Excluding Large Wild Herbivores Reduced Norway Spruce Dominance and Supported Tree Species Richness in a Young, Naturally Regenerated Stand

Bohdan Konôpka 1,2, Vladimír Šebeň 1,* , Jozef Pajtík 1 and Lisa A. Shipley 3

Abstract: Large wild herbivores are important and natural components of forest ecosystems, but through their browsing activities have the potential to influence the structure and composition of forest communities, thus timber production and ecosystem dynamics. To examine the effects of browsing by wild herbivores on a young post-disturbance forest in the Kysuce region of northwestern Slovakia, we established two sets of 2 m radius plots, 15 within a fenced area (5.12 ha) that excluded large wild herbivores, and 15 within an adjacent unfenced area. In each plot, we recorded the species, tree height, stem base diameter, and mutual geographic positions of trees. When we compared tree community characteristics between the unfenced and fenced plots, we found fewer and smaller broadleaved tree species, except silver birch (Betula pendula Roth.) in the unfenced plots. Although common rowan (Sorbus aucuparia L.) was the dominant species within fenced plots, where some individuals were over 6.0 m tall, this species was rare outside the fenced area and usually did not exceed 1.5 m. In contrast, Norway spruce (Picea abies Karts L.) was more abundant and taller within the unfenced area, likely released from competition by suppression of broadleaved trees by herbivores. In addition, fenced plots also showed twice the tree species richness (Shannon index) of unfenced ones. Despite changes in tree communities, total aboveground biomass stock was only slightly but significantly lower in the unfenced than the fenced plots (29.6 kg per 10 m$^2$ vs. 33.5 kg per 10 m$^2$). Our study suggested that browsing pressure by large wild herbivores that focused on most broadleaved tree species, except silver birch (Betula pendula Roth.) in the unfenced plots. Although common rowan (Sorbus aucuparia L.) was the dominant species within fenced plots, where some individuals were over 6.0 m tall, this species was rare outside the fenced area and usually did not exceed 1.5 m. In contrast, Norway spruce (Picea abies Karts L.) was more abundant and taller within the unfenced area, likely released from competition by suppression of broadleaved trees by herbivores. In addition, fenced plots also showed twice the tree species richness (Shannon index) of unfenced ones. Despite changes in tree communities, total aboveground biomass stock was only slightly but significantly lower in the unfenced than the fenced plots (29.6 kg per 10 m$^2$ vs. 33.5 kg per 10 m$^2$). Our study suggested that browsing pressure by large wild herbivores that focused on most broadleaved trees weakened interspecies competition and allowed the expansion of Norway spruce. As a consequence, converting spruce monocultures to mixed species stands is likely unrealistic when faced with heavy browsing pressure by wild large herbivores.

Keywords: aboveground tree biomass; herbivory exclosure; Picea abies; post-disturbance forest; species composition; tree height and diameter

1. Introduction

Wild herbivores are a critical part of forest ecosystems because of their natural ecological interactions with plants and animals and the abiotic environment [1]. However, whether their influence on coupled human and forest ecosystems from a management perspective is positive or negative depends on their population density [2]. In natural systems, large herbivores provide a critical trophic link between plants and large carnivores, and are involved in nutrient cycling through browsing, defecating, and trampling, but their ecological roles are not yet fully understood [1]. The guild of large wild herbivores in the forests of Central Europe, red deer (Cervus elaphus L.), fallow deer (Dama dama L.), European mouflon (Ovis aries musimon), and roe deer (Capreolus capreolus L.) [3] also provide recreational, cultural, and aesthetic values (e.g., [4]). However, high populations of these animals, especially...
red deer, which have resulted from forest and other land management practices and lack of apex predators, can damage ecologically and economically valuable woody plants [5]. Red deer and other large herbivores can decrease timber production [6], worsen wood quality [7], and reduce diversity of trees and other plants [8]. Increasing populations of red deer in Central Europe over the last few decades has created a serious problem in forests maintained for timber production (e.g., [9,10]). For example, in Slovakia, the red deer population was estimated at 33,000 in 2000, but had grown to 51,000 by 2010 [11], 65,000 in 2015, and 75,000 in 2020 [12], which equates to a sustained finite rate of growth of about 1.05. Hence, red deer have reached twice the bearable level predicted by [13].

Red deer and the other large herbivores that reside in forests in Central Europe are generalist herbivores that consume a wide variety of plant species. They mostly prefer grasses, but also consume a substantial amount of leaves, stems, and bark of trees and woody shrubs [3], and select the most nutritious plants and plant parts available [13]. Hence, the intensive trophic pressure of herbivory has had a varied effect on tree species caused both by direct damage from consumption [14], but also indirect effects mediated through their effects on interspecific competition among tree species (e.g., [15–17]). However, quantifying the effect of herbivory in tree stands can be difficult because recent signs of herbivory (e.g., bark peeling and branch bites) are easier to detect and measure (e.g., [18]) than damage that occurred longer ago. Therefore, one of the most effective methods for quantifying the effects of herbivory on plant communities and ecosystem functioning is through the use of herbivore exclosures (fenced areas) in comparison to similar and adjacent control areas (e.g., [1,19–21]). This traditional approach has allowed researchers to examine the effects of larger herbivores not only on forest tree characteristics (e.g., [22]), but also on understory shrubs and herbs (e.g., [8]), and even other animals like invertebrates [23]. However, creating and maintaining large herbivore exclosures over appropriate spatial and temporal scales to study effects of herbivory can be challenging.

Therefore, in this study, we examined the effects of a relatively long term (10 year) and large (about 5 ha) herbivore exclosure on the species composition, height, density, biomass, and spatial distribution of trees in a young Norway spruce (Picea abies L. Karst) dominant forest in the Kysuce region of Slovakia. Mature spruce-dominant stands in this region have experienced especially high levels of forest decline, attributed to historical air pollution (mainly transboundary SO\textsubscript{2} and NO\textsubscript{x} emission from the Silesia region [24]), and the last three decades to climate extremes fostering wind damage and bark beetle outbreaks [25–27]. Therefore, a key management goal has been to convert spruce-dominant stands into mixed conifer/deciduous forests with prevalence of broadleaved species [28,29]. Previous experience has shown that restoring mixed species forests has been difficult, likely because of spontaneous spruce recruitment and possibly browsing by large wild herbivores on broadleaved tree species and silver fir (Abies alba Mill.) in early growth stages [28,30].

We expected that in unfenced areas herbivores would be responsible for promoting a greater proportion of spruce and reducing the proportion of palatable broadleaved species, such as common rowan (Sorbus aucuparia L.), goat willow (Salix caprea L.), trembling aspen (Populus tremula L.), sycamore maple (Acer pseudoplatanus L.), and possibly also other coniferous species, such as silver fir. Consequently, we expected lower tree species richness and lower aboveground tree biomass production in unfenced than fenced areas. Moreover, we hypothesized enhanced variability of vertical stand structure (tree height distribution) and variability in spatial distribution of trees (regular vs. clustered placing) among plots in unfenced areas due to browsing by herbivores.

2. Materials and Methods

2.1. Site and Plot Conditions

The study area was part of a 79.3 ha research–demonstration entity called “Husárík” (RDE, hereinafter) [31]. The RDE is in the northernmost part of the Javorníky Mountains (Kysuce region), located about 5 km southwest of the town of Čadca (Figure 1). The elevation of the RDE ranges from 600 to 800 m, and has a low slope. The climate is cold...
and humid, with an average temperature of up to 16 °C in July and down to −5 °C in January, with a yearly average of 6 °C. The bedrock consists of claystones and shales, and the soil is modally acidic, prevalingly clay. The duration of snow cover is 80 to 120 days a year and annual precipitation reaches 1000 to 1200 mm [24]. RDE is located in the site to Abieto–Fagetum typology [32], with potential natural vegetation of European beech (Fagus sylvatica L.) and silver fir forest. Across the last two centuries, Norway spruce has become the dominant tree type in RDE, like most of the Kysuce region [24]. Spruce monocultures in RDE have been declining since about 2000, mainly due to climatic extremes (e.g., the dry year of 2003) and the subsequent outbreaks of bark beetles. For this reason, they were harvested in 2010 as part of incidental felling (i.e., harvest of individual trees or forest stands related to their unfavorable health status or mortality).

Figure 1. Location of the study area in the Kysuce region, northern Slovakia, and the sampling design where white circles indicate 2 m radius plots within area excluded from large herbivores (hatched line indicates fencing) and dark circles indicate plots open to herbivory.

The RDE is a part of 2860 ha hunting ground that includes 2000 ha of forest and 860 ha of agricultural fields and grasslands. This hunting ground contained 15 red deer, 60 roe deer, 50 mouflon, and 50 fallow deer in 2010 and 35 red deer, 50 roe deer, 30 mouflon and 60 fallow deer in 2020 [12]. Occurrence of natural predators such as gray wolves (Canis lupus) and Eurasian lynx (Lynx lynx) is rare and localized in the region. Hence, the predators likely have not influenced significantly the population density of large herbivores in the last few decades.

In 2011, several experimental plots were developed to assess different reforestation and silvicultural approaches (e.g., natural, artificially planted, and combined; [33]). A fence surrounding an area of 5.12 ha was built on a treeless post-disturbance area [31]. The fence was 2.4 m high made of metal mesh (45 × 45 cm), completely preventing access by large herbivores.

The fence was built to protect experiments on artificial regeneration. However, we took advantage of this exclosure to examine the effects of herbivory on tree community and structure for the subarea covered by young forest originating exclusively from natural regeneration (seed dispersal from mature trees). We selected a portion of the exclosure near the fence outside of artificial restoration plots. Here, inside the fenced area, 15 plots were randomly established with the rule that they had to be at least 10 m apart and within 6–50 m from the fence. Each plot was circular with a radius of 2.0 m (12.57 m²). We also selected 15 circular plots on the opposite side of the fence, also between 6–50 m from the

Figure 1. Location of the study area in the Kysuce region, northern Slovakia, and the sampling design where white circles indicate 2 m radius plots within area excluded from large herbivores (hatched line indicates fencing) and dark circles indicate plots open to herbivory.

The RDE is a part of 2860 ha hunting ground that includes 2000 ha of forest and 860 ha of agricultural fields and grasslands. This hunting ground contained 15 red deer, 60 roe deer, 50 mouflon, and 50 fallow deer in 2010 and 35 red deer, 50 roe deer, 30 mouflon and 60 fallow deer in 2020 [12]. Occurrence of natural predators such as gray wolves (Canis lupus) and Eurasian lynx (Lynx lynx) is rare and localized in the region. Hence, the predators likely have not influenced significantly the population density of large herbivores in the last few decades.

In 2011, several experimental plots were developed to assess different reforestation and silvicultural approaches (e.g., natural, artificially planted, and combined; [33]). A fence surrounding an area of 5.12 ha was built on a treeless post-disturbance area [31]. The fence was 2.4 m high made of metal mesh (45 × 45 cm), completely preventing access by large herbivores.

The fence was built to protect experiments on artificial regeneration. However, we took advantage of this exclosure to examine the effects of herbivory on tree community and structure for the subarea covered by young forest originating exclusively from natural regeneration (seed dispersal from mature trees). We selected a portion of the exclosure near the fence outside of artificial restoration plots. Here, inside the fenced area, 15 plots were randomly established with the rule that they had to be at least 10 m apart and within 6–50 m from the fence. Each plot was circular with a radius of 2.0 m (12.57 m²). We also selected 15 circular plots on the opposite side of the fence, also between 6–50 m from the
fence, which were accessible to large herbivores (Figure 1). The center of each plot was fixed with a metal tube hammered in the ground. The result was 30 plots located approximately in a square within an area of 100 × 100 m that was homogenous in mesohabitat and very similar in climatic and soil conditions. The mature forest on this site was harvested all at the same time during the winter season 2010/2011, which instigated natural regeneration. Therefore, starting conditions for both sets of plots were identical, and we expected the only factor influencing development of the young forest was the presence or exclusion of large herbivores.

2.2. Tree Measurement and Calculations

Measurements on the 30 plots were performed in the growing season of 2020. Tree heights were measured with a hypsometer TruPulse 360° R (Laser Technology, Inc., Centennial, CO, USA) with a precision of ±0.1 m, and stem base diameters with a digital caliper Masser BT (Masser Precision, Rovaniemi, Finland) with a precision ±0.1 mm. Moreover, species and position (FieldMap system; IFER Ltd., Jilove u Prahy, Czech Republic) of each tree (i.e., distance and azimuth regarding central point of plot circle) was recorded. These tree positions were recorded for a local scale, providing information about mutual distances not only between trees within each individual plot, but also between trees among all plots.

In total, about 1000 trees were recorded and measured across all of the plots.

We calculated average tree characteristics per plot, including tree height, stem base diameter, number of trees (expressed per 10 m²), number of species (this was calculated on a plot base, since species richness relates to area size), aboveground biomass (expressed per 10 m²), contribution of tree species to number of trees, and to aboveground biomass. We averaged characteristics within plots calculated from every individual tree by using national allometric models (Table 1) to predict aboveground tree biomass (i.e., stem, branches and foliage combined) from tree diameter at stem base and tree height according to the formula:

\[ B_{\text{abvg}} = e^{(b_0 + b_1 \cdot \ln d_0 + b_2 \cdot \ln h)} \cdot \lambda \] (1)

where:

- \( B_{\text{abvg}} \)—tree aboveground biomass (kg);
- \( d_0 \)—stem base diameter (mm);
- \( h \)—tree height (m);
- \( b_0, b_1, b_2 \)—equation coefficients;
- \( \lambda \)—correction factor (see Marklund [34]).

Table 1. Coefficients (\( b_0, b_1, b_2 \)) and correction factors (\( \lambda \)) for allometric equations (Formula (1)) expressing aboveground tree biomass based on stem base diameter and tree height as independent variables.

| Tree Species           | \( b_0 \)   | \( b_1 \)   | \( b_2 \)   | \( \lambda \) | Source |
|------------------------|------------|------------|------------|-------------|--------|
| Norway spruce          | -0.579    | 2.039      | 0.297      | 1.030       | I      |
| Silver birch           | -1.545    | 2.032      | 0.586      | 1.033       | II     |
| Common rowan           | -1.586    | 2.262      | 0.299      | 1.018       | I      |
| Sycamore maple         | -1.04     | 1.998      | 0.549      | 1.024       | I      |
| Goat willow            | -0.705    | 1.81       | 0.815      | 1.021       | I      |
| Silver fir *           | -0.579    | 2.039      | 0.297      | 1.030       | I      |
| European beech         | -1.236    | 2.124      | 0.521      | 1.038       | I      |
| Trembling aspen        | -1.434    | 2.177      | 0.434      | 1.031       | I      |
| European ash           | -0.589    | 1.838      | 0.754      | 1.032       | I      |

I—models from Paštik et al., 2018; II—own unpublished data; * Silver fir was calculated by using equation derived for Norway spruce.

The models covered eight species, including Norway spruce, silver birch (Betula pendula Roth.), common rowan, sycamore maple, goat willow, European beech, trembling aspen, European ash (Fraxinus excelsior L.). Because a model for silver fir was not available
for the Slovak conditions, one for Norway spruce was implemented. Hence, we were able to express tree aboveground biomass on a tree and plot level.

Finally, we calculated tree metrics of structural and species variation within plots. First, we calculated the Gini index [35] that characterizes uneven trait values for a population. In forestry applications, this index reflects tree height evenness within a stand, thus aspects of vertical structure. The Gini index ranges from a minimum value of 0 if all individuals have the same height, to a theoretical maximum of 1.0, when all but one individual has zero height (maximum unevenness). The Gini index is continuous and directly related to size hierarchy, thus it is well linked to asymmetric competition between trees. It is therefore a good candidate to address the effects of stand inequality on stand productivity.

The Gini index (G) formula is:

\[
G = \frac{\sum_{i=1}^{n} (2i - n - 1) \cdot h_i}{\sum_{i=1}^{n} h_i (n - 1)}
\]  

(2)

where:

\( h_i \) — height of individuals (m);
\( n \) — number of individuals.

Next, we calculated the Clark–Evans aggregation index [36] that describes the nature of the spatial distribution of individuals over an area. The index is the ratio between the observed average distance to the nearest neighbor \( r_S \) and its expected value in the case of random distribution of individuals \( r_T \) in the so-called Poisson’s Forest. Based on the value of the index, it is possible to identify in the stand a deviation from the random distribution either towards a regular or clustered distribution of trees. A value \( R > 1 \) suggests ordering, while \( R < 1 \) suggests clustering.

The Clark–Evans index \( (R) \) is calculated as:

\[
R = \frac{\sum_{i=1}^{n} r_i}{n} \sqrt{\frac{A}{n^2}}
\]

(3)

where:

\( r_i \) — radius from i-individuals to nearest neighbor tree (m);
\( n \) — number of individuals;
\( A \) — area (m²).

Final, we calculated the Shannon index [37], which is used to characterize biological diversity based on richness (number of species or types) and evenness. When most abundance is concentrated to one type, and the other types are very rare (even if there are many of them), Shannon entropy approaches zero. When there is only one type in the dataset, Shannon entropy exactly equals zero (there is no uncertainty in predicting the type of the next randomly chosen entity).

The formula for the Shannon index \( (H) \) is:

\[
H = - \sum_{i=1}^{s} p_i \cdot \ln p_i
\]

(4)

where:

\( s \) — tree species;
\( p_i \) — share of species, calculated as share on basal area related to \( d_0 \).

Differences in stand characteristics between unfenced and fenced plots were tested by two-way ANOVA with main effects of treatment (unfenced vs. fenced plots) and tree species (simplified as Norway spruce, silver birch, common rowan and all other species combined), and the treatment x species interaction, followed by Fisher’s LSD test \( (p < 0.001) \). Differences between unfenced and fenced plots in a number of species per plot, species
3. Results

Overall, the main effect of herbivore exclusion via fencing influenced mean tree height \((F = 93.56; p < 0.001)\) and mean stem base diameter \((F = 51.59; p < 0.001)\), but these effects varied with tree species \((p < 0.001; \text{Figure 2a,b and Tables 2 and 3})\). However, neither tree density \((F = 0.43; p = 0.512)\) nor aboveground biomass \((F = 0.36; p = 0.549)\) was affected by the main effect of treatment \((p > 0.5)\), but did vary by the treatment x species interaction \((p < 0.001; \text{Figure 2c,d and Table 3})\). Although spruces were taller and had a larger stem base diameter, birches, rows and all other species together were shorter and thinner in unfenced than fenced plots \((\text{Fishers LSD test, } p < 0.001; \text{Figure 2a,b and Table 2})\). Spruce trees were significantly more dense and rows less dense in unfenced than fenced plots \((\text{Fishers LSD test, } p < 0.001; \text{Figure 2c and Table 2})\).

![Figure 2. Tree height (a), stem base diameter (b), number of trees (c), and aboveground biomass (d) on unfenced and fenced plots in the study area in the Kyushe region, northern Slovakia. Different letters indicate significant differences (two-way ANOVA followed by Fisher’s LSD test, see also Table 3).](image)

Table 2. Mean (SE) tree characteristics on the plots outside of a fenced area and exposed to browsing by large wild herbivores and inside a fenced area protected from herbivory in the Kysuce region, northern Slovakia, during the growing season of 2020.

| Specific Tree Species or Group of Species | Unfenced Plots | | Fenced Plots | |
|------------------------------------------|----------------|----------------|----------------|----------------|
| Nr. of Measured Trees (individuals)      | Tree Height (m) | Stem Base Diameter (mm) | Tree Density (individuals per 10 m²) | Nr. of Measured Trees (individuals) | Tree Height (m) | Stem Base Diameter (mm) | Tree Density (individuals per 10 m²) |
| Norway spruce (A)                        | 853            | 2.2 (0.1)       | 28.2 (0.1)     | 105            | 1.3 (0.1)       | 23.0 (0.1)     | 5.6 (0.1)               |
| Silver birch (B)                         | 72             | 4.4 (0.2)       | 561 (0.3)      | 34             | 5.2 (0.4)       | 77.1 (0.6)     | 1.8 (0.4)               |
| Common rowan (C)                         | 23             | 0.7 (0.1)       | 10.5 (0.1)     | 292            | 4.6 (0.1)       | 34.0 (0.1)     | 15.5 (2.8)              |
| Sycamore maple (D)                       | 5              | 0.9 (0.3)       | 7.9 (0.2)      | 2              | 0.5 (0.1)       | 7.9 (0.1)      | 0.4 (0.1)               |
| Goat willow (E)                          | 5              | 1.5 (0.3)       | 15.4 (0.4)     | 8              | 0.5 (0.1)       | 7.4 (0.1)      | 0.1 (0.1)               |
| Silver fir (F)                           | 4              | 0.9 (0.3)       | 12.4 (0.3)     | 10             | 2.2 (1.1)       | 16.6 (0.7)     | 0.2 (0.1)               |
| European beech (G)                       | 1              | 0.6 (0.1)       | 9.1 (0.1)      | 2              | 0.5 (0.1)       | 14.0 (0.0)     | 0.1                   |
| Other species (I)                        | 23             | 0.8 (0.1)       | 9.4 (0.1)      | 96             | 2.8 (0.1)       | 24.2 (0.1)     | 5.1 (1.3)               |
| All species together (A–I)               | 473            | 2.4 (0.1)       | 29.1 (1.1)     | 527            | 3.7 (0.1)       | 32.6 (0.1)     | 28.0 (2.2)              |

*Forests 2021, 12, 737*
Table 3. F values and p values from two-way ANOVA for basic stand characteristics considering treatment (unfenced vs. fenced) and tree species (includes Norway spruce, silver birch, common rowan, and others) and their combined effect on the stand characteristics.

| Variable                      | Factor         | F-Value | p-Value |
|-------------------------------|----------------|---------|---------|
| Tree height (m)               | Treatment      | 93.56   | <0.001  |
|                               | Species        | 85.74   | <0.001  |
|                               | Treatment x species | 55.74   | <0.001  |
| Stem base diameter (mm)       | Treatment      | 51.59   | <0.001  |
|                               | Species        | 98.94   | <0.001  |
|                               | Treatment x species | 23.43   | <0.001  |
| Number of trees per 10 m²     | Treatment      | 0.43    | 0.512   |
|                               | Species        | 16.94   | <0.001  |
|                               | Treatment x species | 27.45   | <0.001  |
| Aboveground biomass per 10 m² | Treatment      | 0.36    | 0.549   |
|                               | Species        | 7.11    | <0.001  |
|                               | Treatment x species | 19.46   | <0.001  |

We identified eight tree species on the plots outside and nine species inside the fenced exclosure (Table 2). At the same time, the number of tree species per plot was significantly lower in unfenced than fenced plots (Table 4). Spruce had a greater aboveground biomass and rowan a lower biomass on unfenced than fenced plots (Figure 2d). The species share of the number of trees (Table 4), and to aboveground biomass (Table 4), per plot differed among species. Spruce contributed more to both measures on unfenced than fenced plots, and on the contrary, rowan contributed significantly less (Table 4).

Table 4. A comparison of mean values, standard errors, and coefficients of variability for number of species per plot, species share expressed on number of trees (separately for Norway spruce, silver birch, common rowan, and other species), and species share expressed on aboveground biomass (separately for Norway spruce, silver birch, common rowan, and other species) between unfenced and fenced plots. Statistical differences were proved by Student’s t-test.

| Variable                      | Species                  | Unfenced Plots                      | Fenced Plots                          | Unfenced vs. Fenced Plots |
|-------------------------------|--------------------------|-------------------------------------|---------------------------------------|---------------------------|
|                               |                          | Mean (Standard Error) [Coefficient of Variability] | t-Value (p-Value) |                      |
| Number of species per plot    | all species              | 3.27 (0.31) [0.35]                  | 4.80 (0.37) [0.29]                   | 3.300 (<0.001)           |
| Species share expressed       | Norway spruce            | 71.02 (6.47) [0.34]                 | 21.66 (4.21) [0.19]                  | –6.620 (<0.001)          |
| on number of trees (%)        | silver birch             | 7.99 (6.00) [0.36]                  | 7.85 (4.92) [0.43]                   | –1.719 (0.097)           |
|                               | common rowan             | 4.76 (1.37) [0.93]                  | 51.77 (6.67) [0.48]                  | 7.150 (<0.001)           |
|                               | other species            | 5.80 (1.72) [0.90]                  | 18.73 (5.60) [1.12]                  | 2.285 (0.030)            |
| Species share expressed       | Norway spruce            | 68.82 (9.64) [0.52]                 | 8.45 (2.03) [0.90]                   | –6.346 (<0.001)          |
| on aboveground biomass (%)    | silver birch             | 30.72 (9.71) [1.18]                 | 32.42 (7.12) [0.82]                  | 0.146 (0.884)            |
|                               | common rowan             | 0.16 (0.07) [1.63]                  | 49.44 (8.83) [0.67]                  | 5.778 (<0.001)           |
|                               | other species            | 0.30 (0.21) [1.33]                  | 9.69 (4.56) [1.17]                   | 2.228 (0.034)            |

Although mean tree aboveground biomass on unfenced plots (33.5 kg ± 5.3 per 10 m²) was not significantly different from that on fenced plots (29.6 ± 4.1 kg per 10 m²), their composition regarding species was very different (Table 4). While nearly 69% of tree aboveground biomass on unfenced plots represented spruce trees, this share was only about 8% on fenced plots. On the other hand, rowan trees contributed <1% to tree aboveground biomass on unfenced plots, but as much as 49% on unfenced plots. Biomass of spruce was 17.5 kg per 10 m² greater on unfenced than fenced plots (Figure 3). Rowan biomass clearly dominated on fenced plots, providing 17.2 kg per 10 m² more than on unfenced plots. Other species had relatively small (3.2 kg per 10 m²) to negligible (i.e., birch, 1.0 kg per 10 m²) differences in biomass between treatments.
Trees in unfenced and fenced plots also differed in their frequency among height classes (Figure 4). Although Norway spruce and silver birch were more prevalent in the unfenced than fenced plots in all height classes, rowan and other species showed the opposite pattern. In the unfenced plots, common rowan and other species did not exceed height of 1.5 m, these species occurred in all height classes on the fenced plots. For instance, common rowan trees on fenced plots were most frequently in the height class of 4.6-6.0 m.
Although the Gini index did not differ between unfenced and fence plots ($p = 0.22$), the Clark–Evans index ($p < 0.001$) was higher and Shannon index ($p < 0.001$) was lower in the unfenced than fenced plots (Table 5). Moreover, all three indices manifested higher variability of values (see coefficients of variability in Table 5) among unfenced than among fenced plots.

Table 5. A comparison of mean values, standard errors, and coefficients of variability for Gini, Clark–Evans, and Shannon index between the plots within unfenced (open to herbivores) and fenced (herbivore exclusion) plots. Gini H index (indicates height evenness in stand—the higher value the higher evenness, Clark–Evans index (indicates space distribution of trees in stand—the higher value the more regular tree allocation), and Shannon diversity index (indicates species diversity in stand—the higher value the richer species composition) between unfenced and fenced plots. Statistical differences were proved by Student’s $t$-test.

| Index          | Unfenced Plots (Mean (Standard Error) [Coefficient of Variability]) | Fenced Plots (Mean (Standard Error) [Coefficient of Variability]) | $t$-Value ($p$-Value) |
|----------------|---------------------------------------------------------------------|------------------------------------------------------------------|-----------------------|
| Gini           | 0.36 (0.05) [0.52]                                                  | 0.32 (0.03) [0.35]                                               | −1.250 (0.222)        |
| Clark–Evans    | 0.98 (0.10) [0.38]                                                  | 0.75 (0.04) [0.20]                                               | −3.734 (<0.001)       |
| Shannon        | 0.32 (0.14) [1.64]                                                  | 0.78 (0.17) [0.82]                                               | 3.998 (<0.001)        |

### 4. Discussion

#### 4.1. Herbivores Influence to Basic Stand Characteristics

Our results suggested that presence of large wild herbivores modified tree characteristics in a young post-disturbance forest in the Kysuce region, northern Slovakia. We found that tree species that are both attractive as forage for herbivores and have high regeneration potential, such as rowan and goat willow (e.g., [18,38–40]), were abundant in areas fenced off from herbivores, but nearly absent outside the fenced area. On the other hand, Norway spruce, a tree species generally little consumed by large herbivores because of physical and chemical defenses [13], was larger and more abundant outside of the herbivore exclosure. Silver birch was similar in size and abundance inside and outside of the exclosure. Because it contains plant secondary metabolites such as botulin (a type of terpenoid; ref. [16]), birch is a much less attractive forage for large herbivores [41]. Our findings demonstrate the importance of herbivory on the composition of forests, which in turn could influence production of timber and ecosystem dynamics.

Herbivores have the potential to reduce the overall tree biomass that might influence not only timber resources, but also ecosystem values of the forest. For example, because trees sequestrate carbon, trees play an important role in carbon cycling, which is increasingly important in the face of ongoing climate change (e.g., [42]). A review by Forbes et al. [1] suggested that large herbivores reduce carbon sequestration by reducing tree biomass. However, although browsing by large herbivores in our study area influenced the aboveground biomass of individual tree species, the overall tree biomass stayed nearly the same. By reducing palatable tree species, herbivores created space for the growth of Norway spruce, which was very productive at the site. The stimulated growth of Norway spruce partly compensated for losses of rowan and some other broadleaved species. The biomass of silver birch, a moderately palatable tree species, remained constant regardless of herbivory. The influence of large herbivores on overall tree biomass and carbon sequestration likely depends on the species composition of the forest relative to palatability, among other variables.

Our analysis of tree height frequency indicated that palatable tree species (i.e., rowan and group of other rarer species), nearly exclusively belonged to the first height class (1.5 m). Likely, high pressure for forage by large herbivory prevented these species from growing to the same heights found in the fenced areas, which were up to four times taller. The trees outside the exclosure were either shorter because of repetitive terminal browsing
4.2. Herbivores Influence on Structure and Diversity of Stand

Browsing by large herbivores also influenced aspects of structural diversity in forest plots. Although it did not significantly influence the evenness of tree heights as measured by the Gini index, we found that spatial distribution of trees was more regular (less clustered) in the unfenced plots than fenced ones, as measured by the Clark–Evans index. Although the mechanism for this effect is not entirely clear, we suggest that it might be a secondary effect of browsing via changes in tree species composition. Because young rowan trees grow in clusters [45], browsing by large herbivores reduces the composition of rowan in the stand likely also reduces clustering and increases the Clark–Evans index. However, the Clark–Evans index was also more variable as were the Gini and Shannon indices (expressed as coefficient of variability) in the unfenced than fenced plots, suggesting more unequal height, spatial distribution, and species distribution among sides (in our case represented by individual plots with a size of about 13 m$^2$) under large herbivore pressure. Although seemingly counterintuitive, this difference might be a matter of scale. Herbivores might enhance natural heterogeneity in stand characteristics among microclimates. However, more research is required to understand the influence of herbivory on spatial and structural diversity of mixed forest stands.

Our results indicated that large herbivores reduced species richness and diversity, primarily by lowering the frequency and size of common rowan and goat willow, but also the admixed trace species such as sycamore maple, silver fir and trembling aspen. In other systems, specifically spruce-dominant forests in Czechia, intensive large herbivore pressure led to decreased diversity of young stands [46]. Browsing of infrequent admixed tree species can decrease tree species diversity and sometimes may even lead to species loss [47]. On the other hand, in some situations herbivores might act as “keystone consumers”, where by damaging the most abundant tree species in regeneration they might release other tree species and increase tree diversity [48]. However, the positive effect of herbivores on tree diversity is likely uncommon, because most studies (see review of Bernes et al. [23]) that compared tree species diversity between unfenced and fenced areas have shown increased diversity when herbivores were excluded. For example, in subalpine conditions in Japan, deer-proof fencing was suggested as necessary tool for conservation of endangered and rare plant species [49].

Although much previous work has explored the effects of large herbivores on timber production, forests and wildlife provide a variety of ecosystem services important for humankind (e.g., [50,51]). Mixed forests containing both conifers and a high portion of broadleaves are generally more resistant to a variety of harmful agents, which is increasingly important as the climate continues to change (e.g., [52]). Therefore, maintaining tree species diversity might help mitigate negative impacts of climate change on the functioning of forest ecosystems [53], and understanding the complex relationship between forest herbivores and diversity of forest ecosystems is a critical step in this endeavor.

5. Conclusions

Our results showed that excluding large herbivores as stands were establishing over 10 years increased trees species richness and diversity by reducing the contribution of Norway spruce to tree density and aboveground biomass in forest stands. This finding is somewhat paradoxical because Norway spruce is allochthones (not native) to the region, which provides suboptimal ecological conditions for the species and recently has been declining due to climatic extremes and bark beetle outbreaks. On the other hand, the...
natural regeneration of Norway spruce seedlings is still extremely abundant and dense, appearing even under gradually declining old spruce-dominant stands. Hence, young spruce trees are expanding and competing with other species, despite the attempt of foresters to convert tree species composition towards mixed forests with high portion of broadleaved species.

Therefore, our study, at least on the local scale, suggested that large herbivore browsing pressure retards growth of broadleaved trees (except silver birch) and weakens interspecies competition, thus furthering undesirable expansion of Norway spruce (the species in mature status would be again very prone to damage by harmful agents, especially wind, drought, and bark beetles). Hence, we can conclude that converting spruce monocultures to mixed stands is difficult or impossible in forests faced with heavy browsing pressure by wild large herbivores. Because fencing adequate to exclude large herbivores is extremely expensive, this preventive measure is impractical for reducing herbivory where its populations are high. Hence, reducing herbivore populations, especially red deer, is likely required to establish, protect, and maintain mixed forests in forests of the Kysuce region, and likely within similar temperate forests in across Europe. In a broader view, managing interactions between wild large herbivory and forest ecosystems would be important part of adaptation strategies for forestry under the ongoing climate change.

Author Contributions: Conceptualization, B.K. and V.Š.; data curation, V.Š. and J.P.; funding acquisition, B.K.; investigation, B.K., V.Š. and J.P.; methodology, V.Š. and B.K.; visualization, V.Š.; supervision, B.K.; writing—original draft preparation, B.K. and L.A.S.; writing—review and editing, all authors. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the projects APVV-19-0387, APVV-16-0086, and APVV-18-0086 from the Slovak Research and Development Agency and also by grant “EVA4.0”, No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by OP RDE.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Acknowledgments: The authors would like to express thanks to Ladislav Kulla for establishing and managing the Husárik RDE.

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

References
1. Forbes, E.; Cushman, J.H.; Burkepile, D.E.; Young, T.P.; Klope, M.; Young, H.S. Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. *Funct. Ecol.* 2010, 33, 1597–1610. [CrossRef]
2. Maron, J.L.; Crone, E. Herbivory: Effects on plant abundance, distribution and population growth. *Proc. R. Soc. B* 2006, 273, 2575–2584. [CrossRef]
3. Červený, J.; Hell, P.; Slamečka, J. *Otto’s Encyclopedia Game Management*; Otto’s Publisher: Praha, Czech Republic, 2010; p. 591.
4. Gordon, I.J.; Hester, A.J.; Festa-Bianchet, M. The management of wild large herbivores to meet economic, conservation and environmental objectives. *J. Appl. Ecol.* 2004, 41, 1021–1031. [CrossRef]
5. Spake, R.; Bellamy, C.; Gill, R.; Watts, K.; Wilson, T.; Ditchburn, B.; Eigenbrod, F. Forest damage by deer depends on cross-scale interactions between climate, deer density and landscape structure. *J. Appl. Ecol.* 2020, 57, 1376–1390. [CrossRef]
6. White, M.A. Long-term effects of deer browsing: Composition, structure and productivity in a northeast Minnesota old-growth forest. *For. Ecol. Manag.* 2012, 269, 222–228. [CrossRef]
7. Kiffner, C.; Rössiger, E.; Trisl, O.; Schulz, R.; Rühe, F. Probability of recent bark stripping damage by red deer (*Cervus elaphus*) on Norway spruce (*Picea abies*) in as low mountain range in Germany—A preliminary analysis. *Silva Fenn.* 2008, 42, 125–134. [CrossRef]
8. Schafer, D.; Prati, D.; Schall, P.; Ammer, C.; Fischer, M. Exclusion of large herbivores affects understorey shrub vegetation more than herb vegetation across 147 forest sites in three German regions. *PLoS ONE* 2019, 14, 0218741. [CrossRef] [PubMed]
9. Milner, J.M.; Nilsen, E.B.; Andreassen, H.P. Demographic side effects of selective hunting in ungulates and carnivores. *Conserv. Biol.* 2007, 21, 35–47. [CrossRef] [PubMed]
10. Burbaité, L.; Csányi, S. Red deer population and harvest changes in Europe. *Acta Zool. Litu.* 2010, 20, 179–188. [CrossRef]
11. Bučko, J.; Cibula, R.; Štefančiková, E.; Zimová, L.; Lehocká, K.; Kyšefová, M.; Frič, L. *Game Management Annual Book of the Slovak Republic of 2010*; National Forest Centre: Zvolen, Slovak, 2010; p. 181. (In Slovak)
43. Konopka, B.; Pajtik, B. Why was browsing by red deer more frequent but represented less consumed mass in young maple than ash trees? *J. For. Sci.* 2015, 61, 431–438. [CrossRef]

44. Renaud, P.C.; Verheyden-Tixier, H.; Dumont, B. Damage to saplings by red deer (*Cervus elaphus*): Effect of foliage height and structure. *For. Ecol. Manag.* 2003, 181, 31–37. [CrossRef]

45. San-Miguel-Ayanz, J.; De Rigo, D.; Caudulo, G.; Durrant, T.H.; Mauri, A. *European Atlas of Forest Tree Species*; Publication Office of the European Union: Luxembourg, 2016; p. 200.

46. Merganič, J.; Russ, R.; Beranová, J.; Merganičová, K. Assessment of the impact of deer on the diversity of young trees in forest ecosystems in selected localities of the Czech Republic. *Ekológia* 2009, 28, 424–437. [CrossRef]

47. Martin, J.L.; Daufresne, T. Introduced species and their impacts on the forest ecosystem of Haida Gwaii. In Proceedings of the Cedar Symposium, Haida Gwaii, Canada, 28–30 May 1996; Wiggins, G.G., Ed.; Ministry of Forests: Queen Charlotte Island, BC, Canada, 1999; pp. 69–85.

48. Gill, R.M.A. A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. *Forestry* 1992, 65, 365–388. [CrossRef]

49. Koyama, A.; Uchida, K.; Ozeki, M.; Iwasaki, T.; Nakahama, N.; Suka, T. Conservation of endangered and rare plants requires strategies additional to deer-proof fencing for conservation of sub-alpine plant diversity. *Appl. Veg. Sci.* 2021, 24, e12553. [CrossRef]

50. Harrison, P.A.; Berry, P.M.; Simpson, G.; Haslett, J.T.; Bličarska, M.; Bucur, M.; Dunford, R.; Egoš, B.; Garcia-Llorente, M.; Geamana, N.; et al. Linkages between biodiversity attributes and ecosystem services: A systematic review. *Ecosyst. Serv.* 2014, 9, 191–203. [CrossRef]

51. Mori, A.; Lertzman, K.P.; Gustafsson, L. Biodiversity and ecosystem services in forest ecosystems: A research agenda for applied forest ecology. *J. Appl. Ecol.* 2017, 54, 12–27. [CrossRef]

52. Lindner, M.; Maroschek, M.; Netherer, S.; Kremer, A.; Barbati, A.; Garcia-Gonzalo, J.; Seidl, R.; Delzon, S.; Corona, P.; Kolström, M.; et al. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For. Ecol. Manag.* 2010, 259, 698–709. [CrossRef]

53. Hisano, M.; Searle, E.B.; Chen, H.Y.H. Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. *Biol. Rev.* 2017, 93, 439–456. [CrossRef]