sustainability

MDPI

Article

Floristic and Soil Responses to Shelterwood Regeneration in Pedunculate Oak Forests

Irena Šapić [1], Anamarija Jazbec [2], Krešimir Popić [3,*], Dario Baričević [1], Igor Poljak [4], Ivan Perković [1] and Damir Ugarković [1,*]

[1] Faculty of Forestry and Wood Technology, Institute of Ecology and Silviculture, University of Zagreb, Svetošimunska Cesta 23, 10000 Zagreb, Croatia; isapic@sumfak.unizg.hr (I.Š.); dbaricevic@sumfak.unizg.hr (D.B.); iperkovic@sumfak.unizg.hr (I.P.)
[2] Faculty of Forestry and Wood Technology, Institute of Forest Inventory, Management Planning and Remote Sensing, University of Zagreb, Svetošimunska Cesta 23, 10000 Zagreb, Croatia; ajazbec@sumfak.unizg.hr
[3] Forest Office Lipovac, Forest Department Vinkovci, Croatian Forests Ltd., M. Gupca 5, 32246 Lipovac, Croatia
[4] Faculty of Forestry and Wood Technology, Institute of Forest Genetics, Dendrology and Botany, University of Zagreb, Svetošimunska Cesta 23, 10000 Zagreb, Croatia; ipoljak@sumfak.unizg.hr
* Correspondence: kresimir.popic@hrsume.hr (K.P.); dugarkovic@sumfak.unizg.hr (D.U.)

Abstract

The regular (even-aged) silvicultural system is widely used in the management of pedunculate oak forests to ensure their long-term sustainability and regeneration. This approach maintains an even-aged stand structure by harvesting one tree generation and establishing a new cohort through natural or artificial regeneration. This management simplifies cultivation and exploitation but can have an impact on biodiversity. Research was conducted in the Spačva forest complex in pedunculate oak–common hornbeam stands, including mature forest stands and stands in the seed cut and final cut stages of shelterwood regeneration. This study aimed to assess changes in the floristic composition between the forest and regeneration phases of pedunculate oak stands, and to test whether these changes are associated with shifts in microclimatic conditions, soil microbiological and chemical properties. The study was conducted in the Spačva forest complex across four sites representing regeneration and forest phases, using a total of 20 phytocoenological relevés (10 per phase). Microclimatic data were collected over two years (March 2021–March 2023), while soil chemical, microbiological, and vegetation data were analyzed to compare habitat conditions. Differences between phases were evaluated using Student's *t*-tests, and relationships between diagnostic species and habitat variables were assessed using Spearman rank correlation analysis. The regeneration phase exhibited substantially higher plant species richness than the forest phase, with 84 recorded species compared with 44 in forest stands (approximately a 91% increase), corresponding to mean values of 32 and 19 species per relevé, respectively. There were 12 species with a fidelity index determined as diagnostic for the regeneration phase. Microclimatic, pedological, chemical, and biological soil properties were compared between regeneration and forest phases, and their relationships with the occurrence of 12 diagnostic species were examined to identify ecological drivers relevant to successful and sustainable forest restoration. Increased insolation resulting from canopy opening was identified as the primary factor differentiating regeneration from forest stands, promoting higher plant species richness by enhancing light availability and modifying soil chemical conditions. These findings indicate that shelterwood-induced changes in habitat structure can increase floristic diversity without adversely affecting key soil functions, highlighting the importance of integrating vegetation, soil, and microclimatic indicators into adaptive management strategies for the sustainable restoration and long-term resilience of pedunculate oak forests.

Academic Editor: Ronald C. Estoque

Received: 7 May 2026
Revised: 9 July 2026
Accepted: 15 July 2026
Published: 17 July 2026

Keywords: shelterwood cutting; habitat ecology; sustainable management; species diversity

1. Introduction

Pedunculate oak (*Quercus robur* L.) forests are among the most ecologically and economically important forest ecosystems in Europe, supporting high levels of biodiversity, providing essential ecosystem services, and supplying high-value timber while contributing to climate resilience and sustainable forest management [1,2]. Their distribution extends from Spain in the west to Ukraine in the east and from southern Scandinavia to the Mediterranean region, with the largest areas occurring in France, Germany, and Poland [3].

Although pedunculate oak is a widespread European tree species, its regeneration is increasingly threatened by more frequent drought events, altered hydrological regimes, and interacting biotic stressors associated with climate change. These pressures reduce seedling establishment and survival and may compromise the long-term resilience of oak forests, particularly in lowland floodplain ecosystems experiencing progressive habitat drying [4–7]. Regular or even-aged management of pedunculate oak forests has proven to be the optimal way to guide development during rotation. This approach includes the establishment of a young forest stand, its care during its life cycle and the final regeneration in which the old stand is removed and the space is left to the new generation. Natural regeneration in pedunculate oak forests is commonly achieved through the shelterwood system, in which the overstory is gradually removed over several years to facilitate the establishment of a new tree generation while maintaining partial canopy cover. This approach not only promotes regeneration but also creates temporal changes in light availability, microclimatic conditions, and soil processes, thereby influencing understory vegetation dynamics and ecosystem functioning. In pedunculate oak–common hornbeam stands under normal structural conditions, the regeneration period typically extends from six to eight (up to ten) years [8,9].

According to Ritter et al. [10] and Ugarković et al. [11], forest trees play a fundamental role in shaping microclimatic conditions. Forest canopies regulate solar radiation, air movement, temperature, and humidity, thereby creating stable environmental conditions that support biodiversity and ecosystem functioning, as also highlighted by De Frenne et al. [12]. Organisms inhabiting forest ecosystems are adapted to these specific microclimatic conditions, which differ markedly from those of adjacent open habitats [13,14]. However, forestry interventions can substantially modify canopy structure and consequently alter the forest microclimate [15,16]. Canopy density, vertical vegetation stratification, and tree species composition directly influence light penetration and air circulation within the forest [17]. Tranquillini [18] and Denslow [19] demonstrated that increasing canopy openness enhances solar radiation and air temperature at the forest floor, while Zellweger et al. [20] further showed that these changes can cascade through the ecosystem by affecting understory vegetation, soil processes, and ecosystem resilience.

The belowground environment is also regulated by microclimatic conditions. Soil temperature and moisture strongly influence microbial activity, organic matter decomposition, and nutrient cycling, thereby affecting nutrient availability and plant establishment. These interactions are particularly important in forest ecosystems, where plant species differ in their requirements for light, temperature, and water availability [21]. Microclimatic factors such as soil moisture and temperature are therefore crucial for the establishment and growth of forest species, as demonstrated in studies on the restoration of oak–hornbeam forests and their effects on community composition [22].

Biological components, particularly soil microorganisms and extracellular enzymes, are fundamental drivers of soil functioning and ecosystem resilience. Through their involvement in organic matter decomposition, nutrient mineralization, and biogeochemical cycling, microbial communities regulate soil fertility and support plant productivity, thereby contributing to the maintenance of healthy and resilient forest ecosystems [23–25]. As emphasized by Delgado-Baquerizo et al. [26], soil biodiversity is closely linked to ecosystem multifunctionality and the capacity of ecosystems to sustain multiple ecological processes simultaneously.

Forest soils represent highly diverse microbial habitats dominated by bacteria and fungi. In pedunculate oak forests, saprotrophic fungi are primarily responsible for organic matter decomposition, while mycorrhizal fungi establish mutualistic associations with tree roots that enhance nutrient uptake and improve plant performance under environmental stress. Together with bacterial communities, these organisms play a central role in maintaining soil health and ecosystem stability [27].

Because of their rapid response to environmental change, soil microorganisms and enzyme activities are widely recognized as sensitive indicators of disturbances caused by climate change, tree dieback, or forest management interventions, including shelterwood cutting [28,29]. Their activity is regulated by interactions among climatic conditions, soil properties, organic matter inputs, and vegetation composition [27]. Consequently, soil microbial and enzymatic characteristics provide valuable indicators of restoration success and long-term sustainability by reflecting the recovery of soil functions that underpin forest regeneration and ecosystem resilience, as also highlighted by Bardgett and van der Putten [30]. Soil enzyme activity may therefore serve not only as a predictor of site conditions but also as an indicator of successful oak establishment and regeneration [31].

Forestry interventions that reduce canopy cover create environmental conditions that differ markedly from those in closed-canopy stands by altering light availability, temperature, humidity, and soil moisture regimes [32]. The magnitude of these changes depends on the intensity of canopy opening, with shelterwood treatments creating gradients of microclimatic conditions that influence regeneration trajectories, understory vegetation dynamics, and soil processes. Moderate canopy retention may buffer climatic extremes while providing sufficient light for tree regeneration, whereas more intensive canopy removal can promote pioneer and ruderal species and alter ecosystem functioning. Consequently, understanding how different levels of canopy disturbance affect forest microclimate and the responses of vegetation and soil biota is essential for developing adaptive forest management and restoration strategies that maintain biodiversity, ecosystem resilience, and long-term sustainability in pedunculate oak forests [33]. This relationship between canopy structure and ecological responses has also been emphasized by Decocq et al. [17].

The pedunculate oak–common hornbeam forest community (*Carpino betuli–Quercetum roboris*/Anić 1959/Rauš 1971) is one of the most widespread and extensively studied forest communities in Croatia, covering approximately 110,000 ha, with its largest complexes located in the Spačva Basin and along the Sava River and its tributaries [34]. Despite its ecological and economic importance, this forest type is increasingly exposed to environmental pressures that threaten its long-term resilience and sustainability.

Long-term vegetation studies conducted in the Spačva Basin by Škvorc et al. [6] revealed pronounced shifts in synecological conditions over the last four decades, accompanied by a progressive decline in habitat moisture and changes in floristic composition toward more drought-tolerant and climatogenic communities. The increasing occurrence of species such as *Tilia tomentosa*, *Cornus sanguinea* and *Acer tataricum*, together with the reduction in hygrophilous species, indicates ongoing habitat drying and a loss of characteristic ecological conditions. Similarly, Cestarić et al. [7] demonstrated that the combined effects of hydroamelioration and climate change have accelerated succession from wetter

to drier forest communities, resulting in floristic homogenization, particularly within the shrub and herb layers. These trends suggest a gradual degradation of floodplain forest habitats and highlight the need for adaptive management strategies aimed at enhancing ecosystem resilience and supporting the sustainable restoration of pedunculate oak forests.

Ground vegetation, which includes herbaceous plants, mosses, lichens and low shrubs, is a key component of terrestrial ecosystems, particularly forests, grasslands and wetlands. Due to its close relationship with soil and microclimatic conditions, ground vegetation shows high sensitivity to changes in habitat factors and often responds more quickly and significantly than woody vegetation [35].

The use of indicator species in assessing the effects of forest management interventions offers important methodological and ecological advantages. Because many understory species exhibit narrow ecological amplitudes with respect to light availability, soil moisture, pH-value and nutrient status, changes in their occurrence and abundance provide sensitive measures of alterations in habitat conditions caused by modifications of canopy structure, microclimate, or soil properties [36,37]. Consequently, indicator species are widely used in restoration monitoring as cost-effective biological indicators that integrate multiple environmental drivers and enable the early detection of ecological change. As emphasized by Lindenmayer and Likens [38], bioindicators are particularly valuable for assessing ecosystem condition and evaluating the effectiveness of management actions over time.

Beyond reflecting environmental conditions, indicator species can also help identify ecological thresholds, where relatively small changes in habitat characteristics lead to substantial shifts in community composition or ecosystem functioning. Monitoring such responses is essential for adaptive management, as it enables evaluation of restoration trajectories and timely adjustment of silvicultural interventions. In addition, many indicator species are of conservation importance, allowing simultaneous assessment of biodiversity status and the ecological sustainability of forest management practices [39,40].

Some research has also focused on the impact of various factors, primarily management, on the floristic composition and biodiversity of pedunculate oak forests [41]. The results indicate a significant impact of management methods and cutting intensity on the floristic composition and structure of these forest communities. However, there is a lack of research on the impact of shelterwood cutting on the floristic composition of pedunculate oak forests.

Despite the broad influence of microclimate on the responses of forest ecosystems to global changes, our knowledge of microclimatic changes and impacts on individual members of the forest ecosystem, and of how microclimate shapes biotic responses to global changes, remains insufficient [42]. This is one of the reasons why this research on the impact of shelterwood cutting on microclimatic and microbiological changes in the forest ecosystem was conducted.

Sustainable management of pedunculate oak forests is essential for preserving their ecological stability, biodiversity, and economic value while maintaining the ecosystem services they provide, including carbon sequestration, nutrient cycling, water regulation, and habitat provision, as emphasized by Pan et al. [43]. Successful management requires a comprehensive understanding of forest ecology, particularly the interactions among stand microclimate, microbial processes, soil chemistry, and floristic composition. Changes in temperature, humidity, light availability, and hydrological conditions can affect tree vitality, natural regeneration, and soil functioning, while changes in soil properties and plant communities reflect habitat quality and ecosystem resilience. As highlighted by Bardgett and van der Putten [30], belowground biological processes are fundamental to ecosystem functioning and adaptive capacity. Therefore, monitoring these interconnected indicators enables timely adjustment of management interventions and supports resilience-based

management, climate change adaptation, and the long-term sustainability and restoration of pedunculate oak forests.

The aim of the research is to determine floristic composition changes in the regeneration phase in relation to the forest phase and their connection with microclimatic, microbiological and chemical changes.

We hypothesized that the regeneration phase, characterized by greater canopy openness and increased light availability, would exhibit higher plant species richness and a different floristic composition than the forest phase. We further hypothesized that these differences in vegetation would be associated with corresponding changes in microclimatic conditions and in the chemical and biological properties of the soil, reflecting shifts in ecosystem functioning during forest regeneration.

2. Materials and Methods

2.1. Research Area

The research was conducted in the Spačva forest complex (Figure 1), the largest contiguous pedunculate oak (*Quercus robur* L.) forest complex in Europe, covering approximately 51,000 ha across the border region of Croatia and Serbia. The area extends along the basins of the Spačva and Studva rivers and comprises two main pedunculate oak habitat types: forests on micro-elevations outside the active flood zone and forests on lower terrain periodically influenced by floodwaters. On elevated sites, pedunculate oak forms the association *Carpino betuli–Quercetum roboris* (Anić 1959) Rauš 1971, whereas flood-prone sites are characterized by the association *Genisto elatae–Quercetum roboris* Horvat 1938.

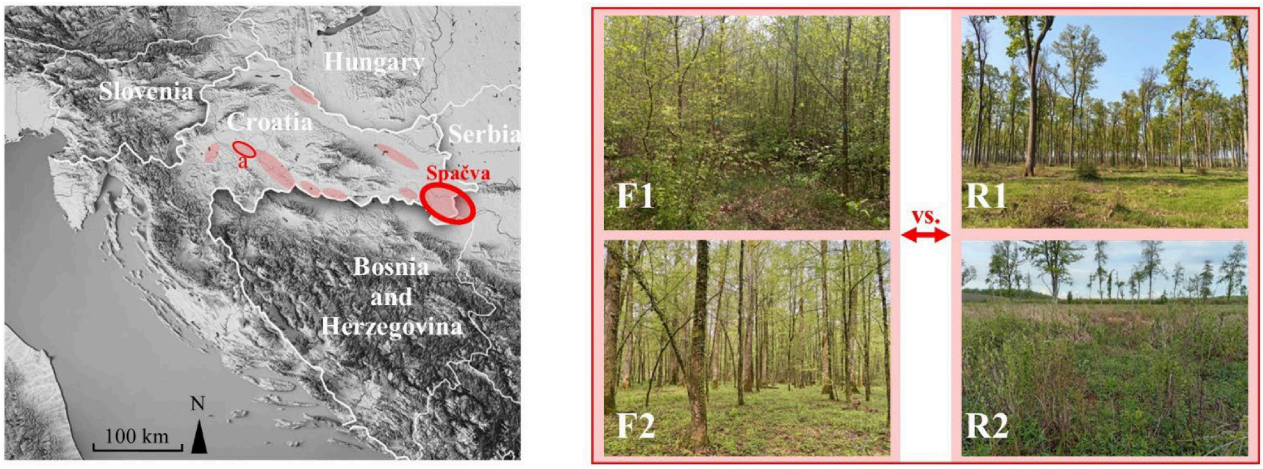

Figure 1. Pedunculate oak forests in Croatia with Spačva as research area—Forest Phase: F1 (n = 5; 14 years old), F2 (n = 5; 131 years old); Regeneration Phase: R1 (n = 5; 152 years old before cutting, with a cutting intensity of 43.66%), R2 (n = 5; 4 years old, with a cutting intensity of 51.21%). Areas colored in light red represent larger contiguous pedunculate oak forest complexes in Croatia. Encircled areas represent research area, Spačva as research area covered in this paper, and ongoing research at western part of the range in Croatia (Turopolje area) marked as "a". Photos were taken by K.P. in June 2022.

The study was conducted exclusively in the *Carpino betuli–Quercetum roboris* community located outside the active flood zone. Although these stands are not directly inundated, the soils become seasonally water-saturated during wetter periods due to groundwater fluctuations and restricted drainage. The soils are developed on Quaternary alluvial deposits and are dominated by Stagnosols, with locally occurring Luvisols, exhibiting slightly acidic to neutral reaction. The stands occur on fresh, drained micro-elevations and ridges that provide more favorable aeration conditions than the surrounding depressions.

The experimental design included stands representing different developmental stages and shelterwood regeneration phases. The forest phase consisted of young (14-year-old) and mature (131-year-old) stands with closed canopies, whereas the regeneration phase included stands after seed cutting (152 years old; 43.66% cutting intensity) and final cutting (4 years old; 51.21% cutting intensity), representing substantially more open canopy conditions. These contrasting stand structures created a gradient of light availability and associated environmental conditions that enabled the assessment of changes in vegetation, soil chemistry, and microbiological properties.

Common hornbeam (*Carpinus betulus*) is a characteristic indicator species of sites with fluctuating groundwater levels, as it tolerates short-term flooding but is sensitive to prolonged waterlogging and persistently high groundwater tables. In addition to pedunculate oak, the tree layer is composed primarily of common hornbeam, field maple (*Acer campestre*), small-leaved lime (*Tilia cordata*), and wild cherry (*Prunus avium*). The shrub layer is relatively species-poor and is dominated by taxa such as *Corylus avellana*, *Cornus sanguinea*, *Euonymus europaeus*, and *Crataegus* spp.

The herb layer reflects the mesic conditions of the oak–hornbeam community and is dominated by shade-tolerant mesophilous forest species, accompanied by hygrophilous plants associated with temporarily moist microsites. Together, these floristic elements indicate the transitional ecological conditions of the habitat, characterized by well-drained micro-elevations with seasonal soil water saturation. The pedunculate oak–common hornbeam forest represents the terminal successional stage of lowland forest vegetation in the region, having developed naturally from the wetter *Genisto elatae–Quercetum roboris* community.

Hydromelioration measures, including drainage and flood protection, have accelerated successional processes in the Spačva forest complex by reducing the frequency and duration of flooding and altering the natural water regime. Previous studies have documented a long-term decline in habitat moisture and a gradual shift in vegetation composition towards more mesophilous forest communities in this region [6,7]. Consequently, the pedunculate oak–common hornbeam community has expanded in areas with suitable site conditions and is currently considered one of the dominant forest types on relatively drier micro-elevations within the Spačva basin.

The study area has a temperate continental climate characterized by pronounced seasonal variability in both temperature and precipitation. Climate characteristics were derived from long-term meteorological records obtained from the Croatian Meteorological and Hydrological Service (DHMZ) [44]. The mean annual air temperature is 11.8 °C, with mean monthly temperatures ranging from 0.6 °C in January to 22.2 °C in July. The mean annual precipitation is approximately 665 mm, with lower monthly precipitation during winter and a maximum in late spring and early summer, reaching an average of 84.6 mm in June. This seasonal climatic pattern results in periodic fluctuations in soil moisture and groundwater availability, which strongly influence natural regeneration processes and understory vegetation dynamics in pedunculate oak forests. The main soil characteristics of the study plots are presented in Table 1.

The experiment was established in four pedunculate oak stands representing the same habitat type but different developmental and management phases (Table 1). Two stands belonged to the forest phase (F1 and F2), whereas two represented the regeneration phase (R1 and R2). The forest phase included a young stand (F1, 14 years old) and a mature stand immediately preceding regeneration (F2, 131 years old), thereby covering the range of stand development from the youngest to the oldest forest stage. The regeneration phase comprised a stand subjected to seed cutting (R1, 152 years old before cutting, with a cutting intensity of 43.66%) and a stand following final cutting (R2, 4 years old, with a cutting intensity of 51.21%) (Figure 1).

Table 1. Site description.

	Forest Phase		Regeneration Phase	
	F1 (n = 5)	**F2 (n = 5)**	**R1 (n = 5)**	**R2 (n = 5)**
Coordinate (long.)	16.798°	19.023°	18.911°	19.018°
Coordinate (lat.)	45.106°	45.020°	45.063°	45.012°
Altitude (m)	80–81	80–81	82–84	79–81
Soil type	Stagnosol	Stagnosol	Stagnosol	Stagnosol
Age (years)	14	131	152	4
Average tree diameter (cm)	15	59	61	1–5
Average tree height (m)	12	38	35	0.6–0.7
Cut intensity (%)	0.00	0.00	43.66	51.21
Density (N ha^{-1})	4500	354	256	64,915
Basal Area (m^2 ha^{-1})	10.00	32.43	28.19	26.87
Volume (m^3 ha^{-1})	50	525	459	405
Pedunculate oak (%)	40.00	64.81	69.81	56.83
Hornbeam (%)	55.00	29.12	3.19	29.84
Narrow leaved-ash (%)	5.00	4.21	25.60	11.15

Each stand covered a relatively large area (29.19–56.02 ha), allowing the establishment of five spatially separated sampling plots. The plots were positioned approximately 200 m apart to capture within-stand variability while reducing spatial autocorrelation. Vegetation surveys, microclimatic measurements, and soil sampling were conducted at all plots using an identical sampling protocol, ensuring methodological consistency and comparability among developmental stages.

2.2. Phytocenological Data

Phytocoenological surveys were conducted in July 2022 in both regeneration sites and forest stands. A total of 20 relevés were recorded, comprising five relevés within each of the four study stands. At each stand, one central plot was established and four additional plots were positioned approximately 200 m apart to ensure representative spatial coverage. In total, 10 relevés represented the regeneration phase and 10 represented the forest phase.

Vegetation was surveyed using the Central European phytocoenological method [45] on 20 × 20 m (400 m^2) plots. The cover and abundance of the tree (A), shrub (B), and herb (C) layers were estimated using the seven-grade Braun–Blanquet scale (r–5), and all relevés were stored in the TURBOVEG database [46]. Shannon's diversity index (H′) and Simpson's diversity index (1 − D) were calculated using PAST version 4.03 based on the recorded plant species data from the phytosociological relevés [47]. The Braun–Blanquet values were used for vegetation classification and the calculation of species fidelity (phi coefficient) in JUICE 7.0. For subsequent statistical analyses Braun-Blanquet grades r and + (coverage less than 1%) were transformed to 1, grade 1 to 2, grade 2 to 3, grade 3 to 4, grade 4 to 5, and grade 5 to 6 (Table S1). Surveys were conducted during a single growing season, when the majority of vascular plant species were fully developed and readily identifiable, providing a representative snapshot of the vegetation composition at the study sites. In order to determine the changes in the floristic composition of the regeneration phase in relation to forest stands, the JUICE 7.0 program [48] was used. Based on the fidelity index, the differential plant species of regeneration phase and forest stands were determined. The nomenclature and affiliation of taxa follows the internet database Euro + Med PlantBase [49], and habitat and socociology follow FloraVeg.EU database [50]. Although the vegetation survey was conducted during a single sampling campaign, the timing coincided with peak vegetation development, maximizing species detectability. Nevertheless, future studies

incorporating repeated seasonal surveys could provide additional insights into temporal variation in understory composition.

2.3. Microclimatic, Chemical and Microbiological Measurements

Microclimatic monitoring was conducted at each study stand using Spectrum WatchDog 2800 meteorological stations (Spectrum Technologies, Inc., Aurora, IL, USA). Air temperature (°C), solar radiation (W m^{-2}), soil temperature (°C), and volumetric soil moisture (%) were recorded. Air temperature sensors were installed at a height of 1.5 m above the ground surface, whereas soil temperature and moisture sensors were positioned at a depth of 10 cm. Volumetric soil moisture was measured using ECHO-25 probes (Spectrum Technologies, Inc., Aurora, IL, USA).

Measurements were recorded automatically at hourly intervals from March 2021 to March 2023. The monitoring equipment was installed and maintained according to the manufacturer's recommendations, and recorded values were routinely checked for consistency and obvious measurement errors before analysis. For statistical analyses, hourly observations were aggregated to representative values for each sampling plot and subsequently used to compare the regeneration and forest phases. Occasional missing records due to technical interruptions represented a negligible proportion of the dataset and were excluded from the analyses without imputation.

Composite soil samples were collected at each site in five replicates from a depth of 0–10 cm using a soil probe. Soil reaction was determined by measuring pH values in aqueous suspension and in 0.01 mol dm^{-3} $CaCl_2$ solution, in accordance with ISO 10390 (2005) [51]. Total carbon and total nitrogen were determined by dry combustion using an NC Soil Flash 112 analyzer (Thermo Scientific, Waltham, MA, USA), following ISO 10694 (1995) [52] and ISO 13878 (1998) [53], respectively.

The concentrations of macro- and microelements were determined by inductively coupled plasma atomic emission spectrometry (ICP-AES) after Mehlich-3 extraction [54]. Before analysis, the instrument was adjusted to stable operating conditions and externally calibrated using a series of standard solutions prepared by dilution of a certified commercial multielement standard. Laboratory quality assurance included the use of calibration blanks, reagent blanks, repeated measurements of selected samples, and regular verification of calibration stability during analytical runs. These procedures were applied to ensure analytical reliability and consistency of the soil chemical data.

Microbiological analyses included the determination of total bacterial abundance using the serial dilution method [55], fungal abundance according to Waksman [56], cellulolytic bacteria and fungi following the procedures described in the *Manual for Soil and Water Testing* [57], and ammonifying microorganisms using the Most Probable Number (MPN) technique on microtiter plates [58]. Dehydrogenase activity was determined using the triphenyltetrazolium chloride (TTC) reduction method [59].

All microbiological determinations were performed according to the protocols described in the cited references, including the recommended culture media, incubation conditions, and quantification procedures for each microbial group. Analyses were carried out in five replicate composite soil samples collected from each study stand, and microbial abundances were expressed according to the units specified for each analytical method.

2.4. Statistical Data Processing

Descriptive statistics (mean, standard deviation and 95% confidence interval) were performed for all microclimatic, pedological, chemical and biological soil variables. In order to determine the habitat differences (univariate) between the regeneration phase and the forest. The sampling plots were treated as independent observational units because

they were spatially separated within large forest stands and established to capture local environmental variability under the same management phase. The difference between microclimatic, pedological, chemical and biological soil properties was tested with Student's *t*-test and if the condition of homogeneity of variance was not met, a Satterthwaite correction was performed. To determine parameters that cause the appearance of 12 species diagnostic for the regeneration phase, a correlation (Spearman rank) of species presence and measured variables was made, but only with parameters statistically significant at a significant level of 5% as well as for "marginal" ($p < 0.065$: C total and C organic) in distinguishing the regeneration and forest phase (Student's *t*-test). For the graphic representation of the correlations of species and selected parameters (variables) as well as the tested plots, we used a biplot based on PCA analysis. All statistical analyses were performed in the SAS9.4 statistical package [60].

3. Results

Shelterwood cutting during the regeneration phase resulted in marked changes in habitat conditions and, consequently, in floristic composition. The synoptic table summarizes the plant species recorded across the 20 phytocoenological relevés (Table 2), together with their frequencies in the regeneration and forest phases and their fidelity indices. The most pronounced difference between the two phases was observed in species richness. A total of 84 plant species were recorded in the regeneration phase (mean = 32 species per relevé), whereas only 44 species were recorded in the forest phase (mean = 19 species per relevé), indicating a substantially richer ground vegetation following canopy opening. In addition to the increase in species richness, several species exhibited high fidelity to the regeneration phase, reflecting compositional shifts associated with shelterwood cutting.

Table 2. Synoptic table with percentage frequency and modified *fidelity* index phi coefficient for regeneration and forest phase. Layers: A—tree layer; B—shrub layer; C—herb layer (first species of each layer within individual sociological category is marked) Dash (-) represent that there is no value.

		Regeneration Phase (10 Relevés)		**Forest Phase (10 Relevés)**	
		Frequency (%)	**Fidelity Index**	**Frequency (%)**	**Fidelity Index**
Alnion incanae					
Quercus robur	(A)	50	-	60	-
Fraxinus angustifolia		10	-	10	-
Ulmus minor		-	-	10	-
Ulmus minor	(B)	50	-	80	-
Fraxinus angustifolia		50	-	50	-
Quercus robur		50	-	40	-
Populus alba		50	-	-	-
Genista tinctoria		10	-	-	-
Ulmus laevis		10	-	-	-
Rumex sanguineus	(C)	100	-	50	-
Rubus caesius		80	-	70	-
Carex remota		50	-	70	-
Quercus robur		60	65.5	-	-
Glechoma hederacea		10	-	30	-
Carex strigosa		10	-	-	-
Cerastium sylvaticum		-	-	20	-
Dryopteris carthusiana		-	-	10	-

Table 2. *Cont.*

		Regeneration Phase (10 Relevés)		Forest Phase (10 Relevés)	
		Frequency (%)	Fidelity Index	Frequency (%)	Fidelity Index
Carpino-Fagetea sylvaticae					
Carpinus betulus	(A)	30	-	60	-
Pyrus pyraster		10	-	-	-
Acer campestre		-	-	30	-
Carpinus betulus	(B)	100	-	70	-
Acer campestre		90	-	90	-
Pyrus pyraster		10	-	10	-
Carex sylvatica	(C)	50	-	100	-
Brachypodium sylvaticum		50	-	60	-
Circaea lutetiana		40	-	70	-
Scrophularia nodosa		50	-	-	-
Euphorbia amygdaloides		20	-	-	-
Carex digitata		10	-	-	-
Carpinus betulus		10	-	-	-
Hedera helix		-	-	50	-
Viola reichenbachiana		-	-	50	-
Athyrium filix-femina		-	-	40	-
Geranium robertianum		-	-	30	-
Vinca minor		-	-	20	-
Arum maculatum		-	-	20	-
Galium odoratum		-	-	10	-
Galeobdolon luteum		-	-	10	-
Mycelis muralis		-	-	10	-
Stachys sylvatica		-	-	10	-
Alnetea gltinosae					
Frangula alnus	(B)	10	-	-	-
Salix cinerea		50	-	10	-
Solanum dulcamara	(C)	90	90.5	-	-
Quercetalia pubescentis					
Quercus cerris	(A)	1	-	-	-
Acer tataricum	(B)	90	61.2	30	-
Quercus cerris		10	-	-	-
Acer tataricum	(C)	-	-	30	-
Ruscus aculeatus		-	-	10	-
Crataego-Prunetea					
Crataegus laevigata	(A)	10	-	10	-
Crataegus monogyna		-	-	10	-
Crataegus monogyna	(B)	60	-	80	-
Crataegus laevigata		40	-	80	-
Cornus sanguinea		80	-	50	-
Euonymus europaeus		20	-	40	-
Rosa canina agg.		20	-	30	-
Rubus hirtus	(C)	-	-	40	-
Euonymus europaeus		-	-	30	-

Table 2. *Cont.*

		Regeneration Phase (10 Relevés)		Forest Phase (10 Relevés)	
		Frequency (%)	Fidelity Index	Frequency (%)	Fidelity Index
Molinio-Arrhenatheretea					
Cirsium palustre	(C)	80	81.6	-	-
Poa trivialis		80	81.6	-	-
Ajuga reptans		10	-	30	-
Lysimachia nummularia		-	-	30	-
Lythrum salicaria		50	-	-	-
Juncus effusus		40	-	-	-
Plantago major		40	-	-	-
Prunella vulgaris		30	-	-	-
Hypericum tetrapterum		10	-	-	-
Ranunculus repens		10	-	-	-
Deschampsia cespitosa		10	-	-	-
Stachys palustris		10	-	-	-
Euphorbia palustris		40	-	-	-
Potentilla reptans		40	-	-	-
Dactylis glomerata		10	-	-	-
Artemisetea vulgaris, Epilobietea angustifolii					
Erigeron annuus	(C)	100	100.0	-	-
Epilobium angustifolium		90	90.5	-	-
Calamagrostis epigejos		90	90.5	-	-
Eupatorium cannabinum		70	73.4	-	-
Solidago gigantea		60	65.5	-	-
Galium aparine		30	-	-	-
Torilis japonica		30	-	-	-
Arctium lappa		20	-	-	-
Tussilago farfara		20	-	-	-
Cirsium vulgare		20	-	-	-
Tanacetum vulgare		10	-	-	-
Galio-Urticetea					
Geum urbanum	(C)	90	-	100	-
Urtica dioica		90	70.4	20	-
Lapsana communis		90	90.5	-	-
Torilis arvensis		20	-	-	-
Lathyrus pratensis		10	-	-	-
Veronica hederifolia		-	-	10	-
Phragmito-Magnocaricetea					
Iris pseudacorus	(C)	50	-	-	-
Galium palustre		30	-	-	-
Carex vulpina		20	-	-	-
Phragmites australis		10	-	-	-
Bidentetea					
Persicaria hydropiper	(C)	40	-	-	-
Bidens tripartita		30	-	-	-
Atriplex prostrata		30	-	-	-

Table 2. *Cont.*

		Regeneration Phase (10 Relevés)		Forest Phase (10 Relevés)	
		Frequency (%)	Fidelity Index	Frequency (%)	Fidelity Index
	Other				
Amorpha fruticosa	(A)	10	-	-	-
Populus tremula		-	-	10	-
Amorpha fruticosa	(B)	30	-	-	-
Populus tremula		30	-	-	-
Salix purpurea		20	-	-	-
Oxalis dillenii	(C)	50	-	-	-
Ambrosia artemisiifolia		50	-	-	-
Carex divulsa		40	-	10	-
Convolvulus arvensis		10	-	-	-
Amorpha fruticosa		10	-	-	-
Erigeron canadensis		10	-	-	-

The regeneration and forest phases were distinguished by 12 species with high fidelity values, all of which were associated with the regeneration phase, indicating substantial compositional changes following shelterwood cutting (Table 2). In addition, several species occurred exclusively in the regeneration phase despite having lower fidelity values, further reflecting the shift in vegetation structure.

From an ecological perspective, the regeneration phase was characterized by an increased representation of species associated with open habitats, wet forest margins, and nutrient-rich disturbed sites. Ruderal taxa belonging to the *Artemisetea vulgaris* and *Epilobietea angustifolii* classes, together with species typical of *Molinio–Arrhenatheretea* and *Bidentetea* communities, were considerably more frequent than in the forest phase. The occurrence of wetland-associated species also indicates locally wetter microsites within regeneration areas.

Many of the species recorded exclusively in the regeneration phase were invasive alien species, including *Amorpha fruticosa*, *Erigeron annuus*, *Solidago gigantea*, *Ambrosia artemisiifolia*, and *Erigeron canadensis*. Their occurrence is likely related to the increased light availability and habitat disturbance associated with shelterwood cutting, which create favorable conditions for the establishment of opportunistic species. Although these species contribute to the higher floristic richness observed during regeneration, their expansion may hinder restoration sustainability by competing with native vegetation and altering successional trajectories. Consequently, monitoring and controlling invasive species during the regeneration phase should be considered an important component of sustainable pedunculate oak forest management.

In contrast to the regeneration phase, no species exhibited a sufficiently high fidelity index to be considered diagnostic of the forest phase. Nevertheless, several species, including *Athyrium filix-femina*, *Galium odoratum*, *Hedera helix* and *Viola reichenbachiana*, occurred more frequently in forest stands. These taxa are characteristic of mesic deciduous forests within the *Carpino-Fagetea sylvaticae* class and reflect the stable environmental conditions maintained under a closed canopy. Reduced light availability, moderated microclimatic fluctuations, and the accumulation of organic matter create favorable conditions for shade-tolerant forest specialists while limiting the establishment of pioneer and disturbance-adapted species. Consequently, the forest phase supports a more homogeneous plant community that is indicative of ecological stability and advanced successional development.

A comparison of microclimatic, pedological, chemical and biological soil properties between the regeneration phase and the forest is shown in Table 3. Average air and soil temperature values did not differ significantly between the two groups ($p > 0.77$). Also, no statistically significant difference was found in soil moisture ($p = 0.3846$). In contrast to the above variables, insolation showed a highly significant difference between regeneration and forest ($p < 0.0001$), with higher values recorded in the regeneration phase.

Table 3. Descriptive statistics and results of Student's *t* test for all analyzed variables.

	Regeneration (n = 10)			Forest (n = 10)			Student's *t* Test	
	Mean	**StdDev**	**95% CI**	**Mean**	**StdDev**	**95% CI**	**t Value**	***p***
Air Temperature (°C)	11.77	4.98	8.21–15.33	11.21	4.48	8.0–14.42	0.26	0.7946
Soil Temperature (°C)	12.06	6.07	7.72–16.41	11.27	6.16	6.86–15.68	0.29	0.7756
Soil Moisture	19.96	7.60	14.53–25.40	22.98	7.53	17.59–28.37	−0.89	0.3846
Insolation	105.60	14.29	95.42–115.87	41.41	30.98	19.25–63.57	5.95 *	<0.0001
pH_{H2O}	6.17	0.26	5.99–6.36	6.46	0.51	6.09–6.82	−1.59 *	0.1346
pH_{CaCl}	5.35	0.31	5.13–5.57	5.69	0.57	5.29–6.11	−1.69	0.1086
N_{tot} (%)	0.22	0.04	0.20–0.25	0.28	0.12	0.19–0.36	−1.40 *	0.1890
C_{org} (%)	2.87	0.41	2.58–3.17	3.78	1.35	2.82–4.76	−2.05 *	0.0659
$C_{org}N$	12.93	1.39	2.58–3.17	13.92	1.66	12.73–15.12	−1.45	0.1647
B (mg/kg)	0.82	0.28	0.62–1.02	0.84	0.26	0.65–1.03	−0.18	0.8618
Ca (mg/kg)	4252.6	567.6	3846.53–4658.67	4500.9	745.4	3967.68–5034.12	−0.84	0.4130
Cu (mg/kg)	1.85	0.21	1.07–2.01	1.85	0.39	1.57–2.14	0.00	1.0000
Fe (mg/kg)	358.2	48.63	323.41–392.99	364.0	46.07	331.04–396.96	−0.27	0.7874
K (mg/kg)	131.6	28.53	111.19–152.01	181.9	36.78	155.59–208.21	−3.42	0.0031
Mg (mg/kg)	609.1	92.38	543.02–675.18	570.3	59.21	527.95–612.65	1.12	0.2782
Mn (mg/kg)	29.82	5.39	25.96–33.68	46.55	22.84	30.21–62.89	−2.25 *	0.0478
Na (mg/kg)	9.60	3.02	7.44–11.76	6.28	1.94	4.89–7.68	2.92	0.0091
P (mg/kg)	12.98	3.51	10.47–15.49	21.19	8.76	14.92–27.46	−2.75 *	0.0179
Zn (mg/kg)	3.12	0.52	2.75–3.49	4.29	0.62	3.85–4.73	−4.57	0.0002
Fungi ($\times 10^5$)	38.87	26.73	19.75–57.99	30.36	13.73	20.54–40.19	0.90	0.3862
Bacteria ($\times 10^6$)	272.3	347.5	23.70–520.89	153.3	69.59	103.51–203.08	1.06 *	0.3140
Amonificator ($\times 10^5$)	359.0	89.77	294.78–423.22	310.2	101.6	237.53–382.87	1.14	0.2699
Celulo Bakteria	47.16	16.17	35.59–58.73	51.29	18.66	37.94–64.64	−0.53	0.6034
Celulo Fungi	28.49	14.07	18.42–38.56	30.77	16.27	19.12–42.42	−0.34	0.7415
Dehydrogenase	3.09	1.67	1.90–4.29	2.63	1.51	1.55–3.71	0.66	0.5197
No. of Species	32.20	5.14	28.52–35.88	18.90	4.77	15.49–22.31	6.00	<0.0001

* Satterthwaite correction for unequal variance.

Soil reaction expressed as pH values in water and $CaCl_2$ did not differ statistically significantly between the phases ($p > 0.10$), although slightly higher mean values were recorded in the forest. Total carbon content, organic carbon and total nitrogen was higher in forest phase than in the regeneration phase, with borderline levels of statistical significance ($p \approx 0.06$–0.19). The C_{org}/N ratio did not show significant differences between phases.

Analysis of macro- and microelements indicated significantly higher concentrations of K ($p = 0.0031$), Mg ($p = 0.0478$), P ($p = 0.0179$) and Zn ($p = 0.0002$) in the forest soil, while sodium was significantly more prevalent in the regeneration ($p = 0.0091$). No significant differences were found for the other analyzed elements (Ca, Mg, Fe, Cu and B).

Figure 2 supports Table 3's findings, which show that insolation and Number of species have a strong correlation and higher average values in the regeneration plots. While the other chosen elements K, Mn, P, and Zn have higher average values in forest plots in addition to having a positive correlation with one another, sodium likewise has a higher average value in favor of regeneration plots. Figure 2 demonstrates the strong correlation between K and P, as well as Mn and Zn. No. of species and insolation had a negative correlation with every variable that was selected, with the exception of Na.

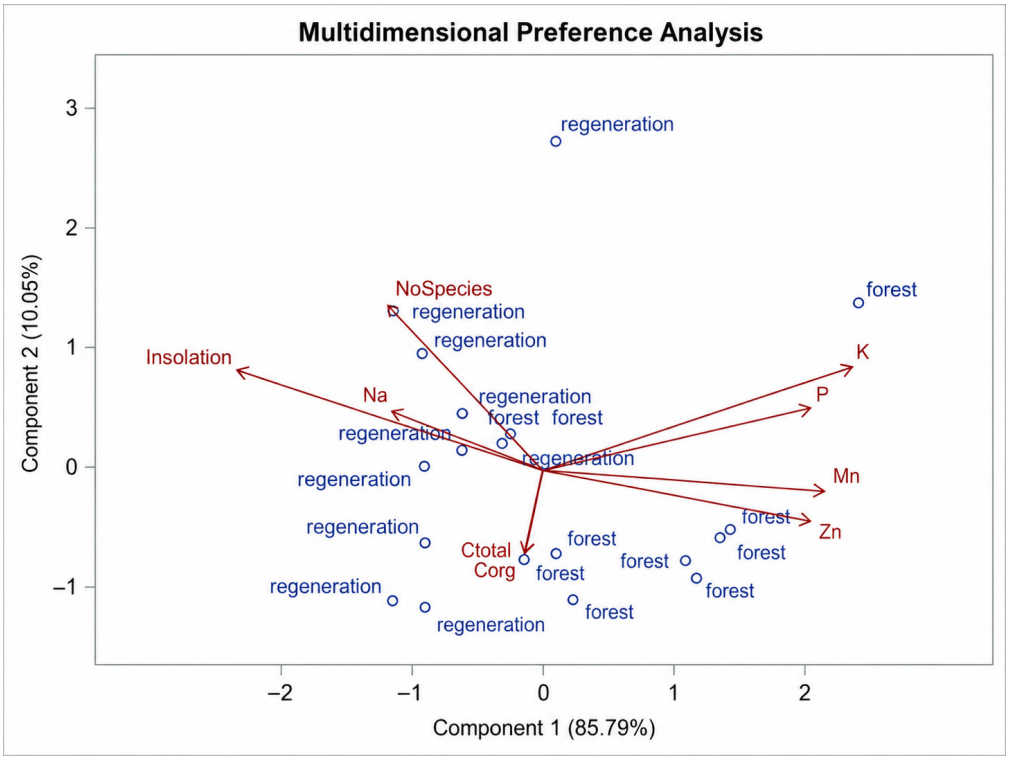

Figure 2. The biplot showing the performance of variables that distinguish forest from regeneration and analyzed plots.

Spearman correlation coefficients (Figure 3) indicate several statistically significant ($r > 0.63$) and ecologically relevant relationships between the analyzed variables ($p < 0.05$).

Insolation shows a statistically significant negative correlation with the species *Erigeron annuus* ($r = -0.64$; $p = 0.048$) and v3 ($r = -0.65$; $p = 0.039$), while *Quercus robur* seedlings and *Acer tataricum* (shrub layer) also show a negative correlation that is not statistically significant, indicating a decrease in these variables with increasing light availability. The negative sign suggests an association with more closed, shady conditions.

A significant positive correlation was observed between *Quercus robur* seedlings and Mn ($r = 0.64$; $p = 0.043$), while it is strongly negatively correlated with the Number of species ($r = -0.79$; $p = 0.006$).

Species *Calamagrostis epigejos* shows a significant negative correlation with manganese ($r = -0.64$; $p = 0.043$) and a very strong positive correlation with the Number of species ($r = 0.77$; $p = 0.006$). A similar pattern is observed for *Epilobium angustifolium*, which is negatively correlated with Mn ($r = -0.68$; $p = 0.030$) and strongly positively with the number of species ($r = 0.84$; $p = 0.001$).

Species *Solidago gigantea* shows a strong negative correlation with Mn ($r = -0.71$; $p = 0.018$) and a very strong positive correlation with the Number of species ($r = 0.86$; $p < 0.001$).

Species *Lapsana communis* shows a significant negative correlation with phosphorus ($r = -0.65$; $p = 0.041$) while the correlation with Zn is borderline significant ($r = -0.62$; $p = 0.054$) and K ($r = -0.60$; $p = 0.069$).

With the corresponding plots, Figure 4 validates the findings from Figure 3. Strong connections between the Number of species and v6, v8, v11, and v12 are evident (Figures 3 and 4). This suggests that these species exist in abundance with other species, whereas v1, v3, v4, and v10 appear when there are few other species (highly negative correlation).

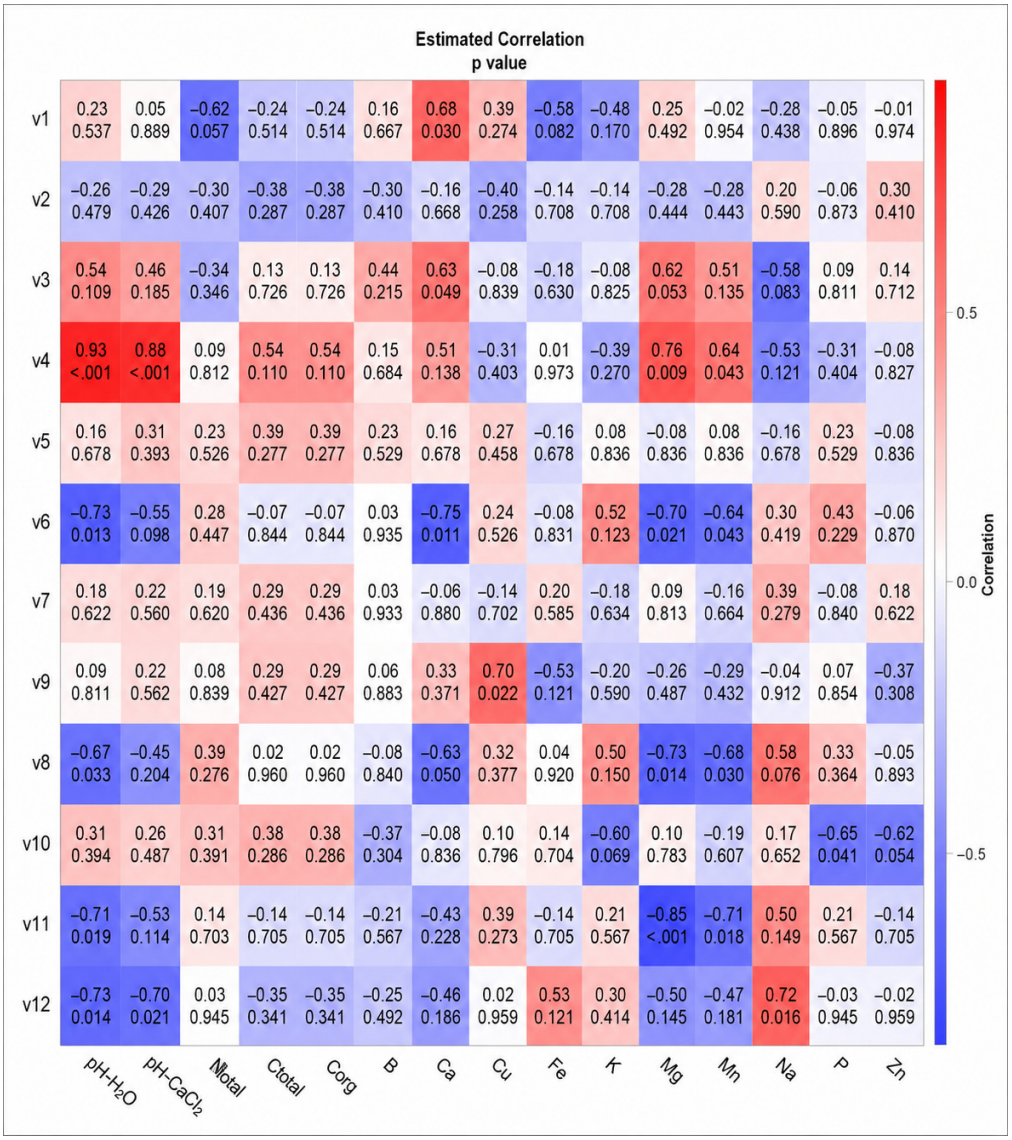

Figure 3. Heatmap for estimated Spearman rank correlation—analyzed species and variables for regeneration phase. Species designation: v1—*Erigeron annuus*, v2—*Urtica dioica*, v3—*Solanum dulcamara*, v4—*Quercus robur* (seedlings), v5—*Acer tataricum* (shrub layer), v6—*Calamagrostis epigejos*, v7—*Cirsium palustre*, v8—*Epilobium angustifolium*, v9—*Eupatorium cannabinum*, v10—*Lapsana communis*, v11—*Solidago gigantea*, v12—*Poa trivialis*.

The positive strong correlations were between Number of species and *Solidago gigantea* (r = 0.86), *Epilobium angustifolium* (r = 0.84), *Calamagrostis epigejos* (r = 0.77) and *Poa trivialis* (r = 0.56; p = 0.092) which indicates the occurrence of those species but also indicates the occurrence of a large number of other species. Also, positive and strong (statistically significant) correlations were between *Quercus robur* seedling and Mn (r = 0.644), which may indicate the importance of this element for some physiological characteristics of the plant species and its regeneration.

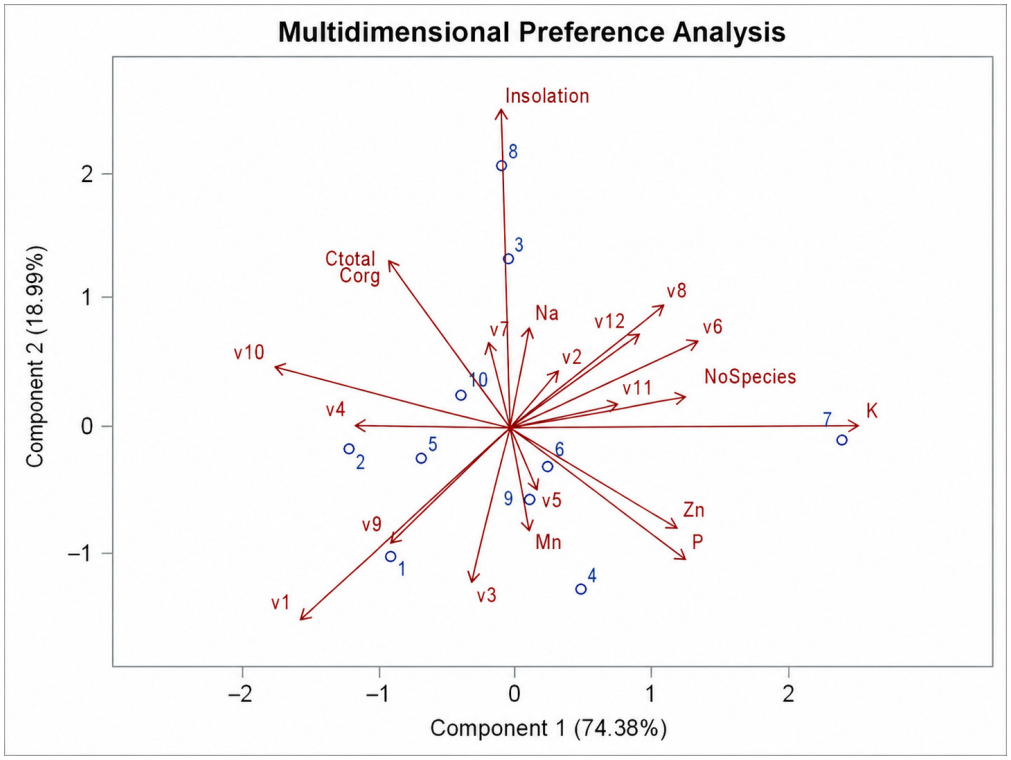

Figure 4. The biplot showing the performance of variables that distinguish forest from regeneration, selected species in regeneration phase and regeneration plots. Species designation: v1—*Erigeron annuus*, v2—*Urtica dioica*, v3—*Solanum dulcamara*, v4—*Quercus robur* (seedlings), v5—*Acer tataricum* (shrub layer), v6—*Calamagrostis epigejos*, v7—*Cirsium palustre*, v8—*Epilobium angustifolium*, v9—*Eupatorium cannabinum*, v10—*Lapsana communis*, v11—*Solidago gigantea*, v12—*Poa trivialis*.

The strongest (statistically significant) negative correlations were between *Quercus robur* seedlings and Number of species (r = −0.79). *Quercus robur* seedlings appear when there are not many other species, it is possible that they represent a stressor or competitive factor in the ecosystem. Similarly, the negative relationships between *Erigeron annuus*, *Solanum dulcamara*, *Lapsana communis* and the Number of species are not statistically significant. There was also a strong negative correlation between Mn and *Solidago gigantea* (r = −0.71), *Epilobium angustifolium* (r = −0.68), and *Calamagrostis epigejos* (r = −0.64). The negative correlation between Mn and these variables may suggest an inhibitory effect of manganese on certain characteristics of plant cover or soil microbial composition. There were also negative statistically significant correlations between *Lapsana communis* and Zn (r = −0.62). For the chosen variables, Figure 4 makes it abundantly evident that v6 and v8 have nearly identical correlation profiles.

The results of the biodiversity analysis show that the regeneration phase (Regeneration) is floristically richer and more diverse compared to the mature forest phase (Forest). A total of 85 plant taxa were recorded in the regeneration phase, while 50 taxa were recorded in the forest phase, indicating a significantly higher species richness in the regeneration stands. The Shannon diversity index (H′) is also higher in the regeneration phase (4.182) than in the forest phase (3.668), indicating a higher overall diversity and more even distribution of species. Similarly, the Simpson diversity index (1 − D) has very high values in both phases but is slightly higher in regeneration (0.9820) than in the forest (0.9701), confirming greater diversity and lower dominance of individual species in the regeneration stands. Overall, the results obtained show that the regeneration phase represents a habitat with greater floristic richness and a higher level of plant diversity compared to the developed forest phase.

4. Discussion

The absence of statistically significant differences in air temperature, soil temperature, and soil moisture between the regeneration and forest phases indicates relatively stable microclimatic conditions at ground level despite differences in vegetation structure. Similar results have been reported in other studies showing that microclimatic differences between open and closed canopy stands are attenuated near the ground surface, particularly in temperate forest ecosystems [10,61]. This buffering capacity of forest vegetation is increasingly recognized as an important mechanism for reducing climatic extremes and enhancing ecosystem resilience under changing environmental conditions [42].

In contrast, the significantly higher insolation observed in regeneration stands confirms the expected effect of a more open canopy structure. Numerous studies have identified light availability as one of the principal factors distinguishing early successional stages from mature forest stands [62,63]. Increased insolation following shelterwood cutting promotes changes in understory vegetation and facilitates natural regeneration, while the retention of partial canopy cover may still preserve important microclimatic buffering functions that contribute to restoration success and long-term ecosystem stability [20]. Increased light availability in regeneration directly affects the composition and structure of the plant cover and indirectly on pedological and biological processes.

Higher values of total and organic carbon and total nitrogen in forest soils are consistent with well-established patterns of organic matter accumulation during forest succession. Mature forest ecosystems receive continuous inputs of leaf litter and woody debris, while relatively slower decomposition promotes the accumulation of soil organic carbon and nitrogen pools [64,65]. Although the differences were not statistically significant in this study, the observed trends suggest progressive improvement in soil chemical properties with forest stand development.

Beyond their role as indicators of soil fertility, increased soil organic carbon stocks contribute to important ecosystem services, including carbon sequestration, nutrient retention, and the maintenance of soil structure and productivity. From the perspective of restoration ecology and sustainable forest management, preserving or enhancing soil organic matter may therefore strengthen ecosystem resilience and support the long-term capacity of pedunculate oak forests to mitigate climate change and sustain ecological functioning [66–68].

Significantly higher concentrations of K, P, Mn and Zn in forests confirm the role of organic matter and microbial activity in retaining and cycling nutrients. According to Attiwill and Adams [69], forest ecosystems allow more efficient internal nutrient cycling, with reduced losses through leaching. P and trace elements such as Zn and Mg are often strongly associated with the organic fraction of the soil, which explains their higher concentrations in forest soils [70,71]. Higher Na concentrations in regeneration may be a consequence of weaker biological binding and greater exposure to abiotic processes in more open habitats [72].

The absence of significant differences in microbiological indicators and enzymatic activity suggests that soil microbial communities remained relatively stable despite changes in vegetation cover. Similar results have been reported by other authors, who emphasize that total microbial biomass often shows greater resistance to changes in vegetation structure than to variations in substrate quality or moisture availability [73,74]. Such stability is consistent with the concepts of microbial resistance and resilience, whereby soil microbial communities are able to maintain or rapidly recover their functional capacity following moderate environmental disturbances [75].

Furthermore, the relatively uniform dehydrogenase activity and abundance of functional microbial groups observed in both regeneration and mature forest stands may reflect

a degree of functional redundancy within the soil microbiome. In this context, different microbial taxa can perform similar ecological functions, allowing key processes such as organic matter decomposition and nutrient cycling to be maintained despite shifts in community composition [76]. These findings suggest that shelterwood cutting, under the conditions studied, does not substantially impair the functional integrity of soil microbial communities.

Increased light availability and greater spatial heterogeneity following canopy opening create conditions that support the coexistence of a larger number of plant species, whereas mature forest stands with a closed canopy are typically dominated by a smaller set of shade-tolerant taxa [77,78]. This pattern is consistent with ecological theories of succession, in which early and intermediate successional stages provide a greater diversity of ecological niches before competitive exclusion becomes more pronounced in later stages. It is also broadly compatible with the Intermediate Disturbance Hypothesis, which predicts that moderate disturbance can promote species richness by preventing competitive dominance and increasing habitat heterogeneity.

The results of the correlation analysis further indicate that light availability represents an important ecological gradient associated with both floristic composition and soil properties. The negative association between insolation and variables related to soil organic matter is consistent with greater carbon accumulation in more closed-canopy stands, reflecting the progressive build-up of litter and organic material during forest succession [64,65]. Together, these findings suggest that shelterwood cutting creates transient environmental conditions that enhance plant diversity while maintaining ecological processes characteristic of sustainable forest regeneration.

Strong negative correlations between manganese (Mn) concentrations and several variables positively associated with species richness indicate that elevated Mn levels were associated with differences in floristic composition. However, these relationships should be interpreted with caution, as the observational design of the study does not permit causal inference. The observed associations may reflect the influence of underlying environmental gradients or interactions among multiple soil properties rather than a direct effect of Mn on plant diversity. Although high Mn concentrations have been reported to exert toxic effects under certain conditions, particularly in acidic soils (Kabata-Pendias [71]), the present results should be regarded as evidence of correlation rather than proof of a limiting effect on floristic diversity.

Extremely strong positive correlations between *Artemisetea vulgaris* and *Epilobietea angustifolii* species (*Calamagrostis epigejos*, *Epilobium angustifolium*, *Solidago gigantea*) and species abundance further confirm that more open habitats (open-compositions) with more favorable soil chemistry support greater biodiversity. Such relationships fit well with succession theory, according to which early and middle successional stages allow for the coexistence of a greater number of species [79,80].

The negative association between phosphorus (P) and several plant species may reflect differences in nutrient availability and cycling between regeneration and mature forest stands, where closed-canopy systems are generally characterized by more efficient internal nutrient retention [69]. Overall, the correlation analysis supports the results of the univariate and multivariate analyses, highlighting consistent associations among light availability, soil chemical properties, and floristic composition that differentiate the regeneration and forest phases.

Manganese (Mn) concentrations were negatively associated with the occurrence of *Calamagrostis epigejos*, *Epilobium angustifolium* and *Solidago gigantea*, whereas sodium (Na) showed positive associations with *Cirsium palustre*, *Epilobium angustifolium* and *Lapsana communis*. Similarly, organic carbon (Corg) were moderately positively associ-

ated with *Acer tataricum* and *Lapsana communis*. These relationships should be interpreted as statistical associations reflecting co-variation among vegetation and environmental variables rather than as evidence of direct ecological mechanisms or causal effects. Additional experimental studies would be required to determine the processes underlying these observed patterns.

Dobrowolska et al. [31] investigated the relationships between stand characteristics, plant species composition, soil enzyme activity, and oak regeneration in stands dominated by Scots pine. According to their research results, one of the most influential factors affecting the number of oak plants was dehydrogenase activity in the humus horizon. According to our research results, dehydrogenase activity was highest in stands with successful regeneration of pedunculate oak.

Forest trees and plants play a key role in shaping the microclimate and have the ability to establish a mosaic of microclimates within the ecosystem. An important example includes the creation of different microclimate gradients by grass species and forest canopy [81]. Namely, within a forest stand, the microclimate differs from the tree layer, the shrub layer to the ground vegetation layer. These changes can have consequences for the growth and abundance of individual plant species.

Microclimate strongly influences soil decomposition, soil biogenicity, and the floristic composition of the plant community [42]. The results of this study showed that the floristic composition differs significantly between the regeneration phase and forest stands of different ages.

Higher light intensity, temperature, and humidity in stands with intensive thinning compared to forest stands were the cause of a greater increase in the diversity of ground vegetation. This is confirmed by the results of the study by Swenson et al. [82].

In pedunculate oak forests, tree felling significantly affects microclimatic conditions, especially the availability of sunlight. The highest amount of light was recorded in stands in the regeneration phase, while forest stands with dense crowns transmitted significantly less light. This increased light availability after felling stimulates the growth of pioneer shrub species and ground vegetation, which is also confirmed by this study.

Changes in plant cover in forest ecosystems due to human activity provide insight into the dynamics of changes and help in understanding vegetation changes through different phases of shelterwood cutting. Changes in floristic composition during regeneration were clearly observed in this study. The number of species differs significantly between different stages of forest development, with the lowest number of species recorded in forest stands and the highest number in the regeneration phase. This change in floristic composition reflects the ecological adaptations of species to changed microclimatic conditions and resource availability.

Shelterwood cutting increases the proportion of pioneer and edge-associated species, while the higher heliophilous index reflects the greater light availability in the understory following canopy opening. These changes create favorable conditions for the establishment of ruderal and light-demanding species, resulting in increased floristic diversity during the regeneration phase.

At the same time, the more open stand structure is associated with increased insolation and altered microenvironmental conditions, which may facilitate the establishment of invasive alien species. Although the present study did not directly assess their long-term ecological impacts, the spread of invasive taxa may represent a potential challenge for restoration by altering competitive interactions with native vegetation and influencing successional trajectories. In some ecosystems, invasive plants have also been associated with changes in nutrient cycling and fuel characteristics, potentially affecting ecosystem functioning and disturbance regimes. These considerations highlight the importance of

monitoring invasive species during forest regeneration to ensure the long-term sustainability and resilience of pedunculate oak ecosystems.

Young individuals of pedunculate oak are present in stands in the regeneration phase, which shows that increased light in the understory is conducive to its regeneration. The entry of a large number of light-loving, ruderal and meadow species explains why the overall floristic diversity is highest precisely in the regeneration phase.

In forest stands with a homogeneous, closed canopy structure, a floristic composition typical of stable, shaded and moderately humid conditions was recorded. Permanent forest species and herbaceous species tolerant to shade dominate, as well as geophytes and hemicryptophytes whose life cycle corresponds to relatively small seasonal oscillations in light and temperature. Comparison with other studies shows similar patterns. Namely, felling increases floral diversity but also creates conditions for the spread of invasive species [83].

The increased occurrence of invasive alien species in regeneration areas illustrates a potential trade-off between enhanced species richness and ecosystem integrity. While canopy opening promotes floristic diversity, it may also increase the susceptibility of restored stands to biological invasions. Therefore, sustainable restoration should combine natural regeneration practices with regular monitoring and timely control of invasive species to maintain native biodiversity and ecosystem resilience.

The findings of this study have broader implications for sustainable forest management and climate adaptation strategies in pedunculate oak ecosystems. Shelterwood cutting created conditions that promoted natural regeneration and increased floristic diversity while maintaining relatively stable soil microbiological activity and key soil properties. Such responses suggest that, when carefully implemented, this silvicultural system can support ecosystem resilience by preserving essential ecological functions despite changes in canopy structure.

From a sustainability perspective, maintaining diverse plant communities and functional soil processes contributes to the long-term provision of ecosystem services, including nutrient cycling, soil conservation, and carbon storage. Moreover, preserving microclimatic buffering and supporting successful natural regeneration may enhance the adaptive capacity of pedunculate oak forests under increasing climatic variability. Nevertheless, the occurrence of invasive alien species in regeneration areas highlights the need for continued monitoring and adaptive management to ensure that restoration measures maintain both biodiversity and ecosystem integrity over the long term.

This study showed that shelterwood cutting in pedunculate oak forests was not associated with significant changes in the measured indicators of soil chemistry, microbiological activity, or ground-level microclimatic conditions. The observed patterns suggest that this silvicultural practice can maintain key ecological functions while promoting natural regeneration and increased floristic diversity.

However, the increased occurrence of ruderal and invasive alien species in regeneration areas indicates that canopy opening may also create opportunities for the establishment of disturbance-associated taxa. Therefore, although the overall results support the compatibility of shelterwood cutting with the principles of sustainable forest management, long-term ecosystem stability depends on continued monitoring and adaptive management to prevent undesirable shifts in vegetation composition and to preserve the ecological integrity and resilience of pedunculate oak forests.

A limitation of the present study is that the phytocoenological survey was conducted during a single sampling campaign in July 2022. Although this period corresponds to peak vegetation development and allows reliable identification of the majority of vascular plant species, repeated surveys across different seasons could capture additional temporal

variability in understory composition and further improve the assessment of vegetation dynamics during forest regeneration.

5. Conclusions

Insolation emerged as one of the principal environmental variables differentiating regeneration and forest habitats, reflecting differences in canopy openness and associated microclimatic conditions. Soil organic matter was consistently associated with successional stage and may serve as a useful indicator of habitat development. Manganese concentrations were negatively associated with several vegetation variables, although the observational nature of the study does not permit conclusions regarding causal ecological effects. Species richness was most strongly associated with the combined influence of light availability and soil chemical characteristics, with the regeneration phase supporting a more diverse plant community under the conditions investigated. Given the limited sample size and correlational design, these findings should be interpreted as indicative patterns that warrant further investigation through long-term and experimental studies.

The observed correlation patterns were generally consistent with the results obtained from the univariate and multivariate analyses, suggesting coherent relationships among vegetation characteristics, soil properties, and environmental conditions. However, given the limited sample size and observational nature of the study, these associations should be regarded as exploratory rather than confirmatory. Nevertheless, they identify potentially important ecological gradients that could be incorporated into future monitoring programs and hypothesis-driven studies aimed at improving restoration assessment and ecological modeling in pedunculate oak forests.

Soil chemical parameters, including Mn, Na, K, Zn, and soil organic components (Corg and Ctot), were associated with the occurrence of several regeneration indicator species, suggesting that variation in soil chemistry is linked to patterns of vegetation development. Although these relationships should not be interpreted as causal, they indicate that soil chemical properties may serve as useful complementary indicators of ecological change during forest regeneration. From a sustainable forest management perspective, integrating soil chemistry with floristic and microbiological assessments could improve the monitoring of restoration progress and support adaptive management aimed at maintaining soil quality, biodiversity, and long-term ecosystem functioning.

Species richness showed the strongest positive associations with *Calamagrostis epigejos*, *Epilobium angustifolium* and *Solidago gigantea*, whereas a negative association was observed with *Quercus robur* seedlings. These patterns reflect shifts in vegetation composition during the regeneration phase rather than unequivocal improvements in ecological quality. Although regeneration areas supported a greater number of plant species, these increases included ruderal and invasive taxa in addition to native species. Consequently, higher species richness should be interpreted with caution, as it does not necessarily indicate enhanced conservation value or ecosystem integrity. Instead, both species richness and community composition should be considered when evaluating restoration success and sustainable forest management.

The regeneration phase showed significantly higher species richness and higher levels of plant diversity than the forest phase, confirming that successional stages with a more open habitat structure contribute to an increase in overall floristic diversity. Maintaining a mosaic of different developmental stages of forest stands may therefore play an important role in biodiversity conservation.

Soil organic matter and essential macro/micronutrients (Mn, Na, K) have significant effects on plant/ecological variables. The integration of soil chemical, floristic, and micro-

biological indicators provide a practical framework for assessing restoration success and guiding adaptive, sustainable management of pedunculate oak forests.

Overall, our results indicate that the combined assessment of floristic composition, soil chemistry, and microbiological properties provides a valuable framework for evaluating the sustainability and climate resilience of pedunculate oak forest restoration under shelterwood management.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/su18147315/s1, Table S1: Species occurrence according to the transformed Braun-Blanquet scale.

Author Contributions: Conceptualization, I.Š. and D.U.; methodology, I.Š., D.U. and A.J.; software, I.Š. and A.J.; validation, I.Š., D.U. and A.J.; formal analysis, A.J.; investigation, K.P., D.B., D.U. and I.P. (Ivan Perković); resources, K.P.; data curation, K.P., D.U., I.Š., A.J., I.P. (Igor Poljak), D.B. and I.P. (Ivan Perković); writing—original draft preparation, D.U. and I.Š.; writing—review and editing, I.Š. and I.P. (Igor Poljak); visualization, I.Š.; supervision, D.U. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding. However, the results of this research were obtained during designing and implementation of the project "The influence of the age of pedunculate oak and common hornbeam stands (*Carpino betuli-Qurcetum roboris*/Anić 1959/Rauš 1971) on the floristic composition, microclimate, pedophysiographic and biological characteristics of the soil—ForEcoForBio". Based on these results the research is now expanded to the western part of the range in Croatia (Turopolje area), in Figure 1 marked as a. The project ForEcoForBio (https://www.croris.hr/projekti/projekt/17837 accessed on 5 May 2026) covers a large number of survey plots evenly distributed in all age classes, throughout the entire rotation and regeneration period.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The original contributions presented in this study are included in the article/Supplementary Materials. Further inquiries can be directed to the corresponding authors.

Conflicts of Interest: Krešimir Popić is employed by Croatian Forests Ltd. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

References

1. Mölder, A.; Meyer, P.; Nagel, R. Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests: An overview. *For. Ecol. Manag.* **2019**, *437*, 324–339. [CrossRef]
2. Krutovsky, K.V.; Popova, A.A.; Yakovlev, I.A.; Yanbaev, Y.A.; Matveev, S.M. Response of Pedunculate Oak (*Quercus robur* L.) to Adverse Environmental Conditions in Genetic and Dendrochronological Studies. *Plants* **2025**, *14*, 109. [CrossRef] [PubMed]
3. Hengeveld, G.M.; Nabuurs, G.J.; Didion, M. A Forest Management Map of European Forests. *Ecol. Soc.* **2017**, *17*, 53. [CrossRef]
4. Krejči, V.; Dubravac, T. Problemi obnove šuma hrasta lužnjaka (*Quercus robur* L.) vlažnog tipa tijekom oplodnih sječa. *Šumarski List* **2004**, *3–4*, 119–126.
5. Ortmann-Ajkai, A.; Lukács, M.; Horváth, F. Regeneration patterns in a pedunculate oak (*Quercus robur* L.) strict forest reserve in Southern Hungary. *Šumarski List* **2017**, *141*, 39–46. [CrossRef]
6. Škvorc, Ž.; Cestarić, D.; Franjić, J.; Krstonošić, D.; Sever, K.; Guzmić, M. Dinamika šumske vegetacije spačvanskog bazena u posljednjih četrdeset godina. In *Zbornik Skupa Šume Hrasta Lužnjaka u Promijenjenim Stanišnim i Gospodarskim Uvjetima*; Matić, S., Anić, I., Eds.; HAZU: Zagreb, Croatia, 2009; pp. 75–101.
7. Cestarić, D.; Škvorc, Ž.; Franjić, J.; Sever, K.; Krstonošić, D. Forest plant community changes in the Spačva lowland area (E Croatia). *Plant Biosyst. Int. J. Deal. All Asp. Plant Biol.* **2016**, *151*, 584–597. [CrossRef]
8. Matić, S. Oak forests (*Quercus* sp.) in Croatia. *Glas. Za Šumske Pokuse* **2000**, *37*, 5–13.
9. Čavlović, J. *Osnove Uređivanja Šuma*; Šumarski Fakultet Sveučilišta u Zagrebu: Zagreb, Croatia, 2013; 322p.

10. Ritter, E.; Dalsgaard, L.; Einhorn, S.K. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. *For. Ecol. Manag.* **2005**, *206*, 15−33. [CrossRef]
11. Ugarković, D.; Tikvić, I.; Popić, K.; Malnar, J.; Stankić, I. Microclimate and natural regeneration of forest gaps as a consequence of silver fir (*Abies alba* Mill) dieback. *Šumarski List* **2018**, *5–6*, 235–245.
12. De Frenne, P.; Zellweger, F.; Rodríguez-Sánchez, F.; Scheffers, B.R.; Hylander, K.; Luoto, M.; Vellend, M.; Verheyen, K.; Lenoir, J. Global buffering of temperatures under forest canopies. *Nat. Ecol. Evol.* **2019**, *3*, 744–749. [CrossRef] [PubMed]
13. von Arx, G.; Dobbertin, M.; Rebetez, M. Spatio-temporal effects of forest canopy on understory microclimate in a long-term experiment. *Agric. For. Meteorol.* **2012**, *166–167*, 144–155. [CrossRef]
14. Barry, R.G.; Blanken, P.D. *Microclimate and Local Climate*; Cambridge University Press: New York, NY, USA, 2016.
15. Lin, H.; Chen, Y.; Song, Q.; Fu, P.; Cleverly, J.; Magliulo, V.; Law, B.E.; Gough, C.M.; Hörtnagl, L.; Di Gennaro, F.; et al. Quantifying deforestation and forest degradation with thermal response. *Sci. Total Environ.* **2017**, *607–608*, 1286–1292. [CrossRef] [PubMed]
16. Ehbrecht, M.; Schall, P.; Ammer, C.; Seidel, D. Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. *Agric. For. Meteorol.* **2017**, *242*, 1–9. [CrossRef]
17. Decocq, G.; Aubert, M.; Dupont, F.; Alard, D.; Saguez, R.; Wattez-Franger, A.; Foucault, B.D.; Delelis-Dusollier, A.; Bardat, J. Plant diversity in a managed temperate deciduous forest: Understorey response to two silvicultural systems. *J. Appl. Ecol.* **2004**, *41*, 1065–1079. [CrossRef]
18. Tranquillini, W. *Physiological Ecology of the Alpine Timberline: Tree Existence at High Altitude with Special Reference to the European Alps*; Ecological Studeies; Springer: Berlin/Heidelberg, Germany; New York, NY, USA, 1979; 140p.
19. Denslow, J.S. Tropical rain forest gaps and tree species diversity. *Annu. Rev. Ecol. Evol. Syst.* **1987**, *18*, 431–451. [CrossRef]
20. Zellweger, F.; De Frenne, P.; Lenoir, J.; Vangansbeke, P.; Verheyen, K.; Bernhardt-Römermann, M.; Baeten, L.; Hédl, R.; Berki, I.; Brunet, J.; et al. Forest microclimate dynamics drive plant responses to warming. *Science* **2020**, *368*, 772–775. Erratum in *Science* **2020**, *368*, eabd3881. https://doi.org/10.1126/science.abd3881. [CrossRef] [PubMed]
21. Bramer, I.; Anderson, B.J.; Bennie, J.; Bladon, A.J.; De Frenne, P.; Hemming, D.; Hill, R.A.; Kearney, M.R.; Körner, C.; Korstjens, A.H.; et al. Advances in monitoring and modelling climate at ecologically relevant scales. In *Next Generation Biomonitoring: Part 1 Advances in Ecological Research*; Elsevier: Amsterdam, The Netherlands, 2018; pp. 101–161.
22. Félegyházi, L.; Horváth, C.V.; Kovács, B.; Kalicz, P.; Gribovszki, Z. Soil moisture dynamic in the regeneration gap cutting of a hornbeam-oak stand. In Proceedings of the EGU General Assembly 2023, Vienna, Austria, 24–28 April 2023; p. EGU23-13030. [CrossRef]
23. Ushio, M.; Kitayma, K.; Balser, T.C. Tree species effects on soil enzyme activities through effects on soil physicochemical and microbial properties in a tropical montane forest on Mt. Kinabalu, Borneo. *Pedobiologia* **2010**, *53*, 227–233. [CrossRef]
24. Das, S.K.; Varma, A. Role of Enzymes in Maintaining Soil Health. In *Soil Enzymology, Soil Biology*; Shukla, G., Varma, A., Eds.; Springer: Berlin/Heidelberg, Germany, 2011; pp. 25–42.
25. Redžepović, S.; Blažinkov, M.; Sikora, S.; Husnjak, S.; Čolo, J.; Bogunović, M. Enzymatic activity and microbiological characteristics of luvic and pseudogley soils in western Slavonia. *Period. Biol.* **2012**, *114*, 111–116.
26. Delgado-Baquerizo, M.; Guerra, C.A.; Cano-Díaz, C.; Egidi, E.; Wang, J.T.; Eisenhauer, N.; Singh, B.K.; Maestre, F.T. The proportion of soil-borne pathogens increases with warming at the global scale. *Nat. Clim. Change* **2020**, *10*, 550–554. [CrossRef]
27. Baldrian, P. Forest microbiome: Diversity, complexity and dynamics. *FEMS Microbiol. Rev.* **2017**, *41*, 109–130. [PubMed]
28. Khatoon, H.; Solanki, P.; Narayan, M.; Tewari, L.; Rai, J. Role of microbes in organic carbon decomposition and maintenance of soil ecosystem. *Int. J. Chem. Stud.* **2017**, *5*, 1648–1656.
29. Muscolo, A.; Settineri, G.; Attinà, E. Early warning indicators of changes in soil ecosystem functioning. *Ecol. Indic.* **2015**, *48*, 542–549. [CrossRef]
30. Bardgett, R.; van der Putten, W. Belowground biodiversity and ecosystem functioning. *Nature* **2014**, *515*, 505–511. [CrossRef] [PubMed]
31. Dobrowolska, D.; Przemysław, K.; Grażyna, O.; Bobolik, L. Effects of stand features and soil enzyme activity on spontaneous pedunculate oak regeneration in Scots pine dominated stands—Implication for forest management. *For. Ecosyst.* **2021**, *8*, 43. [CrossRef]
32. Bonan, G.B. *Ecological Climatology: Concepts and Applications*, 3rd ed.; Cambridge University Press: New York, NY, USA, 2016.
33. De Frenne, P.; Verheyen, K. Weather stations lack forest dana. *Science* **2016**, *351*, 234. [CrossRef] [PubMed]
34. Vukelić, J. *Šumska Vegetacija Hrvatske*; Sveučilište u Zagrebu, Šumarski Fakultet, Državni Zavod za Zaštitu Prirode: Zagreb, Croatia, 2012; 403p.
35. Whittaker, R.H. *Communities and Ecosystems*, 2nd Revise ed.; MacMillan Publishing Co.: New York, NY, USA, 1975.
36. Ellenberg, H.; Weber, H.E.; Düll, R.; Wirth, V.; Werner, W.; Paulißen, D. Zeigwerte von Pflanzen in MittelEuropa. *Scr. Geobot.* **1991**, *18*, 248.
37. Diekmann, M. Species indicator values as an important tool in applied plant ecology—A review. *Basic Appl. Ecol.* **2003**, *4*, 493–506. [CrossRef]

38. Lindenmayer, D.B.; Likens, G.E. *Effective Ecological Monitoring*, 1st ed.; CSIRO Publishing: Clayton, Australia, 2010. [CrossRef]
39. Lindenmayer, D.B.; Margules, C.R.; Botkin, D.B. Indicators of biodiversity for ecologically sustainable forest management. *Conserv. Biol.* **2000**, *14*, 941–950. [CrossRef]
40. Gilg, O. *Old-Growth Forests. Characteristics, Conservation and Monitoring. Habitat and Species Management;* Technical Report No. 74 bis; ATEN: Montpellier, France, 2005. Available online: https://www.researchgate.net/publication/265109043_Old-Growth_Forests (accessed on 5 May 2026).
41. Mikac, S.; Žmegač, A.; Trlin, D.; Paulić, V.; Oršanić, M.; Anić, I. Drought-induced shift in tree response to climate in floodplain forests of Southeastern Europe. *Sci. Rep.* **2018**, *8*, 16495. [CrossRef] [PubMed]
42. De Frenne, P.; Lenoir, J.; Luoto, M.; Scheffers, B.R.; Zellweger, F.; Aalto, J.; Ashcroft, M.B.; Christiansen, D.M.; Decocq, G.; De Pauw, K.; et al. Forest microclimates and climate change: Importance, drivers and future research agenda. *Glob. Change Biol.* **2021**, *27*, 2279–2297. [CrossRef] [PubMed]
43. Pan, Y.; Birdsey, R.A.; Fang, J.; Houghton, R.; Kauppi, P.E.; Kurz, W.A.; Phillips, O.L.; Shvidenko, A.; Lewis, S.L.; Canadell, J.G.; et al. A Large and Persistent Carbon Sink in the World's Forests. *Science* **2011**, *333*, 988–993. [CrossRef] [PubMed]
44. Croatian Meteorological and Hydrological Service (DHMZ). Long-Term Meteorological Records for the Study Area. Available online: https://meteo.hr/ (accessed on 6 February 2026).
45. Braun-Blanquet, J. *Pflanzensoziologie. Grundzüge der Vegetationskunde Plant Sociology. [Basic Course of Vegetation Science]*; Springer: Wien, Austria, 1964; 865p.
46. Hennekens, S.M.; Schaminée, J.H.J. TURBOVEG, a comprehensive data base management system for vegetation data. *J. Veg. Sci.* **2001**, *12*, 589–591. [CrossRef]
47. Hammer, Ø.; Harper, D.; Ryan, P. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontol. Electron.* **2001**, *4*, 9.
48. Tichý, L. JUICE, software for vegetation classification. *J. Veg. Sci.* **2002**, *13*, 451–453. [CrossRef]
49. Euro+Med, 2006-Onwards: Euro+Med PlantBase—The Information Resource for Euro-Mediterranean Plantdiversity. Available online: http://www.europlusmed.org (accessed on 1 February 2026).
50. Chytrý, M.; Řezníčková, M.; Novotný, P.; Holubová, D.; Preislerová, Z.; Attorre, F. FloraVeg.EU—An online database of European vegetation, habitats and flora. *Appl. Veg. Sci.* **2024**, *27*, e12798. [CrossRef]
51. *ISO10390*; Soil Quality—Determination of pH. ISO: Geneve, Switzerland, 1994.
52. *ISO 10694*; Soil Quality—Determination of Organic and Total Carbon After Dry Combustion (Elementary Analysis). ISO: Geneve, Switzerland, 1995.
53. *ISO 13878*; Soil Quality—Determination of Total Nitrogen Content by Dry Combustion (Elemental Analysis). ISO: Geneve, Switzerland, 1998.
54. Zhang, H.; Hardy, D.H.; Mylavarapu, R.; Wang, J.J. Soil Test Methods from the Southeastern United States. Southern Cooperative Series Bulletin No. 419. 2014. Available online: https://aesl.ces.uga.edu/sera6/PUB/MethodsManualFinalSERA6.pdf (accessed on 5 May 2026).
55. Wollum, A.G. Cultural methods for soil microorganism. In *Methods of Soil Analysis: Part 2 Chemical and Microbiological Properties*; Page, A.K., Millar, R.H., Keeney, D.R., Eds.; Agronomy Monograph No 9; ASA-SSSA Publisher: Madison, WI, USA, 1982; pp. 781–814.
56. Atlas, R.M.; Bartha, R. *Microbial Ecology: Fundamentals and Applications*, 2nd ed.; The Benjamin/Cummings Publishing Company, Inc.: Menlo Park, CA, USA, 1987.
57. Anonymous. *Priručnik za Ispitivanje Zemljišta i Voda*, 2nd ed.; JDZP: Beograd, Serbia, 1966.
58. Schmidt, J.M.; Belser, L.W. Autotrophic nitrifying bacteria. In *Methods of Soil Analysis: Part 2 Microbiological and Biochemical Properties*; Bigham, J.M., Ed.; SSSA Book Series No. 5; SSSA: Madison, WI, USA, 1994; pp. 159–177.
59. Casida, L.E., Jr.; Klein, D.A.; Santoro, R. Soil dehydrogenase activity. *Soil Sci.* **1964**, *98*, 371–378. [CrossRef]
60. SAS Institute Inc. *SAS/STAT® User's Guide*, version 9.4; SAS Institute Inc.: Cary, NC, USA, 2004.
61. Chen, J.; Franklin, J.F.; Spies, T.A. Microclimate in forest ecosystems and landscape ecology. *BioScience* **1999**, *49*, 288–297. [CrossRef]
62. Bazzaz, F.A. Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology* **1975**, *56*, 485–488. [CrossRef]
63. Nicotra, A.B.; Chazdon, R.L.; Iriarte, S.V.B. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* **1999**, *80*, 1908–1926. [CrossRef]
64. Post, W.M.; Kwon, K.C. Soil carbon sequestration and land-use change: Processes and potential. *Glob. Change Biol.* **2000**, *6*, 317–327. [CrossRef]
65. Six, J.; Conant, R.T.; Paul, E.A.; Paustian, K. Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils. *Plant Soil* **2002**, *241*, 155–176. [CrossRef]
66. Lal, R. Managing soils for negative feedback to climate change and positive impact on food and nutritional security. *Soil Sci. Plant Nutr.* **2020**, *66*, 1–9. [CrossRef]

67. Chabbi, A.; Rumpel, C.; Hagedorn, F.; Schrumpf, M.; Baveye, P.C. Carbon Storage in Agricultural and Forest Soils. *Front. Environ. Sci.* **2022**, *10*, 848572. [CrossRef]
68. Popić, K. Ekološko-Vegetacijski Odnosi u Oplodnim Sječama Sastojina Hrasta Lužnjaka i Običnog Graba (*Carpino betuli—Quercetum roboris*/Anić 1959/Rauš 1971). Ph.D. Thesis, Sveučilište u Zagrebu, Fakultet Šumarstva I Drvne Tehnologije, Zagreb, Croatia, 2025; 193p.
69. Attiwill, P.M.; Adams, M.A. Nutrient cycling in forests. *New Phytol.* **1993**, *124*, 561–582. [CrossRef] [PubMed]
70. Hinsinger, P. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: A review. *Plant Soil* **2001**, *237*, 173–195. [CrossRef]
71. Kabata-Pendias, A. *Trace Elements in Soils and Plants*, 4th ed.; CRC Press: Boca Raton, FL, USA, 2011.
72. Brady, N.C.; Weil, R.R. *The Nature and Properties of Soils*, 15th ed.; Pearson Education: New York, NY, USA, 2016.
73. Wardle, D.A. *Communities and Ecosystems: Linking the Aboveground and Belowground Components*; Princeton University Press: Princeton, NJ, USA, 2002.
74. Bardgett, R.D.; Bowman, W.D.; Kaufmann, R.; Schmidt, S.K. A temporal approach to linking aboveground and belowground ecology. *Trends Ecol. Evol.* **2005**, *20*, 634–641. [CrossRef] [PubMed]
75. Shade, A.; Peter, H.; Allison, S.D.; Baho, D.L.; Berga, M.; Bürgmann, H.; Huber, D.H.; Langenheder, S.; Lennon, J.T.; Martiny, J.B.; et al. Fundamentals of Microbial Community Resistance and Resilience. *Front. Microbiol.* **2012**, *3*, 417. [CrossRef] [PubMed]
76. Louca, S.; Polz, M.F.; Mazel, F.; Albright, M.B.N.; Huber, J.A.; O'Connor, M.I.; Ackermann, M.; Hahn, A.S.; Srivastava, D.S.; Crowe, S.A.; et al. Function and functional redundancy in microbial systems. *Nat. Ecol. Evol.* **2018**, *2*, 936–943. [CrossRef] [PubMed]
77. Tilman, D. *Resource Competition and Community Structure*; Princeton University Press: Princeton, NJ, USA, 1982.
78. Gilliam, F. *The Herbaceous Layer in Forests of Eastern North America*; Oxford University Press: Oxford, UK, 2014; pp. 1–688. [CrossRef]
79. Connell, J.H. Diversity in tropical rain forests and coral reefs. *Science* **1978**, *199*, 1302–1310. [CrossRef] [PubMed]
80. Grime, J.P. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*; Wiley: Chichester, UK, 2001.
81. Vandvik, V.; Skarpaas, O.; Klanderud, K.; Telford, R.J.; Halbritter, A.H.; Goldberg, D.E. Biotic rescaling reveals importance of species interactions for variation in biodiversity responses to climate change. *Proc. Natl. Acad. Sci. USA* **2020**, *117*, 22858–22865. [CrossRef] [PubMed]
82. Swenson, N.G.; Enquist, B.; Pither, J.; Kerkhoff, A.; Boyle, B.; Weiser, M.; Elser, J.J.; Fagan, F.W.; Forero, J.; Fyllas, N.; et al. The biogeography and filtering of woody plant functional diversity in North and South America. *Glob. Ecol. Biogeogr.* **2012**, *21*, 798–808.
83. Wolde, B.; Lal, P. Invasive-Plant-Removal Frequency—Its Impact on Species Spread and Implications for Further Integration of Forest-Management Practices. *Forests* **2018**, *9*, 502. [CrossRef]