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# Drivers of Understory Plant Diversity in Thermophilous Oak Forests Dominated by *Quercus frainetto* and *Quercus cerris*: Topographic, Edaphic, and Stand Structure Factors

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## Abstract

Oak forests are important components of temperate forest ecosystems, yet the factors shaping understory plant diversity in Southeast European thermophilous oak forests remain insufficiently understood. This study investigates understory plant diversity in forests dominated by *Quercus frainetto* and *Quercus cerris* in the protected area of Kosmaj (Serbia) and examines its relationships with topographic, edaphic, and stand structure factors. Species richness, Shannon diversity, and Pielou's evenness were used to characterize diversity patterns. Understory diversity was shaped by multiple environmental factors, with stand structure variables showing the highest independent contribution to species richness and Shannon diversity, whereas topographic variables were more closely associated with Pielou's evenness. Humus content showed positive associations with Shannon diversity and Pielou's evenness, whereas higher phosphorus and potassium availability showed negative associations with diversity indices, particularly Shannon diversity. Younger stands showed a tendency toward higher species richness, while Shannon diversity showed a similar but weaker pattern, although differences among stand age classes were not significant. Geological substrate was associated with variation in diversity patterns, with limestone showing greater species richness, whereas silicate substrates showed slightly higher Shannon diversity and evenness. These findings highlight that variation in understory plant diversity in thermophilous oak forests reflects the combined influence of stand characteristics, soil conditions, and topographic gradients, providing insights for biodiversity conservation and adaptive forest management through the maintenance of stand structural complexity, soil quality, and environmental heterogeneity.

**Keywords:** thermophilous oak forests; understory vegetation; plant diversity; environmental drivers; Serbia



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## 1. Introduction

Forest ecosystems play a key role in global carbon cycling and biodiversity conservation but are increasingly threatened by ongoing climate change, which affects their stability and functioning [1]. These changes are particularly evident in European forests [2], where shifts in temperature, precipitation regimes, and extreme climatic events influence forest growth, vitality, carbon storage, and species distributions [3]. Mixed-species forests are increasingly recognized for their role in maintaining biodiversity and ecosystem stability, as species interactions may enhance resistance to environmental stress and support more efficient resource use [4–7]. In this context, thermophilous oak forests dominated by *Quercus frainetto* and *Q. cerris* represent important forest communities in Southeastern Europe, supporting diverse understory vegetation and contributing to regional biodiversity conservation.

European temperate *Quercus* forests have experienced changes in species composition over the past century, largely driven by anthropogenic influences, including thermophilization, eutrophication, and biotic homogenization [8]. Despite ongoing environmental pressures, several widespread oak species in Central and Southeastern Europe, including *Quercus petraea*, *Q. frainetto*, and *Q. cerris*, display relatively high drought tolerance and adaptive capacity under changing climatic conditions and are widely recognized as key examples of resilience among temperate forest tree species [9–11]. Given the ongoing changes in species composition and climate conditions, understanding the drivers of understory diversity in temperate oak forests is particularly important, as these ecosystems play a key role in maintaining biodiversity and ecosystem stability across Europe. In Southeastern Europe, thermophilous oak forests are expected to become more important due to their relatively high tolerance to drought and warming, potentially supporting biodiversity and ecosystem resilience under future climate conditions. Their broad distribution and high biogeographical significance further highlight their role in regional forest ecosystems [12–14]. Within this group, forests dominated by *Quercus frainetto* and *Q. cerris* are widely distributed throughout Southeastern Europe, including Serbia and its neighboring countries, and they occur across diverse site conditions and on a wide range of geological substrates and elevations [15,16]. In Serbia, these forests represent the most extensive zonal forest type, up to approximately 600 m a.s.l., occurring under a wide range of site conditions and environmental gradients [17]. This environmental heterogeneity leads to considerable variation in understory species composition, shaped by multiple interacting factors, including soil properties, light availability, moisture, and temperature. Thermophilous oak forests are among Europe's most species-rich forest communities, largely due to the high proportion of thermophilous and light-demanding herbaceous species [18].

Forest understory vegetation is one of the most responsive components of forest ecosystems, exhibiting rapid shifts in species composition, diversity, and functional characteristics in response to changes in light availability, microclimatic conditions, soil properties, and disturbance regimes. Consequently, understory vegetation is increasingly recognized as a valuable ecological indicator for assessing forest ecosystem responses to environmental change and forest management practices [19]. At the local scale, understory plant diversity is shaped by complex interactions among multiple environmental gradients, with topographic, edaphic, and stand structural factors often acting simultaneously and differing in their relative influence [20–22]. Soil properties affect nutrient availability, water-holding capacity, and microbial activity, thereby influencing plant performance and species interactions [23]. Topography modifies microclimatic conditions, particularly temperature and moisture regimes, by creating fine-scale variation in radiation, exposure, and drainage [24], while stand structure regulates both the amount and spatial heterogeneity of light reaching the forest floor [25].

Although previous studies have highlighted the importance of climatic, edaphic, and structural factors in shaping forest understory diversity, the relative importance and interactive effects of these drivers vary among forest types and spatial scales. In thermophilous oak forests, however, these relationships remain insufficiently understood, particularly at local spatial scales [26]. Therefore, the aim of this study is to identify the main drivers of understory plant diversity in oak forests dominated by *Quercus frainetto* and *Quercus cerris* in the Kosmaj region, thereby improving our understanding of ecosystem processes and supporting sustainable forest management under ongoing environmental change. We hypothesized that understory plant diversity is shaped by multiple interacting environmental factors, including stand characteristics, soil properties, geological substrates, and topographic conditions.

## 2. Materials and Methods

### 2.1. Study Area

The study was conducted in coppice oak forests dominated by *Quercus frainetto* Ten. and *Quercus cerris* L. in the Kosmaj Mountain area, Serbia. Kosmaj is a relatively low mountain massif (626 m a.s.l.), most of which was designated as a protected area in 2005, covering a total of 3514.50 ha, of which 688.30 ha are forested. The study area is located between 44°26′32″–44°29′11″ N and 20°33′05″–20°36′04″ E. According to the Thornthwaite climate classification, the region has a moist subhumid climate (C2 type). The mean annual air temperature is 12.3 °C, rising to 18.9 °C during the vegetation period. Precipitation averages 696 mm annually, with approximately 57% falling during the vegetation period [27]. Geologically, Mount Kosmaj is an isolated massif composed of Cretaceous flysch and limestone, with local occurrences of serpentinite and granitoid. This heterogeneous geological structure has led to pronounced variability in soil conditions across the landscape.

Thermophilous deciduous oak forests dominated by *Q. frainetto* and *Q. cerris* are the main vegetation type in the study area. These forests primarily occur at lower elevations (300–550 m a.s.l.), on warmer exposures and gentle slopes (6–24°), and are associated with diverse geological substrates including flysch, limestone, and serpentinite. The studied stands are secondary coppice forests characterized by the strong resprouting capacity of the dominant oak species and a well-developed shrub and herb layer.

### 2.2. Data Collection and Processing

A total of 28 phytosociological relevés, each representing a distinct forest stand, were used to analyze the floristic composition of oak forests in the Kosmaj area (Figure 1). Sampling plots were selected in floristically homogeneous forest stands representing the range of stand and site conditions observed in the study area, including differences in geological substrate, elevation, and stand age. Floristic sampling was carried out using 900 $m^2$ (30 × 30 m) plots. In each plot, a complete list of vascular plant species was recorded separately for the tree, shrub, and herb layers, using the Braun–Blanquet scale [28]. Cover-abundance values were transformed according to Van der Maarel [29] before statistical analyses.

For each sample plot, topographic and stand variables were recorded. The altitude of the plot center was measured with a Trimble Juno GPS device (Trimble Inc., Sunnyvale, CA, USA). Slope was measured in the field using a Haglöf Vertex hypsometer (Haglöf Sweden AB, Långsele, Sweden). Aspect was recorded with a hand compass and expressed in degrees relative to true north. Because aspect is a circular variable, where 0° and 360° represent the same direction, aspect values were transformed using the cosine transformation proposed by Beers et al. [30]. The transformed aspect index ranges from 0 to 2, with lower values representing warmer southwest-facing slopes and higher values representing

cooler northeast-facing slopes. Stand age for each plot was obtained from official forest management plans. For subsequent analyses, plots were classified into three altitudinal classes: 300–400 m a.s.l., 400–500 m a.s.l., and >500 m a.s.l. Geological substrates were grouped into two main categories: limestone and silicate. Forest stands were classified into three 20-year age classes (20–40, 40–60, and 60–80 years). This classification was used to facilitate comparison among stand developmental stages and to reduce variability in stand age data.

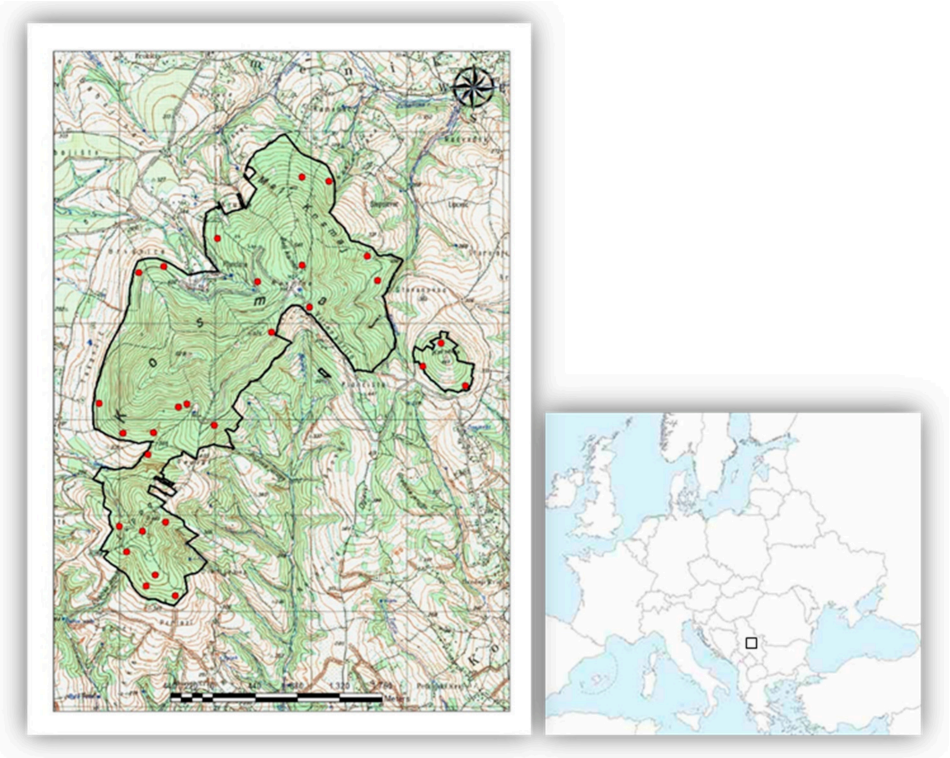

**Figure 1.** Study area and location of the 28 sampling plots in oak forest. The black box indicates the study area, and red dots indicate the locations of the sampling plots.

Soil samples were collected from the same 28 plots used for vegetation sampling. In each plot, soil was sampled in triplicate from a depth of 0–30 cm, and composite samples were prepared for each plot. Samples were air-dried and sieved before laboratory analyses. Soil chemical properties included humus content, determined by the Tyurin method [31]; total nitrogen, determined by the Kjeldahl method [32]; and available phosphorus and potassium, determined by the AL method according to Egner–Riehm [33]. Soil active acidity (pH in $H_2O$) was measured potentiometrically according to SRPS EN ISO 10390:2022 [34] . The sum of exchangeable base cations (S) and hydrolytic acidity (H) was determined by the Kappen method [33], while the total cation exchange capacity (T) and base saturation (V) were subsequently calculated using standard equations.

### 2.3. Data Analysis

Three measures of biodiversity were used: species richness, the Shannon diversity index, and Pielou's evenness index. These diversity indices were calculated based on species recorded in the shrub and herb layers, which were considered as the understory vegetation component of the studied forests. Species richness was calculated as the total number of herbaceous and shrub species per plot. The Shannon diversity index [35] quantified species diversity, while Pielou's evenness index [36] assessed species evenness. All diversity indices were calculated using JUICE 7.0 software [37]. Statistical analyses were performed in

R software (version 4.5.2). Differences in biodiversity indices among groups defined by altitudinal zones, stand age, and geological substrate were tested using the Mann–Whitney U test (for two groups) and the Kruskal–Wallis test (for three or more groups).

Relationships between biodiversity parameters and environmental variables (aspect, slope, and canopy cover) were assessed using Spearman's rank correlation coefficient (ρ), due to deviations from normality and the assumption of monotonic relationships. The relationship between stand age and canopy cover was also evaluated using the same approach. Statistical significance was set at $p < 0.05$ for all tests.

The effects of soil properties on plant diversity were further evaluated using multiple linear regression models. Species richness, the Shannon diversity index, and Pielou's evenness index were used as dependent variables, while soil chemical properties were included as predictors. Standardized regression coefficients (β) were calculated to compare the relative importance of predictors. Before analysis, soil organic matter-related variables (total N and C/N ratio) were excluded to avoid potential multicollinearity among predictors, and humus content was retained as a proxy for soil organic matter. The correlation structure among soil variables considered during model selection is provided in Supplementary Table S1. The final models included pH, humus, $P_2O_5$, and $K_2O$. Regression diagnostics, including variance inflation factors (VIFs) and Cook's distance values, are provided in Supplementary Table S2. All predictors showed acceptable levels of multicollinearity (VIF < 5). Cook's distance was examined to identify potentially influential observations. For regression models, statistical significance was set at $p < 0.05$, while marginal trends were considered at $0.05 \leq p < 0.10$.

Variation partitioning analysis (VPA) was performed using the vegan package (version 2.7.3) to quantify the independent and shared contributions of environmental predictor groups to variation in understory plant diversity. Three sets of explanatory variables were considered: stand structure variables (stand age and canopy closure), topographic variables (elevation, slope, and aspect), and edaphic/geological variables (pH, humus, $P_2O_5$, $K_2O$, and geological substrate). These predictor groups were defined based on their ecological relevance and represent major environmental components potentially influencing understory vegetation. The explanatory power of variation partitioning models was evaluated using adjusted $R^2$ values. The significance of individual predictor groups was assessed using permutation tests based on redundancy analysis (RDA) with 999 permutations.

The study area map and the distribution of sampling plots were created using ArcGIS 10.8.

## 3. Results

### 3.1. Vegetation Composition and Diversity

A total of 172 vascular plant species were recorded across all sampled plots (Supplementary Table S3). The tree layer was dominated by *Quercus cerris* and *Quercus frainetto*, which together formed the main canopy structure, while other tree species occurred at low cover values, indicating a typical coppice-origin oak forest with a mixed canopy composition. The shrub layer was well developed and characterized by a high cover of *Crataegus monogyna*, *Ligustrum vulgare*, *Prunus spinosa*, and *Fraxinus ornus*, reflecting a structurally heterogeneous understory. The herb layer exhibited the highest species richness and was strongly dominated by *Brachypodium sylvaticum*, together with frequent forest species such as *Melica uniflora*, *Poa nemoralis*, *Helleborus odorus*, and *Galium sylvaticum*. Species richness in the herb layer ranged from 19 to 48 species per plot, with 44 species classified as rare, occurring in less than 1% of the sampled plots. The most species-rich families were *Rosaceae* (11%), *Lamiaceae* (9%), *Fabaceae* (9%), *Poaceae* (8%), and *Asteraceae* (6%). The Shannon diversity index (H') ranged from 2.49 to 3.34, while Pielou's evenness index (J') ranged from 0.78 to 0.90 (Table 1).

**Table 1.** Descriptive statistics of species diversity, topography, stand structure, and soil properties (mean ± SE, minimum and maximum).

| Variable | Mean ± SE | Min | Max |
|---|---|---|---|
| Species richness | 34.29 ± 1.4 | 19.00 | 48.00 |
| Shannon diversity index (H′) | 2.99 ± 0.04 | 2.49 | 3.34 |
| Pielou's evenness index (J′) | 0.84 ± 0.01 | 0.78 | 0.90 |
| Elevation (m) | 418.9 ± 10 | 336 | 558 |
| Aspect (cosine-transformed) | 0.693 ± 0.120 | 0 | 1.924 |
| Slope (°) | 16.00 ± 0.89 | 5 | 24 |
| Age | 52.96 ± 3.07 | 22 | 70 |
| Canopy cover (%) | 73.93 ± 2.30 | 60 | 90 |
| pH ($H_2O$) | 5.23 ± 0.59 | 4.66 | 6.89 |
| Base saturation (%) | 59.87 ± 15.34 | 36.11 | 88.56 |
| Humus (%) | 2.99 ± 1.16 | 1.74 | 4.98 |
| Total N (%) | 0.23 ± 0.06 | 0.16 | 0.34 |
| C/N ratio | 7.12 ± 2.35 | 2.89 | 9.76 |
| $P_2O_5$ (mg $kg^{-1}$) | 13.1 ± 8.9 | 1.5 | 28.2 |
| $K_2O$ (mg $kg^{-1}$) | 179.1 ± 50.2 | 118.5 | 286.4 |

In addition to vegetation characteristics, the study plots exhibited considerable variation in topographic conditions, stand structure, and soil chemical properties, providing a broad environmental gradient for subsequent analyses.

### *3.2. Effects of Elevation, Stand Age and Geology on Understorey Plant Diversity*

Species richness, the Shannon diversity index (H′), and evenness varied moderately along the altitudinal gradient (Figure 2). Species richness was lowest at 300–400 m a.s.l. (Mdn = 31), increased to 39 at 400–500 m a.s.l., and peaked at 40.5 at elevations above 500 m a.s.l. Differences among altitude classes were statistically significant (Kruskal–Wallis $\chi^2 = 6.50$, df = 2, $p = 0.039$), although Dunn's post hoc test with Holm correction did not identify significant pairwise differences among individual altitude classes. The Shannon diversity index increased slightly with altitude, from approximately 2.90 at 300–400 m a.s.l. to 3.15 at 400–500 m a.s.l., before decreasing slightly to approximately 3.04 at elevations above 500 m a.s.l. These differences were not statistically significant (Kruskal–Wallis $\chi^2 = 3.85$, df = 2, $p = 0.146$). Evenness showed a weak decreasing trend with increasing altitude, with median values of 0.84 at low, 0.83 at middle, and 0.82 at high elevations. Despite the observed decreasing trend, differences in evenness among altitudinal classes were not statistically significant (Kruskal–Wallis $\chi^2 = 0.81$, df = 2, $p = 0.668$).

Stand age showed a tendency to influence diversity patterns (Figure 3). Younger stands (20–40 years) exhibited the highest species richness and Shannon diversity index values with median values of 39 and 3.15, respectively. Both indices showed a slight decreasing trend with increasing stand age, with a slight recovery of Shannon diversity in the oldest stands, although differences among stand age classes were not statistically significant (species richness: Kruskal–Wallis $\chi^2 = 5.24$, df = 2, $p = 0.073$; Shannon diversity: $\chi^2 = 2.42$, df = 2, $p = 0.298$). The oldest stands showed the highest variability in species richness among age classes. In contrast, evenness showed a slight increasing trend with stand age, but differences among age classes were not statistically significant ($\chi^2 = 0.22$, df = 2, $p = 0.897$).

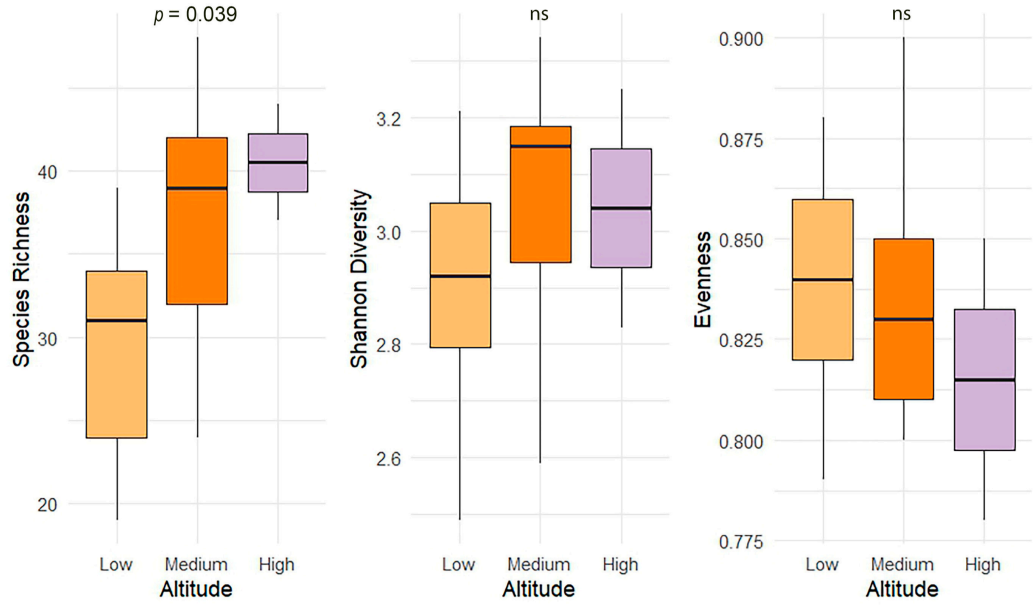


**Figure 2.** Variation in species richness, Shannon diversity, and Pielou's evenness across altitude classes. Statistical significance was assessed using Kruskal–Wallis tests. *p*-values are shown on the graphs; ns indicates non-significant differences ($p > 0.05$).

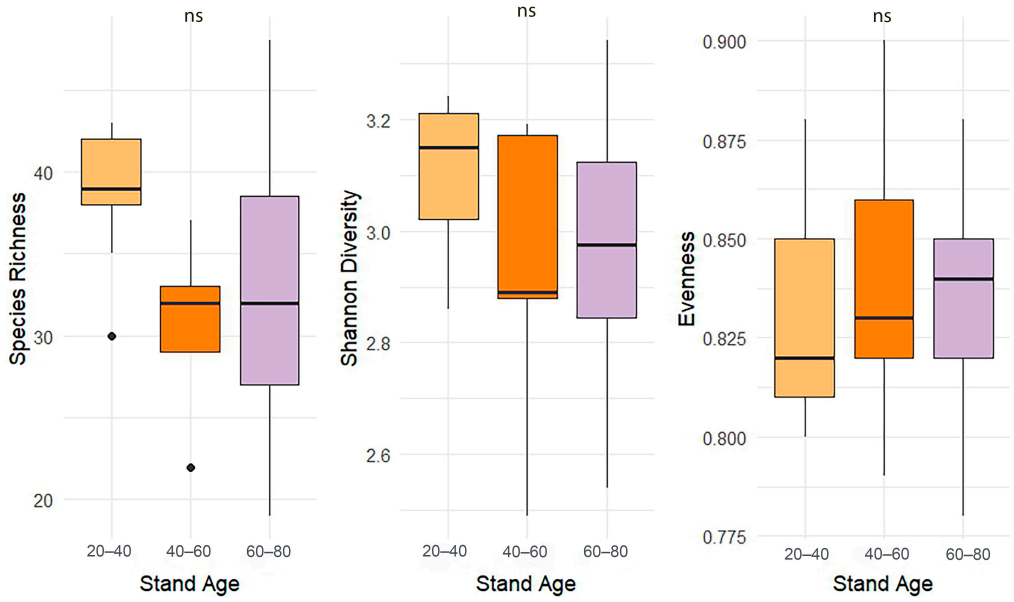


**Figure 3.** Variation in species richness, Shannon diversity index, and Pielou's evenness across stand age classes. Statistical significance was assessed using Kruskal–Wallis tests. *p*-values are shown on the graphs; ns indicates non-significant differences ($p > 0.05$).Black dots indicate outliers beyond the whiskers of the boxplots.

Differences in plant diversity were also observed among geological substrates (Figure 4). Species richness showed higher median values on limestone substrates compared to silicate substrates (37 and 33, respectively), whereas Shannon diversity and evenness tended to be slightly higher on silicate substrates (median values of 3.07 and 2.89 for Shannon diversity, and 0.84 and 0.82 for evenness, respectively). Overall, these results suggest that a geological substrate may be associated with variations in diversity patterns and community structure, with limestone showing higher species richness, while silicate substrates tended to show slightly higher Shannon diversity. However, differences

between geological substrates were not statistically significant for species richness, Shannon diversity, or evenness (Mann–Whitney U tests, all $p > 0.05$; Table 2).

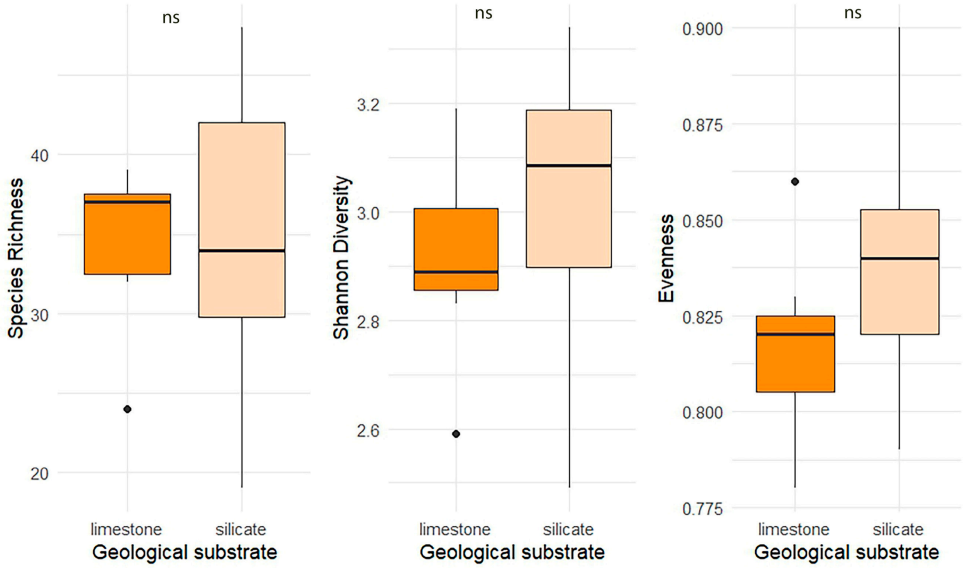


**Figure 4.** Variation in species richness, Shannon diversity index, and Pielou's evenness across geological substrate types. Statistical significance was assessed using Mann–Whitney U tests. *p*-values are shown on the graphs; ns indicates non-significant differences ($p > 0.05$). Black dots indicate outliers beyond the whiskers of the boxplots.

**Table 2.** Results of Kruskal–Wallis and Mann–Whitney U tests for species richness, Shannon diversity, and evenness across altitude, stand age, and geological substrate groups.

| Factor | Groups (*n*) | Diversity Index | Test | Statistic | df | *p*-Value |
|---|---|---|---|---|---|---|
| Altitude | 300–400 m ($n = 11$)<br>400–500 m ($n = 12$)<br>>500 m ($n = 5$) | Richness | Kruskal–Wallis | $\chi^2 = 6.501$ | 2 | 0.039 |
| | | Shannon | | $\chi^2 = 3.847$ | 2 | 0.146 |
| | | Evenness | | $\chi^2 = 0.807$ | 2 | 0.668 |
| Stand age | 20–40 years ($n = 9$)<br>40–60 years ($n = 5$)<br>60–80 years ($n = 14$) | Richness | Kruskal–Wallis | $\chi^2 = 5.237$ | 2 | 0.073 |
| | | Shannon | | $\chi^2 = 2.424$ | 2 | 0.298 |
| | | Evenness | | $\chi^2 = 0.217$ | 2 | 0.897 |
| Geological substrate | Limestone ($n = 5$)<br>Silicate ($n = 23$) | Richness | Mann–Whitney U | W = 57.5 | – | 1.000 |
| | | Shannon | | W = 43.0 | – | 0.401 |
| | | Evenness | | W = 37.5 | - | 0.239 |

### *3.3. Relationships of Topographic Gradients and Canopy Cover with Understory Plant Diversity*

Spearman's correlation analysis revealed no significant relationships between species richness and the environmental variables examined: aspect ($\rho = -0.029$, $p = 0.882$), slope ($\rho = 0.045$, $p = 0.821$), and canopy cover ($\rho = 0.156$, $p = 0.428$) (Figure 5). Similarly, the Shannon diversity index did not significantly correlate with aspect ($\rho = -0.048$, $p = 0.814$), slope ($\rho = 0.301$, $p = 0.12$), or canopy cover ($\rho = 0.372$, $p = 0.051$), although a marginal, non-significant positive relationship was observed with canopy cover. Pielou's evenness index, however, showed a significant positive correlation with slope ($\rho = 0.452$, $p = 0.016$), indicating higher evenness on steeper slopes. No significant relationships were found between Pielou's evenness index and aspect ($\rho = 0.294$, $p = 0.143$) or canopy cover ($\rho = 0.342$,

$p$ = 0.075). Additionally, stand age was not significantly correlated with canopy cover (Spearman's ρ = 0.18, $p$ = 0.363), suggesting that variations in canopy structure were not strongly related to stand age across the studied plots.

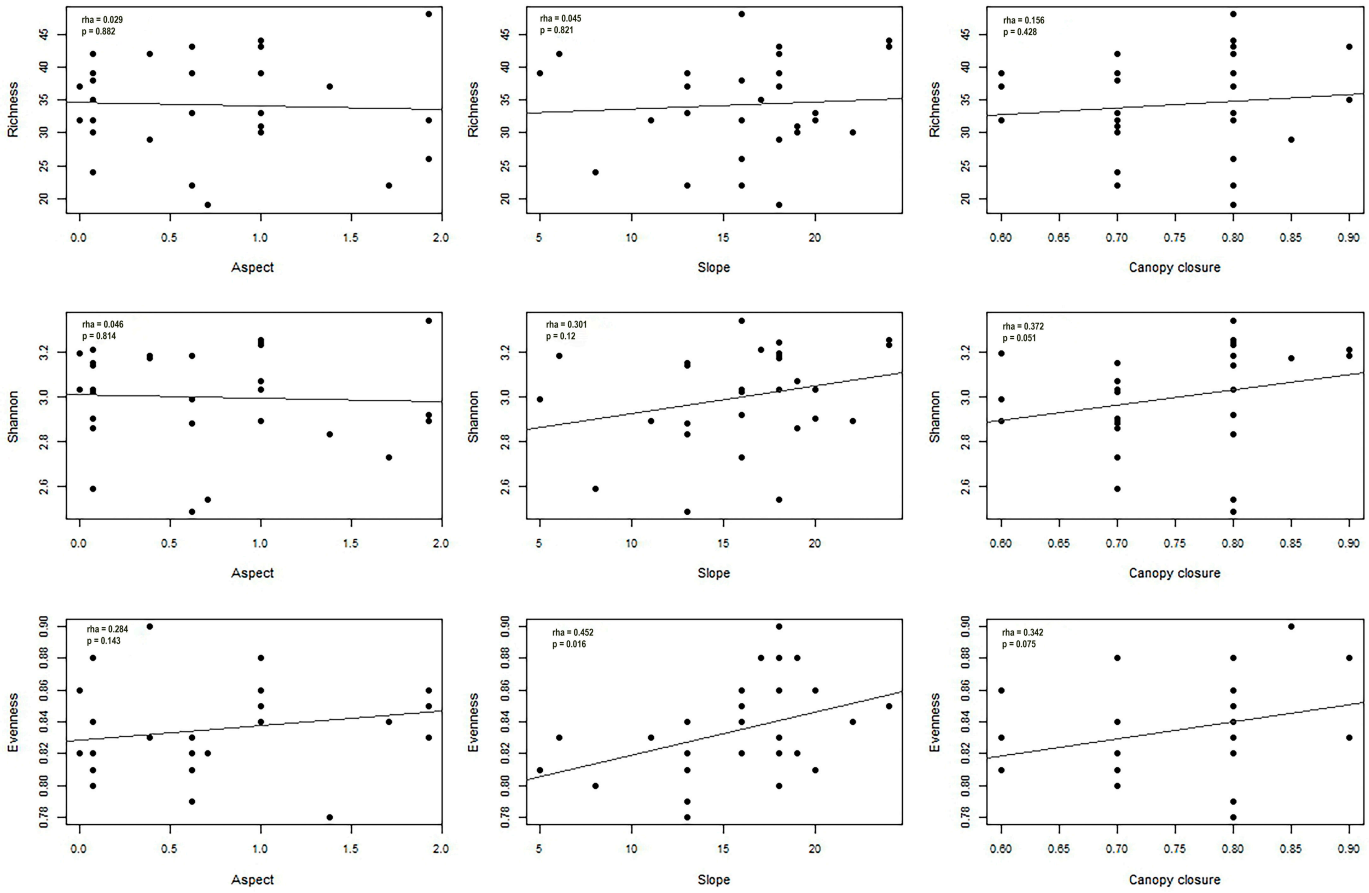


**Figure 5.** Relationships between plant diversity indices and topographic and stand structure.

### *3.4. Effects of Soil Chemical Properties on Understory Plant Diversity*

Soil chemical properties displayed moderate variability across the sampled plots (Table 1). Soil pH ($H_2O$) ranged from 4.66 to 6.89, with a mean of 5.23 ± 0.59, indicating moderately acidic conditions. Base saturation varied considerably (36.11%–88.56%), with a mean of 59.87 ± 15.34%. Soil organic matter content (humus) ranged from 1.74% to 4.98%, with an average of 2.99 ± 1.16%, corresponding to moderately humus-rich soils. Total nitrogen content ranged from 0.16% to 0.34%, with a mean of 0.23 ± 0.06%. The C/N ratio varied from 2.89 to 9.76, with an average of 7.12 ± 2.35, suggesting relatively rapid organic matter turnover. Available phosphorus ($P_2O_5$) and potassium ($K_2O$) exhibited wider ranges, with mean values of 13.1 ± 8.9 mg $kg^{-1}$ and 179.1 ± 50.2 mg $kg^{-1}$, respectively.

Soil chemical properties showed relationships with biodiversity indices (Figure 6; Table 3). The regression model for species richness explained a moderate proportion of the variation ($R^2$ = 0.53; adjusted $R^2$ = 0.21). Among the predictors, humus content showed a positive but non-significant association with species richness, whereas available phosphorus ($P_2O_5$) showed a marginal negative association ($p$ = 0.079). Soil pH and $K_2O$ were not significant predictors (Table 3). The model for the Shannon diversity index explained a higher proportion of the variability ($R^2$ = 0.80; adjusted $R^2$ = 0.67). Humus content was positively and significantly associated with Shannon diversity, whereas $P_2O_5$ and $K_2O$ were negatively and significantly associated with this index. Soil pH was not a significant predictor of Shannon diversity. The model for Pielou's evenness index showed moderate

explanatory power ($R^2$ = 0.68; adjusted $R^2$ = 0.47). Humus content was positively and significantly associated with evenness, whereas $P_2O_5$ and $K_2O$ showed marginal negative associations. Soil pH was not a significant predictor of evenness.

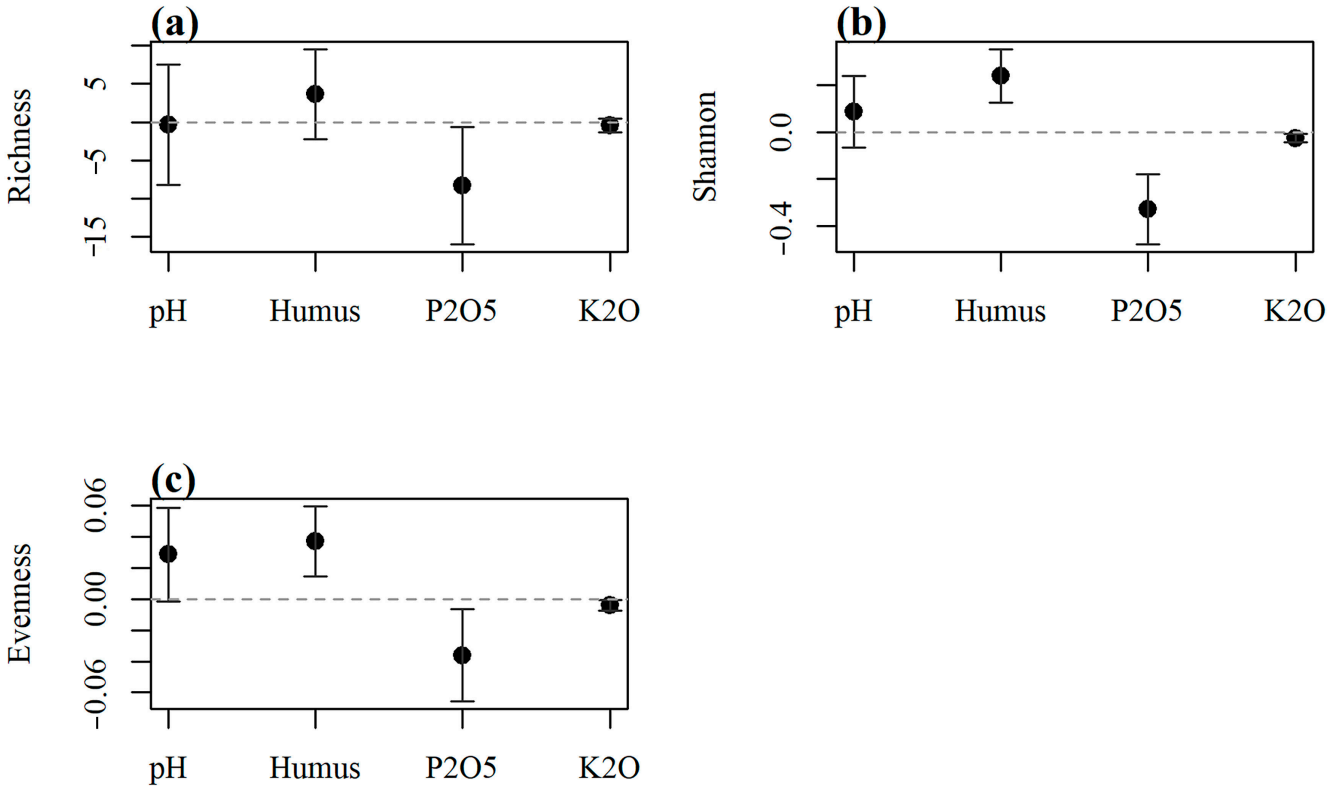


**Figure 6.** Effects of soil chemical properties on: (**a**) species richness, (**b**) Shannon diversity, and (**c**) Pielou's evenness index. The dashed lines indicate the zero reference line.

**Table 3.** Multiple linear regression models examining the effects of soil properties on species richness, Shannon diversity (H), and Pielou's evenness (J).

| Variable | Predictor | β | Estimate | SE | t | *p*-Value | 95% CI |
|---|---|---|---|---|---|---|---|
| Species richness | pH | −0.027 | −0.354 | 4.024 | −0.088 | 0.933 | −10.200 to 9.492 |
| | Humus | 0.551 | 3.631 | 2.989 | 1.215 | 0.270 | −3.683–10.944 |
| | $P_2O_5$ | −0.969 | −8.317 | 3.929 | −2.117 | 0.079 | −17.930–1.297 |
| | $K_2O$ | −0.298 | −0.456 | 0.465 | −0.979 | 0.365 | −1.595–0.683 |
| Shannon diversity index (H′) | pH | 0.223 | 0.085 | 0.078 | 1.101 | 0.313 | −0.104–0.275 |
| | Humus | 1.216 | 0.237 | 0.058 | 4.117 | 0.006 | 0.096–0.378 |
| | $P_2O_5$ | −1.294 | −0.329 | 0.076 | −4.341 | 0.005 | −0.514–−0.143 |
| | $K_2O$ | −0.573 | −0.026 | 0.009 | −2.891 | 0.028 | −0.048–−0.004 |
| Pielou's evenness index (J′) | pH | 0.472 | 0.029 | 0.015 | 1.849 | 0.114 | −0.009–0.066 |
| | Humus | 1.201 | 0.037 | 0.011 | 3.224 | 0.018 | 0.009–0.065 |
| | $P_2O_5$ | −0.905 | −0.036 | 0.015 | −2.405 | 0.053 | −0.073–0.001 |
| | $K_2O$ | −0.587 | −0.004 | 0.002 | −2.349 | 0.057 | −0.009–0.000 |

β = standardized regression coefficient; SE = standard error; CI = confidence interval.

### *3.5. Integrated Assessment of Environmental Drivers of Understory Diversity*

Variation partitioning analysis was used to quantify the independent contributions of three groups of predictors: stand structure variables (stand age and canopy closure), topographic variables (elevation, slope and aspect), and edaphic factors, including geological substrate (soil pH, humus, $P_2O_5$, $K_2O$ and substrate type).

The full variation partitioning model explained 12.5% of the variation in species richness, whereas it showed negligible explanatory power for Shannon diversity (adjusted $R^2 = -0.060$) and limited explanatory power for Pielou's evenness (adjusted $R^2 = 0.083$) (Table 4).

**Table 4.** Adjusted $R^2$ values of full variation partitioning models for plant diversity indices.

| Response Variable | Full-Model Adjusted $R^2$ |
|---|---|
| Species richness | 0.125 |
| Shannon diversity | −0.060 |
| Pielou's evenness | 0.083 |

Variation partitioning revealed that stand structure variables made the largest independent contribution to species richness, accounting for 27.0% of the explained variation. Stand structure variables also showed the largest independent contribution to Shannon diversity (12.1%), whereas topographic variables represented the largest independent contribution to Pielou's evenness, accounting for 2.5% of the explained variation (Figure 7). Edaphic and geological factors showed low or negative independent contributions across diversity indices after accounting for the effects of the other predictor groups.

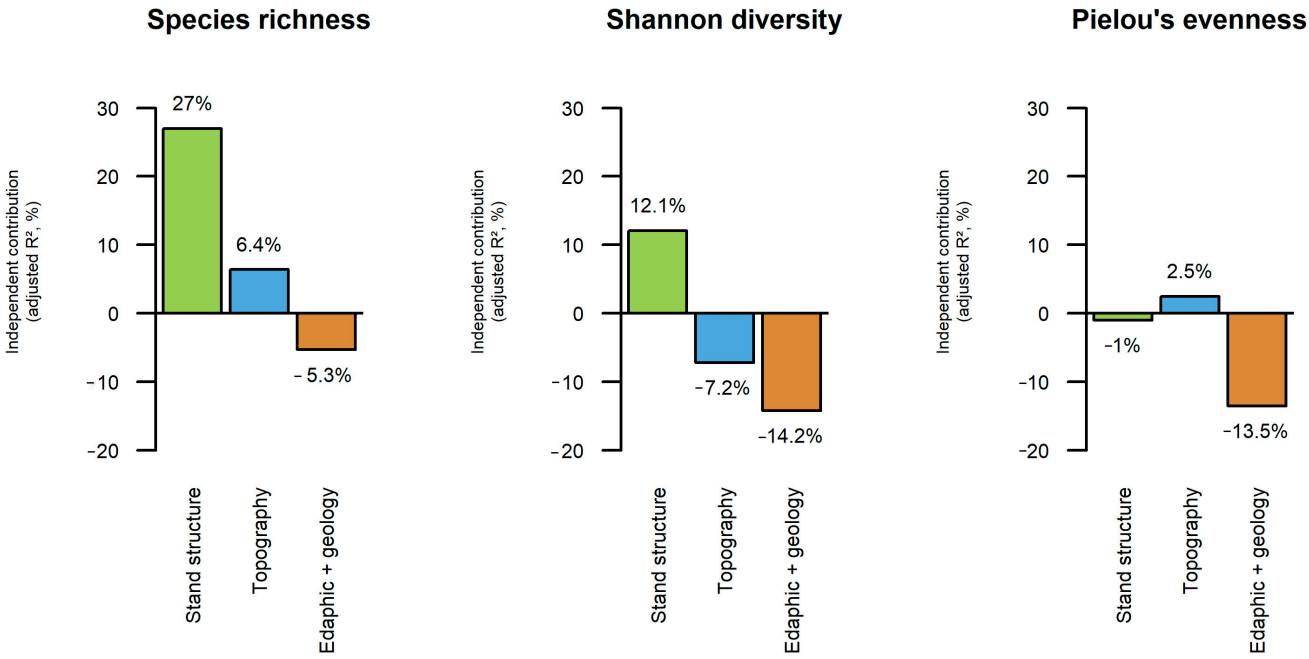


**Figure 7.** Variation partitioning of plant diversity indices showing the independent and shared contributions of stand structure, topographic, and edaphic/geological predictor groups.

## 4. Discussion

The relatively high number of vascular plant species (172) recorded across all plots indicates considerable habitat heterogeneity, suggesting that these oak-dominated forests are structurally and compositionally diverse. Similar patterns of high understory diversity have been reported in semi-natural oak forests of Central Europe, where structural complexity and environmental heterogeneity promote species coexistence [38]. Understory diversity in forest ecosystems is strongly influenced by variations in light availability, soil conditions, and stand structure, while broader-scale vegetation patterns are also shaped by topographic and edaphic gradients. Previous studies have shown that such environmental factors are important predictors of species richness and community composition in

deciduous oak forests [39]. Consistent with these findings, substantial variation in understory plant diversity was observed among the sampled stands, suggesting the influence of multiple interacting environmental drivers. The following discussion examines the relative importance of topographic, edaphic, geological, and stand structure variables in shaping understory diversity patterns.

### 4.1. Effects of Elevation, Stand Age and Geology

Among the environmental factors examined, elevation, geological substrate, and stand age showed different patterns of association with understory diversity.

In this study, species richness showed an increasing trend with elevation, a pattern that contrasts with the commonly reported decreasing or unimodal elevational trends [40]. This pattern may reflect locally favorable conditions at higher elevations within the study area, potentially including increased habitat heterogeneity and resource availability. Similar positive relationships between elevation and understory diversity have also been reported in some oak [38] and beech forest systems [41], suggesting that elevational effects can be context-dependent and strongly influenced by local environmental conditions.

Shannon diversity showed a weak unimodal pattern, with the highest values at mid-elevations, whereas evenness declined at higher elevations. The relatively narrow elevational range investigated in this study may contribute to this pattern, as higher elevations did not reach levels typically associated with climatic limitations on plant diversity. Similar mid-elevation peaks in species diversity are frequently reported along elevational gradients and are often associated with more favorable environmental conditions and greater habitat heterogeneity at intermediate elevations [42]. In oak-dominated forests, stand closure and canopy structure may further influence these patterns by regulating light availability and understory microenvironmental conditions [43]. The lower evenness observed at higher elevations may reflect stronger environmental filtering, leading to increased dominance by a smaller number of species adapted to more restrictive environmental conditions.

Geological substrate was associated with variations in understory diversity patterns, although differences between substrate types were not statistically significant. Limestone substrates showed higher species richness, whereas silicate substrates tended to have slightly higher Shannon diversity and evenness, suggesting that substrate-related differences may contribute to variation in different components of understory diversity. These patterns may reflect variations in soil properties, nutrient availability, and pH conditions that are often associated with contrasting substrate types. Similar patterns have been reported in oak forests, where bedrock strongly influences understory composition and richness [38]. Overall, variability within both substrate types highlights the importance of local-scale environmental heterogeneity. The observed substrate-related variation may reflect indirect effects of geology on soil development and nutrient availability, which may contribute to the differences in understory diversity.

Stand age showed a tendency to influence understory diversity, with younger stands showing higher richness and Shannon diversity. This pattern may reflect differences in stand development, habitat complexity, and resource availability during forest succession [44,45]. Although canopy closure is often considered an important mechanism regulating understory communities during stand development, the lack of a significant relationship between stand age and canopy cover in the present study suggests that other aspects of stand development and habitat structure may have contributed to the observed diversity patterns. Pielou's evenness remained relatively stable across age classes, indicating that changes in species richness were not accompanied by substantial shifts in species dominance structure [46]. Furthermore, the absence of a significant relationship between

stand age and canopy cover suggests that differences in canopy structure among plots were not primarily explained by stand development.

### 4.2. Topographic Gradients and Canopy Cover as Drivers of Understory Diversity

Most topographic and structural variables showed weak or nonsignificant relationships with species richness and Shannon diversity in the studied oak forests, suggesting that these factors had a limited influence on overall diversity patterns within the studied plots. In contrast, the significant positive relationship between slope and Pielou's evenness suggests that steeper terrain may reduce dominance by competitively superior species, promoting a more balanced distribution of species abundances. This pattern is consistent with findings that environmental gradients often drive shifts in species dominance through competitive filtering rather than changes in species richness [47]. This may be attributed to shallower soils, increased surface runoff, and greater microhabitat heterogeneity on steeper slopes, which limit competitive exclusion and reduce the advantage of dominant mesophytic species. Such conditions are consistent with studies highlighting the role of microtopographic heterogeneity, soil depth variation, and microclimatic buffering in shaping understory plant communities in temperate forests [48,49].

Canopy cover showed positive but non-significant relationships with both Shannon diversity and evenness, suggesting that canopy structure may contribute to variation in understory conditions by modifying light availability and microclimatic conditions [50]. Canopy effects on understory diversity may reflect differences in understory environmental conditions associated with canopy structure, potentially influencing the balance between competitive and stress-tolerant species [25]. However, the weak statistical support indicates that these effects are context-dependent and may vary with stand structure, management intensity, and successional stage [51]. Overall, these findings are consistent with previous studies emphasizing the role of forest structure in shaping understory vegetation dynamics. Increased structural complexity has been shown to support greater herb-layer diversity [52,53], whereas dense and more homogeneous canopies are often linked to reduced species richness and simplified understory composition in temperate oak forests [22].

### 4.3. Influence of Soil Chemical Properties on Understory Diversity

Soil organic matter plays a central role in forest ecosystem functioning by influencing nutrient availability, water retention, and soil structure. In oak-dominated forests, the accumulation and decomposition of organic matter are largely determined by litter quality and environmental conditions, which together regulate nutrient cycling and humus formation [54]. Differences in litter characteristics among oak species may further affect these processes, as *Quercus cerris* litter decomposes more slowly than *Quercus frainetto* litter, potentially contributing to variation in organic matter accumulation and nutrient availability [55].

In this study, soil humus content and nutrient availability emerged as important individual edaphic predictors of understory diversity in the investigated oak forests. Humus content showed a positive relationship with understory diversity, particularly with Shannon diversity and Pielou's evenness, whereas available phosphorus and potassium showed predominantly negative relationships with these indices. The positive relationship between humus content and diversity metrics suggests that higher levels of soil organic matter create more favorable conditions for understory vegetation by enhancing nutrient supply and increasing environmental heterogeneity. The mineralization of organic litter and humus formation are strongly influenced by the C/N ratio and climatic conditions (temperature and moisture), with narrower C/N ratios generally promoting faster decomposition and

more rapid nutrient release. Higher humus content is generally associated with lower C/N ratios, which represent an important ecological gradient influencing understory vegetation in temperate forest ecosystems, including oak-dominated stands [56]. Such conditions may contribute to nutrient cycling and soil fertility, which are widely recognized as key drivers of plant diversity in these ecosystems.

In contrast to humus content, available phosphorus showed predominantly negative associations with diversity parameters. In forest ecosystems developed on heterogeneous substrates, phosphorus availability is often highly variable and may reflect both parent material and long-term soil development processes [57]. Although positive associations between phosphorus availability and vascular plant richness have been reported [58], our results are more consistent with the findings of Hrivnák et al. [59]. A possible explanation is that increased phosphorus availability may modify competitive interactions among understory plant species by favoring a subset of species better able to utilize available resources, potentially reducing coexistence and resulting in lower diversity [60,61]. A similar but weaker negative trend was observed for available potassium, suggesting that higher potassium availability may favor a subset of competitive species at the expense of overall understory diversity. However, compared to phosphorus, the ecological effects of potassium are generally more indirect and context-dependent and are more strongly influenced by interactions with other soil properties and site-specific conditions [62].

### *4.4. Integrated Effects of Environmental Drivers on Understory Diversity*

Variation partitioning analysis provided an integrated assessment of the relative contribution of different environmental components to understory diversity patterns and showed that the importance of predictor groups varied among diversity indices. Stand structure variables showed the highest independent contribution to species richness, suggesting that differences in stand development and canopy conditions may influence understory species richness patterns by modifying site conditions and resource availability. Stand structure variables also showed the largest independent contribution to Shannon diversity, although the overall explanatory power of the full model for this index was negligible. For Pielou's evenness, topographic variables represented the largest independent contribution, indicating that topographic variation may influence the relative abundance structure of understory communities rather than overall species richness.

Although edaphic and geological variables showed low or negative independent contributions in the variation partitioning analysis, individual soil properties were associated with diversity patterns, particularly through the effects of humus content and nutrient availability identified by regression models. The limited explanatory power of the full variation partitioning models, particularly for Shannon diversity and Pielou's evenness, indicates that the environmental predictor groups considered here explained only a limited proportion of the variation in understory diversity patterns. Therefore, the identified environmental factors should be interpreted as contributing factors shaping understory diversity patterns rather than as exclusive drivers.

## 5. Conclusions

This study shows that understory plant diversity in *Quercus frainetto–Quercus cerris* forests is shaped by multiple interacting environmental factors, including stand structure, topography, and soil conditions. Variation partitioning analysis showed that the relative contribution of these environmental components differed among diversity indices. Stand structure variables had the highest independent contribution to species richness and Shannon diversity, whereas topographic variables showed the highest independent contribution to Pielou's evenness. Soil humus content was positively associated with Shannon diversity

and Pielou's evenness, highlighting the importance of organic matter accumulation in maintaining plant diversity in the understory layer. In contrast, higher phosphorus and potassium availability showed negative associations, particularly with Shannon diversity, indicating that increased nutrient availability does not necessarily promote higher understory diversity in these forests. Although edaphic and geological variables showed lower independent contributions in the integrated models, individual soil properties remained important predictors of diversity patterns. Stand age and geological substrate showed variable associations with diversity components, although these relationships were not statistically significant.

From a management perspective, maintaining environmental heterogeneity, preserving stands at different developmental stages, and conserving soil quality are important for sustaining understory plant diversity in thermophilous oak forests. These findings emphasize that variation in understory plant diversity in *Q. frainetto*–*Q. cerris* forests reflects the combined effects of stand characteristics, topographic gradients, and edaphic conditions. However, the results should be interpreted within the spatial context of the studied area, and further research across broader geographic scales is needed to evaluate the general applicability of these patterns.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f17080924/s1, Table S1: Pearson correlation matrix among soil variables considered for predictor selection for multiple linear regression models; Table S2: Regression diagnostics for multiple linear regression models; Table S3: Mean percentage cover (±SEM) of tree, shrub, and herb layer species across 28 mixed-oak stands.

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