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Quercus pyrenaica Forests Under Contrasting Management Histories in Northern Portugal: Carbon Storage and Understory Biodiversity

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Abstract

Old-growth forests are crucial for biodiversity conservation and climate change mitigation due to their high carbon storage, structural complexity, and resilience to environmental stressors. Yet, such ecosystems are rare in Europe, and their ecological functioning remains poorly understood. This study assesses the capacity of *Quercus pyrenaica* forests in the Montesinho-Nogueira Natura 2000 site (Bragança, Portugal) to develop maturity attributes under different forest management histories. We compare an area with low human intervention for over 80 years (10.2 ha) to two areas harvested for traditional small-scale firewood and timber extraction around 30 years ago (11.4 ha and 2.73 ha). Dendrometric measurements, carbon storage, floristic inventories of understory vegetation, and regeneration surveys were conducted across 42 sub-plots during June–July 2024. Results show that older forests store significantly more carbon and support greater biodiversity, evenness and regeneration, while younger forests present higher values of species richness, including several rare taxa. Our findings suggest that under favorable conditions, secondary forests can recover substantial biomass and carbon stocks within a few decades, while mature stands continue to accumulate carbon and maintain complex structures. Differences in floristic composition between sites may also reflect distinct silvopastoral practices between patches, such as itinerant grazing through forest patches, which historically characterized the Montesinho landscape. These results highlight the value of preserving a mosaic of successional stages, as both mature and intermediate-phase forests, together with compatible human activities, provide complementary biodiversity benefits and contribute to the multifunctionality of Mediterranean agroforestry systems.

Keywords: old-growth forests; carbon storage; biodiversity conservation; forest management; Natura 2000; species richness; climate change mitigation

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1. Introduction

Forests play a crucial role in mitigating climate change, acting as important carbon sinks, providing habitat for threatened biodiversity, buffering extreme climatic events, and offering a wide range of essential ecosystem services [1–3]. In this context, the European Union has established ambitious ecological restoration goals, including the definition of clear indicators to assess forest ecosystem health [4]. Special attention has been given to the preservation of primary and old-growth forests, recognized as key elements in achieving the goals of the EU Biodiversity Strategy for 2030. Despite their scarcity—in Europe, they are estimated to cover 2.0% of the forest area—these forests represent significant carbon reservoirs, maintain higher humidity levels, and support specialized biological communities [5]. At the landscape scale, forests with long-standing tree presence also tend to host more complex and diverse vegetation mosaics [6]. Consequently, their mapping and protection are key priorities under the EU Biodiversity and Forest Strategies for 2030 [7,8].

Despite their importance, scientific knowledge about their allometric structure (e.g., tree volume or biomass) and their function for hosting biodiversity remains limited across Europe, particularly in the Mediterranean region, where such studies are even more scarce [9,10].

Pyrenean oak (*Quercus pyrenaica* Willd.) is a deciduous tree distributed throughout the western Atlantic–Mediterranean regions. It typically grows in mid-mountain areas with sub-humid to semi-arid Mediterranean climates being well adapted to siliceous soils [11–13]. The species covers approximately 660,000 hectares in Spain and 81,700 hectares in Portugal, reflecting its ecological importance across the Iberian Peninsula [14–16], and is currently protected by European legislation [11]. Despite its adaptability, the species faces challenges from climate change, primarily due to its limited migration capacity, increased vulnerability to pests and diseases, and habitat loss [17,18]. The projected decline in suitable habitats, particularly in southern regions, further highlights conservation concerns [17,19], underscoring the need for targeted conservation efforts. Additionally, in the Iberian Peninsula, *Quercus* spp. stands, such as *Q. pyrenaica*, have historically integrated timber and non-timber forest uses with seasonal grazing, contributing not only to biodiversity conservation but also to wildfire prevention and local economies [20], reinforcing the threats of habitat loss to ecosystem services.

Quercus pyrenaica forests are typically associated with a rich understory of sciaphilous grasses, herbs, and geophytes [6]. In Portugal, one of the most extensive and oldest areas of *Q. pyrenaica* occurs in the Montesinho, Coroa and Nogueira mountain system [21], part of the Natura 2000 site Montesinho/Nogueira (PTCON0002). Initially classified as a Site of Community Importance (SCI), the area is now designated as both a Special Area of Conservation (SAC-MN) and a Special Protection Area (SPA). Covering over 108,000 ha in the Trás-os-Montes region, the SAC-MN spans several municipalities (Bragança, Vinhais, Chaves, and Macedo de Cavaleiros) and lies at the interface between the Mediterranean and Eurosiberian biogeographic regions [22,23].

The SAC-MN is characterized by a habitat mosaic, shaped by diverse environmental conditions—altitudinal gradients, geology, and geomorphology—as well as traditional land uses, such as extensive grazing. This variety of habitats supports significant mountain biodiversity from the transition between the Mediterranean (southern) and Atlantic (northern) biogeographical regions [22,24]. Besides *Q. pyrenaica* forests, notable vegetation types include vegetation of serpentine soils such holm oak forests (*Quercus rotundifolia* Lam.), characterized by slow growth; the locally named *lameiros* (characteristic mountain pastures in the region); the hygrophilous heaths of *Erica tetralix* L. and *Ulex minor* Roth., the non-littoral heaths, the *cervunais* (dominated by *Nardus stricta* L.) and the hazels (*Corylus avellana* L.) [22,23]. Moreover, the SAC-MN constitutes a pastoral agroforestry landscape where forest resources (including oaks and chestnut), crops, and extensive grazing have historically coexisted, forming the typical silvopastoral system of northwestern Iberia [25].

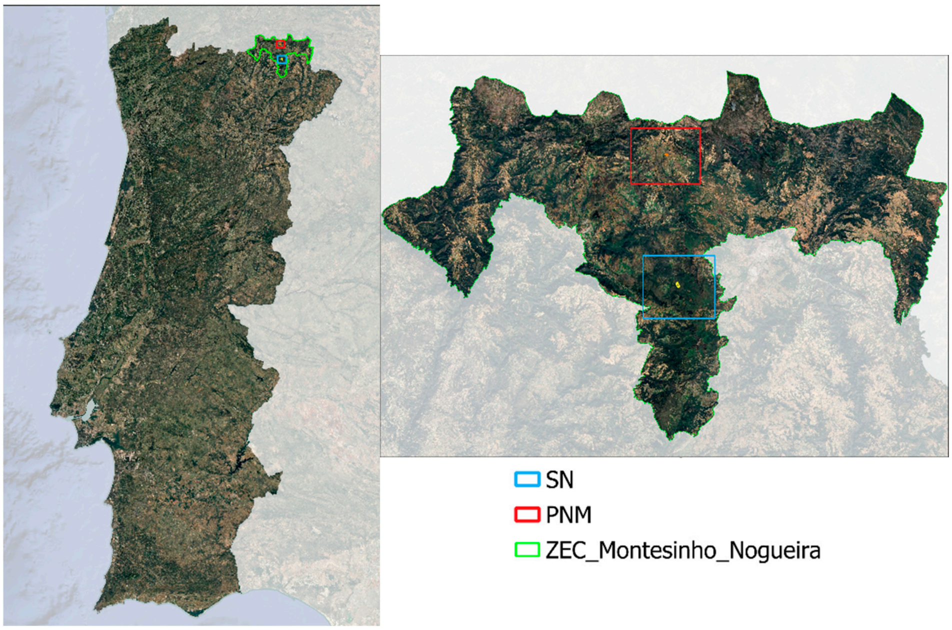
Regarding *Q. pyrenaica*, the SAC-MN contains the most extensive and well-preserved forests in the country. However, their characteristics and properties as mature/old-growth forests have never been studied. Combined with the site's ecological, social, and historical significance, this makes the SAC-MN a living laboratory area for mature/old-growth forests studies in Portugal.

In this context, the main objective of this study is to evaluate the effect of forest age—understood as time since last human intervention—on *Q. pyrenaica* forest in the SAC-MN. The assessment focuses on parameters related to forest maturity, including dendrometric variables (wood volume, biomass, and carbon stocks), floristic diversity (species richness and Shannon diversity indices). The implications for forest management and traditional activities in the forest such as traditional small-scale firewood collection, occasional timber extraction, and itinerant grazing are discussed.

2. Materials and Methods

2.1. Study Area

The study area is in the special area of conservation Montesinho/Nogueira (SAC-MN) (Portugal). Three areas of *Q. pyrenaica* were selected, two young stands (last intervention 30 years ago) and one considered as mature (last intervention 80 years ago) (Figure 1).



(**a**) (**b**)

Figure 1. (**a**) Location of the SAC Montesinho Nogueira in Portugal (green); (**b**) Location of the study sites within the Serra de Noguera (SN) (blue) and Natural Park of Montesinho (PNM) (red) (Google Earth Pro).

Two of these areas are located in the Serra de Nogueira (SN). SN is at a southern location and is characterized by extensive patches of *Q. pyrenaica* forests. Both areas at SN are communally owned, and on a slope with NW-W and S-SW exposure, near the village of Carrazedo (Bragança municipality). One of the areas (SN-80) (41°46′33.77″ N; 6°52′45.01″ W, 10.2 ha, perimeter 1461 m and an altitude range of 854–972 m) has not been subjected to any intervention for over 80 years, and is considered in this study the mature/old-growth forest sample (non-intervened area). The other area (SN-30) (41°46′18.03″ N; 6°52′45.71″ W, 11.4 ha, perimeter 1405 m, and altitude range 862–943 m) was subjected to traditional small-scale firewood and timber extraction about 30 years ago, mainly involving the selective removal of branches or a limited number of trees. These interventions resulted in a low density of timber removal, although no quantitative records are available. This forest is therefore considered a young forest (intervened area).

The third area (PNM-30) is located in the Montesinho Natural Park (*Parque Natural de Montesinho*—PNM) in northern Portugal. The PNM is characterized by a mosaic of small land-use patches, where forest stands are interspersed with agricultural fields and pastures, and where a long-standing tradition of itinerant grazing is notably more prevalent than in the SN sites. The selected area (41°54′31.08″ N, 6°53′41.87″ W, 2.72 ha, perimeter, range of altitude 893–935 m) is situated on a slope with NW-N exposure and located near the village of Zeive. This area, intervened for firewood and timber (similar to SN-30) around 30 years ago, is considered a young forest. A brief climate description is provided in the Supplementary Materials (Figure S1).

2.2. Experimental Design and Field Work

For dendrometric measurements, circular plots were established according to the density and extent of each forest site. In SN-80, 16 plots of 250 m^2 were randomly selected (total sampled area = 4000 m^2, 882 trees). In SN-30, 10 plots of 250 m^2 were established (2500 m^2, 1250 trees), with fewer plots required due to higher tree density. In PNM-30, 8 plots of 500 m^2 were used (4000 m^2, 307 trees), the difference in plot size and number reflecting the smaller extent of the study site. To ensure comparability, all variables were standardized either per hectare or per tree, depending on the analysis. The minimum distance among the circular plots was 20 m. The plot radius was adjusted to account for slope. Plots were delimited using a tape measure, with the center marked by an iron stake. The tape measure was fixed at this central point, and the circumference was defined by walking clockwise from North (determined using a compass). The total sampling area in the Serra de Nogueira was 21.6 hectares, with the 'non-intervened' area covering 10.2 hectares and the 'intervened' area covering 11.4 hectares. In the PNM the total area was 2.72 hectares.

Dendrometic parameters (height and DBH) were measured in the field. From April to July 2024, all living trees within the plots were numbered and identified. The height and DBH trees with a greater than 7.5 cm DBH and a minimum height of 1.30 m (measured from the ground) were measured in the plots. Thus, in SN and PNM, the assessment was carried out on a total of 2162 and 284 individuals, respectively. The total height of the trees was obtained by measuring the distance between the base of the stem and the apex of the crown, using a Vertex hypsometer Haglöf 5 (Haglöf, Sweden AB, Långsele, Sweden).

For the plant diversity, a total of 16 and 10 floristic inventories in SN and PNM respectively, were accomplished (Figure 2). The different number of floristic inventories is due to the smaller size of the selected PNM area, which did not allow a higher number of independent plots of adequate size. In the center of each plot, a 20-m transect following a north direction was established using a tape measure. Sampling points were placed every 20 cm, resulting in a total of 100 points per 20-m transect. An iron pointer was placed next to the tape, and plant species, along with the number of individuals touching the pointer, were recorded, totaling 100 sampling points in each sampling plot. Floristic inventories were accomplished between 5 and 31 of July 2024. To support that sampling effort was sufficient and comparable across sites species accumulation curves were constructed (Supplementary Materials, Figure S2).

The number and size of sampling plots were defined based on the representativeness of the parameters studied and the need to obtain an acceptable relative sampling error (less than 10%) for a 95% confidence interval. Since the intervened areas had a higher tree density than the non-intervened areas, more plots were required to ensure adequate representativeness.

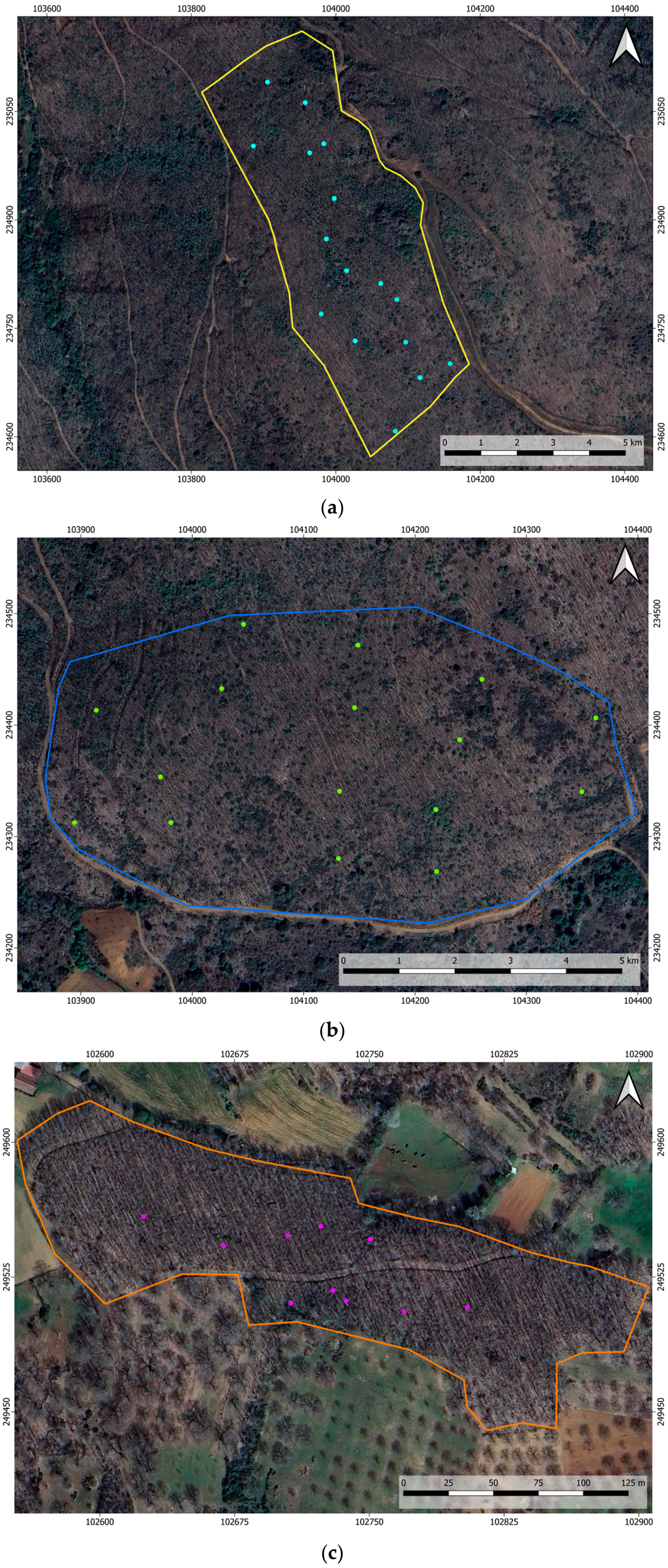


Figure 2. Maps of the study areas. (**a**) Oak forest without intervention for 80 years in Serra de Nogueira (yellow); (**b**) oak forest cut for firewood/timber 30 years ago in Serra de Nogueira (blue); (**c**) oak forest cut for firewood/timber 30 years ago in the Natural Park of Montesinho (orange) (Google Earth Pro 7.3.6.10201 (64-bit)). Points represent sample locations in the study area.

2.3. Indirect Dendrometric Parameters

The total volume, biomass and carbon per tree were calculated as follows:

The total volume per tree (v) was calculated using the following Equation (1) for oak and other hardwoods [26]:

$$v = \frac{\beta_0}{1000}\left(DBH^2h\right)^{\beta_1}, \tag{1}$$

where β_0 = 0.08011; DBH—diameter at breast height; h—height; β_1 = 0.9220

The green biomass per tree of living trees was calculated using Equation (2):

$$\text{Biomass} = \text{v dens}, \tag{2}$$

where v is the total volume (the summatory of all trees volume); dens—average density of oak wood (0.600 g/cm^3) [27].

Finally, the stored carbon reserves in the wood per tree were quantified using the following Equation (3) [28]:

$$C = \text{Biomass} * 0.5 \tag{3}$$

2.4. Diversity and Evenness Metrics

We calculated the species richness (S), Shannon diversity (H′), Simpson diversity (D), and Hill evenness at the transect level. The richness (S) was calculated as the number of plant species. The Shannon Diversity Index (H′) (Equation (4)) was calculated as:

$$H' = \sum_{i=1}^{S} p_i \ln p_i, \tag{4}$$

where S is the richness, p_i is the relative abundance of each species i, which results from the proportion of records for a species to the total number of individuals in the community, and *ln* is the natural logarithm. Larger values indicate more diverse communities, integrating richness and evenness.

Simpson index (D) was computed as Equation (5). For interpretation and subsequent analyses, we used the Gini–Simpson form, $1-D$, which approaches 1 when dominance is low:

$$D = \sum_{i=1}^{S} p_i^2 \tag{5}$$

Hill evenness (Hill) was calculated using Equation (6), interpretable as the effective number of common species relative to richness:

$$\text{Hill} = e^{H'}/S \tag{6}$$

2.5. Data Analysis

2.5.1. Dendrometric Parameters

To assess the effect of forest history on dendrometric variables—specifically tree volume, aboveground biomass, and carbon content—we applied Generalized Additive Models for Location, Scale, and Shape (GAMLSS) using the gamlss package 5.4.22 [29] in R 4.4.1 [30]. This modeling framework was selected after standard models (e.g., linear mixed models or generalized linear models) failed to meet assumptions of homoscedasticity and normality of residuals, as confirmed by residual diagnostics. GAMLSS allowed us to flexibly model the distribution of the response variable, including its skewness and kurtosis, which were essential due to the continuous and strictly positive nature of the data. Each response variable (volume, biomass, and carbon) was modeled as a function of the fixed effect "area" (forest site and age class: PNM-30, SN-30, and SN-80) and the random effect "plot". Five families were tested per variable to account for data distribution characteristics:

GA (Gamma with variable variance), IG (Inverse Gaussian), LOGNO (Log-normal), GG (Generalized Gamma), and BCPE (Box–Cox Power Exponential).

Model selection was based on Akaike Information Criterion (AIC) using the AICtab function from the bbmle package 1.0.25.1 [31]. The BCPE distribution consistently yielded the best fit for all three response variables. Model diagnostics were conducted through graphical checks of standardized (centile) residuals—i.e., residuals transformed based on their position within the fitted distribution (this approach is particularly suitable for GAMLSS models) and included QQ-plots, histograms, and residuals versus fitted plots. These indicated a satisfactory fit, with no strong deviations or patterns in residuals. To assess differences between areas, we re-fitted the best model for each response without the random effect (to obtain marginal means), and conducted post hoc comparisons using estimated marginal means via the emmeans package 1.10.2 [32]. Group differences were evaluated using Sidak-adjusted pairwise comparisons ($\alpha = 0.05$).

2.5.2. Robustness and Sensitivity Analyses

Because plot size and number differed among areas, we implemented complementary checks to ensure that inferences were not driven by sampling design. First, dendrometric variables were standardized to a hectare basis at the plot level for stand-scale response and summarized per tree for individual-scale comparisons. Second, we performed tree rarefaction by subsampling to the minimum number of trees across areas (1000 iterations). Third, we ran leave-one-plot-out (LOPO) analyses at the plot scale to evaluate the influence of any single plot on stand-level estimates. Finally, as a model-based sensitivity, we fitted linear mixed-effects models for carbon per hectare with area as a fixed effect and plot as a random intercept, and compared these results with a specification including area weighting. Conclusions were considered robust if effect signs, relative magnitudes, and uncertainty ranges remained stable across checks. Analyses were performed in R 4.4.1 (packages dplyr 1.1.4 [33]; purrr 1.0.2 [34], lme4 1.1.35.3 [35], tidyr 1.3.1 [36]).

2.5.3. Vegetation Community Composition

To analyse differences in plant community composition between old and young forest plots in SN and PNM, we constructed a Venn diagram and performed a Non-metric Multidimensional Scaling (NMDS) ordination based on Bray–Curtis dissimilarities of species abundance data. To account with the different number of floristic inventories, abundance data were pondered by the number of sampling plots in the different areas, when the three areas (PNM-30, SN-30, and SN-80) were analyzed together. To minimize the influence of dominant species on compositional patterns, species were classified as abundant (total count > 80) or rare ($\leq$80), based on the inflection point of the species abundance distribution curve (Figure S2, Supplementary Materials). A log(x + 1) transformation was applied to reduce the effect of highly dominant species.

NMDS ordination was conducted using two dimensions with the *metaMDS* function (parameters: trymax = 100, set.seed(123)) from the vegan package 2.6.6.1 [37] in R 4.4.1 [30]. Species vectors that best explained variation in community composition were fitted using the envfit function with 999 permutations from the same package. The Venn diagram was created using the venn.diagram function from the VennDiagram package 1.7.3 [38].

To test for significant differences in species composition among environments, a Permutational Multivariate Analysis of Variance (PERMANOVA) was performed using the adonis2 function from vegan, with 999 permutations and Bray–Curtis dissimilarity. Bray–Curtis was chosen because it is well-suited for ecological community data, as it accounts for species abundance while ignoring joint absences, making it appropriate for sparse and zero-inflated species matrices. Pairwise post hoc comparisons between PNM-30, SN-30, and SN-80 were conducted using a custom function (pairwise_permanova, Supplementary File S1), which iteratively applies adonis2 to all pairwise group combinations. Resulting *p*-values were adjusted using the Holm correction.

To assess whether observed differences were due to shifts in community centroids (i.e., composition) or group dispersions (i.e., beta diversity), we used the betadisper and permutest functions from vegan 2.6.6.1, based on Bray–Curtis dissimilarities. Significance was tested using ANOVA from base R.

Preliminary analyses indicated that the species composition in PNM-30 differed markedly from that in SN-30 and SN-80. Including PNM-30 in the NMDS caused the ordination to be dominated by the separation between PNM and SN sites, leading to an artificially low stress value and masking more subtle gradients within the SN sites—particularly for abundant species (Figure S3, Supplementary Materials). Therefore, PNM-30 was excluded from the final NMDS to enable clearer visualization of compositional differences among SN plots. This decision was supported by PERMANOVA and PERMDISP results (see Section 3).

2.5.4. Vegetation Diversity and Evenness Metrics

To assess structural patterns in vegetation communities across forest types, we first fitted an LDA with S, H′, Gini D, and Hill evenness as predictors and forest type as the grouping factor using the lda funtion from MASS [39]. Predictors were z-standardized. To assess the LDA homoscedasticity assumption we ran Box's M on the standardized predictors by group (function boxM from biotools 4.3 package [40]). Because Box's M indicated unequal covariance matrices and LDA accuracy was modest, we then used regularized discriminant analysis (RDA; rda funtion from klaR 1.7.3 package [41]), which shrinks group covariance estimates toward diagonal/spherical targets. We tuned the regularization parameters (λ, γ) on a small grid via LOOCV with equal class priors, and selected $\lambda = 1$, $\gamma = 1$. For visualization we plotted an RDA log-odds biplot in the $K - 1 = 2$ dimensional space of posterior probabilities (baseline SN-80): the axes are log[*p*(PNM-30)/*p*(SN-80)] and log[*p*(SN-30)/*p*(SN-80)]. We overlaid 95% normal-theory filled ellipses by group (sample mean/covariance) and plotted group centroids. To aid interpretation, we reported Pearson correlations (r) between each standardized predictor (cor function from stats package in base R) and the RDA axes. We also quantified pairwise separation along each axis using Cohen's d (cohens_d function from effectsize 0.8.8 package [42]) using a pooled SD and no small-sample correction.

To statistically evaluate group differences among forest types, a PERMANOVA was applied to a Euclidean distance matrix computed from the z-standardized values of S, H′, $1 - D$, and Hill. Euclidean distance was selected because it is appropriate for continuous, non-compositional variables on a common scale after standardization. The analysis was performed with the adonis2 function (vegan 2.6.6.1 package [37]; 9999 permutations). Pairwise comparisons between forest types were conducted using the same custom function (pairwise_permanova), and *p*-values were adjusted using the Holm method.

To determine whether differences were due to changes in centroid position or within-group variability, a PERMDISP was carried out using betadisper and permutest on the same distance matrix. This allowed us to distinguish between true shifts in multivariate structure and differences in dispersion among groups.

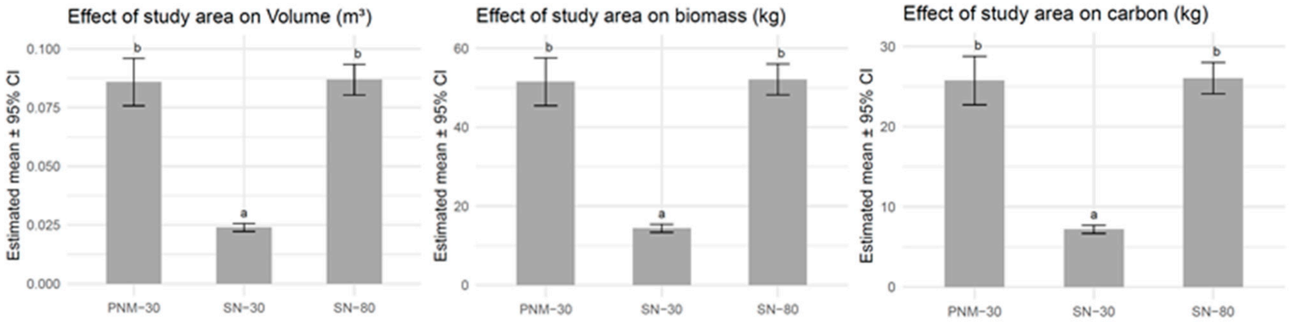
3. Results

3.1. Dendrometric Parameters

The area with no-intervention (SN-80) presented superior values of wood volume (241.6 ± 22.17 m^3/ha), biomass (147.8 ± 13.56 Mg/ha) and carbon stored per hectare

(73.9 ± 6.78 Mg/ha) while the values were inferior in the area with intervention (SN-30) with a wood volume of 146.4 ± 14.52 m^3/ha, biomass of 93.32 ± 9.26 Mg/ha and carbon stored per hectare of 46.66 ± 6.07 Mg/ha. In PNM-30 the wood volume was 171.6 ± 8.51 m^3/ha, the biomass 102.98 ± 5.11 and the carbon stored 51.49 ± 5.55 Mg/ha.

These values highlight that, at the stand scale (per hectare), the non-intervened SN-80 accumulated more biomass and carbon than the other sites. However, when evaluated at the tree scale, patterns differed. The mean volume per tree differed significantly between forest sites (GAMLSS model using the BCPE distribution). Compared to PNM-30, SN-30 showed a significantly lower mean volume (*Estimate* = –0.064, *SE* = 0.004, *t value* = −16.410, $p < 0.001$), whereas no significant difference was found between PNM-30 and SN-80 (*Estimate* = –0.002, *SE* = 0.005, *t value* = −0.450, $p = 0.653$) (Table S2). Post hoc pairwise comparisons revealed two homogeneous groups: SN-30 (group "a") and PNM-30 together with SN-80 (group "b"). These results indicate that tree volume was significantly reduced in SN-30, but comparable between the longer undisturbed stand SN-80 and PNM-30 (Figure 3a).



(**a**) (**b**) (**c**)

Figure 3. Effect of the forest (Natural Park of Montesinho last intervened 30 years ago—PNM-30, Serra da Nogueira last intervened 30 years ago SN-30, and 80 years SN-80) on three dendrometric measurements per individual trees (**a**) tree volume (m^3), (**b**) aboveground biomass (kg), (**c**) carbon content (kg). Bars represent estimated means (± 95% confidence intervals) from GAMLSS models fitted without random effects. Letters indicate significant differences between areas based on post hoc comparisons (Sidak-adjusted).

A similar effect was observed for tree biomass and carbon storage. The mean biomass per tree also differed significantly between forest sites (GAMLSS model using the BCPE distribution). Compared to PNM-30, SN-30 exhibited a significantly lower mean biomass (Estimate = −38.489, SE = 2.347, t value = −16.398, $p < 0.001$), while no significant difference was observed between PNM-30 and SN-80 (*Estimate* = −1.226, *SE* = 2.697, *t value* = −0.455, $p = 0.649$) (Table S2). Post hoc pairwise comparisons identified two groups: SN-30 (group "a") and PNM-30 together with SN-80 (group "b"). These findings suggest that tree biomass was significantly reduced in SN-30, but remained similar between SN-80 and PNM-30 (Figure 3b).

Carbon storage per tree followed the same pattern: the GAMLSS model revealed that SN-30 had significantly lower mean carbon content compared to PNM-30 (*Estimate* = −19.245, *SE* = 1.174, *t value* = −16.398, $p < 0.001$), whereas SN-80 did not differ significantly from PNM-30 (*Estimate* = −0.614, *SE* = 1.349, *t value* = −0.455, $p = 0.649$) (Table S2). Post hoc comparisons again indicated two homogeneous groups: SN-30 (group "a") and SN-80 with PNM-30 (group "b"), highlighting a strong reduction in carbon storage in SN-30 compared to the other sites (Figure 2c). These results indicate that, although SN-80 stores more carbon at the stand level, average carbon storage per tree is similar in SN-80 and PNM-30, reflecting differences in stand density between the sites.

3.2. Robustness and Sensitivity Analyses

Area rarefaction confirmed the ordering PNM-30 < SN-30 < SN-80 for volume, biomass, and carbon per hectare (e.g., median carbon $\approx$ 25.8, 46.7, 73.9 t C ha^{-1}, respectively). Tree rarefaction showed markedly smaller trees in SN-30 (per-tree volume $\approx$ 0.031 m^3) compared to SN-80 and PNM-30 (both $\approx$ 0.112 m^3). LOPO analyses did not alter effect directions, indicating no single plot drove the results. The mixed-effects model estimated SN-30—PNM-30 $\approx$ +21.7 t C ha^{-1} and SN-80—SN-30 $\approx$ +24.4 t C ha^{-1}, consistent with the non-parametric checks.

3.3. Plant Community

3.3.1. Vegetation Community Composition

A total of 75 species (66 genera) belonging to 28 families were recorded, comprising 6449 individual occurrences. The most abundant families (92% of total individuals) were Poaceae (N = 3809), followed by Fagaceae (N = 856), Rubiaceae (N = 467), Rosaceae (N = 369), Fabaceae (N = 856), and Caryophyllaceae (N = 129). The most abundant species (accounting for 73% of individuals) were *Festuca elegans* (N = 1404, Poaceae), *Brachypodium pinnatum* (N = 910, Poaceae), *Quercus pyrenaica* (N = 848, Fagaceae), *Festuca rothmaleri* (N = 431, Poaceae), *Rubia peregrina* (N = 406, Rubiaceae), *Poa nemoralis* (N = 315, Poaceae), *Genista falcata* (N = 196, Fabaceae), and *Crataegus monogyna* (N = 173, Rosaceae) (Table S1, Supplementary Materials).

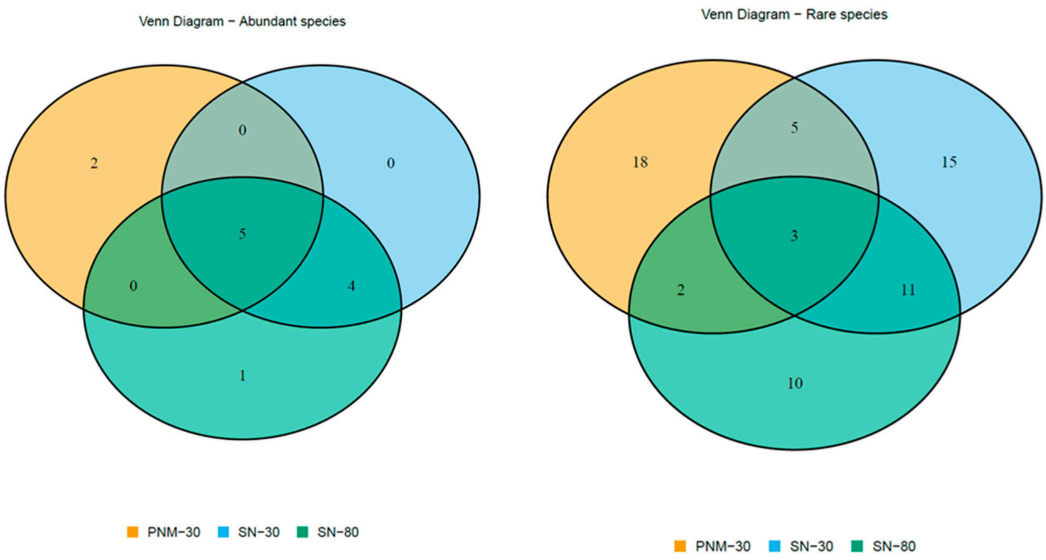
In SN-80, 34 species (35 genera, 16 families) were recorded, totaling 2242 individuals. The most abundant families (90% of individuals) were Poaceae (N = 1146), Fagaceae (N = 465), Rubiaceae (N = 226), and Rosaceae (N = 190). The most abundant species (86%) were *Festuca elegans* (N = 541), *Quercus pyrenaica* (N = 464), *Brachypodium pinnatum* (N = 390), *Rubia peregrina* (N = 217), *Holcus lanatus* (N = 165), and *Crataegus monogyna* (N = 155). A total of 28 species had fewer than 80 occurrences. Ninety-three records corresponded to bare soil. Mean species richness (S) per transect was 13, ranging from 5 to 19 species. The number of individuals (N) per transect ranged from 101 to 211.

In SN-30, 41 species (42 genera, 28 families) were identified, totaling 2624 individuals. The most abundant families (86%) were Poaceae (N = 1694), Rubiaceae (N = 208), Fagaceae (N = 192), and Fabaceae (N = 171). The most abundant species (84%) were *Festuca elegans* (N = 862), *Brachypodium pinnatum* (N = 520), *Poa nemoralis* (N = 249), *Quercus pyrenaica* (N = 192), *Rubia peregrina* (N = 198), and *Genista falcata* (N = 189). A total of 35 species had fewer than 80 occurrences. Bare soil was not recorded in any transect. Mean species richness was 11 species per transect, ranging from 7 to 15, and N per transect ranged from 120 to 195.

In PNM-30, 34 species (33 genera, 16 families) were recorded, with a total of 1183 individuals. The most abundant families (83%) were Poaceae (N = 669), Fagaceae (N = 199), Rosaceae (N = 60), and Caprifoliaceae (N = 58). The most abundant species (77%) were *Festuca rothmaleri* (N = 431), *Brachypodium rupestre* (N = 231), *Quercus pyrenaica* (N = 192), and *Lonicera periclymenum* ssp. *hispanica* (N = 58). Thirty-one species had fewer than 80 records. Bare soil accounted for 185 records. Mean species richness was 12 species per transect (range: 6–19), with the number of individuals per transect ranging from 74 to 162.

3.3.2. Species Turnover and Ordination

The Venn diagram (Figure 4) showed that all the abundant species in SN-30 were present in SN-80 while SN-80 had one exclusive species (*Holcus lanatus*). *Brachypodium pinnatum*, *Rubia peregrina*, *Poa nemoralis* and *Crataegus monogyna* were abundant in both SN-30 and SN-80 but not recorded in PNM. *Festuca rothmaleri* and *Brachypodium rupestre* were abundant in the PNM but not recorded in SN sites. Five species (*Quercus pyrenaica*, *Genista falcata*, *Rubus ulmifolius*, *Arenaria montana* and *Festuca elegans*) were abundant in all areas.



(**a**) (**b**)

Figure 4. Venn diagrams showing the distribution of (**a**) abundant and (**b**) rare plant species across the three oak forest areas located in Serra de Nogueira (SN) and Natural Park of Montesinho (PNM) untouched for 30 (SN-30, PNM-30) or 80 years (SN-80). Each set represents the unique and shared species composition among areas. Species were classified as abundant or rare based on a total abundance threshold of 80 individuals across all samples.

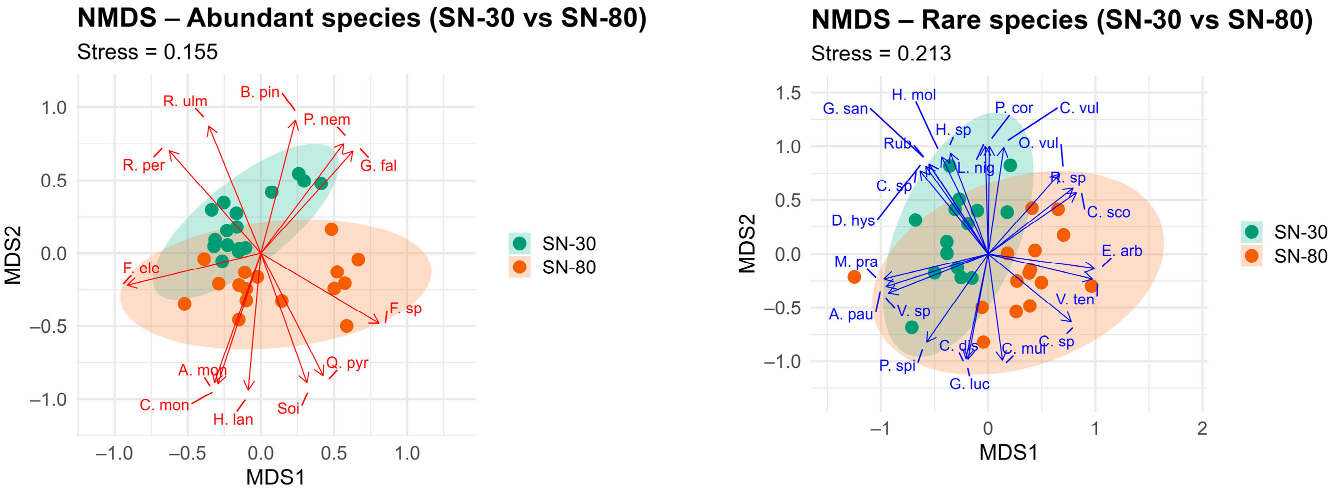
Regarding the rare species, the three areas presented more than 10 exclusive species. Eleven species were shared between the areas at SN, while overlap between PNM and SN was lower.

The PERMANOVA comparing the three areas (PNM-30, SN-30, and SN-80) showed that community composition differed significantly among them ($F = 9.780$, $R^2 = 0.334$, $p < 0.001$). Pairwise tests revealed significant differences between all pairs. The largest difference was observed between PNM-30 and SN-30 ($F = 11.0$, $R^2 = 0.315$, $p = 0.003$), followed by PNM-30 vs. SN-80 ($F = 9.99$, $R^2 = 0.294$, $p = 0.003$), and SN-30 vs. SN-80 ($F = 7.38$, $R^2 = 0.198$, $p = 0.003$).

However, the test for homogeneity of multivariate dispersions (PERMDISP) indicated significant differences in beta diversity dispersion among areas ($F_{2,39} = 11.02$, $p < 0.001$), violating the assumption of equal multivariate dispersion required for valid PERMANOVA inferences. Visual inspection (Figure S4, Supplementary Materials) showed that dispersion in PNM-30 plots differed notably from SN plots. Therefore, PNM-30 was excluded from subsequent ordination analyses and pairwise comparisons to ensure valid interpretation of community differences.

A separate PERMANOVA including only SN-30 and SN-80 confirmed that community composition differed significantly between these two environments ($F = 5.36$, $R^2 = 0.152$, $p < 0.001$). In this case, PERMDISP indicated no significant difference in beta diversity dispersion between areas ($F_{1,30} = 0.012$, $p = 0.914$), supporting the robustness of the PERMANOVA results.

The NMDS analysis (Figure 5) for abundant species yielded a stress value of 0.155, indicating a good representation of the data in reduced dimensions. The ordination revealed a clear separation between SN-30 and SN-80 plots, suggesting notable differences in the composition of abundant species between the two successional stages. Environmental ellipses showed relatively tight clustering of samples within each environment, reflecting consistent community structure.



(**a**) (**b**)

Figure 5. Non-metric multidimensional scaling (NMDS) ordination plots based on Bray–Curtis dissimilarity of plant species. (**a**) Abundant species (>80 records); (**b**) Rare species (≤80 records). Points represent transects, filled by two *Quercus pyrenaica* forest areas located in Serra de Nogueira (SN) untouched for 30 (SN-30) and 80 years (SN-80). Ellipses indicate 95% confidence intervals around environments. Red (abundant species) and blue arrows (rare species) represent the direction and strength of species most strongly associated with the ordination axes. Stress values are indicated in each panel. Species abbreviations are in Table S1.

Vectors representing the most strongly associated abundant records included *Quercus pyrenaica*, *Crataegus monogyna*, *Arenaria montana*, and bare soil in association with SN-80; and *Genista falcata*, *Rubus ulmifolius*, *Rubia peregrina*, *Brachypodium pinnatum*, and *Poa nemoralis* with SN-30.

For rare species, the NMDS solution had a higher stress value of 0.213, which is acceptable but indicates a more complex or variable pattern in the data. Despite this, some degree of separation between SN-30 and SN-80 plots was observed. The broader spread of points compared to the abundant species analysis reflects greater heterogeneity in the distribution of rare species across plots.

Several rare records, such as *Vicia tenuifolia*, *Carex distachya*, *Origanum vulgare*, and *Rosa* sp., were associated with SN-80. Others, including *Clinopodium vulgare*, *Physospermum cornubiense*, *Geranium sanguineum*, *Lathyrus niger*, *Dianthus hyssopifolius*, and *Hypericum montanum*, were linked to SN-30. However, the considerable overlap among plots suggests that rare species are less predictive of environmental differentiation than abundant ones, likely due to their lower frequency and abundance.

3.3.3. Vegetation Diversity and Evenness Metrics

Box's M indicated unequal covariance matrices among groups (χ^2 = 34.67, df = 20, p = 0.022). Under RDA, LOOCV overall accuracy reached 52.4% (95% CI 36.4–68.0%). Class-wise accuracies were 60.0% (PNM-30), 37.5% (SN-30) and 62.5% (SN-80). The LOOCV confusion matrix (rows = real; columns = predicted) was PNM-30 [PNM-30: 6, SN-30: 2, SN-80: 2]; SN-30 [PNM-30: 6; SN-30: 6; SN-80: 4] and SN-80 [PNM-30: 3, SN-30: 3, SN-80: 10]. Pairwise separation was strongest between PNM-30 and SN-80, moderate for SN-30 vs. SN-80, and weakest for PNM-30 vs. SN-30.

In the RDA log-odds biplot (baseline SN-80), RDA1 (PNM-30 vs. SN-80) correlated negatively with H' ($r = -0.68$), Gini–Simpson ($1 - D$) ($r = -0.87$) and Hill evenness ($r = -0.84$), and near-zero with S ($r = -0.08$), indicating lower diversity/evenness in PNM-30 relative to SN-80. RDA2 (SN-30 vs. SN-80) correlated positively with S ($r = 0.46$) and negatively with H' ($r = -0.18$), $1{-}D$ ($r = -0.50$) and Hill ($r = -0.97$), indicating higher richness but lower diversity/evenness in SN-30 relative to SN-80. Standardized separations were large (Cohen's d with 95% CIs): 0.98 [0.13, 1.81] for PNM-30 vs. SN-80 on RDA1; 0.86 [0.13, 1.58] for SN-30 vs. SN-80 on RDA2. Thus, SN-30 tends to lower Gini-D, H' and Hill evenness and higher S relative to SN-80, with PNM-30 intermediate, while SN-80 remains the most distinct group in this predictor space (Figure 6).

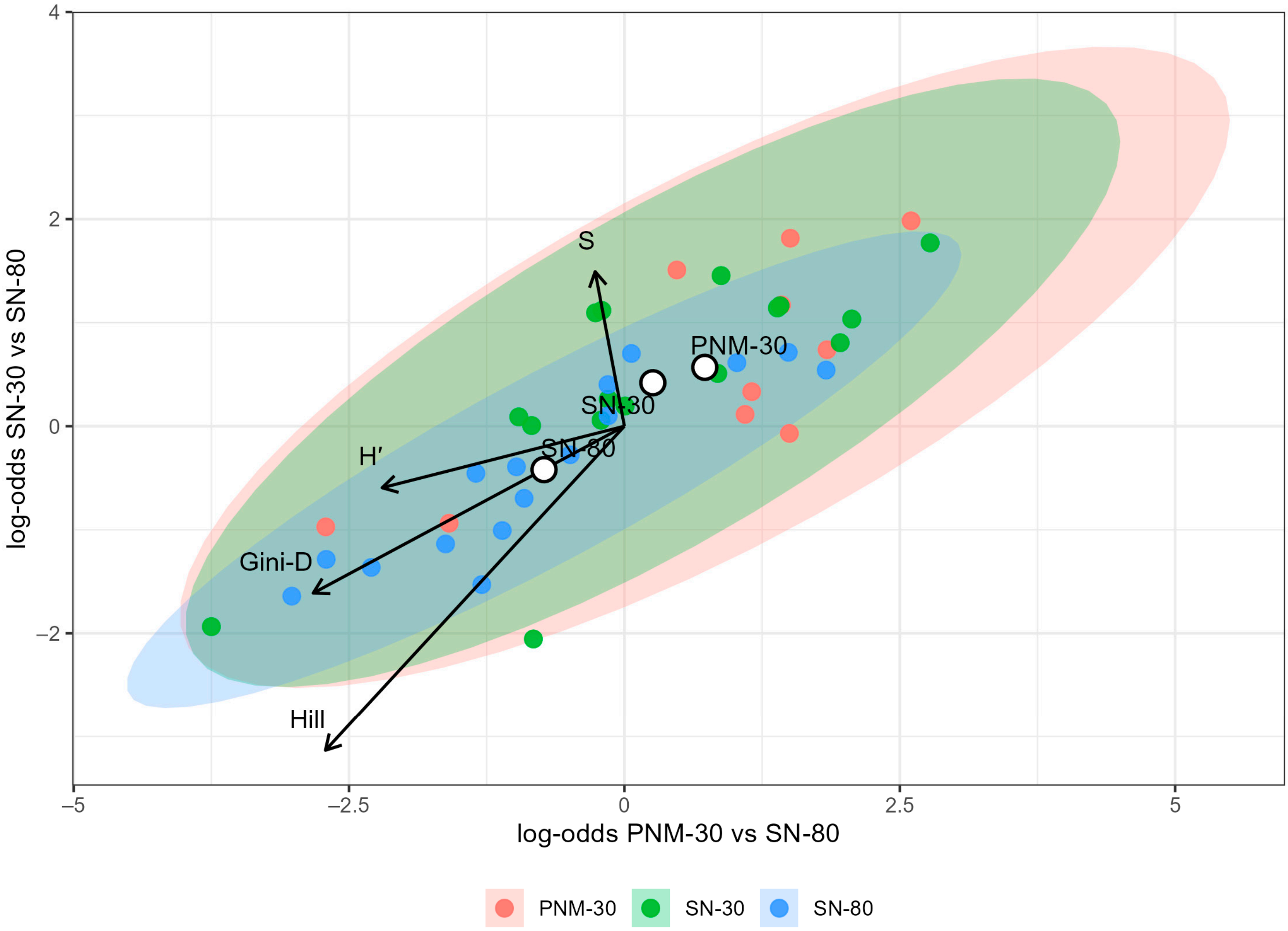


Figure 6. Regularized discriminant analysis (RDA) log-odds biplot for *Quercus pyrenaica* forests in Serra de Nogueira (SN) and the Natural Park of Montesinho (PNM), in untouched stands for 30 years (SN-30, PNM-30) and 80 years (SN-80). Axes are RDA1 = log[p(PNM-30)/p(SN-80)] and RDA2 = log[p(SN-30)/p(SN-80)]; Points are transects; 95% normal-theory filled ellipses and white-filled centroid dots summarize each forest type. Arrows show correlations between z-standardized predictors—S (richness), H' (Shannon), Gini-D ($1 - D$), and Hill [$\exp(H')/S$]—and the axes; arrow length is proportional to r (Pearson correlation between each standardized predictor and each RDA axis) and direction indicates increasing values of the corresponding predictor.

A PERMANOVA on Euclidean distances of z-standardized S, H', $1{-}D$ and Hill did not detect overall differences among forest types ($F = 1.49$, $R^2 = 0.071$, $p = 0.207$; 9999 permutations). Pairwise tests were likewise non-significant after Holm adjustment: PNM-30 vs. SN-80 ($F = 2.61$, $R^2 = 0.098$, $p = 0.250$), SN-30 vs. SN-80 ($F = 1.83$, $R^2 = 0.057$,

$p = 0.335$), and PNM-30 vs. SN-30 ($F = 0.399$, $R^2 = 0.016$, $p = 0.677$). No significant differences in multivariate dispersion were detected (PERMDISP: $F = 1.83$, $p = 0.174$).

Supervised classification (RDA) shows moderate predictive structure, whereas PERMANOVA does not support statistically significant centroid differences; accordingly, between-forest contrasts are interpreted as indicative trends.

4. Discussion

This study suggests that both the duration of non-intervention and local ecological factors influence forest structure, carbon accumulation, and plant biodiversity in *Q. pyrenaica* forests. As expected, the Serra da Nogueira forest, last intervened 80 years ago (SN-80), had higher tree volume, biomass, and carbon storage than the forest in the same area last intervened 30 years ago (SN-30), highlighting the role of maturity in carbon sequestration. However, when comparing sites with the same non-intervention period, SN-30 showed markedly lower values than PNM-30, suggesting that differences in ecological conditions—such as soil properties or microclimate [43]—can strongly condition recovery. The fact that PNM-30 reached similar values to SN-80 indicates that, under favorable conditions, secondary forests can regain substantial biomass and carbon stocks within a few decades. These results are consistent with findings by Martin-Benito et al. [44] in *Q. petraea*, where centuries of low disturbance promoted structural stability and high aboveground biomass.

The high biomass and carbon values in SN-80 align with observations from mature European forests, where carbon accumulation and structural complexity continue well beyond typical harvesting ages [2]. It should be noted, however, that this study quantified only the aboveground biomass of large trees, and did not assess other important carbon pools such as small trees, understory, deadwood, and fine roots [45], which represents a limitation in fully evaluating total ecosystem carbon storage.

Regarding the biodiversity patterns and floristic composition, the *Q. pyrenaica* forests studied exhibited distinct floristic patterns linked to their age and disturbance history. In PNM-30, the high within-group dispersion suggests a heterogeneous structure, possibly shaped by local conditions or past disturbances. This pattern is consistent with the fine-grained forest–agriculture–pasture mosaic of Montesinho Natural Park, where itinerant grazing has historically been prevalent and likely contributed to structural heterogeneity. Similar dynamics have also been reported for rear-edge forests in Sierra Nevada [17], where distinct population groups of oaks are associated with specific environmental variables. These findings emphasize the importance of identifying local population differentiation for modeling species distribution and forecasting the impact of global change, thus highlighting the relevance of local-scale studies, in agreement with our results.

Besides environmental factors, important drivers influencing differences in floristic patterns may be human activities, such as the traditional silvopastoral systems prevalent in the PNM. These systems are characterized by itinerant grazing that often passes through forest patches [25], a practice facilitated by the small size and mosaic structure of properties in the PNM when compared with SN. As Santiago-Freijanes et al. [25] note for the PNM, this mosaic historically integrated forest stands, crop areas, and grazing routes, forming a multifunctional agroforestry landscape. It is important to note that the gradual decline or modification of these practices, along with other land-use changes (e.g., the replacement of dryland crops with chestnut plantations) may have significant implications for vegetation structure, species composition, and the long-term resilience of these forests.

Several phytosociological associations have been described for *Q. pyrenaica* forests in the Iberian Peninsula [46–49]. In the Orensano-Sanabriense sector, where our study areas are located, two associations are recognized as climatophilous oak forests: *Holco* *mollis—Quercetum pyrenaicae* and *Genisto falcatae—Quercetum pyrenaicae*, corresponding to higher and lower altitudes, respectively [43,50,51].

The abundance of species such as *Festuca rothmaleri* (Litard.) Markgr.-Dann., *Brachypodium rupestre* (L.) P. Beauv, and *Lonicera periclymenum* L., alongside frequent occurrences of *Rubus ulmifolius* Schott, *Cytisus scoparius* (L.) Link, *Prunus avium* (L.) L. and *Erica australis* L., suggests that the oak forest in the PNM corresponds to an advanced secondary stage of the *Genisto falcatae—Quercetum pyrenaicae* association characteristic of subserial communities on acidic soils recovering toward more stable, mesic oak forests. In SN-80, the dominance of plants such as *Festuca rothmaleri* (Litard.) Markgr.-Dann., *B. rupestre*, *R. ulmifolius* along with the presence of *Holcus lanatus* L., *Rubia peregrina* L., and *Crataegus monogyna* Jacq. and a high rate of oak regeneration points to the *Holco mollis—Quercetum pyrenaicae* association. This is typical of mature, mesophilous *Q. pyrenaica* forests on siliceous, oligotrophic soils in humid to hyperhumid supramediterranean conditions in the northwestern Iberian Peninsula [46,49,51]. In contrast, SN-30 is characterized by a high abundance of herbaceous plants such as *Festuca elegans* Boiss, *Brachypodium pinnatum* (L.) P.Beauv., *Poa nemoralis* L. and scrubs such as *Genista falcata* Brot., and *R. ulmifolius*, with additional species such as *Clinopodium vulgare* L., *Melampyrum pratense* L., *Dianthus hyssopifolius* L., and *Geranium sanguineum* L. This floristic composition is probably indicative of the *Genisto falcatae—Quercetum pyrenaicae* association in earlier or intermediate successional stages, representing more open or regenerating stands. The lower rate of oak regeneration and greater structural heterogeneity suggest higher light availability, consistent with younger or more disturbed forest phases [43,52].

Within the SN sites, the younger forest (SN-30) tends to display higher species richness compared to SN-80, whereas SN-80 showed greater diversity (Shannon index, Gini-Simpson) and evenness. This pattern is consistent with an earlier-stage stand where light-demanding, competitive taxa may inflate richness, but a few species dominate, reducing evenness, e.g., [53]; by contrast, the more mature SN-80 appears structurally more complex and supports more even assemblages, as commonly expected [54]. We treat these contrasts as tendencies (PERMANOVA non-significant), but the supervised RDA suggests a coherent ecological gradient from richer-but-less-even communities (SN-30/PNM-30) toward more even, mature stands (SN-80). The strong association of SN-80 with *Q. pyrenaica* regeneration and increased bare soil coverage further supports its classification as a mature forest, consistent with post-fire regeneration patterns described by Calvo et al. [55].

Importantly, SN-30 was associated with rare species such as *D. hyssopifolius*, *Hypericum montanum* L., *Geranium sanguineum* L., and *Lathyrus niger* (L.) Bernh. Some of these taxa are considered near-threatened [56], reinforcing the ecological value of maintaining heterogeneous, partially disturbed systems where light availability promotes understory diversity. *Vicia tenuifolia* Freyn was linked to SN-80, showing that late successional stages also harbor unique and rare species.

Overall, in light of our results, differentiated management interventions can be recommended to conserve biodiversity within these *Q. pyrenaica* forests. In SN-30, small-scale, patchy interventions (e.g., selective canopy openings and fine-grain structural heterogeneity) may help maintain higher species richness while avoiding further losses of evenness by limiting the dominance of a few taxa. In turn, the conservation of older, structurally stable forests like SN-80—which could be designated as a conservation microreserve—would help preserve late-successional species, interior forest habitats, natural regeneration, and overall forest integrity. In areas such as the PNM, promoting intermediate stages through traditional activities like grazing, may also contribute to wildfire prevention and support local economies. In this sense, Castro et al. [57] showed that combining mechanical clearing with sheep grazing in open *Quercus faginea* Lam. and *Q. suber* L. woodlands can reduce shrub biomass and wildfire risk, although the short-term effects on floristic diversity may vary. Integrating such practices into a broader silvopastoral management framework could help maintain the multifunctional role of Mediterranean agroforestry landscapes. In sum, preserving a diversity of successional stages can enhance long-term forest resilience, while providing firewood, timber, and cattle forage resources for local inhabitants.

Several limitations should be considered when interpreting our results. First, our findings must be contextualized within the specific Mediterranean mountain environment of the study area, characterized by a reversal-type rainfall pattern (trend inversion around 1967; see Supplementary Materials) and by heterogeneous historical disturbances such as itinerant grazing and small-scale firewood and timber collection. These distinct climatic and socio-ecological conditions may constrain the generalizability of our conclusions, and extrapolations to other Mediterranean or temperate forests should be made with caution. Second, belowground carbon pools were not assessed in this study; root biomass (both coarse and fine) was excluded from the carbon accounting. Given that root biomass can constitute a substantial fraction of total tree carbon and may scale nonlinearly with stand age and structure, this omission likely leads to underestimation of absolute stocks in older, undisturbed stands and complicates direct comparisons across management histories. Despite these limitations, the study provides valuable insights into aboveground carbon dynamics and structural recovery of *Q. pyrenaica* forests under contrasting disturbance legacies.

5. Conclusions

This study underlines the combined importance of forest maturity and site-specific ecological conditions in shaping the structure, carbon storage, and biodiversity of *Quercus pyrenaica* forests. Our findings suggest that under favorable conditions, secondary forests can recover substantial biomass and carbon stocks within a few decades, while mature stands continue to accumulate carbon and maintain complex structures. Differences in floristic composition between sites highlight the value of preserving a mosaic of successional stages, as both mature and intermediate-phase forests provide complementary biodiversity benefits, including habitat for rare and threatened species.

In the context of Mediterranean agroforestry systems, such as the silvopastoral mosaics of PNM, traditional practices, such as itinerant grazing and small-scale firewood harvesting, have historically contributed to maintaining structural heterogeneity, controlling shrub biomass, and supporting species adapted to open woodland conditions. Integrating these practices into selected younger forests—while conserving the unique characteristics of old-growth stands—could sustain the multifunctional role of these landscapes, enhance their resilience to climate change, and reinforce their socio-economic value for local communities.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/land14101953/s1, Figure S1: Annual rainfall records (mm) at Celas Station (03P/01U) and Montesinho Station (02Q/01UG); Figure S2: Species accumulation curves by forest type.Species–transect accumulation curves for PNM-30, SN-30, and SN-80 built from incidence (presence/absence) per transect. Solid lines show the mean expected richness as transects accumulate; shaded ribbons are 95% CIs. Axes: x = number of transects (sampling effort), y = accumulated species richness. Curves approaching an asymptote and overlapping CIs at the same effort indicate sufficient and comparable sampling among groups; divergence suggests effort or compositional differences. Figure S3: Total abundance of each species, ranked from most to least frequent, pondered by the number of sampling plots in the different areas. A red dashed line indicates the threshold (n = 80) used to distinguish between 'abundant' (left) and 'rare' species (right); Figure S4: Non-metric multidimensional scaling (NMDS) ordination plots based on Bray–Curtis dissimilarity of plant species. (a) Abundant species (>80 records); (b) Rare species (≤80 records). Points represent transects, filled by the three oak forest areas located in Serra de Nogueira (SN) and Natural Park of Montesinho (PNM) untouched for 30 (SN-30, PNM-30) or 80 years (SN-80). Ellipses indicate 95% confidence intervals around environments. Blue arrows represent the direction and strength of species most strongly associated with the ordination axes. Stress values are indicated in each panel. Plants abbreviations are in Table S1; Figure S5: Multivariate dispersion (PERMDISP) among environments based on Bray–Curtis distances calculated from log-transformed species abundance data. Distances to group centroids (environmental groups) in multivariate space (a) and corresponding boxplot (b); Table S1: Number of records for each plant species identified in Quercus pyrenaica forests in the Natural Park of Montesinho (PNM) and Serra da Nogueira (SN), with stand ages of 30 years (PNM-30, SN-30) and 80 years (SN-80). Records are classified as Abundant (>80 records) or Rare ($\leq$80 records). For each species, the genus, family, abundance group, total number of records, and the number of occurrences per environment are shown. Abb: abbreviations used in ordination plots; Table S2: Outputs from GAMLSS models (family BCPE) including the estimates, standard errors (SE), t-values and *p*-values for the parameters of the response distribution: mean (μ), dispersion (σ), skewness (ν), and kurtosis (τ) of volume per tree, biomass, and carbon storage. The link function used for each parameter is indicated in parentheses; Scrip S1: Supplementary_File_S1_Function: Custom R Function for Pairwise PERMANOVA.

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Data Availability Statement: The dataset supporting this study is archived in the Zenodo repository (https://doi.org/10.5281/zenodo.17171771) under Restricted Access. Access is limited to ensure proper documentation and contextual information. Data can be made available upon request through the repository.

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