Herbivory Exclosure

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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.

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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][16][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][20][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.

2. 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][24][25][26]), 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 [27]. 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., [28]). 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 or because smaller individuals persisted by hiding from herbivores within the shelter from groups of large trees, mostly clustered Norway spruces and silver birches. Similarly, our previous work [29] showed that branch and terminal browsing on broadleaved species by red deer occurred most frequently (about 70% of all cases) at 76–

150 cm from the ground level. The heights at which trees are browsed decrease with body size, typically focusing at the height of their shoulders [30].

3. 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 [31], 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 [32]. Browsing of infrequent admixed tree species can decrease tree species diversity and sometimes may even lead to species loss [33]. 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 [34]. 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 [35].

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., [36][37]). 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., [38]). Therefore, maintaining tree species diversity might help mitigate negative impacts of climate change on the functioning of forest ecosystems [39], and understanding the complex relationship between forest herbivores and diversity of forest ecosystems is a critical step in this endeavor.

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