Geoinf.* **2015**, *37*, 142–151. [[CrossRef](#)]
79. Alcaraz-Segura, D.; Reyes, A.; Cabello, J. Changes in vegetation productivity according to teledetection. In *Global Change Impacts in Sierra Nevada: Challenges for Conservation*; Zamora, R., Pérez-Luque, A., Bonet, F., Barea-Azcón, J., Aspizua, R., Eds.; Consejería de Medio Ambiente y Ordenación del Territorio: Junta de Andalucía, Spain, 2016; pp. 142–145.
80. Lorite, J.; Salazar, C.; Peñast, J.; Valle, F. Phytosociological review on the forests of *Quercus pyrenaica* Willd. *Acta Bot. Gall.* **2008**, *155*, 219–233. [[CrossRef](#)]
81. Gavilán, R.G.; Escudero, A.; Rubio, A. Effects of disturbance on floristic patterns of *Quercus pyrenaica* forests in Central Spain. In *Vegetation Science in Retrospect and Perspective—Proceedings 41st IAVS Symposium*; Opulus Press: Uppsala, Sweden, 2000; pp. 226–229.
82. Jiménez Olivencia, Y. *Los Paisajes de Sierra Nevada: Cartografía de los Sistemas Naturales de una Montaña Mediterránea*; Universidad de Granada: Granada, Spain, 1991.
83. Camacho-Olmedo, M.; García-Martínez, P.; Jiménez-Olivencia, Y.; Menor-Toribio, J.; Paniza-Cabrera, A. Dinámica evolutiva del paisaje vegetal de la Alta Alpujarra granadina en la segunda mitad del s. XX. *Cuad. Geográficos* **2002**, *32*, 25–42.
84. Al Aallali, A.; López-Nieto, J.M.; Pérez-Raya, F.; Molero-Mesa, J. Estudio de la vegetación forestal en la vertiente sur de Sierra Nevada (Alpujarra Alta granadina). *Itinera Geobot.* **1998**, *11*, 387–402.
85. Valbuena-Carabaña, M.; Gil, L. Centenary coppicing maintains high levels of genetic diversity in a root resprouting oak (*Quercus pyrenaica* Willd.). *Tree Genet. Genomes* **2017**, *13*, 28. [[CrossRef](#)]
86. Valbuena-Carabaña, M.; Gil, L. Evaluación de la estructura genética de poblaciones marginales de *Quercus Pyrenaica* Willd. y su evolución. Implicaciones para la conservación de sus recursos genéticos. In *Proyectos de Investigación en Parques Nacionales, 2007–2010*; Ramírez, L., Asensio, B., Eds.; Naturaleza y Parques Nacionales; Serie Investigación en la Red; Organismo Autónomo Parques Nacionales: Madrid, Spain, 2011; pp. 175–204.
87. Médail, F.; Diadema, K. Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *J. Biogeogr.* **2009**, *36*, 1333–1345. [[CrossRef](#)]
88. Gómez, A.; Lunt, D.H. Refugia within Refugia: Patterns of Phylogeographic Concordance in the Iberian Peninsula. In *Phylogeography of Southern European Refugia*; Weiss, S., Ferrand, N., Eds.; Springer: Dordrecht, The Netherlands, 2007; pp. 155–188. [[CrossRef](#)]
89. Blanco-Pastor, J.L.; Fernández-Mazuecos, M.; Coello, A.J.; Pastor, J.; Vargas, P. Topography explains the distribution of genetic diversity in one of the most fragile European hotspots. *Divers. Distrib.* **2019**, *25*, 74–89. [[CrossRef](#)]
90. Brewer, S.; Cheddadi, R.; de Beaulieu, J.L.; Reille, M. The spread of deciduous *Quercus* throughout Europe since the last glacial period. *For. Ecol. Manag.* **2002**, *156*, 27–48. [[CrossRef](#)]
91. Olalde, M.; Herrán, A.; Espinel, S.; Goicoechea, P.G. White oaks phylogeography in the Iberian Peninsula. *For. Ecol. Manag.* **2002**, *156*, 89–102. [[CrossRef](#)]
92. Rodríguez-Sánchez, F.; Hampe, A.; Jordano, P.; Arroyo, J. Past tree range dynamics in the Iberian Peninsula inferred through phylogeography and palaeodistribution modeling: A review. *Rev. Palaeobot. Palynol.* **2010**, *162*, 507–521. [[CrossRef](#)]
93. Petit, R.J.; Brewer, S.; Bordacs, S.; Burg, K.; Cheddadi, R.; Coart, E.; Cottrell, J.; Csaikl, U.M.; van Dam, B.; Deans, J.D.; et al. Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *For. Ecol. Manag.* **2002**, *156*, 26. [[CrossRef](#)]
94. Bhagwat, S.A.; Willis, K.J. Species persistence in northerly glacial refugia of Europe: A matter of chance or biogeographical traits? *J. Biogeogr.* **2008**, *35*, 464–482. [[CrossRef](#)]
95. Birks, H.J.B.; Willis, K.J. Alpines, trees, and refugia in Europe. *Plant Ecol. Divers.* **2008**, *1*, 147–160. [[CrossRef](#)]
96. Gavin, D.G.; Fitzpatrick, M.C.; Gugger, P.F.; Heath, K.D.; Rodríguez-Sánchez, F.; Dobrowski, S.Z.; Hampe, A.; Hu, F.S.; Ashcroft, M.B.; Bartlein, P.J.; et al. Climate refugia: Joint inference from fossil records, species distribution models and phylogeography. *New Phytol.* **2014**, *204*, 37–54. [[CrossRef](#)]
97. Blanco Castro, E.; Costa-Tenorio, M.; Morla y Juaristi, C.; Sanz-Ollero, H. *Los Bosques ibéricos: Una Interpretación Geobotánica*; Planeta: Barcelona, Spain, 2005.

98. García, I.; Jiménez, P. 9230 Robledales de *Quercus pyrenaica* y robledales de *Quercus robur* y *Quercus pyrenaica* del noroeste ibérico. In *Bases Ecológicas Preliminares Para la Conservación de los Tipos de Hábitat de Interés Comunitario en España*; Ministerio de Medio Ambiente, y Medio Rural y Marino: Madrid, Spain, 2009; pp. 1–66.
99. del Río, S.; Herrero, L.; Penas, A. Bioclimatic analysis of the *Quercus pyrenaica* forests in Spain. *Phytocoenologia* **2007**, *37*, 541–560. [[CrossRef](#)]
100. Gavilán, R.G.; Mata, D.S.; Vilches, B.; Entrocassi, G. Modelling current distribution of Spanish *Quercus Pyrenaica* Forests Using Climatic Parameters. *Phytocoenologia* **2007**, *37*, 561–581. [[CrossRef](#)]
101. Pereira, P.; Oliva, M.; Misiune, I. Spatial interpolation of precipitation indexes in Sierra Nevada (Spain): Comparing the performance of some interpolation methods. *Theor. Appl. Climatol.* **2016**, *126*, 683–698. [[CrossRef](#)]
102. Martínez-Parras, J.M.; Molero-Mesa, J. Ecología y fitosociología de *Quercus Pyrenaica* Willd. En La Prov. Bética. Los Melojares Béticos Y Sus Etapas De Sustitución. *Lazaroa* **1982**, *4*, 91–104.
103. Gómez, J. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. *For. Ecol. Manag.* **2003**, *180*, 125–134. [[CrossRef](#)]
104. Gómez-Aparicio, L.; Pérez-Ramos, I.M.; Mendoza, I.; Matías, L.; Quero, J.L.; Castro, J.; Zamora, R.; Marañón, T. Oak seedling survival and growth along resource gradients in Mediterranean forests: Implications for regeneration in current and future environmental scenarios. *Oikos* **2008**, *117*, 1683–1699. [[CrossRef](#)]
105. Mendoza, I.; Zamora, R.; Castro, J. A seeding experiment for testing tree-community recruitment under variable environments: Implications for forest regeneration and conservation in Mediterranean habitats. *Biol. Conserv.* **2009**, *142*, 1491–1499. [[CrossRef](#)]
106. Gómez, J.; Gómez-Aparicio, L.; Zamora, R.; Montes, J. *Problemas de Regeneración de Especies Forestales Autóctonas en el Espacio Natural Protegido de Sierra Nevada*; Sociedad Española de Ciencias Forestales: Granada, Spain, 2001.
107. Guisan, A.; Thuiller, W. Predicting species distribution: Offering more than simple habitat models. *Ecol. Lett.* **2005**, *8*, 993–1009. [[CrossRef](#)]
108. Urbieto, I.R.; Pérez-Ramos, I.M.; Zavala, M.A.; Marañón, T.; Kobe, R.K. Soil water content and emergence time control seedling establishment in three co-occurring Mediterranean oak species. *Can. J. For. Res.* **2008**, *38*, 2382–2393. [[CrossRef](#)]
109. Sánchez de Dios, R.; Benito-Garzón, M.; Sainz-Ollero, H. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecol.* **2009**, *204*, 189–205. [[CrossRef](#)]
110. López-Tirado, J.; Hidalgo, P.J. A high resolution predictive model for relict trees in the Mediterranean-mountain forests (*Pinus sylvestris* L., *P. nigra* Arnold and *Abies pinsapo* Boiss.) from the south of Spain: A reliable management tool for reforestation. *For. Ecol. Manag.* **2014**, *330*, 105–114. [[CrossRef](#)]
111. Navarro-González, I.; Pérez-Luque, A.J.; Bonet, F.J.; Zamora, R. The weight of the past: Land-use legacies and recolonization of pine plantations by oak trees. *Ecol. Appl.* **2013**, *23*, 1267–1276. [[CrossRef](#)] [[PubMed](#)]
112. Jump, A.S.; Cavin, L.; Hunter, P.D. Monitoring and managing responses to climate change at the retreating range edge of forest trees. *J. Environ. Monit.* **2010**, *12*, 1791–1798. [[CrossRef](#)] [[PubMed](#)]
113. Hampe, A.; Jump, A.S. Climate Relicts: Past, Present, Future. *Annu. Rev. Ecol. Evol. Syst.* **2011**, *42*, 313–333. [[CrossRef](#)]