forests

Article

The Impact of Structural Indicators and Game Browsing on the Natural Regeneration of Forest–Steppe Ecosystems Dominated by Deciduous Oak Species—A Case Study from the Krupina Plateau, Slovakia

Zuzana Parobeková [1,*], Denisa Sedmáková [1], Ján Pittner [1], Ivana Sarvašová [2] and Ivan Lukáčik [1,2]

[1] Faculty of Forestry, Technical University in Zvolen, T.G. Masaryka 24, 960 01 Zvolen, Slovakia; denisa.sedmakova@tuzvo.sk (D.S.); pittner@tuzvo.sk (J.P.); ivan.lukacik@tuzvo.sk (I.L.)
[2] Borova Hora Arboretum, Technical University in Zvolen, Borovianska 66, 960 01 Zvolen, Slovakia; ivana.sarvasova@tuzvo.sk
* Correspondence: parobekova@tuzvo.sk

Abstract: Forest–steppe ecosystems represent a heterogeneous small-patch landscape important as a biodiversity hotspot and habitat for many endangered species. In this work, we examine threatened forest–steppe communities using structural indices, browsing intensity and indices that consider herbivorous game preferences. The study aims to assess the abundance of natural regeneration and the browsing intensity in relation to different stand structures and to identify woody species threatened by selective browsing at three study sites on the Krupina Plateau in the southern part of central Slovakia. At each study site, three circular permanent research plots (PRPs), each 500 m^2 in size, were established for stand structure analysis. Within each PRP, nine circular subplots with a radius of 2 m were established for detailed analysis of natural regeneration. The results of this study suggest that forest patches in the forest–steppe mosaic suffer from a long-term lack of natural regeneration, which is induced mainly by increasing aridity and ungulate pressure. Positive effects on the amount of natural regeneration were noted in association with the aggregated structure of forest patches and the presence of dead wood. Differentiated stand structure influenced the regeneration number in a negative way and at the same time significantly increased browsing intensity. In relation to a more advanced regeneration, shrubs had a protective effect against browsing. The feeding preferences of the animals can positively modulate the species composition and eliminate the imbalances in the regeneration in favor of the increasingly rare *Quercus pubescens* Willd.

Keywords: extreme drought; game browsing; selectivity; Quercus pubescens; Quercus cerris

check for updates

Citation: Parobeková, Z.; Sedmáková, D.; Pittner, J.; Sarvašová, I.; Lukáčik, I. The Impact of Structural Indicators and Game Browsing on the Natural Regeneration of Forest–Steppe Ecosystems Dominated by Deciduous Oak Species—A Case Study from the Krupina Plateau, Slovakia. *Forests* **2024**, *15*, 2057. https://doi.org/10.3390/f15122057

Academic Editor: Giovanna Battipaglia

Received: 16 September 2024
Revised: 8 November 2024
Accepted: 18 November 2024
Published: 21 November 2024

1. Introduction

The forest–steppe represents a mosaic of broadleaf deciduous forest patches and meadow–steppe or steppified meadows extending from the Carpathians to the Ural Mountains [1]. The distribution of forest–steppe communities is strongly determined by aridity, which in the temperate climate of Central Europe is mainly determined by edaphic factors, topography and wild herbivores [2]. The fragile interplay of all the factors allows the existence of a heterogeneous small-patch landscape, which provides important habitats for many endangered species and represents a biodiversity hotspot [3].

In the Pannonian ecoregion, which also includes the southern regions of Slovakia, processes of forest and shrub expansion at the expense of grassland have been observed [4,5]. However, climate change scenarios predict a considerable increase in mean annual temperature and summer drought in this zone [6], which might lead to the opposite process—an increase in the cover of grassland in the future. Negative impacts of drought are observed in many aspects of forest health including seedling recruitment, productivity and mortality of mature trees, susceptibility to pathogen or insect attack, and vulnerability to damage from fire, see, e.g., [7–9]. In addition, generally milder climatic conditions and less intensive game management lead to an overabundance of herbivorous game, which greatly amplifies the effect of climate change on tree species distribution [2,10–12]. Plant removal and erosion have a direct effect on the microclimate, which tends to become drier, warmer and less buffered against climatic extremes on grazed sites [13]. What is more, selective browsing on woody species can modify the interactions between competing species and thus change overall patterns of plant diversity in the forest–steppe. A less intensively browsed, more drought-tolerant tree species may have an opportunity for expansion to other areas currently dominated by tree species suffering from both drought- and ungulate-induced damage [14]. The strongly influenced structure, composition, growth, and succession of forest patches may lead not only to tree species loss but also to wide-ranging indirect effects on the entire biota [15,16]. Browsing may also affect human interests by reducing species diversity and productivity of commercially used plants or by limiting the protective functions of the forest or other social demands [12]. Understanding the drivers of ungulate browsing is of outmost importance from both ecological and forestry-management standpoints.

The relationship between ungulate density and browsing intensity is well known, but other factors such as food availability and animal preferences cause plant biomass to have a stronger relationship with browsing intensity than with ungulate density [12,16]. Browsing intensity perfectly illustrates temporal and spatial changes in herbivory pressure, but it needs to be complemented by information on the tree species preferred among the available vegetation. One of the widely used indicators which expresses the imbalance between usage and availability is the Jacobs selectivity index [17].

Existing forest communities also significantly modify their environment and may favor establishment, growth and survival of tree seedlings [4]. For example, dense thorny shrubs or a high abundance of more palatable species may shield tree seedlings against browsing [18]. The importance of positive species interactions for plant community structure and dynamics has been increasingly recognized, especially in stress-exposed and low-productivity habitats [19,20]. Biodiversity and variety of growth patterns in forest ecosystems are closely related to structural complexity, which is conveniently described by structural indices [21,22]. Structural indices are commonly used to describe the vertical and horizontal shape of a forest [23,24]. Their undeniable advantages, which are important for our study, include, for example, equal emphasis on horizontal and vertical diversity, insensitivity to tree size and insensitivity to tree distribution [21].

In light of all the above-mentioned facts, the development of the forest–steppe communities is highly uncertain. Study concerning tree seedling abundance, browsing intensity and their interconnections with the compositional and structural characteristics of the forest patches are highly requested for the development of reliable management and above all, conservation strategies for the near future [2–5,21]. In this work, we therefore decided to comprehensively evaluate threatened forest–steppe communities using structural indices, browsing intensity and the Jacobs selectivity index, which consider herbivorous game preferences. We aim to combine these approaches to (i) evaluate the natural regeneration abundance and the browsing intensity depending on different stand structures; (ii) determine which woody species are seriously threatened by selective browsing; and (iii) forecast the development of the woody species composition based on the research results.

2. Material and Methods

2.1. Study Area

The study was conducted at three study sites—Medovarce (MED), Plášťovce (PLA) and Drienovo (DRI), all located on the Krupina Plateau, situated in the southern part of central Slovakia with altitudinal range from the lowland to the sub-mountain level (300–650 m a. s. l.) (Figure 1). The plateau has been inhabited and extensively used by humans since the Neolithic time. The original plant cover has been unevenly preserved, mainly as forest–steppe communities in the southern and south-western parts. These habitats occur on steep andesitic rocky slopes (50–70%) and ridges with clay to clay-loam soils. The study sites are under the influence of the dry and hot Pannonian climate. Relatively low rainfall, relief and permeable subsoil make these habitats very dry, which is the main limiting factor for woody and herbaceous plants [25]. The investigated part of the plateau belongs to the warm region with a mean annual air temperature of 10.7–12.3 °C (Figure 2) and precipitation of 560–580 mm [26]. More detailed information on the course of climatic indicators is available in Figure 2.

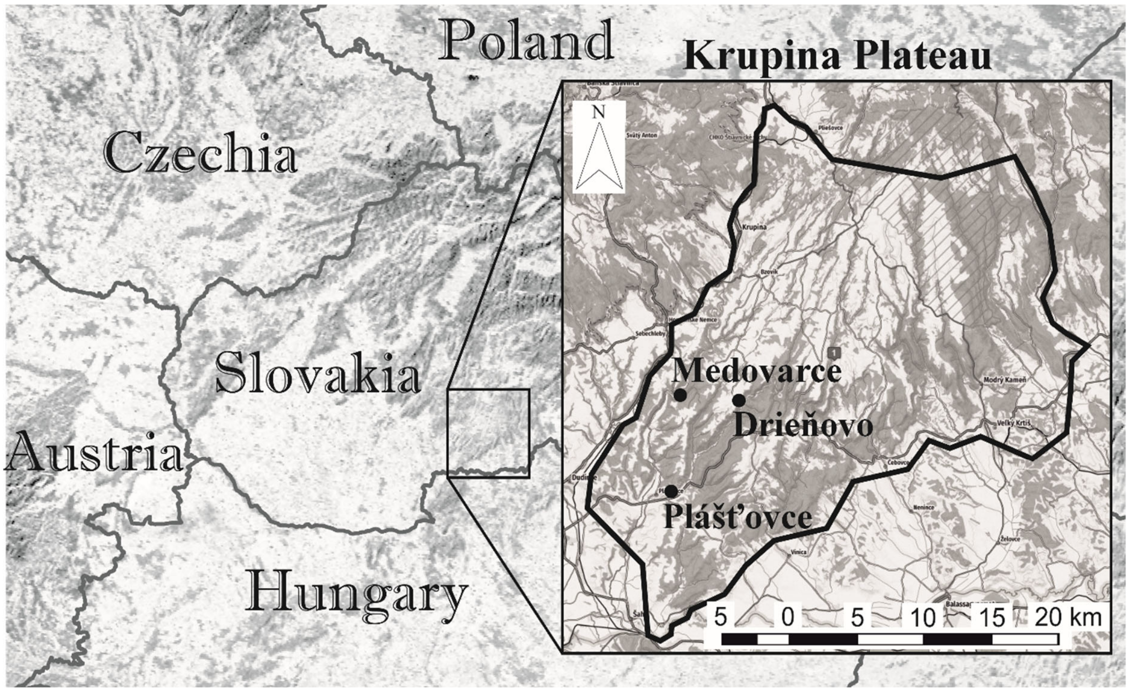

Figure 1. Study site location within Slovakia and surrounding countries.

	MED	PLA	DRI
Mean monthly air temperature (°C)			
Annual	10.7	10.9	12.3
May-July	21.3	21.6	21.5
April-Sept.	17.3	17.6	17.5
Mean monthly air humidity (%)			
Annual	77.8	73.5	72.2
May-July	70.0	63.3	64.9
April-Sept.	70.4	64.0	65.2
Mean monthly soil temperature (°C)			
Annual	12.1	11.9	11.9
May-July	20.2	20.4	20.3
April-Sept.	17.1	17.5	17.2
Mean monthly soil moisture (%)*			
Annual	23.9	23.5	20.7
May-July	21.6	13.2	17.3
April-Sept.	23.1	18.4	18.5

*soil water content

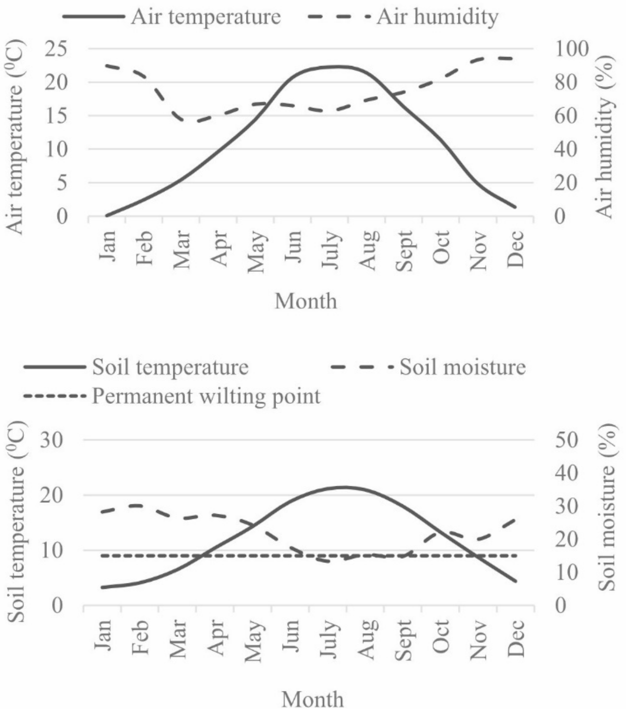

Figure 2. Climatic characteristics of study sites and their average annual course.

Local forest–steppe communities predominantly consist of thermophilic and xerothermic plant species. Forest patches are composed mainly of oak species (*Quercus pubescens* Willd., *Quercus cerris* L., *Quercus dalechampii* Ten.) and other tree species—maples (*Acer campestre* L., *Acer tataricum* L.), European hornbeam (*Carpinus betulus* L.), wild pear (*Pyrus communis* L.), service tree (*Sorbus domestica* L.) and wild service tree (*Sorbus torminalis* L.). There is usually a well-developed shrub layer with typical shrubby species (*Cornus mas* L., *Ligustrum vulgare* L., *Prunus spinosa* L., *Rosa canina* L., *Crataegus* species) (according to our survey).

Currently, the most common species of wild ungulate in the Krupina Plateau are red deer (*Cervus elaphus)*, roe deer (*Capreolus capreolus)*, fallow deer *(Dama dama*), mouflon (*Ovis musimon*) and wild boar (*Sus scrofa*). According to the annual state-wide game census, the abundant amount of all the mentioned species greatly exceeds the model population of the game (in order: 1.94; 1.15; 3.21; 1.6; 2.0 times) [27].

2.2. Data Collection and Analysis

The identification of relevant ecological factors affecting the state of natural regeneration requires knowledge of the site's climatic characteristics. For microclimate measurements, at each study site, a weather station was established (using Environmental Measuring Systems®, Brno, Czech Republic). The weather stations recorded the air temperature and the air humidity at a height of 1.3 m above the ground, and the soil moisture and soil temperature at a depth of 35 cm. Data were measured every hour and recorded by data loggers from 1 April 2020 to 31 October 2023. Soil moisture was measured as the soil water content (SWC %). The permanent wilting point was approximately determined according to water-holding capacity of the clay-loam soil type (SWC 17%) [28] (Figure 2).

Analysis of the stand structure of each study site was based on the data from three permanent research plots (PRPs). PRPs had a circular shape with an area of 500 m^2 (r = 12.6 m). The centers of the PRPs were stabilized by a ground anchor and geolocated using a GPS device. In the PRPs, all living stems and standing deadwood (snags) with diameter at breast height 1.3 m (dbh) $\geq$ 2 cm were recorded. For all standing stems, we registered their exact location within the plot (using Field Map® technology, IFER—Monitoring and Mapping Solutions, LTD., Jílové u Prahy, Czech Republic), tree species, dbh, height and status (living or dead). For living stems, we also recorded crown base height.

In two cases, species were pooled together within a genus or species because their individual identification was not reliable enough, which could lead to confusing interpretations and conclusions. *Quercus virgiliana* Ten. is closely associated with *Quercus pubescens* Willd., considered as its ecomorphotype [29]. Young individuals in particular were difficult to distinguish, so we decided to pool this species under one, *Quercus pubescens* Willd. Similarly complicated was the identification of species belonging to the genus *Crataegus*. Their taxonomic identification was extremely complicated due to extensive hybridization and introgression among all native species [30]. *Crataegus oxyacantha* L., *Crataegus monogyna* Jacq. and their hybrids were pooled under *Crataegus* species.

As additional characteristics of stand structure, we calculated for all PRPs the following structural indices: distance-independent (also non-spatial)—Gini coefficient for heights [31] and standardized diversity [32]; as well as distance-dependent (also spatial)—aggregation index [32,33], diameter-differentiation index [34] and structural complexity index [35].

The Gini coefficient (G) is one of the vertical structural characteristics that characterizes the inequity in the distribution of tree heights and ranges from 0 (maximum uniformity, all trees have the same height) to 1 (maximum non-uniformity). The standardized diversity (E) reaches a maximum value of 1 in the case of equal representation of tree species in the stand and decreases to 0 with increasing differences. The aggregation index (R) is a measure of the spatial distribution of stems on the plot. The index indicates the deviation from random (value 1) to regular (>1) or aggregated (<1) distribution. The diameter differentiation index (T) is a measure of the size differentiation (dbh) between the three nearest neighbors. T ranges from 0 to 1 (highly differentiated stands). The structural complexity index (SCI) incorporates tree size differentiation (h, dbh) and horizontal spatial positioning. The SCI is based on a spatial tessellation that creates a triangular irregular network of non-overlapping triangles of tree neighbors that are as equilateral as possible. The lowest SCI value is 1 (all trees are of the same size), with no upper limit [22].

The density of natural regeneration (dbh $\leq$ 2 cm) was registered on a series of 9 circular subplots with a radius of 2 m distributed over each PRP. One plot was in the center of the PRP and the next two plots were situated at distances of 5 and 10 m in four radii in two perpendicular directions (gradient and contour line). Each individual of natural regeneration was assigned a tree species and height category (height $\leq$ 10 cm and > 10 cm) and was assessed for damage. Damage was recorded as no damage and damaged. Damage was defined as the loss of the terminal bud during the current growing season.

For each subplot, two indices determining the competitive effect of the surrounding trees on natural regeneration were calculated. The index of canopy closure (C) [36] can be calculated for any point within the forest. It is based on the three-dimensional stereo geometry of trees in the vicinity of a focal individual or point. The modified diameter-distance index (D) [37] is a sum of the ratios of the diameters of a subject tree and its competitors weighted by the distance from the subject tree. In our case, we used the heights of trees, as we considered very young individuals of natural regeneration.

Plant–herbivore interactions were analyzed by browsing intensity and Jacob's selectivity index. Browsing intensity is the percent proportion of browsed vegetation among available vegetation. Jacob's index of selectivity [17,38] is a quantity of imbalance between availability and consumption of a given species in total available regeneration. The index ranges from -1 to 1, with a negative value indicating that the taxon is avoided and a positive value indicating that the taxon is selected. The value 0 indicates consumption in equal proportion to its availability.

To assess the differences between PRPs for the key indicators, one-factorial analysis of variance was performed. Correlation analysis (Spearman's rank correlation) was performed to reveal the connections of stand characteristics with the amount of natural regeneration and browsing intensity. Since it was not appropriate to calculate some structural indices for subplots (required minimal area), they were calculated for PRPs and analyzed only within the Krupina Plateau, to ensure a sufficient number of cases entering the analysis. All statistical analyses were performed using STATISTICA 12 software.

3. Results

PRPs of all study sites are situated on steep slopes (50%–70%) with a predominantly southern orientation with shallow soil and locally protruding parent rock. These factors determine the extreme climatic conditions, which are summarized in Figure 2. Air and soil temperatures are comparable between localities with almost identical annual courses. According to air humidity, PLA and DRI are more arid, which is even more reflected in soil moisture. The average soil water content at the depth of 35 cm declines below the permanent wilting point in summer months, which can cause permanent damage due to vegetation rooting shallower. Extremely low values of water content were achieved mainly in the locality PLA in the months May–July.

To evaluate the joint effects of stand structure and large herbivores on abundance, composition and browsing damages of natural regeneration, we must focus in detail on the structure of the forest patches. All study sites were of relatively low tree height and basal area, consisting mainly of deciduous oak species (92%–99%) (Table 1). Other woody species were represented as other tree species in lower dbh classes (up to 18 cm) and shrubs (Figure 3). The shrub layer was better developed in the localities MED and PLA, which significantly increased the stand density and the number of species in the lower dbh classes (Figure 3, Table 1). The amount of regeneration and the number of species in regeneration were by a large margin the highest at study site MED, where browsing intensity was the lowest. Nevertheless, low upper-tree height ($H_{10\%}$), which was achieved by almost all individual trees, and the predominant representation of trees in the middle dbh classes caused considerable uniformity and insignificant differences in vertical and horizontal stand structure (T, SCI, G) (Table 1, Figure 3). Significant differences were visible in a number of species and their even representation in stands according to basal area (E_{BA}). Other tree species and shrubs in PLA were represented in higher dbh classes than in the other study sites and the range of classes was narrower. In DRI, the number of species was by a large margin the lowest, but the species were relatively evenly distributed across the dbh classes (Figure 3), which in both cases caused higher values of standardized diversity according to basal area (E_{BA}). Although other tree species and shrubs were quite numerous in MED and PLA, differences in the standardized diversity derived from tree density (E_N) were insignificant. Regarding the spatial distribution of trees and shrubs on PRPs, the highest value of the aggregation index (R) was observed in DRI, where it pointed to random distribution, and aggregation indexes of MED and PLA, in contrast, indicated aggregation of stems (Table 1).

Table 1. Stand structure characteristics.

Study Site	MED	PLA	DRI
Stand density (psc/ha)	1033.0 ± 296.9 a	1160.0 ± 423.3 a	640.0 ± 60.0 b
Basal area (m^2/ha)	25.4 ± 4.2	24.7 ± 2.1	19.6 ± 3.4
Q. cerris *	62.0 ± 5.3	52.0 ± 18.5	35.3 ± 17.5
Q. pubescens *	35.0 ± 5.5	34.2 ± 11.9	48.6 ± 14.9
Q. dalechampii *	0.9 ± 1.3 b	5.7 ± 3.4 ab	15.0 ± 8.8 a
Other tree species *	1.5 ± 0.8	4.9 ± 3.8	0.9 ± 1.2
Shrubs *	1.2 ± 1.7	3.3 ± 3.6	0.2 ± 0.4
Snags (m^2/ha)	1.3 ± 2.0	1.6 ± 0.5	1.3 ± 1.4
$H_{10\%}$ (m)	14.4 ± 2.5	15.8 ± 4.0	13.9 ± 4.3
Number of species (pcs)	8.0 ± 2.0 a	6.7 ± 0.6 ab	5.3 ± 0.6 b
Regeneration (thous. pcs/ha)	57.18 ± 32.6 a	13.4 ± 3.9 b	16.5 ± 6.2 b
Number of species in regeneration (pcs)	5.9 ± 2.1 a	3.4 ± 1.2 b	3.1 ± 1.3 b
Browsing intensity (%)	51.2 ± 28.8 b	68.9 ± 27.9 a	56.2 ± 28.8 ab
G	0.3 ± 0.0	0.3 ± 0.0	0.2 ±0.0
E_N	0.7 ± 0.1	0.8 ± 0.1	0.8 ± 0.1
E_{BA}	0.5 ± 0.1 b	0.7 ± 0.1 a	0.7 ± 0.1 a
R	0.8 ± 0.0 b	0.8 ± 0.1 b	1.0 ± 0.0 a
T	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.1
SCI_{dbh}	7.1 ± 1.8	4.7 ± 0.5	4.7 ± 0.9
SCI_h	2.7 ± 0.6	2.4 ± 0.2	1.9 ± 0.3

Study sites: MED—Medovarce; PLA—Plášťovce; DRI—Drienovo; * % of basal area; $H_{10\%}$—height of the top 10% tallest trees; G—Gini coefficient; E_N—standardized diversity according to tree density; E_{BA}—standardized diversity according to basal area; R—aggregation index; T—diameter differentiation index; SCI_{dbh}—structural complexity index according to dbh; SCI_h—structural complexity index according to height, ±standard deviation. Letters indicate statistically significant differences (ANOVA, $p \leq 0.05$).

Natural regeneration was registered in 81 subplots evenly distributed over study sites and permanent research plots (see above). We considered all wooden taxa independent of their occurrence frequency. A total of 17 species were recorded: 12 tree species (*Quercus cerris* L., *Quercus pubescens* Willd., *Quercus dalechampii* Ten., *Quercus petraea* (Matt.) Liebl., *Quercus polycarpa* Schur, *Acer campestre* L., *Acer tataricum* L., *Carpinus betulus* L., *Pyrus communis* L., *Sorbus domestica* L., *Sorbus torminalis* L., *Tilia cordata* Mill.) and 5 shrubby species (*Cornus mas* L., *Ligustrum vulgare* L., *Prunus spinosa* L., *Rosa canina* L., *Crataegus* species). *Tilia cordata* Mill. and two species of the genus *Quercus* (*Q. polycarpa* Schur, and *Q. petraea* (Matt.) Liebl.) were detected additionally compared to the species composition of the mother stands. Nevertheless, the number of species in natural regeneration was in all study sites lower than the number of species represented in mother stands (Table 1). For some species, the number of occurrences was low (10 or less) (*Quercus polycarpa* Schur, *Quercus petraea* (Matt.) Liebl., *Tilia cordata* Mill., *Sorbus domestica* L., *Carpinus betulus* L. and

Cornus mas L.), so the calculation of the Jacob's index of selectivity for these species was of no predictive value and therefore we did not include them in further results.

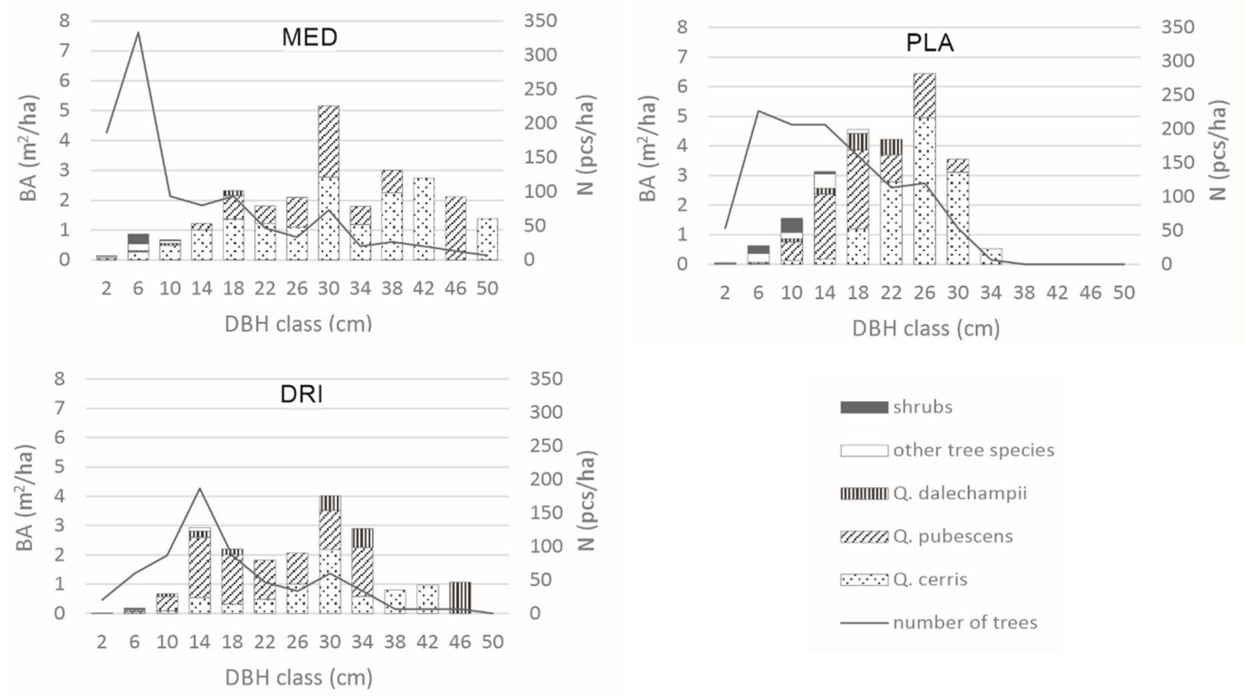

Figure 3. Basal area and diameter distributions for study sites (MED—Medovarce; PLA—Plášťovce; DRI—Drienovo) according to classes of diameter at breast height and tree species.

In Figure 4, it is visible that the only study site with a higher number of regenerated individuals and a good ability to transition to the category above 10 cm was MED. In PLA, natural regeneration was strongly limited and almost only shrubs were able to survive in the category above 10 cm. Regeneration in DRI was also limited, with a higher share of *Quercus cerris* in both height categories and with a minimal share of other tree species and shrubs in the category above 10 cm. In general, it may be stated that insufficient regeneration of *Quercus pubescens* was observed in all localities.

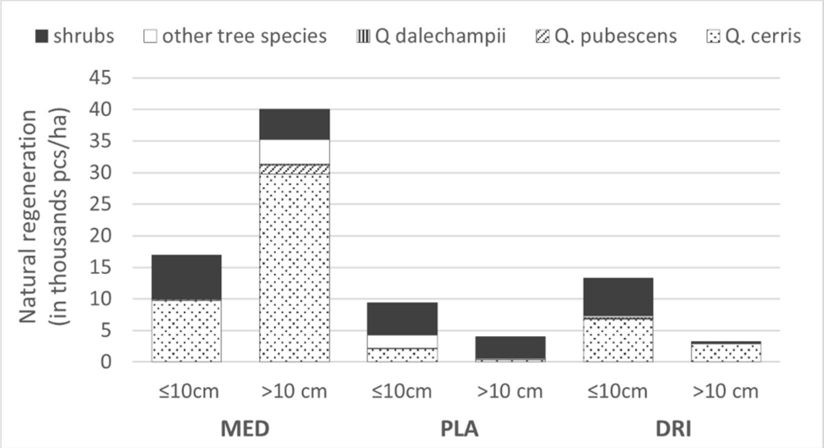

Figure 4. Number and composition of natural regeneration on study sites according to height categories (MED—Medovarce; PLA—Plášťovce; DRI—Drienovo).

The significance of correlation coefficients (Spearman's R) of indices countable for subplots provided information about the unequal response of the natural regeneration number in individual study sites to stand characteristics (Table 2). In general, for the whole investigated locality, we can confirm the positive effect of the occurrence of snags on the frequency of natural regeneration in the category above 10 cm, which may be connected to the free space, higher light supply and possible improvement of the ambient humidity regime. Quite the opposite influence of stumps was visible in MED, where their significantly negative impact on a category up to 10 cm may be related to a massive expansion of the shrub layer. The shrub layer influenced natural regeneration in MED mostly in a negative way, which is significant in the category above 10 cm. The number of species did not significantly influence the amount of natural regeneration within the locality, with the exception of the study site PLA, which may be related to the presence of a dense shrubby layer and a relatively high proportion of other tree species (Figure 3). Indices related to canopy closure and competition between individuals (tree density, basal area, C, D) had no effect on the amount of natural regeneration within the investigated locality. A positive correlation was detected only in study site DRI regarding the competitive diameter-distance index (D) (Table 2). We assume, that DRI was the most unfavorable study site, as basal area and upper height were the lowest (Table 1). In such harsh conditions, young individuals survived more successfully under the cover of parent trees that provided at least intermittent shade, which significantly enhanced microclimatic conditions. From these findings, it was concluded that some factors influencing natural regeneration did not seem to be important within the locality, but in the specific conditions of individual sites, they played an important role.

Table 2. Correlation analysis of natural regeneration amount and stand structure characteristics.

	Krupina Plateau		**MED**		**PLA**		**DRI**	
Height category	**≤10 cm**	**>10 cm**	**≤10 cm**	**>10 cm**	**≤10 cm**	**>10 cm**	**≤10 cm**	**>10 cm**
Tree density	−0.015	0.097	0.129	−0.167	−0.288	0.163	0.014	−0.298
Basal area	−0.107	0.061	−0.149	0.015	−0.373	0.046	0.183	0.177
Shrubs *	−0.118	−0.123	−0.202	**−0.514**	−0.204	−0.013	−0.228	−0.256
Snags *	−0.034	**0.275**	**−0.656**	−0.338	−0.076	0.155	0.300	−0.338
Nr. of species	−0.121	0.194	−0.025	−0.286	**−0.401**	0.101	−0.185	−0.213
C	0.005	0.141	0.137	−0.130	−0.302	0.182	0.120	−0.214
D	0.042	0.113	−0.036	−0.065	−0.355	0.092	**0.450**	0.271
$H_{10\%}$	0.113	**0.306**	-	-	-	-	-	-
G	−0.058	0.001	-	-	-	-	-	-
E_N	**0.347**	**0.581**	-	-	-	-	-	-
E_{BA}	**0.354**	0.145	-	-	-	-	-	-
R	−0.185	**−0.301**	-	-	-	-	-	-
T	**−0.360**	**−0.380**	-	-	-	-	-	-
SCI_{dbh}	**−0.322**	**−0.300**	-	-	-	-	-	-
SCI_h	−0.110	0.157	-	-	-	-	-	-

Study sites: MED—Medovarce; PLA—Plášťovce; DRI—Drienovo; * % of basal area; C—index of canopy closure D—diameter-distance index; $H_{10\%}$—height of the 10% tallest trees; G—Gini coefficient; E_N—standardized diversity according to tree density; E_{BA}—standardized diversity according to basal area; R—aggregation index; T—diameter differentiation index; SCI_{dbh}—structural complexity index according to dbh; SCI_h—structural complexity index according to height). Significant correlations ($p < 0.05$) are indicated by bold font.

Diversified structure (expressed by T, SCI_{dbh}) negatively correlated with the natural regeneration amount of both categories within the investigated locality. Positive correlation with standardized diversity (E), which assesses the evenness of tree species representation in the stand, was self-evident because its higher values were the result of sufficient and continuous natural regeneration in study sites. A negative correlation with the aggregation index (R) followed from the nature of the index, whose decrease to 0 indicated the aggregation of the stand. Aggregate structure provided more varied environmental conditions, which could increase the frequency (Table 2) and diversity of natural regeneration (Table 1).

Browsing damage was analyzed across the entire Krupina Plateau. Herbivory pressure intensified with the increasing height of the seedlings and more than 80% of the seedlings were browsed in the category above 10 cm (Table 3). Calculation of the availability, consumption and Jacob's selectivity index was based on total available regeneration regardless of species and category. According to Jacob's selectivity index, individuals of regeneration up to 10 cm were less sought after than individuals of a higher category (Table 3). In the category above 10 cm, three species were avoided by herbivorous game (*Quercus pubescens* Willd., *Quercus dalechampii* Ten., *Acer tataricum* L.). The other species were preferred by game at different levels. The most selected were *Quercus cerris* L., *Acer campestre* L. and *Pyrus communis* L.

Table 3. Browsing intensity (BI %), availability (A), consumption (C) and Jacob's selectivity index (S).

	BI		**A**		**C**		**S**	
Height category	**≤10 cm**	**>10 cm**	**≤10 cm**	**>10 cm**	**≤10 cm**	**>10 cm**	**≤10 cm**	**>10 cm**
Quercus cerris	38.5	79.0	0.229	0.226	0.182	0.357	−0.372	0.333
Q. pubescens	30.0	58.7	0.004	0.014	0.002	0.015	−0.598	−0.175
Q. dalechampii	25.0	66.7	0.003	0.001	0.002	0.001	−0.728	−0.017
Rosa canina	38.8	81.8	0.158	0.006	0.088	0.006	−0.524	0.003
Crataegus sp.	37.3	97.6	0.034	0.030	0.031	0.042	−0.527	0.203
Prunus spinosa	7.7	88.8	0.010	0.003	0.005	0.004	−0.648	0.119
Ligustrum vulgare	50.1	98.6	0.123	0.052	0.103	0.063	−0.370	0.226
Acer campestre	41.9	96.4	0.045	0.012	0.030	0.026	−0.461	0.376
Acer tataricum	8.0	56.3	0.009	0.003	0.003	0.002	−0.859	−0.197
Sorbus torminalis	12.9	72.6	0.017	0.013	0.011	0.020	−0.577	0.144
Pyrus communis	66.7	100.0	0.003	0.003	0.004	0.007	−0.225	0.317

BI—the proportion of browsed individuals among total natural regeneration of the plot in percentage terms; A—the proportion of species in the total natural regeneration of the plot; C—the contribution of species to the total browsing in the plot; S—ranges between −1 to 1, a negative value indicates that the taxon is avoided, a positive value that the taxon is selected.

Browsing intensity was negatively influenced by the appearance of shrubs (Table 4). On the other hand, a significant positive relationship was found between diameter differentiation of stand (T, SCI_{dbh}) and browsing.

Table 4. Correlation analysis of browsing intensity and stand structure characteristics.

	Krupina Plateau	
Height Category	**≤10 cm**	**>10 cm**
Tree density	0.010	−0.209
Basal area	0.060	−0.013
Shrubs *	−0.118	**−0.253**
Snags *	−0.071	−0.084
Nr. of species	−0.062	−0.216
C	0.002	−0.223
D	0.147	0.018
$H_{10\%}$	−0.043	0.030
G	0.041	0.197
E_N	**−0.333**	**−0.433**
E_{BA}	**−0.223**	−0.247
R	0.170	0.121
T	**0.330**	**0.305**
SCI_{dbh}	**0.346**	**0.443**
SCI_h	0.005	0.104

* % of basal area; C—index of canopy closure; D—diameter-distance index; $H_{10\%}$—height of the top 10% tallest trees; G—Gini coefficient; E_N—standardized diversity according to tree density; E_{BA}—standardized diversity according to basal area; R—aggregation index; T—diameter differentiation index; SCI_{dbh}—structural complexity index according to dbh; SCI_h—structural complexity index according to height. Significant correlations ($p < 0.05$) are indicated by bold font.

4. Discussion

Forest–steppe communities form the southern distribution boundary of the temperate deciduous forest biome. Their occurrence is conditioned by aridity, which prevents the formation of a closed forest. The investigated forest–steppe area falls within the range of temperatures and precipitation totals that determine the occurrence of the forest–steppe in Central Europe (8.25–13.5 °C, 420–600 mm) [2,5], but as the distribution of precipitation within the year fluctuates considerably, arid phases of different length occur regularly.

The Pannonian Basin is periodically exposed to droughts during the late summer and early autumn months [6], which in combination with local soil or topographic conditions limits the occurrence of deciduous trees, as their distribution is strictly determined by soil moisture availability [39,40]. As the amount of natural regeneration was strongly limited by aridity (Figure 2, Table 1) and on arid sites the transition to a higher category (>10 cm) (Figure 4) decreased, low soil moisture seems to be the most serious cause of poor seedling emergence and growth. The soil water content reached the permanent wilting point in the months of July, August and September simultaneously with culmination of temperatures in July and August (Figure 2). Evidence of longer outages in natural regeneration was also seen in the small number of trees in the lowest DBH classes (Figure 3).

It is well documented that tree species adapted to arid climatic regimes generally have higher root-to-shoot ratios and deeper, more rapidly developing root systems because the topsoil dries faster [8,9,41]. Rapid and deep rooting has been shown to be beneficial for plant growth and survival under water-limited conditions. In investigated study sites, the shallow rocky soils and steep slopes limited deep rooting, and the permeable subsoil did not guarantee higher soil moisture in deeper layers. As the aggregated structure of forest patches significantly increases the frequency of natural regeneration (Table 2), we assume that this is due to the provision of more varied environmental conditions. Young individuals could survive mostly in posts with locally better soil conditions, and/or in better microclimatic conditions created by the structure of the forest patches. According to our findings, the presence of dead wood may also significantly improve microclimatic conditions. Soil-attached deadwood is characterized by humid conditions and can serve as a water supply for the surrounding area [42].

In general, indices related to canopy closure and competition between individuals had neither positive nor negative effects on the amount of natural regeneration within the investigated locality. Species of the genus *Quercus* are light-demanding to semi-shade-tolerant, but at the seedling stage they can tolerate shady conditions under trees [43]. In arid climates, canopy cover improves the soil water balance, so seedlings may find optimal conditions for establishment and growth under canopies, where the water status of seedlings is improved as a result of increased shading and soil moisture availability [44]. Indeed, the positive effect of canopy, expressed as a diameter-distance index (D), was observed in the study site with the lowest annual water content (DRI) (Table 2, Figure 1). In contrast, in the study site with the highest water availability (MED), a particularly negative effect of shrubs was observed, mainly in relation to more developed seedlings. As water supply is a crucial factor during oak germination and seedling development, shady conditions may be compensated by higher moisture, but the line between the positive and the negative influence of shading is narrow, and depends on microclimatic conditions, species mixture or developmental stage of regeneration [2,18,40].

Indices of diversified structure (T, SCI) were negatively correlated with the natural regeneration amount of both categories within the investigated locality. In a highly structured system, occupation of both above- and below-ground space causes strong competing pressures on natural regeneration, similar to the ingrowth stage of a forest-development cycle, where natural regeneration no longer succeeds, see, e.g., [22,24]. In the arid habitat of the study site PLA, even the number of tree species in the parent stand had a significant negative effect on the abundance of natural regeneration (Table 2). Mixed species with contrasting resource-use strategies can reduce forest vulnerability to extreme events. Individual species can distinctively modulate the effect of heat and drought on their hydraulic traits. However, some studies have documented that species mixture can mitigate the adverse drought impact for some species, but enhance them for others [20,45]. Species mixtures therefore have the potential to shape drought impacts in unpredictable ways, which may result in the persistence of some species and the vulnerability of others. These negative interactions are prominent under extreme drought, where even trees with complementary resource-use strategies compete for water resources [7,19,46].

In contrast, differentiated stand structures with the presence of shrubs may facilitate natural regeneration in cases of heavy browsing pressure [18,47,48]. According to our findings, shrubs protected young individuals from browsing, but differentiated structure without the appearance of shrubs significantly increased browsing intensity. In heterogeneous, semi-open landscapes, such as forest–steppe, ungulates prefer to graze in open areas and seek shelter in the shade of compact forest patches [2]. These sites are severely affected by biomass removal through grazing and trampling with subsequent erosion and by damage to old trees through bark abrasion. In addition, the preference for south-facing slopes in winter significantly increases ungulate concentration and browsing probability [12]. Long-term exposure to browsing can lead to a strong reduction in canopy cover, which may allow grassland species to invade forest patches and eventually convert them to steppe [40,49].

There was an alarming decrease in the amount and species diversity of regeneration with transition to the high category above 10 cm (Figure 4, study sites PLA and DRI). Under the investigated conditions, the most resilient species persisting under extreme drought in advanced regeneration were *Quercus cerris* L. and mainly some shrubby species such as *Crataegus* species and *Ligustrum vulgare* L. (see Table 3). Diversity loss and an insufficient number of young individuals can alter or completely disrupt the life cycles of forest patches in favor of shrub occurrences, as was also documented in other studies, e.g., [2,44]. The situation is particularly alarming for *Quercus pubescens* Willd., generally rare in the regeneration (Figure 4, Table 2), which, in connection with its deteriorating health (expressed by total defoliation) and unfavorable sociological position [50], predisposes its representation in the species composition to decline.

The situation of insufficient natural regeneration amount and low biodiversity is further complicated by the pressure of herbivorous game. Plant communities in areas with high browsing intensity used to have lower species richness and cover, and exhibit reduced stem heights, increased mortality, reduced abundance and a lack of mature individuals, which can alter successional trajectories [16]. In the investigated locality, the intensity of browsing increased dramatically as the wood species grew into higher categories (Table 3). In the category above 10 cm, more than 80% of the individuals had observable feeding traces, or even severely altered shape. Although competition strongly influences seedling survival, dense herbaceous cover and the high abundance of other, more palatable species can effectively protect seedlings from browsing [4,17,40,46]. When seedlings emerge above the herbaceous layer and, more importantly, above the winter snow cover, they are fully exposed to herbivorous game. In winter conditions, woody plants such as trees and shrubs make up the majority of the browsed species, although only a small number of browsed species normally make up the bulk of the food [51]. According to the selectivity of woody species estimated by Jacob's selectivity index, only three species were avoided—*Quercus pubescens* Willd., *Quercus dalechampii* Ten. and *Acer tataricum* L. Among the most selected species, *Quercus cerris* L., *Acer campestre* L. and *Pyrus communis* L. were represented. Boulanger et al. (2009) [17] also recorded a global increase in the selectivity of the mentioned species, as an increase in the deer population forced the animals to feed more on species that were previously avoided or that they were indifferent to. The palatability of species is often related to the density of trichomes, the presence of thorns or specific substances such as tannins, see, e.g., [52,53]. Leaves of *Quercus pubescens* Willd. are green-greyish and densely pubescent at the beginning of their development, soon after, all hairs on the upper side fall off, and the leaves become leathery and dark green [29]. On the other hand, the lower tannin content and high edible quality of relatively large acorns (51% less tannin and 35% less fiber than *Quercus cerris* L.) are probably responsible for their significant feeding preference and consequently low availability for regeneration [53]. Severely damaged *Quercus cerris* L. sprouts in coppice forests in central Italy show that it is not even possible to rely on vegetative renewal in times of ungulate overpopulation [54–56].

5. Conclusions

The results of this study suggest that forest patches in the forest–steppe mosaic suffer from a long-term lack of natural regeneration, mainly due to increasing aridity and ungulate pressure. A significant decrease in the amount and diversity of natural regeneration is also manifested in the absence of the lower stem sizes in forest patches, indicating the long-term persistence of the problem. Taking into account the deteriorating health condition of adult *Quercus pubescens* Willd. individuals, we can suppose the opening of the closed forest patches in favor of shrub or grass communities, which means that the future of the forest–steppe is at least doubtful.

Based on our results, we can highly recommend retention of deadwood within the forest patches, in extreme cases even active deadwood-enrichment strategies in the sense of an increase in its quantity. Partial reduction of heavily diversified stands, especially in places with more advanced regeneration, also seems to be advisable. In any case, the adjustment of the browsing pressure to sustainable levels is certainly a critical measure. This appears to be the most important factor with respect to facing the mentioned threats and effectively solving the problem of woody species regeneration. Reducing animal numbers would not only reduce browsing, but also eliminate secondary damage such as trampling, erosion and subsequent aridization. Under more favorable conditions for natural regeneration, the feeding preferences of animals can positively modulate the species composition of forest patches and to some extent eliminate the imbalances in the regeneration of woody species, for example, in favor of the increasingly rare *Quercus pubescens* Willd.

Author Contributions: Conceptualization, Z.P. and I.S.; Methodology, Z.P., D.S. and J.P.; Formal analysis, Z.P.; Investigation, Z.P. and D.S.; Data curation, D.S. and J.P.; Writing—original draft, Z.P.; Supervision, I.L. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Scientific Grant Agency of the Ministry of Education, Science, Research and Sport of the Slovak Republic [under the Contract no. VEGA 1/0515/23], Slovak Research and Development Agency [under the Contract no. APVV-21-0199] and the Operational Programme Integrated Infrastructure funded by the ERDF [Project HYSPED ITMS2014+ 313010BWC9].

Data Availability Statement: The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

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

References

1. Lukanina, E.; Shumilovskikh, L.; Novenko, E. Vegetation and fire history of the East-European forest-steppe over the last 14,800 years: A case study from Zamostye, Kursk region, Russia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2022**, *605*, 111218. [CrossRef]
2. Chytrý, K.; Willner, W.; Chytrý, M.; Divíšek, J.; Dullinger, S. Central European forest–steppe: An ecosystem shaped by climate, topography and disturbances. *J. Biogeogr.* **2022**, *49*, 1006–1020. [CrossRef]
3. Bátori, Z.; Erdős, L.; Kelemen, A.; Deák, B.; Valkó, O.; Gallé, R.; Bragina, T.M.; Kiss, P.J.; Kröel-Dulay, G.; Tölgyesi, C. Diversity patterns in sandy forest-steppes: A comparative study from the western and central Palaearctic. *Biodivers. Conserv.* **2018**, *27*, 1011–1030. [CrossRef]
4. Erdős, L.; Tölgyesi, C.; Horzse, M.; Tolnay, D.; Hurton, Á.; Schulcz, N.; Körmöczi, L.; Lengyel, A.; Bátori, Z. Habitat complexity of the Pannonian forest-steppe zone and its nature conservation implications. *Ecol. Complex.* **2014**, *17*, 107–118. [CrossRef]
5. Erdős, L.; Kröel-Dulay, G.; Bátori, Z.; Kovács, B.; Németh, C.; Kiss, P.J.; Tölgyesi, C. Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics. *Biol. Conserv.* **2018**, *226*, 72–80. [CrossRef]
6. Ministry of Environment of the Slovak Republic. The Seventh National Communication of the Slovak Republic on Climate Change [in Slovak] Bratislava. Available online: https://unfccc.int/sites/default/files/resource/976840315_Slovakia-NC7-1-7NC_SVK.pdf (accessed on 16 February 2024).
7. Martínez-Vilalta, J.; Lloret, F.; Breshears, D. Drought-induced forest decline: Causes, scope and implications. *Biol. Lett.* **2011**, *8*, 689–691. [CrossRef]
8. Comas, L.H.; Becker, S.R.; Cruz, V.M.V.; Byrne, P.F.; Dierig, D.A. Root traits contributing to plant productivity under drought. *Front. Plant Sci.* **2013**, *4*, 442. [CrossRef]

9. Brunner, I.; Herzog, C.; Dawes, M.A.; Arend, M.; Sperisen, C. How tree roots respond to drought. *Front. Plant Sci.* **2015**, *6*, 547. [CrossRef]
10. Petersson, L.K.; Milberg, P.; Bergstedt, J.; Dahlgren, J.; Felton, A.M.; Götmark, F.; Salk, C.; Löf, M. Changing land use and increasing abundance of deer cause natural regeneration failure of oaks: Six decades of landscape-scale evidence. *For. Ecol. Manag.* **2019**, *444*, 299–307. [CrossRef]
11. Carpio, A.J.; Apollonio, M.; Acevedo, P. Wild ungulate overabundance in Europe: Contexts, causes, monitoring and management recommendations. *Mammal Rev.* **2021**, *51*, 95–108. [CrossRef]
12. Donini, V.; Corlatti, L.; Ferretti, F.; Carmignola, G.; Pedrotti, L. Browsing intensity as an index of ungulate density across multiple spatial scales. *Ecol. Indic.* **2024**, *163*, 112131. [CrossRef]
13. De Frenne, P.; Zellweger, F.; Rodríguez-Sanchez, 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]
14. Katona, K.; Kiss, M.; Bleier, N.; Székely, J.; Nyeste, M.; Kovács, V.; Terhes, A.; Fodor, Á.; Olajos, T.; Rasztovits, E.; et al. Ungulate browsing shapes climate change impacts on forest biodiversity in Hungary. *Biodivers. Conserv.* **2013**, *22*, 1167–1180. [CrossRef]
15. Schulze, E.D.; Bouriaud, O.; Wäldchen, J.; Eisenhauer, N.; Walentowski, H.; Seele, C.; Heinze, C.; Pruschitzki, E.; Danila, U.; Marin, G.; et al. Ungulate browsing causes species loss in deciduous forests independent of silvicultural management in Central and Southeastern Europe. *Ann. For. Res.* **2014**, *57*, 267–288. [CrossRef]
16. Sample, R.D.; Delisle, Z.J.; Pierce, J.M.; Swihart, R.K.; Caudell, J.N.; Webster, C.R.; Jenkins, M.A. Predicting and indexing ungulate browse intensity from local to regional scales. *Ecol. Indic.* **2023**, *154*, 110564. [CrossRef]
17. Boulanger, V.; Baltzinger, C.; Saïd, S.; Ballon, P.; Picard, J.F.; Dupouey, J.L. Ranking temperate woody species along a gradient of browsing by deer. *For. Ecol. Manag.* **2009**, *258*, 1397–1406. [CrossRef]
18. Jensen, A.M.; Löf, M. Effects of interspecific competition from surrounding vegetation on mortality, growth and stem development in young oaks (*Quercus robur*). *For. Ecol. Manag.* **2017**, *392*, 176–183. [CrossRef]
19. Haberstroh, S.; Werner, C. The role of species interactions for forest resilience to drought. *Plant Biol.* **2022**, *24*, 1098–1107. [CrossRef]
20. Mas, E.; Cochard, H.; Deluigi, J.; Didion-Gency, M.; Martin-StPaul, N.; Morcillo, L.; Valladeras, F.; Vilagrosa, A.; Grossiord, C. Interactions between beech and oak seedlings can modify the effects of hotter droughts and the onset of hydraulic failure. *New Phytol.* **2023**, *241*, 1021–1034. [CrossRef]
21. Staudhammer, C.L.; LeMay, V.M. Introduction and evaluation of possible indices of stand structural diversity. *Can. J. For. Res.* **2001**, *31*, 1105–1115. [CrossRef]
22. Parobeková, Z.; Pittner, J.; Kucbel, S.; Saniga, M.; Filípek, M.; Sedmáková, D.; Vencurik, J.; Jaloviar, P. Structural diversity in a mixed spruce-fir-beech old-growth forest remnant of the Western Carpathians. *Forests* **2018**, *9*, 379. [CrossRef]
23. Keren, S.; Svoboda, M.C.; Janda, P.; Nagel, T.A. Relationships between structural indices and conventional stand attributes in an old-growth forest in Southeast Europe. *Forests* **2019**, *11*, 4. [CrossRef]
24. Alterio, E.; Cislaghi, A.; Bischetti, G.B.; Sitzia, T. Exploring correlation between stand structural indices and parameters across three forest types of the southeastern Italian Alps. *Forests* **2021**, *12*, 1645. [CrossRef]
25. Miklós, L. *Landscape Atlas of the Slovak Republic*, 1st ed.; MŽP SR: Bratislava, Slovakia, 2002; p. 342. ISBN 80-88833-27-2.
26. KNMI Climate Explorer. Available online: https://climexp.knmi.nl/start.cgi (accessed on 16 February 2024).
27. National Forestry Centre. Hunting Statistical Yearbook of the Slovak Republic. Available online: https://www.forestportal.sk/wp-content/uploads/2023/09/Polovnicka-statisticka-rocenka-SR-2022.pdf (accessed on 16 February 2024).
28. EMS Brno. SM100 Soil Moisture Sensor. Available online: http://www.emsbrno.cz/r.axd/Datasheets__manuals_v_Spectrum__Technologies__WaterScout__SM100_v_SM100__userman_u_pdf.jpg?ver= (accessed on 16 February 2024).
29. Pasta, S.; De Rigo, D.; Caudullo, G. Quercus pubescens in Europe: Distribution, habitat, usage and threats. In *European Atlas of Forest Tree Species*, 1st ed.; San Miguel Ayanz, J., De Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A., Eds.; Publications Office of the EU: Luxembourg, 2016; pp. 156–157. Available online: https://w3id.org/mtv/FISE-Comm/v01/e019e5c (accessed on 16 February 2024).
30. Baranec, T. Biosystematické štúdium rodu *Crataegus* L. na Slovensku. *Acta Dendrobiol.* **1986**, *11*, 1–118.
31. Latham, P.A.; Zuuring, H.R.; Coble, D.W. A method for quantifying vertical forest structure. *For. Ecol. Manag.* **1998**, *104*, 157–170. [CrossRef]
32. Shanon, C.E. A mathematical theory of communication. *Bell Syst. Tech. J.* **1948**, *27*, 379–423. [CrossRef]
33. Clark, P.J.; Evans, F.C. Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology* **1954**, *35*, 445–453. [CrossRef]
34. Donnelly, K. Simulations to determine the variance and edge effect of total nearest neighbour distance. In *Simulation Methods in Archaeology*; Hodder, J.R., Ed.; Cambridge University Press: London, UK, 1978; pp. 91–95.
35. Füldner, K. Zur Strukturbeschreibung in Mischbeständen. *Forstarchiv* **1995**, *66*, 235–240.
36. Lieberman, M.; Lieberman, D.; Peralta, R. Forests Are Not Just Swiss Cheese: Canopy Stereogeometry of Non-Gaps in Tropical Forests. *Ecology* **1989**, *70*, 550–552. [CrossRef]
37. Lorimer, C.G. Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Manag.* **1983**, *6*, 343–360. [CrossRef]

38. Dumont, B.; Renaud, P.C.; Morellet, N.; Mallet, C.; Anglard, F.; Verheyden-Tixier, H. Seasonal variations of red deer selectivity on a mixed forest edge. *Anim. Res.* **2005**, *54*, 369–381. [CrossRef]
39. Walter, H.; Breckle, S.W. *Spezielle Ökologie der Gemäßigten und Arktischen Zonen Euro-Nordasiens*, 2nd ed.; G. Fischer Verlag Stuttgart: Jena, Germany, 1986; 726 p, ISBN 3-8252-8022-5.
40. Erdős, L.; Szitár, K.; Öllerer, K.; Ónodi, G.; Kertész, M.; Török, P.; Baráth, K.; Tölgyesi, C.; Bátori, Z.; Somay, L.; et al. Oak regeneration at the arid boundary of the temperate deciduous forest biome: Insights from a seeding and watering experiment. *European J. For. Res.* **2021**, *140*, 589–601. [CrossRef]
41. Koevoets, I.T.; Venema, J.H.; Elzenga, J.T.M.; Testerink, C. Roots withstanding their environment: Exploiting root system architecture responses to abiotic stress to improve crop tolerance. *Front. Plant Sci.* **2016**, *7*, 1335. [CrossRef] [PubMed]
42. Uhl, B.; Krah, F.S.; Baldrian, P.; Brandl, R.; Hagge, J.; Müller, J.; Thorn, S.; Tlaskal, V.; Bässler, C. Snags, logs, stumps, and microclimate as tools optimizing deadwood enrichment for forest biodiversity. *Biol. Conserv.* **2022**, *270*, 109569. [CrossRef]
43. Milios, E.; Pipinis, E.; Kitikidou, K.; Batziou, M.; Chatzakis, S.; Akritidou, S. Are sprouts the dominant form of regeneration in a lowland *Quercus pubescens–Quercus frainetto* remnant forest in Northeastern Greece? A regeneration analysis in the context of grazing. *New For.* **2014**, *45*, 165–177. [CrossRef]
44. Lookingbill, T.R.; Zavala, M.A. Spatial pattern of *Quercus ilex* and *Quercus pubescens* recruitment in *Pinus halepensis* dominated woodlands. *J. Veg. Sci.* **2000**, *11*, 607–612. [CrossRef]
45. Forner, A.; Valladares, F.; Bonal, D.; Granier, A.; Grossiord, C.; Aranda, I. Extreme droughts affecting Mediterranean tree species' growth and water-use efficiency: The importance of timing. *Tree Physiol.* **2018**, *38*, 1127–1137. [CrossRef]
46. Gentilesca, T.; Camarero, J.J.; Colangelo, M.; Nolã, A.; Ripullone, F.; Nole, A. Drought-induced oak decline in the western Mediterranean region: An overview on current evidences, mechanisms and management options to improve forest resilience. *IForest* **2017**, *10*, 796–806. Available online: https://hdl.handle.net/11563/131318 (accessed on 16 February 2024). [CrossRef]
47. Barrere, J.; Petersson, L.K.; Boulanger, V.; Collet, C.; Felton, A.M.; Löf, M.; Saïd, S. Canopy openness and exclusion of wild ungulates act synergistically to improve oak natural regeneration. *For. Ecol. Manag.* **2021**, *487*, 118976. [CrossRef]
48. Alias, S.; Bianchi, L.; Calamini, G.; Gregori, E.; Sioni, S. Shrub facilitation of *Quercus ilex* and *Quercus pubescens* regeneration in a wooded pasture in central Sardinia (Italy). *Iforest-Biogeosci. For.* **2010**, *3*, 16. [CrossRef]
49. Zachar, Z.; Pápay, G.; Csontos, P.; Szabó, G.; Zimmermann, Z.; Saláta, D.; Szentes, S.; Pajor, F.; Fuchs, M.; Penksza, K. The effects of different management methods on restored grasslands in potential temperate forest zones. *Diversity* **2022**, *14*, 551. [CrossRef]
50. Sedmáková, D.; Sarvašová, I.; Parobeková, Z.; Pittner, J.; Ďurica, P.; Lukáčik, I. Stagnation of natural regeneration of Pubescent oak in steppe woods in Krupinska planina. In Proceedings of the Central European Silviculture—21st International Conference, virtual, 14–15 April 2021; Volume 10, pp. 37–47.
51. Bergqvist, G.; Wallgren, M.; Jernelid, H.; Bergström, R. Forage availability and moose winter browsing in forest landscapes. *For. Ecol. Manag.* **2018**, *419*, 170–178. [CrossRef]
52. Schindler, J.R.; Fulbright, T.E.; Forbes, T.D.A. Influence of thorns and tannins on white-tailed deer browsing after mowing. *J. Arid. Environ.* **2003**, *55*, 361–377. [CrossRef]
53. Backhaus, S.; Wiehl, D.; Beierkuhnlein, C.; Jentsch, A.; Wellstein, C. Warming and drought do not influence the palatability of *Quercus pubescens* Willd. leaves of four European provenances. *Arthropod-Plant Interact.* **2014**, *8*, 329–337. [CrossRef]
54. Bonacchi, A.; Bartolommei, P.; Gasperini, S.; Manzo, E.; Cozzolino, R. Acorn choice by small mammals in a Mediterranean deciduous oak forest. *Ethol. Ecol. Evol.* **2017**, *29*, 105–118. [CrossRef]
55. Cutini, A.; Bongi, P.; Chianucci, F.; Pagon, N.; Grignolio, S.; Amorini, E.; Apollonio, M. Roe deer (*Capreolus capreolus* L.) browsing effects and use of chestnut and Turkey oak coppiced areas. *Ann. For. Sci.* **2011**, *68*, 667–674. [CrossRef]
56. Chianucci, F.; Mattioli, L.; Amorini, E.; Giannini, T.; Marcon, A.; Chirichella, R.; Appollonio, M.; Cutini, A. Early and long-term impacts of browsing by roe deer in oak coppiced woods along a gradient of population density. *Ann. Silvic. Res.* **2015**, *39*, 32–36. [CrossRef]