forests

MDPI

Regeneration of Native Forest Species in Mainland Portugal: Identifying Main Drivers

Tiago Monteiro-Henriques[ID] and Paulo M. Fernandes *[ID]

Centro de Investigação e Tecnologias Agroambientais e Biológicas, CITAB, Universidade de Trás-os-Montes e Alto Douro, UTAD, Quinta dos Prados, Apartado 1013, 5000-801 Vila Real, Portugal; tmh@isa.ulisboa.pt
* Correspondence: pfern@utad.pt; Tel.: +351-259-350-484

check for updates

Abstract: Persistence of native forests is a global concern. We aimed at unveiling the main factors affecting tree recruitment in Portuguese native forests, modelling sapling data collected during the 5th Portuguese Forest Inventory, for five main *Quercus* taxa. Zero-inflated count data models allowed us to examine simultaneously (i) the absence of tree recruitment and (ii) the density of tree recruitment. Using Akaike weights, we obtained importance values for 15 relevant explanatory variables. Results showed that seed availability and climatic variables were determinant to understand regional absence of regeneration for all taxa. Seed availability was also an important driver of sapling density, except for *Quercus suber*. Other variables impacted on regeneration density: grazing hindered *Q. suber* regeneration; regeneration of *Q. rotundifolia* and *Q. suber* was lower in flat areas; recurrent fire hampered the regeneration of *Q. robur* and *Q. pyrenaica*; *Q. broteroi* and *Q. pyrenaica* showed depressed regeneration in regions where forest plantations abound, while *Q. robur* and *Q. suber* seemed selectively protected. We conclude that caution is warranted when analysing pooled data for *Quercus* spp. regeneration, as different variables affected *Quercus* taxa differently. Finally, we suggest dedicated management actions to enhance the establishment of new native forests.

Keywords: native forest; Portugal; *Quercus*; regeneration; sapling; zero-inflated count data model

1. Introduction

Native forests are of great concern for nature conservation [1]. On the one hand, they are known to shelter significantly more biodiversity than planted forests [2–9]; on the other hand, they have been exploited by man since long and eventually replaced on a large scale with agriculture, urban fabric and other land uses [10].

Native forests are nowadays subjected to new challenges that endanger their long-term persistence, such as regeneration failure [11–13], climatic changes [14,15] and replacement with non-native forest species [1]. The latter are already widely distributed in Portugal. Portuguese native forests were reduced to less than 7% of the territory by the end of the 19th century [16,17] and never recovered conspicuously [17,18] for three main reasons: (i) during the first half of the 20th century, *Pinus pinaster* Aiton was the preferred forestry species [17]; (ii) during the second half of the 20th century, preference was given to the exotic *Eucalyptus globulus* Labill., which is currently the most abundant forest species in Portugal, corresponding to 26% of the forested areas [17,19]; and (iii) since the end of the 20th century, a great increase in the extent of wildfires [20], which recurrently burn shrublands [21], delaying the progression of ecological succession.

Forest regeneration and its possible failure have long worried scientists [22]. A considerable number of scientific studies have shown that a very large set of variables affects forest regeneration. We list some examples of such variables, non-exhaustively: air temperature [23,24]; moisture [25]; light [26–29]; aspect [30]; nurse-effect of shrubs or trees [30–32]; animal mediated seed dispersal [33,34];

grazing and browsing [23,35]; proximity to seed source [36]; disturbance regimes like those emerging from fire patterns [12,37]; soil nutrients [26,27]; soil organic layer depth [11,38]; soil texture [11]. Modelling forest regeneration is thus challenging, as a vast set of variables is known to possibly affect it. Additionally, the effects of such variables can have opposite signals among different contexts. For example, Caldeira et al. [39] showed that under Mediterranean climate (where summer drought is pronounced), tree canopy cover negatively affected seedlings growth but facilitated seedlings survival of *Quercus suber* L. and *Q. rotundifolia* Lam., while low soil moisture, high soil temperature and herb biomass decreased their survival. Similarly, Plieninger et al. [11] have associated *Q. suber*, *Q. rotundifolia* and *Q. pyrenaica* Willd. regeneration failure with more open, uniform, and/or aged woodlands. Conversely, under temperate climate, where water availability is not as limiting, tree regeneration might depend much more on competitive growth and gap-dynamics [29,40,41]. Other variables can have two-fold effects even on the same species under similar contexts, depending on their frequency patterns. for example, relatively infrequent fires can trigger or promote tree regeneration and diversity [42–44], while recurrent fires can strongly and negatively affect forest regeneration, eventually compromising it in the long-term [45].

"Foundation species" sensu Dayton [46], constitute fundamental taxa for the structuring of the whole community. Dominant trees are foundation species within the forest ecosystem they thrive in and are intimately connected to the existing biodiversity. Here we approach forest regeneration focusing on dominant tree recruitment. In particular we considered five *Quercus* taxa that dominate zonal native forests in mainland Portugal, namely: *Quercus robur* L., *Q. pyrenaica* Willd., *Q. faginea* Lam. subsp. *broteroi* (Cout.) A. Camus, *Q. suber* L. and *Q. rotundifolia* Lam. [47]. Although other genera can dominate zonal native forests in mainland Portugal, for example, *Juniperus*, *Pinus*, *Olea*, *Ceratonia* and *Betula* [48], the five referred *Quercus* taxa account for 93% of the potential zonal native forests area in mainland Portugal [47]. Currently, in Portugal, 21.5% of the mainland territory is included in the National System of Classified Areas [49]. However, forests devoted to biodiversity conservation occupy about 145 000 ha [50], representing 4.5% of the forested area and 1.6% of the Portuguese mainland territory, once mostly covered by forests [47,51–54].

Our single objective is to comprehensively understand the regeneration of these native forest taxa in mainland Portugal, testing a wide collection of high-quality explanatory variables, answering the question: which are the most relevant factors driving tree recruitment in Portuguese native forests? Unveiling such factors is of ultimate importance not only to devise inclusive guidelines targeting the expansion of native forests but also to underpin forest management strategies and best practices.

We concluded that even if some variables affected all the studied taxa similarly, some other variables showed very different relevance between taxa. This allowed us to point out basic dedicated management actions to enhance the establishment of new native forests.

2. Materials and Methods

2.1. Base Data

We used data from the 5th National Forest Inventory (NFI5) [55], which surveyed around 6800 forest plots (of 500 to 2000 m^2) on a regular grid (2 × 2 km) within mainland Portugal, during 2005 and 2006. In particular, we used as dependent variable the number of "small trees" of each of the five oak taxa already referred (*Q. robur*, *Q. pyrenaica*, *Q. faginea* subsp. *broteroi*, *Q. suber* and *Q. rotundifolia*). *Q. faginea* subsp. *faginea* occurs scattered among *Q. suber* and *Q. rotundifolia* forests in the northeast of Portugal [56] and some very rare forests are dominated by this subspecies in the same region [57]. However, since the spatial resolution of NFI5 does not seem sufficient to capture these very rare forests and very little regeneration of that subspecies was recorded, *Q. faginea* subsp. *faginea* regeneration was not modelled. Pooling the two subspecies was not an option, given the substantially different conditions (climate, land use, orography) under which they thrive. Henceforth, *Q. faginea* subsp.

broteroi is denoted simply as *Q. broteroi*. The NFI5 considers as "small trees" those taller than 0.50 m but with a diameter at breast height (1.30 m) inferior to 7.5 cm. Hereafter we denote "small tree" as sapling.

We searched for high-resolution/high-quality variables, as the NFI5 dataset has high spatial accuracy (the maximum admissible positioning error of the plots centre was 6 m). Aiming at covering the widest possible range of variable types, we gathered 15 putative explanatory variables known to affect forest regeneration. We describe these variables in the following paragraphs.

From data collected during the NFI5, we used basal area (G), tree density (N), evidence of grazing (GRAZI) and evidence of understory clearing (UnderClear). Also using data from the NFI5 on the dominant and co-dominant trees, we built maps of the density of plots dominated or co-dominated by each of the studied *Quercus* taxa, within three different predefined neighbourhoods (2 km, 5 km and 10 km). Such maps (Figures S1–S5 within Supplementary Materials) were obtained using the *focal* function from R *raster* package [58] and statistically estimate the local to regional presence of adult trees, being fair proxies of (local to regional) seed availability (SeedAvail). SeedAvail derived for a taxon (e.g., *Q. robur*) was used only for modelling the regeneration of that same taxon (i.e., *Q. robur* saplings), thus this variable can be summarized as "the density of plots with conspecific adult trees, in a predefined neighbourhood". In the same way, using the dominant and co-dominant species information coming from NFI5, we calculated the density of plots dominated or co-dominated by *Pinus pinaster* trees (DensPp) and the density of plots dominated or co-dominated by *Eucalyptus globulus* trees (DensEg) (Figures S6 and S7 in Supplementary Materials). With such variables we wanted to test if (local to regional) forestry intensity could influence *Quercus* regeneration.

Using data from the Portuguese digital fire atlas (available online at http://www2.icnf.pt/portal/florestas/dfci/inc/mapas) we produced two variables: fire frequency (FireFreq), as the number of fires experienced by each plot between 1975 and 2006 and time since last fire (TSLFire) coded as a factor with two levels ("≤5 years" and ">5 years"). In this way we could test if regeneration is hindered where fire recurrence is high or if it is triggered by a recent fire.

Concerning climatic data, Monteiro-Henriques et al. [59] published 13 climatological indices for mainland Portugal. From those we chose the summer quarter ombrothermic index (OMBRO) and the compensated thermicity index (THERM), as these are fairly uncorrelated and synthesise important climatological information known to affect plant species distribution [60]. OMBRO is related to climatic summer drought, which is important to discriminate between Mediterranean and temperate bioclimates and THERM reflects annual average temperature with extra weight given to winter temperatures, which are known to limit plant growth and distribution.

Using the digital elevation model produced by the Shuttle Radar Topography Mission version 4.1 [61] we obtained two physiographic variables (TRASP and SLOPE) and one edaphic variable (SoilMoist). TRASP was calculated as described in Evans [62], transforming topographic aspect into a 0 to 1 scale, higher values indicating the sunniest/driest aspects (S-SW exposures); flat stands were treated as if exposed southwards. SLOPE, that is, drop per distance, was obtained using TAUDEM 5.06 (Terrain Analysis Using Digital Elevation Model) D-infinity method [63,64]. SoilMoist, that is, the logarithm of the contributing area, was also calculated using TAUDEM (D8 method) and R STATISTICAL SOFTWARE 3.0.1 [65]. Several packages were used in the process: *lattice* 0.20-9 [66], *permute* 0.7-0 [67], *foreign* 0.8-55 [68], *raster* 2.1-49 [69], *rgdal* 0.8-10 [70] and *sp* 1.0-11 [71,72]. *rgdal* package relied on libraries GDAL version 1.10.0 and PROJ4 version 4.8.0 [PJ_VERSION: 480]. We calculated two variants of SoilMoist using two different weights: (i) OMBRO, which reflects summer soil moisture; and (ii) the annual ombrothermic index (AOI) [59], which reflects the accumulated soil moisture throughout the year. In order to calculate OMBRO and AOI for the Iberian Peninsula we merged precipitation interpolations coming from Nicolau [73] and Gonzalo Jiménez [74] and used data on temperature, for the Iberian Peninsula, coming from Hijmans et al. [75,76]. In this way we obtained two datasets for the Iberian Peninsula (with 35-m resolution) of weighted contributing areas. Further information can be found at http://home.isa.utl.pt/~tmh/ as well as links to download the contributing area variables and other associated hydrologic variables.

Soil parent material types (SPMType) were also tested as an edaphic explanatory variable, derived from the 1/500,000 Portuguese Geologic Map [77]. Appendix A details the methodology used to construct this variable; see also, in the same appendix, Tables A1 and A2 where further information is given on the construction of SPMType and Figure A1 where a map of SPMType is presented.

Table 1 lists the 15 putative explanatory variables, the respective abbreviations, an informal classification of the variable type and the physical phenomenon related to each variable.

Table 1. List of putative explanatory variables of *Quercus* regeneration and their succinct characterization.

Abbreviation	Variable Name (Units or Levels)	Variable Type	Related Physical Phenomenon
G	Basal area (m^2 ha^{-1}).	Forest structure	Light/space availability (proxy).
N	Tree density, independently of the species (no. of trees per m^2).	Forest structure	Light/space availability (proxy).
GRAZI	Evidence of grazing by domestic animals, that is, cattle, equine, sheep, goat or swine ("yes", "no").	Anthropic (animal husbandry)	Vegetation disturbance.
UnderClear	Evidence of bushes removal, that is, mechanical removal, prescribed fire, manual removal, etc. ("yes", "no").	Anthropic (management)	Vegetation disturbance/space availability.
SeedAvail	Density of plots with conspecific adult trees (no. of plots in a predefined neighbourhood).	Seed source	Local to regional seed availability/conspecific adult presence.
DensPp	Density of plots with adult *P. pinaster* trees (no. of plots in a predefined neighbourhood).	Anthropic (land-use)	Local to regional forestry intensity (*P. pinaster*).
DensEg	Density of plots with adult *E. globulus* trees (no. of plots in a predefined neighbourhood).	Anthropic (land-use)	Local to regional forestry intensity (*E. globulus*).
FireFreq	Fire frequency (no. of fires between 1975–2006).	Fire	Recurrent vegetation disturbance.
TSLFire	Time since last fire ("≤5 years", ">5 years").	Fire	Vegetation disturbance/space availability.
OMBRO	Summer quarter ombrothermic index (mm °C^{-1}).	Climatic	Summer climatic moisture (proxy).
THERM	Compensated thermicity index (°C*10).	Climatic	Air temperature.
TRASP	Transformed aspect (0 to 1).	Physiographic	Relative solar radiation; also related to moisture, temperature and wind shelter (proxy).
SLOPE	Slope (drop/distance).	Physiographic	Soil deepness (proxy); accessibility (proxy).
SoilMoist	Logarithm of the contributing area weighted by OMBRO or AOI (mm °C^{-1}).	Hydrologic/edaphic	Summer soil moisture/annual soil moisture (proxy).
SPMType	Soil parent material types ("alluvia", "siliceous light", "siliceous loamy", "siliceous heavy", "intermediate loamy", "basic heavy", "ultramafic heavy").	Edaphic	Parent material base richness and potential soil texture.

2.2. Data Pre-Treatments

Pearson correlation coefficient (*r*) among all variable pairs was checked and multicollinearity was further assessed calculating the variance inflation factors for each taxon dataset using function *vif* from R package *usdm* [78]. For all taxa datasets *r* among all possible pairs of variables used in models was lower than 0.7 (see Figures S8–S12 in Supplementary Materials.). Variance inflation factors were under 2.8 (9.0 excluding zero saplings) for *Q. broteroi* and under 2.9 (5.2 excluding zero saplings) for all other species, showing low multicollinearity levels. Tables S1–S5 in Supplementary Materials present summary statistics for all variables in all datasets.

The presence of spatial autocorrelation on saplings data was checked with the Mantel test and 10,000 Monte Carlo permutations using *mantel.rtest* function from package *ade4* [79]. For all taxa, the simulated *p*-values were between 0.75 and 0.97, indicating no correlation between saplings data (excluding zero saplings) and the respective Euclidean distance matrices.

Extreme observations can bring additional ecological insight. However, it was not feasible to compare the fitting results with and without extreme observations, due to the long computation time of the fitting process. After inspecting saplings boxplots for each species, we decided to exclude a few clearly isolated data points corresponding to suspicious extremely high counts; Figure S13 in Supplementary Materials shows the boxplots produced and Table 2 indicates the number of extreme observations removed. Table 2 shows, additionally, which soil parent material types (SPMType) were tested for each taxon and the total number of plots used to implement the models for each taxon (i.e., the total number of plots with available information on both saplings and the 15 explanatory variables).

Table 2. SPMType tested classes for each taxon and total no. of plots used in modelling.

Taxa	No. of Removed Extreme Observations	SPMType Tested Classes [1]	Total No. of Plots Used in Modelling
Q. robur	0	1, 2	4167
Q. pyrenaica	2	1, 2, 4	4461
Q. broteroi	1	1, 2, 3, 4	4631
Q. suber	3	1, 2, 4	4485
Q. rotundifolia	1	1, 2, 3, 4	4642

[1] SPMType: 1 "siliceous loamy", 2 "siliceous heavy", 3 "intermediate loamy", 4 "basic heavy".

2.3. Zero-Inflated Count Data Models

Zero-inflated count data models (ZICDM) are two-component mixture models that extend the classical generalized linear models (GLM) to account for excess of zeros in the dataset. One component incorporates a point mass at zero while the other corresponds to a count distribution such as Poisson or negative binomial. Therefore, zeros might come both from the point mass and from the count component. ZICDM using a negative binomial count model include a dispersion parameter θ in the modelling procedure, enabling the incorporation of both the excess of zeros and over-dispersion [80].

Following Zeileis et al. [80] the regression equation for the mean of a ZICDM, using the canonical log link for the count component, can be written as:

$$\mu_i = (1 - \pi_i) \cdot e^{(\beta_0 + x_{1i}\beta_1 + \ldots + x_{mi}\beta_m)} \tag{1}$$

where π_i is the probability of belonging to the point mass component, that is, in our case, the probability that regeneration is absent (zero saplings). The second component $e^{(\beta_0 + x_{1i}\beta_1 + \ldots + x_{mi}\beta_m)}$ is simply the conditional mean coming from the count model (as in a classical Poisson or negative binomial GLM). β's correspond to the m coefficients of the count model (β_0 the intercept), which multiply by each of the m selected explanatory variables (x_i).

The unobserved probability π_i is modelled, simultaneously, by a binomial GLM, which conditional mean can be written, using the standard logit link, as:

$$\pi_i = \frac{1}{1 + e^{(\gamma_0 + z_{1i}\gamma_1 + \ldots + z_{ni}\gamma_n)}} \tag{2}$$

where γ's correspond to the n coefficients of the zero inflation component (γ_0 the intercept), which multiply by each of the n selected explanatory variables (z_i) [80].

The coefficients β and γ, as well as the dispersion parameter θ (for the negative binomial count model) can be estimated, simultaneously, by maximum likelihood [80–82]. ZICDM are particularly appropriate to model saplings count data coming from national forest inventories. As count data, saplings number is appropriately handled by the count component of the model (by using Poisson or negative binomial distributions). Additionally, it is plausible that some species do not regenerate in some regions due to, for example, environmental constraints (which ultimately result in the absence

of that species in that regions); as a result, an excessive number of zeros occur in the data. However, in the regions where regeneration is more probable, plots presenting zero saplings can still occur (e.g., by a simple matter of chance); these zeros are modelled by the count component.

Interestingly, by combining a logistic response (zero inflation component) with an exponential response (count component), it is possible for ZICDM to fit unimodal responses for a variable (thus, not only monotonic, as logistic or exponential by their own, when using first-degree polynomial terms). Additionally, such combined responses can also be asymmetric/skewed in shape. This added flexibility is only achievable when the variable in question is included in both components of the ZICDM.

2.4. Model Fitting

All the 15 chosen variables were tested as predictors in the count component. Regarding the zero inflation component, however, we decided to test OMBRO, THERM, SeedAvail and SoilMoist (i.e., as predictors of the absence of saplings). Other variables such as FireFreq, GRAZI, UnderClear can completely hinder regeneration (e.g., through very high fire frequency or overgrazing) but extremes in FireFreq are very rare in the studied area, thus not expected to produce a true inflation of zeros, neither the number of grazed or managed plots justifies their testing as zero inflating variables. Inversely, climatic variables can impede regeneration over extensive areas, for example, low OMBRO values represent severe summer drought, which in southern Portugal is expected to completely preclude the regeneration of temperate species like *Q. robur*. Another variable able to produce zero inflation is SPMType (e.g., *Q. suber* is known to be calcifuge); however, as it is a categorical variable, to avoid numerical problems and perfect fittings we decided simply to remove from the analysis the classes of SPMType presenting less than 10 sapling occurrences, for *Q. robur*, *Q. pyrenaica*, *Q. suber* and *Q. rotundifolia*, and, exceptionally, 5 for *Q. broteroi* (as the number of sapling occurrences was considerably lower).

To sample the number of saplings, NFI5 used two different subplot sizes, depending on the species dominating the forest plot, respectively 200 m^2 subplots in plots dominated by *Q. suber* or *Q. rotundifolia* and 50 m^2 subplots for all other species. Consequently, the logarithm of the subplot area was used as an offset in all of the fitted models, ensuring that saplings density was correctly modelled.

To decide between the Poisson and negative binomial distribution we firstly looked at the mean and variance of the response variable and checked the Wald-tests of log(θ).

Model fitting was performed in R STATISTICAL SOFTWARE 3.2.0 [83] using packages *stats*, *utils*, *parallel* [83], *vegan* [84] and *pscl* [85]. After rescaling continuous independent variables to zero mean and unit variance using function *decostand* (*vegan* package), we used *zeroinfl* function (*pscl* package) to fit the models and function *AIC* from package *stats* to extract the Akaike Information Criteria (AIC) of each model.

As variables influence is expected to vary between taxa, we individually fitted models for each *Quercus* taxon. Even if we understand that the inclusion of interactions between variables could certainly improve the obtained models [13,38], including 2-way interactions would have raised the number of possible model formulas to an impracticable number. Therefore we opted to not include interaction terms, focusing only on the main terms importance. In this way, the 15 variables used for the count component of the model and the 4 variables selected for the zero inflation component were combined in all possible ways using function *combn* from *utils* package to produce 524,288 different model formulas for each taxon.

We performed two sequential runs. In the first run we used: (i) SeedAvail with 2-km neighbourhoods, as we hypothesized that local scale effects on seed availability would be stronger than regional effects, due to the limited seed dispersal range usually found in the *Quercus* genus [33,34]; (ii) DensPp and DensEg with 10-km neighbourhoods, as we supposed the wider scale would best capture forestry intensity effects on regeneration; (iii) SoilMoist weighted by OMBRO, as the gradient of summer precipitation is pronounced in mainland Portugal and is an important limiting variable

for the survival of seedlings and saplings. Therefore, in a first run we fitted models for all possible combinations of:

- On the count component: G, N, GRAZI, UnderClear, SeedAvail (2 km), DensPp (10 km), DensEg (10 km), FireFreq, OMBRO, THERM, TRASP, SLOPE, SoilMoist (summer) and SPMType;
- On the zero inflation component: SoilMoist (summer), OMBRO, THERM and SeedAvail (10 km).

After fitting all models and sorting them by increasing AIC we checked if SeedAvail, DensPp and DensEg were selected amongst the best model (lower AIC), or on some of the alternative models (ΔAIC < 2). In case one (or more) of those variables was extant in this set of best models, we studied if other neighbourhood size (or a combination of neighbourhood sizes) minimized AIC further. Finally, when AIC decreased by replacing the neighbourhood size(s), we performed a second run, again fitting all the 524,288 combinations but now using the neighbourhood(s) which decreased AIC. Simultaneously, we also checked for AIC changes by replacing SoilMoist (summer) by SoilMoist (annual), whenever this variable was present in the set of best models. In case the replacement produced a decrease in AIC, we used SoilMoist (annual) in the second run. Even if we wanted to sense the differences between the different neighbourhood sizes and SoilMoist weights, we must stress that we expected minimal changes in the model performance, as the changes in neighbourhood or weight produced, generally, highly correlated variables (see Figures S8–S12 in Supplementary Materials.).

2.5. Variables Importance Value

AIC difference to the best model was calculated for each of the fitted models ($\Delta_i = \text{AIC}_i - \text{AIC}_{min}$). As the relative likelihood is directly proportional to a simple calculation using the Δ_i's ($\mathcal{L}(g_i|\text{data}) \propto e^{-(1/2)\Delta_i}$), Akaike weights ($w_i$) can be computed for each model as:

$$w_i = \frac{e^{-(1/2)\Delta_i}}{\sum_{k=1}^{K} e^{-(1/2)\Delta_k}} \tag{3}$$

where *K* is the total number of models.

Finally, variable importance values were obtained for each of the tested variables, summing the Akaike weights of all models containing the variable:

$$w_+(j) = \sum_{i \text{ for } x_j \in g_i} w_i \tag{4}$$

See [86,87] for further information.

Besides variable importance, we found essential to inspect the signal of the effect (i.e., positive or negative), in order to discuss the results from an eco-physiological point of view. We examined the signal of the fitted coefficients in the following way: after ordering all models by their respective Akaike weight (w_i), we selected the first *j* models that totalized 0.95 of summed w_i and checked if each variable sign was positive or negative among those models. A variable signal was considered consistent when always positive or negative within the first *j* models.

3. Results

As expected, a large proportion of plots had zero saplings; moreover, saplings variance was systematically greater than the mean (Table 3). Therefore the negative binomial distribution was used and, inspecting the set of best models, the logarithm of the dispersion parameter $\log(\theta)$ was always significant in the Wald-test for all taxa.

Table 3. Percentage of zeros, mean and variance of sapling by taxon.

Taxa	% Plots without Saplings	Excluding Plots without Saplings		Including Plots without Saplings	
		Saplings Mean	Saplings Variance	Saplings Mean	Saplings Variance
Q. robur	96.0%	4.7	35.5	0.2	2.3
Q. pyrenaica	96.8%	7.8	113.3	0.3	5.5
Q. broteroi	99.3%	2.0	2.0	0.01	0.04
Q. suber	94.6%	3.1	15.5	0.2	1.3
Q. rotundifolia	95.2%	8.2	128.8	0.4	9.3

Neighbourhood sizes and SoilMoist weights producing lower AIC values varied among the studied taxa. Considering SeedAvail, 2-km neighbourhoods produced better models for *Q. robur* and *Q. pyrenaica*, yet for *Q. broteroi* and *Q. rotundifolia* higher values were chosen. For DensPp, 10-km produced lower AIC values for *Q. robur* and 2-km for *Q. pyrenaica*, while for DensEg, the 10-km neighbourhood was selected both for *Q. broteroi* and *Q. suber*. Table 4 summarizes best neighbourhoods results, as well as SoilMoist best weight (summer or annual ombrothermic index).

Table 4. Neighbourhood dimensions and soil moisture weight selected for final run; shown only when significant (*p*-value < 0.05) in the Wald-test in some of the best models of the final run.

Taxa	SeedAvail (count)	DensPp (count)	DensEg (count)	SoilMoist (count)	SeedAvail (zero)	SoilMoist (zero)
Q. robur	2 km	10 km	-	-	10 km	summer
Q. pyrenaica	2 km	2 km	-	-	5 km	-
Q. broteroi	5 km	-	10 km	annual	10 km	annual
Q. suber	-	-	10 km	-	2 km	-
Q. rotundifolia	10 km	-	-	-	2 km	-

The number of models used to study variable signal consistency was quite different among taxa (Table 5), meaning that, for some of the studied taxa, Akaike weights were more concentrated within the first models with lower AIC, than for other taxa. Figures S14–S18 in Supplementary Materials show graphically, for each taxon, the sorted AIC of all models and the proportion of the first (sorted) models that summed up to 0.95 of Akaike weight.

Table 5. Number of models where coefficients signals were examined.

Taxa	No. of Models
Q. robur	5289
Q. pyrenaica	1275
Q. broteroi	16,249
Q. suber	4272
Q. rotundifolia	18,551

Importance values based on Akaike weights (w_+), both for the count and zero inflation components, allowed us to identify the most and the least relevant variables for the regeneration of each taxon. Table 6 presents the obtained importance values (values greater than 75% are in bold). On the side of each importance value the result of the signal consistency analysis is also presented: an up arrow indicates a consistent positive effect of the variable in the taxon regeneration; a down arrow indicates a consistent negative effect; if both arrows are present, signal was not consistent in the analysed models. Signals were consistent for all variables with importance values greater than 80%.

In order to allow the inspection of (the best) obtained fits, we present in Tables S6–S10 in Supplementary Materials the summary outputs of the best model (lower AIC) for each taxon.

Table 6. Variable importance values based on Akaike weights both for the count and zero inflation components and respective signal consistency.

Variable		Variable Importance Values (Based on Model Akaike Weights)				
		Q. robur	*Q. pyrenaica*	*Q. broteroi*	*Q. suber*	*Q. rotundifolia*
Count component	G	**95.8%** (↑)	72.1% (↓)	26.7% (↑↓)	**99.9%** (↑)	28.3% (↑↓°)
	N	**86.0%** (↓)	63.1% (↓)	66.6% (↑↓°)	45.8% (↓)	33.2% (↑↓°)
	GRAZI	45.2% (↓)	61.6% (↓)	40.2% (↓)	**98.9%** (↓)	30.1% (↑°↓)
	UnderClear	56.6% (↓)	**99.4%** (↓)	35.1% (↓)	29.8% (↓)	31.5% (↑)
	SeedAvail	**100.0%** (↑)	**99.9%** (↑)	**99.9%** (↑)	34.9% (↑)	**98.8%** (↑)
	DensPp	**76.4%** (↑)	**78.0%** (↓)	31.2% (↑↓)	30.7% (↑)	32.8% (↑↓°)
	DensEg	29.3% (↑↓)	41.5% (↓)	**81.8%** (↓)	**92.5%** (↑)	28.1% (↑↓)
	FireFreq	**100.0%** (↓)	**93.6%** (↓)	29.2% (↑↓)	31.9% (↑)	60.8% (↑°↓)
	TSLFire	34.0% (↑)	27.7% (↑↓)	47.4% (↑°↓)	27.9% (↑↓°)	73.0% (↓)
	OMBRO	**93.8%** (↓)	**99.5%** (↓)	**75.8%** (↑°↓)	**99.0%** (↓)	54.5% (↑↓°)
	THERM	36.5% (↑°↓)	29.9% (↑↓)	73.9% (↑)	29.0% (↑↓)	62.0% (↑°↓)
	TRASP	**83.7%** (↓)	**94.2%** (↓)	68.5% (↑↓°)	40.9% (↓)	63.6% (↓)
	SLOPE	27.5% (↑°↓)	33.1% (↓)	35.6% (↑)	**100.0%** (↑)	**100.0%** (↑)
	SoilMoist	48.6% (↑)	28.6% (↑↓)	69.4% (↑°↓)	30.6% (↓)	41.5% (↑)
	SPMType	28.8%	**99.8%**	29.3%	15.2%	71.9%
Zero inflation component	SeedAvail	**100.0%** (↓)	**100.0%** (↓)	**100.0%** (↓)	**100.0%** (↓)	**100.0%** (↓)
	OMBRO	**100.0%** (↓)	**100.0%** (↓)	**100.0%** (↑°↓)	**99.8%** (↓)	**96.7%** (↑)
	THERM	**92.1%** (↓)	**100.0%** (↑)	76.5% (↑°↓)	39.1% (↓)	67.2% (↑↓°)
	SoilMoist	**75.5%** (↓)	48.7% (↑)	69.1% (↑°↓)	30.4% (↓)	57.4% (↓)

(↑) consistent positive signal; (↓) consistent negative signal; (↑↓) inconsistent signal. When only a smaller proportion (<25%) of models containing the variable contributed to signal inconsistency, the less frequent signal is indicated with ° on the right of the respective arrow.

4. Discussion

4.1. Zero Inflation Component

Importance values for the zero inflation components of all studied taxa were very high for climatic variables, particularly OMBRO and, to a less extent, THERM. This was expected, as mainland Portugal encompasses two distinct macrobioclimates, temperate in the NW and Mediterranean in the rest of the territory [59,88] and climate is known to determine species absence from entire regions [89]. However, species and/or regeneration can be missing from areas that are climatically suitable. In fact, seed availability (SeedAvail), at relatively much smaller scales (from 2 to 10 km), presented also very high importance values, showing that the presence of nearby adult trees is critical for regeneration to occur. SoilMoist was less relevant by far. Still, zero-sapling occurrences of *Q. robur* decreased towards higher summer moisture areas (i.e., the bottom of the hills and valleys in areas with rainier summers), which agrees with the species preference for deep, cool soils under temperate climate [25,90].

4.2. Count Component

As expected, variable importance values were much different among each taxon. Notwithstanding, local to regional seed availability (SeedAvail) resulted positively linked to higher sapling densities for all taxa except *Q. suber*; the importance of nearby seed sources in Iberian *Quercus* regeneration was also found relevant by Gómez-Aparicio et al. [91]. OMBRO was also relevant for all taxa and its selection on both count and zero inflation components (with the same signal) indicates the modelling of non-monotonic responses. We now highlight other important variables for each taxon.

4.2.1. *Q. robur*

Q. robur regeneration was dependent on forest structure, increasing with basal area (G). In fact *Q. robur* ability to regenerate under intermediate to low levels of light is well-known [92,93]. However, higher tree densities (N) showed an opposite effect, which can be related to regeneration failure in younger and denser forests, probably plantations, where very low light levels can end up hindering

Q. robur regeneration [94,95]. Fire frequency (FireFreq) was particularly relevant at hindering *Q. robur* regeneration, which agrees with this species sensitivity to recurrent fires that can lead to its replacement by shrubland [45]. DensPp had a moderate positive effect on *Q. robur* sapling density. Fast-growing pine plantations have long been introduced in the Mediterranean countries assuming they would facilitate hardwoods in the long-term [96]. In Portugal, this strategy was mostly unsuccessful but some old growth pine stands in the centre and north of Portugal currently comprise a substantial *Q. robur* component. We believe this relates to the effect found for DensPp, alongside with greater awareness of this species value. Sapling density was lower in southern aspects (TRASP), where summer water deficit is likely to be higher (or more severe) than in less sun-exposed terrain aspects.

4.2.2. *Q. pyrenaica*

The negative response of regeneration to higher basal area (G) or denser forests (N) concurs with [41], who studied the regeneration patterns of *Q. pyrenaica* and linked it to shade-intolerant species. *Q. pyrenaica* regeneration particularly suffered with understory clearing (UnderClear) and, to a lesser extent, with grazing (GRAZI). Indeed, this species occupies northern mountains where human settlements are scattered but extensive livestock grazing is still practiced [18,56]. Northern mountains display the highest fire frequency in Portugal, due to intricate relationships between land use, climate and topography [20,97]; accordingly, FireFreq affected sapling density negatively, as it did for *Q. robur*. Soils with heavier textures and higher base content (SPMType) had a positive effect on sapling abundance, similarly to Plieninger et al. [11] findings. *Q. pyrenaica* stands on such clayish and base-rich soils are rare in Portugal and are mainly limited to the NE region, where very dense stands with high and rapid regeneration have been described [56].

Although *Q. pyrenaica* occurrence is linked to the transitional areas between temperate and Mediterranean macrobioclimates, thus enduring summer drought better than *Q. robur*, southern aspects (TRASP) had lower sapling densities, like *Q. robur*. Contrariwise, DensPp had a negative effect on *Q. pyrenaica*, which might be related to forest management actions (as shown also by UnderClear) and possibly to the additional pressure this species suffers from its use as firewood [98].

4.2.3. *Q. broteroi*

After SeedAvail, regeneration of *Q. broteroi* was chiefly negatively affected by the regional density of *E. globulus* stands (DensEg). *Q. broteroi* use for firewood is documented in the centre west of Portugal, where it comprises a considerable proportion of burned firewood [99]. *E. globulus* stands planted for pulp production are widespread in this region. This possibly explains the regeneration depression in these areas due to both forest management practices and the overuse of *Q. broteroi* for firewood.

4.2.4. *Q. suber*

Basal area (G) affected *Q. suber* regeneration positively, in agreement with other studies where a nursing effect of tree cover was reported [39,100]. It is striking to note that *Q. suber* was the only taxon for which saplings density did not increase with the density of stands dominated or co-dominated by *Q. suber* adult trees in the neighbourhood (SeedAvail). In fact, regeneration failure in the *montado* system is a well-known and well-studied phenomenon [11,101,102] and most Portuguese *Q. suber* stands appear in the form of such cultural systems [103].

Grazing (GRAZI) is a common component of the agro-silvo-pastoral *montado* system and was highly relevant in depressing *Q. suber* regeneration, in agreement with studies showing that the *montado* sustainability is threatened by overgrazing, among other factors [101,102,104,105]. Slope arose also as an important variable, with flat areas associated with a decrease in regeneration; interestingly, *montados* are usually associated with flat areas [106]. Additionally, steeper terrain is usually less accessible, being less prone to human disturbances, as referred by Maia et al. [107].

Another remarkable finding is that *Q. suber* regeneration was positively associated to *E. globulus* stands, which was unexpected but it is justifiable. On one hand, *E. globulus* currently occupies a great

fraction of the most oceanic *Q. suber* potential area in Portugal [19,47]. On the other hand, in this central-western part of Portugal it is common to find *Q. suber* trees exploited for cork, mainly in marginal areas, as a source of extra income for landowners. High environmental suitability for *Q. suber* and its presence either as scattered individuals or small stands, might explain its denser regeneration in those *E. globulus* dominated regions.

Q. suber is known to prefer siliceous substrata [90]. Considering SPMType, its saplings occurred in more than 10 stands for "siliceous loamy" (34.3%), "siliceous heavy" (60.7%) and "basic" (5%) types. Stands on "basic" substrata are considerably less in number, clearly evidencing its preferences. Yet, the variable did not result important as expected. We believe that the 15 stands on "basic" substrata might mainly result from mapping generalization errors (recall base data was on a scale of 1:500,000; see Appendix A) or from sites located in rainy areas where soil characteristics might change due to leaching.

4.2.5. *Q. rotundifolia*

From all studied taxa, *Q. rotundifolia* is the one able to withstand higher summer drought [108]. Its aptitude to thrive under dry climates is documented [109,110]. In fact, it was the only *Quercus* for which the probability of zero saplings increased with summer climatic moisture (OMBRO). As for the other *Quercus*, this was compensated by OMBRO in the count component (thus producing a non-monotonic response, as the others); however, it reflects the fact that sapling presence is concentrated towards summer drier regions, which are extensive in the centre and south of Portugal [59].

Recent fire events (TSLFire) triggered *Q. rotundifolia* regeneration, most probably linked to resprouting. Notwithstanding, high Firefreq resulted also negative for *Q. rotundifolia* regeneration but less importantly than for the temperate sub-Mediterranean species.

As for *Q. suber*, *Q. rotundifolia* is also frequently found dominating the tree layer of the Portuguese *montado* system. Yet, it is also commonly observed dominating residual and marginal forests throughout the Mediterranean areas of mainland Portugal. In Spain, the agro-silvo-pastoral system similar to *montado*, the *dehesa*, is also associated with a regeneration failure of *Q. rotundifolia* [106]. Yet, grazing (GRAZI) did not result relevant in obstructing *Q. rotundifolia* regeneration, as it did for *Q. suber*. This is somehow puzzling, as a similar pattern would be expected. However, both species co-occur frequently in Portugal and herbivore preference for *Q. suber* is documented [111,112], which can shed some light on why grazing affected these species differently. Nevertheless, as with *Q. suber*, slope resulted equally very relevant, with flat areas (common in *montados*) having decreased regeneration.

4.3. Selected Neighbourhoods

For all taxa, the most important variable affecting regeneration was the density of conspecific trees, that is, the proxy of local to regional seed availability (SeedAvail), being determinant in modelling regeneration absence (producing excess of zeros) and with the exception of *Q. suber*, it was also positively linked to sapling abundance. *Quercus* spp. seeds are known to be recalcitrant, with viabilities usually shorter than one year [113]. Thus, *Quercus* do not form a seed bank and, as expected, the proximity of adult trees resulted relevant for regeneration. Although different neighbourhoods performed differently for SeedAvail, changing neighbourhoods did not produce relevant changes in models. Nevertheless, for the temperate species *Q. robur* and *Q. pyrenaica*, 2-km neighbourhoods performed better (confirming our initial hypothesis), while for the Mediterranean species *Q. broteroi* and *Q. rotundifolia*, respectively, 5-km and 10-km performed better. In the case of *Q. broteroi* the neighbourhood increase might relate with the low number of adult stands in the dataset. The neighbourhood increase in *Q. rotundifolia* might relate with the highly continuous and even occurrence of this species in the southeast of Portugal.

Concerning DensPp and DensEg (which reflect local to regional forestry intensity), the 10-km neighbourhoods performed better in *Q. robur*, *Q. broteroi* and *Q. suber* models, as initially hypothesized.

For *Q. pyrenaica* the 2-km neighbourhood was the best performing one; in this case we believe the relatively simpler rural landscapes where this species generally occurs allows the smaller neighbourhood to capture forestry pressure more readily. SeedAvail, DensPp and DensEg different neighbourhood performance could be better clarified by further work.

5. Conclusions

Mediterranean taxa sapling abundance (*Q. suber* and *Q. rotundifolia*) increased on less accessible sites, reflecting the long lasting and widespread anthropization of such landscapes. Actually, *Q. suber* regeneration was particularly impeded by cultural practices, namely grazing.

P. pinaster and *E. globulus* plantations had a negative effect on less noble essences (*Q. broteroi* and *Q. pyrenaica*), which are selectively collected for firewood in their regions of occurrence. Results suggest the more valuable *Q. robur* and *Q. suber* saplings are selectively protected under plantations, especially the latter, which is kept for cork harvesting and is strictly protected by law.

Disturbance is a well-known trigger of regeneration as it creates site availability. From the set of chosen variables, FireFreq, TSLFire, UnderClear and GRAZI are vegetation disturbances known to be very frequent in the Portuguese context. Wildfires became very frequent in mainland Portugal since the 1970s. Fire triggered the regeneration of *Q. rotundifolia* (TSLFire), nonetheless, high FireFreq reduced the abundance of its saplings. FireFreq was particularly relevant in hampering the regeneration of temperate sub-Mediterranean taxa (*Q. robur* and *Q. pyrenaica*). Although *Quercus* species resprout after fire [114], frequent fires can exhaust belowground storage reserves precluding further resprouting and kill saplings that have not yet stored enough reserves for resprouting [115].

Pooled analyses, for example, Vayreda et al. [116], although relevant for the study of more general traits (e.g., pines vs. broadleaves), can mislead the importance and relevance of variables. Vayreda et al. [116] concluded that climate and even disturbances, were less relevant drivers of regeneration. In fact, climate cannot be expected to be much relevant in a pooled analysis, as *Quercus* spp. are ubiquitous in the Iberian Peninsula, thus pooling them is likely to result in a no-effect for climatic variables. In this study we showed that different disturbances, as well as climatic variables, can be important and their relevance changes from taxon to taxon. Eventually, sapling density, as well as sapling absence, showed strong correlation to climate, thus, climatic changes are expected to impact regeneration in the future.

In a nutshell, management actions aiming at improving native forests regeneration should consider fire control (*Q. robur*, *Q. pyrenaica* and *Q. rotundifolia*), thinning of existing forest plantations, for example, *P. pinaster* (*Q. robur* and *Q. pyrenaica*) and avoiding practices that eliminate the taxon, like understory clearing (*Q. pyrenaica* and *Q. broteroi*), firewood overexploitation (*Q. broteroi*) and overgrazing (*Q. suber*).

(n = 4167), Table S2: Summary statistics for the *Q. pyrenaica* dataset (n = 4461), Table S3: Summary statistics for the *Q. broteroi* dataset (n = 4631), Table S4: Summary statistics for the *Q. suber* dataset (n = 4485), Table S5: Summary statistics for the *Q. rotundifolia* dataset (n = 4642), Figure S13: Sapling counts boxplots for all datasets. Whiskers extend 1.5 times the interquartile range. Outside whiskers, circles indicate observations that were used in the analysis, while crosses those removed, Figure S14: Top: Sorted AIC of all 524 288 fitted models for *Q. robur*. Bottom: Sorted model Akaike weights, for *Q. robur* and the respective fraction of the first models, which sum up to 0.95 and 0.99 of Akaike weight, Figure S15: Top: Sorted AIC of all 524 288 fitted models for *Q. pyrenaica*. Bottom: Sorted model Akaike weights, for *Q. pyrenaica* and the respective fraction of the first models, which sum up to 0.95 and 0.99 of Akaike weight, Figure S16: Top: Sorted AIC of all 524 288 fitted models for *Q. broteroi*. Bottom: Sorted model Akaike weights, for *Q. broteroi* and the respective fraction of the first models, which sum up to 0.95 and 0.99 of Akaike weight, Figure S17: Top: Sorted AIC of all 524 288 fitted models for *Q. suber*. Bottom: Sorted model Akaike weights, for *Q. suber* and the respective fraction of the first models, which sum up to 0.95 and 0.99 of Akaike weight, Figure S18: Top: Sorted AIC of all 524 288 fitted models for *Q. rotundifolia*. Bottom: Sorted model Akaike weights, for *Q. rotundifolia* and the respective fraction of the first models, which sum up to 0.95 and 0.99 of Akaike weight, Table S6: Summary output of the best fitted model for *Q. robur*, Table S7: Summary output of the best fitted model for *Q. pyrenaica*, Table S8: Summary output of the best fitted model for *Q. broteroi*, Table S9: Summary output of the best fitted model for *Q. suber*, Table S10: Summary output of the best fitted model for *Q. rotundifolia*.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript and in the decision to publish the results.

Appendix A

This appendix details how the variable SPMType (soil parent material types) was constructed.

The chemical composition and texture/grain size of the parent material influence pedogenesis and mostly determine soil richness and texture, which also strongly depend on other important factors such as climate, biota and so forth. Soil parent material types were obtained by reclassifying the Portuguese Geological Map 1:500,000 [77]. We reclassified each geological map unit (rock types and formations) into seven classes, crossing the associated potential soil base richness and potential soil texture (see Table A1). To position each rock type/formation in each of the seven classes we used information on the richness in SiO_2, K and Ca and also information on texture/grain size of the parent material. Table A2 presents a detailed characterization of the seven used classes, namely presenting the relative content in SiO_2, K and Ca of the parent material, the central (potential) soil texture (i.e., usually associated with that parent material) and finally the rock types/formations that were included in each class (mainly in view of the context of mainland Portugal geologic principal features).

Table A1. Potential richness-textural classes used to classify soil parent material.

		Textural Classes		
		Light (Sandy)	**Loamy**	**Heavy (Silty or Clayish)**
Base richness	**Siliceous**	siliceous light	siliceous loamy	siliceous heavy
	Intermediate		intermediate loamy	
	Basic			basic heavy
	Ultramafic			ultramafic heavy

Table A2. Detailed characterization of the defined classes: relative content of SiO$_2$, K and Ca, central (potential) soil texture and included rock types/formations.

Class	Relative Content in			Central Soil Texture	Rock Types/Formations
	SiO$_2$	K	Ca		
siliceous light	++++	-	-	very light (sandy)	Siliceous sand formations.
siliceous loamy	+++	++	-	(light to) loamy	Chert (flint, radiolarite), siliceous/ferric sandstone, consolidated dunes, siliceous conglomerate, quartz syenite, quartz trachyte, acid tuff, granite, rhyolite, syenite, trachyte, siliceous gneiss, siliceous paragneiss, arkose, quartz, quartz monzonite, quartz latite, quartzite.
siliceous heavy	++	+	+	(loamy to) heavy	Siliceous schist, clayish conglomerate, greywacke, siliceous phyllite, clayish sandstone, turbidite, mica schist, clayish schist, slate, lydite rich metasediments, claystone, clay, mudstone (shale, argilite), metapelite, silt, silty phyllite, siltstone, ampelite, silty arkose, expansive clays.
intermediate loamy	+	-	++	(light to) loamy (to heavy)	Granodiorite, monzonite, latite, foid syenite, phonolite, tonalite, tonalitic gneiss, quartz monzodiorite, monzodiorite, siliceous schist/phyllite with carbonated or calc-silicate layers, calciturbidite, quartz diorite, diorite, quartz monzogabbro.
basic heavy	-	-	+++	(loamy to) heavy	Carbonate sandstone, carbonate breccia/conglomerate, sandstone + marlstone, sandstone + limestone, andesite, quartz gabbro, monzogabbro, basaltic andesite, mafic lamprophyre, diabase/dolerite, gabbro, foid gabbro, basalt, tephrite, marlstone + sandstone, limestone + sandstone, amphibolite, limestone + marlstone, marble, limestone.
basic very heavy	-	-	+++	very heavy	Marlstone + limestone, marlstone, dolomite rock.
ultramafic heavy	- -	- *	var.	heavy	Basanite (igneous), ultramafic lamprophyre, pyroxenite, serpentinite, peridotite, metaperidotite, dunite.

Legend: + and - signs indicate relative richness; * generally poor but rare exceptions occur; var.: very variable content.

Igneous rocks were positioned mainly using data from QAPF diagrams (Quartz, Alkali feldspar, Plagioclase and Feldspathoid) and the TAS (Total Alkali vs. Silica) diagram [118,119] and other specific mineralogical information of each rock type/formation, gathered in geological and similar publications. Sedimentary and metamorphic rocks/formations were positioned following specific mineralogical information of the respective rock type/formation, gathered in geological and similar publications. For the present work, the "basic heavy" and "basic very heavy" classes of Table A2 were merged into one single class called "basic heavy".

After the reclassification, the new map was entered into a Geographical Information System (GIS) and orthoimagery was used to improve the map accuracy. In particular, using ESRI ARCMAP 10.0 SP5 *Spatial Adjustment* tools (rubersheet method) the obtained polygons were adjusted to the Portuguese official boundary [120], a highly accurate dataset of the Portuguese border, as well as, adjusted to match natural boundaries when unequivocally recognized in the orthoimagery provided by ESRI (ESRI basemaps, 50 cm resolution otrthoimages from DGRF collected from 2004 to 2006). Several natural boundaries between geological units could be recognized and were very useful to improve the map georeferencing, for instance:

(i) boundaries between granitoid rocks and metasediments were sometimes recognizable in the orthoimages and particularly valuable in the centre and north of mainland Portugal.

(ii) in the south, the transition between limestone and metasediments was often distinguishable in the orthoimages.

(iii) ultramafic rocks, which are known to affect greatly the vegetation cover, allowed to add some correction points in the north-east of mainland Portugal, using the shift to other basic rocks.

(iv) alluvial plains have usually dendritic shapes, matched to the easily recognizable river networks; additionally, their limits are also identifiable straightforwardly in orthoimages, as they often produce clear-cut geomorphologic transitions to the surrounding hills. Therefore, almost all the patches corresponding to alluvial sediments produced several georeferencing correction points.

In total 9875 (circa 25% on the border, 75% inland) control points were used to improve spatial accuracy of the produced dataset. Adjustments were slight (most, up to 600 m) but significantly improved by the matching with natural shapes and with the Portuguese border, thus certainly contributing to overall accuracy of the dataset. This spatial adjustment is, in practice, not much relevant at the 1:500,000 scale (recall 600 m correspond to 1.2 mm in the printed map) but is of utmost importance if the researcher wants to cross the dataset with other data with high spatial accuracy (e.g., point data coming from global positioning devices), as it was performed in the present article.

Some geological formations are composed of intricate layers of very different types of rocks (sometimes very thick) that might point to different classes. In such cases, we kept such information by defining different levels of classes. Although it is difficult to determine which of those complex layers dominate in terms of outcropping matter, based mostly on geological literature, we produced a first level of information (Level 0) where only the dominant class is mentioned. In Level 1 we ascribed (when present) up to two classes to such complex formations (thus, including the co-dominant class). In Level 2 we ascribed all the occurring classes, preserving the original geological information. In the present work, we used Level 0 (dominant class only, see Figure A1). This information can be downloaded from: http://home.isa.utl.pt/~tmh/.
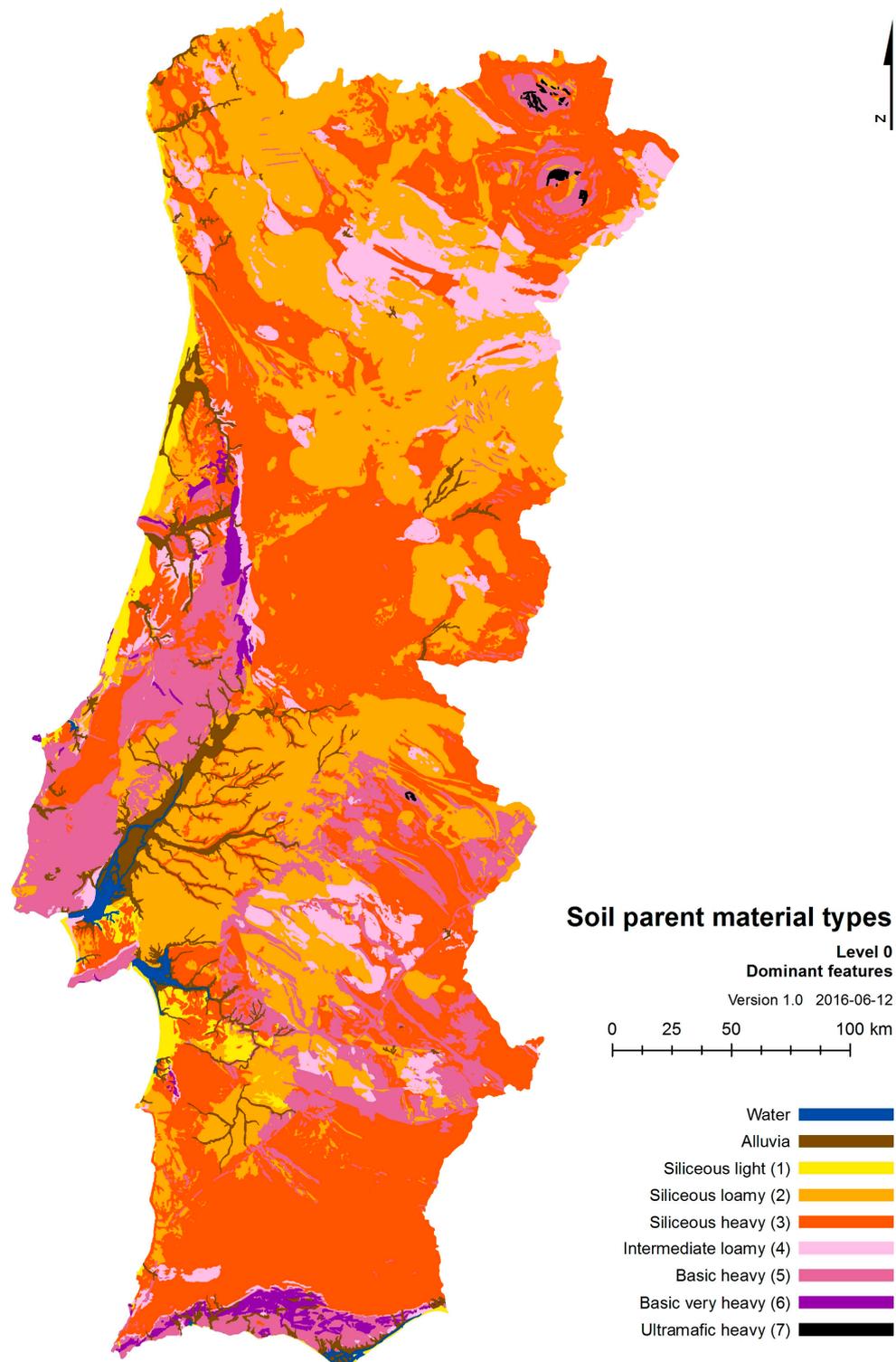
Soil parent material types

Level 0
Dominant features

Version 1.0   2016-06-12

Legend	
Water	
Alluvia	
Siliceous light (1)	
Siliceous loamy (2)	
Siliceous heavy (3)	
Intermediate loamy (4)	
Basic heavy (5)	
Basic very heavy (6)	
Ultramafic heavy (7)	

Figure A1. Soil parent material types map. The map contains other two classes: "alluvia" which are not easily classifiable within any of the defined classes, as their chemical composition and texture vary and "water", corresponding to rivers, estuaries, etc.

References

1.   Food and Agriculture Organization of the United Nations. *Global Forest Resources Assessment 2010: Main Report*; FAO Forestry Paper; Food and Agriculture Organization of the United Nations: Rome, Italy, 2010; ISBN 978-92-5-106654-6.

2. Bongiorno, S.F. Land use and summer bird populations in northwestern galicia, Spain. *Ibis* **1982**, *124*, 1–20. [CrossRef]

3. Kwok, H.K.; Corlett, R.T. The bird communities of a natural secondary forest and a Lophostemon confertus plantation in Hong Kong, South China. *For. Ecol. Manag.* **2000**, *130*, 227–234. [CrossRef]

4. Barlow, J.; Mestre, L.A.M.; Gardner, T.A.; Peres, C.A. The value of primary, secondary and plantation forests for Amazonian birds. *Biol. Conserv.* **2007**, *136*, 212–231. [CrossRef]

5. Farwig, N.; Sajita, N.; Böhning-Gaese, K. Conservation value of forest plantations for bird communities in western Kenya. *For. Ecol. Manag.* **2008**, *255*, 3885–3892. [CrossRef]

6. Calviño-Cancela, M.; Rubido-Bará, M.; van Etten, E.J.B. Do eucalypt plantations provide habitat for native forest biodiversity? *For. Ecol. Manag.* **2012**, *270*, 153–162. [CrossRef]

7. Calviño-Cancela, M. Effectiveness of eucalypt plantations as a surrogate habitat for birds. *For. Ecol. Manag.* **2013**, *310*, 692–699. [CrossRef]

8. Pina, J.P. Breeding bird assemblages in eucalyptus plantations in Portugal. *Ann. Zool. Fenn.* **1989**, *26*, 287–290.

9. Proença, V.M.; Pereira, H.M.; Guilherme, J.; Vicente, L. Plant and bird diversity in natural forests and in native and exotic plantations in NW Portugal. *Acta Oecol. Int. J. Ecol.* **2010**, *36*, 219–226. [CrossRef]

10. Williams, M. *Deforesting the Earth: From Prehistory to Global Crisis: An Abridgment*; University of Chicago Press: Chicago, IL, USA, 2006; ISBN 0-226-89947-0.

11. Plieninger, T.; Rolo, V.; Moreno, G. Large-scale patterns of *Quercus ilex*, *Quercus suber* and *Quercus pyrenaica* regeneration in central-western Spain. *Ecosystems* **2010**, *13*, 644–660. [CrossRef]

12. Carnicer, J.; Coll, M.; Pons, X.; Ninyerola, M.; Vayreda, J.; Peñuelas, J. Large-scale recruitment limitation in Mediterranean pines: The role of *Quercus ilex* and forest successional advance as key regional drivers. *Glob. Ecol. Biogeogr.* **2014**, *23*, 371–384. [CrossRef]

13. Benavides, R.; Escudero, A.; Coll, L.; Ferrandis, P.; Ogaya, R.; Gouriveau, F.; Penuelas, J.; Valladares, F. Recruitment patterns of four tree species along elevation gradients in Mediterranean mountains: Not only climate matters. *For. Ecol. Manag.* **2016**, *360*, 287–296. [CrossRef]

14. Benito-Garzón, M.; Ruiz-Benito, P.; Zavala, M.A. Interspecific differences in tree growth and mortality responses to environmental drivers determine potential species distributional limits in Iberian forests. *Glob. Ecol. Biogeogr.* **2013**, *22*, 1141–1151. [CrossRef]

15. Stevens-Rumann, C.S.; Kemp, K.B.; Higuera, P.E.; Harvey, B.J.; Rother, M.T.; Donato, D.C.; Morgan, P.; Veblen, T.T. Evidence for declining forest resilience to wildfires under climate change. *Ecol. Lett.* **2017**. [CrossRef] [PubMed]

16. Mather, A.S.; Pereira, J.M.C. Transição Florestal e Fogo em Portugal. In *Incêndios Florestais em Portugal: Caracterização, Impactes e Prevenção*; Pereira, J.S., Pereira, J.M.C., Rego, F.C., Silva, J.M.N., da Silva, T.P., Eds.; ISAPress: Lisboa, Portugal, 2006; pp. 257–282.

17. Louro, G.; do Monteiro, M.L.; Constantino, L.; Tomé, M.; Rego, F. Evolução do material lenhoso de pinheiro-bravo e eucalipto. *Silva Lusit.* **2010**, *18*, 133–149.

18. Moreira, F.; Rego, F.C.; Ferreira, P.G. Temporal (1958–1995) pattern of change in a cultural landscape of northwestern Portugal: Implications for fire occurrence. *Landsc. Ecol.* **2001**, *16*, 557–567. [CrossRef]

19. Costa, A.; Madeira, M.; Santos Lima, J. Is cork oak (*Quercus suber* L.) woodland loss driven by eucalyptus plantation? A case-study in southwestern Portugal. *IFor. Biogeosci. For.* **2014**, *7*, 193–203. [CrossRef]

20. Fernandes, P.M.; Loureiro, C.; Guiomar, N.; Pezzatti, G.B.; Manso, F.T.; Lopes, L. The dynamics and drivers of fuel and fire in the Portuguese public forest. *J. Environ. Manag.* **2014**, *146*, 373–382. [CrossRef] [PubMed]

21. Nunes, M.C.S.; Vasconcelos, M.J.; Pereira, J.M.C.; Dasgupta, N.; Alldredge, R.J.; Rego, F.C. Land cover type and fire in Portugal: Do fires burn land cover selectively? *Landsc. Ecol.* **2005**, *20*, 661–673. [CrossRef]

22. Watt, A.S. On the causes of failure of natural regeneration in British oakwoods. *J. Ecol.* **1919**, *7*, 173–203. [CrossRef]

23. Buckley, D.S.; Sharik, T.L.; Isebrands, J.G. Regeneration of northern red oak: Positive and negative effects of competitor removal. *Ecology* **1998**, *79*, 65–78. [CrossRef]

24. Carnicer, J.; Barbeta, A.; Sperlich, D.; Coll, M.; Peñuelas, J. Contrasting trait syndromes in angiosperms and conifers are associated with different responses of tree growth to temperature on a large scale. *Front. Plant Sci.* **2013**, *4*. [CrossRef] [PubMed]

25. Čater, M.; Batič, F. Groundwater and light conditions as factors in the survival of pedunculate oak (*Quercus Robur* L.) Seedlings. *Eur. J. For. Res.* **2006**, *125*, 419–426. [CrossRef]

26. Latham, R. Co-occurring tree species change rank in seedling performance with resources varied experimentally. *Ecology* **1992**, *73*, 2129–2144. [CrossRef]

27. Bazzaz, F.; Miao, S. Successional status, seed size and responses of tree seedlings to CO_2, light and nutrients. *Ecology* **1993**, *74*, 104–112. [CrossRef]

28. Canham, C.; Finzi, A.; Pacala, S.; Burbank, D. Causes and consequences of resource heterogeneity in forests: Interspecific variation in light transmission by canopy trees. *Can. J. For. Res. Rev.* **1994**, *24*, 337–349. [CrossRef]

29. Rodríguez-Calcerrada, J.; Pardos, J.A.; Gil, L.; Reich, P.B.; Aranda, I. Light response in seedlings of a temperate (*Quercus petraea*) and a sub-Mediterranean species (*Quercus pyrenaica*): Contrasting ecological strategies as potential keys to regeneration performance in mixed marginal populations. *Plant Ecol.* **2008**, *195*, 273–285. [CrossRef]

30. Gómez-Aparicio, L.; Zamora, R.; Gómez, J.M.; Hódar, J.A.; Castro, J.; Baraza, E. Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants. *Ecol. Appl.* **2004**, *14*, 1128–1138. [CrossRef]

31. Callaway, R. Effect of Shrubs on Recruitment of *Quercus-Douglasii* and *Quercus-Lobata*. *Ecology* **1992**, *73*, 2118–2128. [CrossRef]

32. Smit, C.; den Ouden, J.; Diaz, M. Facilitation of *Quercus ilex* recruitment by shrubs in Mediterranean open woodlands. *J. Veg. Sci.* **2008**, *19*, 193–200. [CrossRef]

33. Vander Wall, S.B. The evolutionary ecology of nut dispersal. *Bot. Rev.* **2001**, *67*, 74–117. [CrossRef]

34. 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]

35. Tilghman, N. Impacts of white-tailed deer on forest regeneration in Northwestern Pennsylvania. *J. Wildland Manag.* **1989**, *53*, 524–532. [CrossRef]

36. Hewitt, N.; Kellman, M. Tree seed dispersal among forest fragments: II. Dispersal abilities and biogeographical controls. *J. Biogeogr.* **2002**, *29*, 351–363. [CrossRef]

37. Boiffin, J.; Aubin, I.; Munson, A.D. Ecological controls on post-fire vegetation assembly at multiple spatial scales in eastern North American boreal forests. *J. Veg. Sci.* **2015**, *26*, 360–372. [CrossRef]

38. Coll, M.; Peñuelas, J.; Ninyerola, M.; Pons, X.; Carnicer, J. Multivariate effect gradients driving forest demographic responses in the Iberian Peninsula. *For. Ecol. Manag.* **2013**, *303*, 195–209. [CrossRef]

39. Caldeira, M.C.; Ibáñez, I.; Nogueira, C.; Bugalho, M.N.; Lecomte, X.; Moreira, A.; Pereira, J.S. Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oaks. *J. Appl. Ecol.* **2014**, *51*, 349–358. [CrossRef]

40. Busing, R.T. Canopy cover and tree regeneration in old-growth cove forests of the Appalachian Mountains. *Vegetatio* **1994**, *115*, 19–27.

41. Camisón, Á.; Miguel, R.; Marcos, J.L.; Revilla, J.; Tardáguila, M.Á.; Hernández, D.; Lakicevic, M.; Jovellar, L.C.; Silla, F. Regeneration dynamics of *Quercus pyrenaica* Willd. in the Central System (Spain). *For. Ecol. Manag.* **2015**, *343*, 42–52. [CrossRef]

42. Lorimer, C.; Chapman, J.; Lambert, W. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* **1994**, *82*, 227–237. [CrossRef]

43. Hannon, G.E.; Bradshaw, R.; Emborg, J. 6000 years of forest dynamics in Suserup Skov, a seminatural Danish woodland. *Glob. Ecol. Biogeogr.* **2000**, *9*, 101–114. [CrossRef]

44. Pausas, J.C.; Llovet, J.; Rodrigo, A.; Vallejo, R. Are wildfires a disaster in the Mediterranean basin?—A review. *Int. J. Wildland Fire* **2008**, *17*, 713–723. [CrossRef]

45. Carrión, Y.; Kaal, J.; Antonio Lopez-Saez, J.; Lopez-Merino, L.; Martinez Cortizas, A. Holocene vegetation changes in NW Iberia revealed by anthracological and palynological records from a colluvial soil. *Holocene* **2010**, *20*, 53–66. [CrossRef]

46. Ellison, A.M.; Bank, M.S.; Clinton, B.D.; Colburn, E.A.; Elliott, K.; Ford, C.R.; Foster, D.R.; Kloeppel, B.D.; Knoepp, J.D.; Lovett, G.M.; et al. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* **2005**, *3*, 479–486. [CrossRef]

47. Capelo, J.; Mesquita, S.; Costa, J.C.; Ribeiro, S.; Arsénio, P.; Neto, C.; Monteiro-Henriques, T.; Aguiar, C.; Honrado, J.; Espírito-Santo, D.; et al. A methodological approach to potential vegetation modeling using GIS techniques and phytosociological expert-knowledge: Application to mainland Portugal. *Phytocoenologia* **2007**, *37*, 399–415. [CrossRef]

48. Costa, J.C.; Neto, C.; Aguiar, C.; Capelo, J.; Espírito Santo, M.D.; Honrado, J.; Pinto-Gomes, C.; Monteiro-Henriques, T.; Sequeira, M.; Lousã, M.; et al. Vascular plant communities in Portugal (Continental, the Azores and Madeira). *Glob. Geobot.* **2012**, *2*, 1–180. [CrossRef]

49. Costa, J.C.; Monteiro-Henriques, T.; Neto, C.; Arsénio, P.; Aguiar, C. The application of the habitats directive in Portugal. *Fitosociologia* **2007**, *44*, 23–28.

50. Eira, J.; Pinho, J.; Santos, C.; Buxo, J.; Godinho Ferreira, P.; Uva, J.; Moreira, J. *Global Forest Resources Assessment 2010-Country Report-Portugal*; Food and Agriculture Organization: Rome, Italy, 2010.

51. Svenning, J.-C. A review of natural vegetation openness in north-western Europe. *Biol. Conserv.* **2002**, *104*, 133–148. [CrossRef]

52. Bradshaw, R.H.W.; Hannon, G.E.; Lister, A.M. A long-term perspective on ungulate-vegetation interactions. *For. Ecol. Manag.* **2003**, *181*, 267–280. [CrossRef]

53. Mitchell, F.J.G. How open were European primeval forests? Hypothesis testing using palaeoecological data. *J. Ecol.* **2005**, *93*, 168–177. [CrossRef]

54. Carrión, J.S.; Fernández, S.; González-Sampériz, P.; Gil-Romera, G.; Badal, E.; Carrión-Marco, Y.; López-Merino, L.; López-Sáez, J.A.; Fierro, E.; Burjachs, F. Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. *Rev. Palaeobot. Palynol.* **2010**, *162*, 458–475. [CrossRef]

55. Direcção-Geral dos Recursos Florestais. *Resultados do Inventário Florestal Nacional 2005/2006, 5a Revisão*; Direcção-Geral dos Recursos Florestais: Lisboa, Portugal, 2007; p. 70.

56. Aguiar, C. Flora e Vegetação da Serra de Nogueira e do Parque Natural de Montesinho. Ph.D. Thesis, Universidade Técnica de Lisboa-Instituto Superior de Agronomia, Universidade Técnica de Lisboa (TULisbon), Lisboa, Portugal, 2001.

57. Monteiro-Henriques, T. Landscape and Phytosociology of the Paiva River's Hydrographical Basin. Ph.D. Thesis, Instituto Superior de Agronomia, Universidade Técnica de Lisboa (TULisbon), Lisboa, Portugal, 2010.

58. Hijmans, R.J. Raster: Geographic Data Analysis and Modeling (Version 2.3-40). Available online: http://CRAN.R-project.org/package=raster (accessed on 28 December 2015).

59. Monteiro-Henriques, T.; Martins, M.J.; Cerdeira, J.O.; Silva, P.; Arsénio, P.; Silva, Á.; Bellu, A.; Costa, J.C. Bioclimatological mapping tackling uncertainty propagation: Application to mainland Portugal. *Int. J. Climatol.* **2016**, *36*, 400–411. [CrossRef]

60. Gavilán, R. The use of climatic parameters and indices in vegetation distribution. A case study in the Spanish Sistema Central. *Int. J. Biometeorol.* **2005**, *50*, 111–120. [CrossRef] [PubMed]

61. Jarvis, A.; Reuter, H.I.; Nelson, A.; Guevara, E. Hole-Filled SRTM for the Globe Version 4. Available online: http://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1 (accessed on 9 April 2014).

62. Evans, J. Topographic Radiation Index-ArcScripts. Available online: http://arcscripts.esri.com/details.asp?dbid=12643 (accessed on 12 April 2016).

63. Tarboton, D.G. A New method for the determination of flow directions and contributing areas in grid digital elevation models. *Water Resour. Res.* **1997**, *33*, 309–319. [CrossRef]

64. Tarboton, D.G. TAUDEM: Terrain Analysis Using Digital Elevation Model (Version 5.0.6). Available online: http://hydrology.usu.edu/taudem/taudem5/downloads5.0.html (accessed on 1 December 2013).

65. R Core Team. R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria (Version 3.0.1). Available online: http://www.R-project.org/ (accessed on 1 December 2013).

66. Sarkar, D. *Lattice: Multivariate Data Visualization with R*; Use R! Springer: New York, NY, USA, 2008; ISBN 978-0-387-75968-5.

67. Simpson, G.L. Permute: Functions for Generating Restricted Permutations of Data (Version 0.7-0). Available online: http://CRAN.R-project.org/package=permute (accessed on 1 December 2013).

68. R Core Team. Foreign: Read Data Stored by Minitab, S, SAS, SPSS, Stata, Systat, dBase, . . . (Version 0.8-55). Available online: http://CRAN.R-project.org/package=foreign (accessed on 1 December 2013).

69. Hijmans, R.J. Raster: Geographic Data Analysis and Modeling (Version 2.1-49). Available online: http://CRAN.R-project.org/package=raster (accessed on 1 December 2013).

70.　Bivand, R.; Keitt, T.; Rowlingson, B. Rgdal: Bindings for the Geospatial Data Abstraction Library (Version 0.8-10). Available online: http://CRAN.R-project.org/package=rgdal (accessed on 1 December 2013).

71.　Pebesma, E.J.; Bivand, R.S. Classes and methods for spatial data in R. *R News* **2005**, *5*, 9–13.

72.　Bivand, R.S.; Pebesma, E.J.; Gomez-Rubio, V. *Applied Spatial Data Analysis with R*; Springer: New York, NY, USA, 2008.

73.　Nicolau, R. (Maria Rita Rodrigues Carmona Nicolau) Modelação e Mapeamento da Distribuição Espacial de Precipitação-Uma Aplicação a Portugal Continental. Ph.D. Thesis, Universidade Nova de Lisboa-Faculdade de Ciências e Tecnologia, Lisboa, Portugal, 2002.

74.　Gonzalo Jiménez, J. *Diagnosis Fitoclimática de La España Peninsular: Hacia Un Modelo de Clasificación Funcional de La Vegetación Y de Los Ecosistemas Peninsulares Españoles*, 1st ed.; Serie Técnica Naturaleza y Parques Nacionales; Organismo Autónomo de Parques nacionales, Ministerio de Medio Amiente y Medio Rural y Marino de España: Madrid, Spain, 2010; ISBN 978-84-8014-787-3.

75.　Hijmans, R.J.; Cameron, S.E.; Parra, J.L.; Jones, P.G.; Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **2005**, *25*, 1965–1978. [CrossRef]

76.　Hijmans, R.J.; Cameron, S.E.; Juan, L.P.; Jones, P.G.; Jarvis, A.; Richardson, K. Worldclim. Available online: http://www.worldclim.org/ (accessed on 31 May 2009).

77.　Serviços Geológicos de Portugal. *Carta Geológica de Portugal na Escala 1:500 000*; SGP: Lisboa, Portugal, 1992.

78.　Naimi, B. Usdm: Uncertainty Analysis for Species Distribution Models (Version 1.1-12). Available online: https://rdrr.io/cran/usdm/ (accessed on 25 February 2016).

79.　Chessel, D.; Dufour, A.B.; Thioulouse, J. The ade4 package—I: One-table methods. *R News* **2004**, *4*, 5–10.

80.　Zeileis, A.; Kleiber, C.; Jackman, S. Regression models for count data in R. *J. Stat. Softw.* **2008**, *27*. [CrossRef]

81.　Mullahy, J. Specification and testing of some modified count data models. *J. Econ.* **1986**, *33*, 341–365. [CrossRef]

82.　Lambert, D. Zero-Inflated Poisson Regression, with an Application to Defects in Manufacturing. *Technometrics* **1992**, *34*, 1–14. [CrossRef]

83.　R Core Team. R Core Team. R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria (Version 3.2.0). Available online: http://www.R-project.org/ (accessed on 25 December 2015).

84.　Oksanen, J.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, P.R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Wagner, H. Vegan: Community Ecology Package (Version 2.2-1). Available online: http://CRAN.R-project.org/package=vegan (accessed on 25 February 2016).

85.　Jackman, S. *Pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory (Version 1.4.9)*; Department of Political Science, Stanford University: Stanford, CA, USA, 2015.

86.　Burnham, K.P.; Anderson, D.R.; Burnham, K.P. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed.; Springer: New York, NY, USA, 2002; ISBN 978-0-387-95364-9.

87.　Burnham, K.P.; Anderson, D.R.; Huyvaert, K.P. AIC model selection and multimodel inference in behavioral ecology: Some background, observations and comparisons. *Behav. Ecol. Sociobiol.* **2010**, *65*, 23–35. [CrossRef]

88.　Rivas-Martínez, S.; Rivas Sáenz, S.; Penas, Á. Worldwide bioclimatic classification system. *Glob. Geobot.* **2011**, *1*, 1–634. [CrossRef]

89.　Woodward, F.I.; Williams, B.G. Climate and plant distribution at global and local scales. *Vegetatio* **1987**, *69*, 189–197. [CrossRef]

90.　Franco, J. do *Quercus* L. In *Flora iberica: Plantas Vasculares de la Península Ibérica e Islas Baleares*; Castroviejo, S., Laínz, M., López González, G., Montserrat, P., Muñoz Garmendia, F., Paiva, J., Villar, L., Eds.; Real Jardín Botánico-Consejo Superior de Investigaciones Científicas: Madrid, Spain, 1990; Volume II, pp. 15–36. ISBN 84-00-07034-8.

91.　Gómez-Aparicio, L.; Zavala, M.A.; Bonet, F.J.; Zamora, R. Are pine plantations valid tools for restoring mediterranean forests? An assessment along abiotic and biotic gradients. *Ecol. Appl.* **2009**, *19*, 2124–2141. [CrossRef] [PubMed]

92.　Van Hees, A.F.M. Growth and morphology of pedunculate oak (*Quercus robur* L) and beech (*Fagus sylvatica* L) seedlings in relation to shading and drought. *Ann. Sci. For.* **1997**, *54*, 9–18. [CrossRef]

93.　Welander, N.T.; Ottosson, B. The influence of shading on growth and morphology in seedlings of *Quercus robur* L. and *Fagus sylvatica* L. *For. Ecol. Manag.* **1998**, *107*, 117–126. [CrossRef]

94.　Ziegenhagen, B.; Kausch, W. Productivity of young shaded oaks (*Quercus robur* L.) as corresponding to shoot morphology and leaf anatomy. *For. Ecol. Manag.* **1995**, *72*, 97–108. [CrossRef]

95.　Valladares, F.; Chico, J.M.; Aranda, I.; Balaguer, L.; Dizengremel, P.; Manrique, E.; Dreyer, E. The greater seedling high-light tolerance of *Quercus robur* over Fagus sylvatica is linked to a greater physiological plasticity. *Trees Struct. Funct.* **2002**, *16*, 395–403. [CrossRef]

96.　Pausas, J.G.; Blade, C.; Valdecantos, A.; Seva, J.P.; Fuentes, D.; Alloza, J.A.; Vilagrosa, A.; Bautista, S.; Cortina, J.; Vallejo, R. Pines and oaks in the restoration of Mediterranean landscapes of Spain: New perspectives for an old practice—A review. *Plant Ecol.* **2004**, *171*, 209–220. [CrossRef]

97.　Fernandes, P.M.; Loureiro, C.; Magalhães, M.; Ferreira, P.; Fernandes, M. Fuel age, weather and burn probability in Portugal. *Int. J. Wildland Fire* **2012**, *21*, 380–384. [CrossRef]

98.　Cerqueira, M.; Gomes, L.; Tarelho, L.; Pio, C. Formaldehyde and acetaldehyde emissions from residential wood combustion in Portugal. *Atmos. Environ.* **2013**, *72*, 171–176. [CrossRef]

99.　Gonçalves, C.; Alves, C.; Pio, C. Inventory of fine particulate organic compound emissions from residential wood combustion in Portugal. *Atmos. Environ.* **2012**, *50*, 297–306. [CrossRef]

100.　Tiscar-Oliver, P. Patterns of shrub diversity and tree regeneration across topographic and stand-structural gradients in a Mediterranean forest. *For. Syst.* **2015**, *24*, 11. [CrossRef]

101.　Bugalho, M.N.; Caldeira, M.C.; Pereira, J.S.; Aronson, J.; Pausas, J.G. Mediterranean cork oak savannas require human use to sustain biodiversity and ecosystem services. *Front. Ecol. Environ.* **2011**, *9*, 278–286. [CrossRef]

102.　Simões, M.P.; Belo, A.F.; Fernandes, M.; Madeira, M. Regeneration patterns of *Quercus suber* according to montado management systems. *Agrofor. Syst.* **2015**, 1–9. [CrossRef]

103.　Capelo, J. Nemorum Transtaganae Descriptio: Sintaxonomia Numérica das Comunidades Florestais e Pré-florestais do Baixo Alentejo. Ph.D. Thesis, Universidade Técnica de Lisboa-Instituto Superior de Agronomia, Lisboa, Portugal, 2007.

104.　Plieninger, T. Compatibility of livestock grazing with stand regeneration in Mediterranean holm oak parklands. *J. Nat. Conserv.* **2007**, *15*, 1–9. [CrossRef]

105.　Pulido, F.; Garcia, E.; Obrador, J.J.; Moreno, G. Multiple pathways for tree regeneration in anthropogenic savannas: Incorporating biotic and abiotic drivers into management schemes. *J. Appl. Ecol.* **2010**, *47*, 1272–1281. [CrossRef]

106.　Pulido, F.J.; Diaz, M.; de Trucios, S.J.H. Size structure and regeneration of Spanish holm oak *Quercus ilex* forests and dehesas: Effects of agroforestry use on their long-term sustainability. *For. Ecol. Manag.* **2001**, *146*, 1–13. [CrossRef]

107.　Maia, P.; Keizer, J.; Vasques, A.; Abrantes, N.; Roxo, L.; Fernandes, P.; Ferreira, A.; Moreira, F. Post-fire plant diversity and abundance in pine and eucalypt stands in Portugal: Effects of biogeography, topography, forest type and post-fire management. *For. Ecol. Manag.* **2014**, *334*, 154–162. [CrossRef]

108.　Rivas-Martínez, S.; Sáenz Laín, C. Enumeración de los quercus de la península ibérica. *Rivasgodaya* **1991**, *6*, 101–110.

109.　Corcuera, L.; Camarero, J.J.; Gil-Pelegrín, E. Effects of a severe drought on *Quercus ilex* radial growth and xylem anatomy. *Trees Struct. Funct.* **2004**, *18*, 83–92. [CrossRef]

110.　Corcuera, L.; Notivol, E. Differences in photosynthetic activity might explain the large-scale shifts in pine recruitment in favour of oaks in continental Mediterranean climates. *Forestry* **2015**, *88*, 248–256. [CrossRef]

111.　Bugalho, M.N.; Milne, J.A.; Racey, P.A. The foraging ecology of red deer (*Cervus elaphus*) in a Mediterranean environment: Is a larger body size advantageous? *J. Zool.* **2001**, *255*, 285–289. [CrossRef]

112.　Bugalho, M.N.; Milne, J.A. The composition of the diet of red deer (*Cervus elaphus*) in a Mediterranean environment: A case of summer nutritional constraint? *For. Ecol. Manag.* **2003**, *181*, 23–29. [CrossRef]

113.　Pasquini, S.; Mizzau, M.; Petrussa, E.; Braidot, E.; Patui, S.; Gorian, F.; Lambardi, M.; Vianello, A. Seed storage in polyethylene bags of a recalcitrant species (*Quercus ilex*): Analysis of some bio-energetic and oxidative parameters. *Acta Physiol. Plant.* **2012**, *34*, 1963–1974. [CrossRef]

114.　Catry, F.X.; Pausas, J.G.; Moreira, F.; Fernandes, P.M.; Rego, F. Post-fire response variability in Mediterranean Basin tree species in Portugal. *Int. J. Wildland Fire* **2013**, *22*, 919–932. [CrossRef]

115.　Clarke, P.J.; Lawes, M.J.; Midgley, J.J.; Lamont, B.B.; Ojeda, F.; Burrows, G.E.; Enright, N.J.; Knox, K.J.E. Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. *New Phytol.* **2013**, *197*, 19–35. [CrossRef] [PubMed]

116. Vayreda, J.; Gracia, M.; Martinez-Vilalta, J.; Retana, J. Patterns and drivers of regeneration of tree species in forests of peninsular Spain. *J. Biogeogr.* **2013**, *40*, 1252–1265. [CrossRef]

117. Murdoch, D.; Chow, E.D. Ellipse: Functions for Drawing Ellipses and Ellipse-Like Confidence Regions (Version 0.3-8). Available online: http://CRAN.R-project.org/package=ellipse (accessed on 31 May 2013).

118. Le Bas, M.; Streckeisen, L. The IUGS systematics of igneous rocks. *J. Geol. Soc. Lond.* **1991**, *148*, 825–833. [CrossRef]

119. Le Maitre, R.W.; Streckeisen, A.; Zanettin, B.; Le Bas, M.J.; Bonin, B.; Bateman, P.; Bellieni, G.; Dudeck, A.; Efremova, S.; Keller, J.; et al. *Igneous Rocks: A Classification and Glossary of Terms: Recommendations of the International Union of Geological Sciences, Subcommission on the Systematics of Igneous Rocks*, 2nd ed.; Cambridge University Press: Cambridge, NY, USA, 2004; ISBN 978-0-521-61948-6.

120. Direção-Geral do Território Carta Administrativa Oficial de Portugal-Versão 2011. Available online: http://www.dgterritorio.pt/cartografia_e_geodesia/cartografia/carta_administrativa_oficial_de_portugal__caop_/caop__download_/carta_administrativa_oficial_de_portugal___versao_2011/ (accessed on 26 September 2011).