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Heavy Ungulate Pressure behind the Disappearance of Regeneration in Hungarian Forests

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Abstract: Ungulate populations have surged to unsustainable levels in multiple areas in recent decades due to human intervention, making forestry and conservation practices arduous. The population of ungulates is also currently displaying a rising trend in Hungary, prompting decision-makers to commence substantial reduction efforts. Our study examined the ungulate impact in three forested regions of Hungary, employing field survey sampling plots on almost 50,000 hectares. Our findings revealed that regeneration browsing and soil disturbance were evenly high in these areas, while the cover of the regeneration layer was extremely low. Ungulate pressure was suspected as the cause of the lack of regeneration. Based on habitat and vegetation conditions, we divided our sample as favourable and unfavourable for regeneration. The cover of the regeneration categories was not significantly different between the two sets. The evidence of the direct indicators, including browsing and soil disturbance, coupled with the lack of regeneration, leads us to infer indirect signs of ungulate pressure. The absence of older and taller vegetation in the area also suggests long-standing ungulate pressure. Our investigation suggests that the high ungulate population can cause low abundance, even the lack of regeneration, not only locally but also at a regional scale.

Keywords: ungulate impact; browsing; soil disturbance; overabundance; regeneration failure

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1. Introduction

Ungulates are integral parts of forest communities. Due to the eradication of top predators, the extinction of large herbivores, the support of economically valuable ungulates and the development of organised forestry, the effects of these animals are manifested in different ways now. Under natural conditions, herbivores consume less than 10% of the biomass [1], and they provide a biodiversity-enhancing function through moderate soil disturbance (as a biotic natural disturbance) [2] and selective foraging [3]. Since ungulates can transform communities through their role of herbivory, they can also be considered keystone species [4]. Ungulate damage occurs when foraging behaviour (grazing, browsing, bark stripping, rooting, etc.) and habitat modification (soil compaction, erosion) initiate changes in the ecosystem or reach such a magnitude, which adversely affects conservation and management goals.

Since the second half of the 20th century, the ungulate population in Europe has been increasing [5] to such an extent that some populations have often reached a local overabundance [6,7]. Despite management efforts to keep the population at an acceptable level, the legislative changes, afforestation activities, abandonment of agricultural lands, conscious propagation in support of trophy hunting, and the introduction of alien species promoted their growth [8]. Attempts have already been made to determine the ungulate density negatively affecting the ecosystem [9–11]. Apart from the population density, the intensity of the ungulate pressure is determined by the interplay of landscape attributes, land use, climate, and forest composition and structure [12,13]. These properties need to be studied further, since there are few results about their relationship with ungulate pressure [14].

By trampling, soil disturbance, bark stripping and browsing, overabundant ungulate populations can obstruct forest growth, cause economic damage, threaten ecological stability, and reduce biodiversity and the effectiveness of the forest's protective function [8,15]. Wild boars (*Sus scrofa* L.) dig out tree propagules (masts), rhizomes, and bulbs of herbaceous plants and associated fungi from the soil, causing direct damage [16]. Due to soil disturbance, they provide a constantly renewed surface, thus promoting the establishment and spread of invasive and nitrophilous plants that can compete with tree regeneration [17]. Through their continuous, repeated browsing, herbivorous mammals can even make trees and shrubs completely unviable [1]. The lethality of browsing could be easily underestimated because of the disappearance of dead plants [11]. Intensive browsing can result in a transformation to grasslands or even a complete loss of forest habitats [18]. The pressure on regeneration can be quite high, especially in winter, when no other food is available [11].

Hungary has recently observed a dramatic increase in ungulate populations (Table 1). Ungulate pressure is widespread and significantly influences the composition and the structure of tree regeneration (Figure 1). This statement is supported by the results from 300 experimental plots of a nationwide monitoring project ("Assessment of Game Damages in Forests") between 2001 and 2008 [19] and by forestry practice. However, some studies have found that the effects of ungulates have an impact on a local rather than a regional scale [20,21]. Nowadays, the situation seems so severe that in some places, reforestation cannot be successful without installing ungulate exclusion fences, even during the African Swine Fever (ASF) epidemic [22]. Degradation due to ungulate damage is also a severe problem in valuable conservation areas, demonstrated by exclusion experiments (e.g., [23,24]). Still, according to some viewpoints, this effect may be overemphasised [25].

Table 1. Estimated ungulate population sizes and harvest numbers in 1960 and 2020 in Hungary [26].

Ungulate Species	Population (10^3 ind.)		Harvest (10^3 ind.)	
	1960	2020	1960	2020
Red deer (*Cervus elaphus* L.)	14.0	119.1	3.8	65.6
European fallow deer (*Dama dama* L.) *	0.9	40.9	0.7	16.9
Roe deer (*Capreolus capreolus* L.)	68.8	375.5	3.7	108.7
European mouflon (*Ovis aries musimon* Pall.) *	1.4	12.8	0.2	3.6
Wild boar (*Sus scrofa* L.)	8.3	83.0	3.9	181.1

* Not native to Hungary.

Figure 1. (**A**) A common scene in Hungary, where there is no regeneration and shrub layer, and no shoots can survive below c.a. 1.5 m. (**B**) In gaps and forest edges, unviable woody regeneration with a distorted, bonsai-like physiognomy is quite common.

A field survey of 59,616 sampling points was carried out in an area of nearly 50,000 ha within the framework of the "Multipurpose assessment serving biodiversity conservation in the Carpathian region of Hungary" project ("Swiss Contribution Project"—hereafter SCP) [27]. Data on tree regeneration, ungulate damage and habitat characteristics were collected, among other variables. Based on these data, here we present an overview of the abundance and condition of tree regeneration and the possible role of ungulate pressure, with a particular focus on exploring possible causes of the widespread lack of tree regeneration at a regional scale. We are aware that even in the complete lack of ungulate pressure, certain conditions (e.g., too young, too dense canopy layer) do not favour tree regeneration. To resolve this, we divided our sample into two groups, characterised by favourable and unfavourable conditions for regeneration, and then we compared these two groups.

2. Materials and Methods

2.1. Study Areas

The study areas are located in the Börzsöny, Mátra and Aggtelek Mts. of Hungary (Figure 2). The bedrock of the Börzsöny Mts. is predominantly andesite of volcanic origin. Its highest peak is 939 m. The mean annual temperature is 7.5–9.0 °C [28], and the annual precipitation is 600–850 mm [29]. The Mátra Mts. are also volcanic, with bedrock composed mainly of andesite and rhyolite tuff. Its highest peak is also the country's highest point, at 1014 m. The mean annual temperature is 7.0–9.0 °C, and the annual precipitation is 550–800 mm [30]. The Aggtelek Mts. are of limestone origin. Its highest peak is 605 m. The mean annual temperature is 8.5–9.0 °C, and the annual precipitation is 650–700 mm [31].

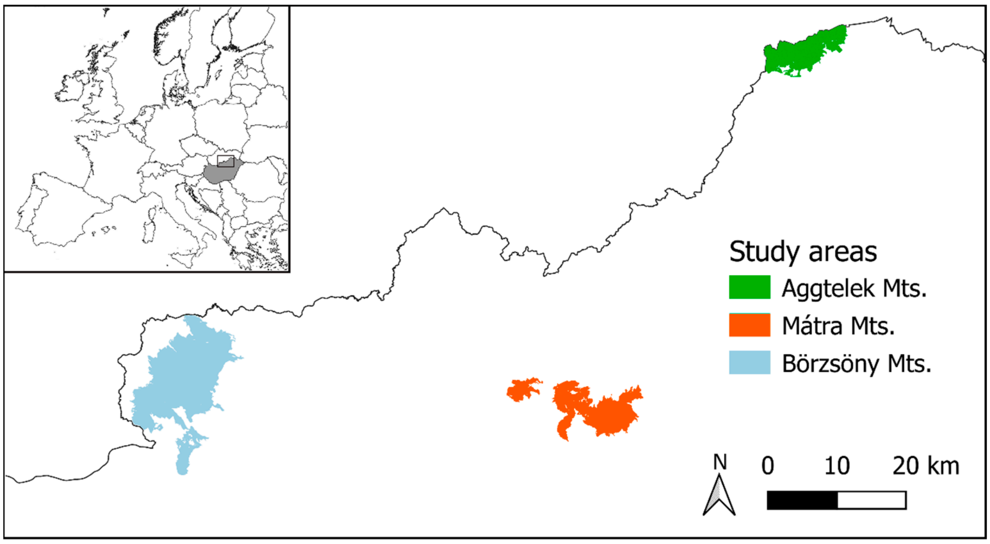

Figure 2. Location of the study areas along the northern border of Hungary.

At lower elevations in the Börzsöny and Mátra Mts., vegetation is characterised by stands of sessile oak (*Quercus petraea* (Matt.) Liebl.) and Turkey oak (*Quercus cerris* L.). The forests above this vegetation zone are dominated by common hornbeam (*Carpinus betulus* L.) and sessile oak. In the highest areas, on north-facing slopes and in valleys, European beech (*Fagus sylvatica* L.) dominates. Because of the occurrence of limestone bedrock and varied karst geomorphology, vegetation in the Aggtelek Mts. is more diverse with mixed oak-hornbeam forests, beech woods and characteristic scrub woods with pubescent oak (*Quercus pubescens* Willd.).

Most of the studied forests are managed according to a uniform shelterwood system, resulting in even-aged forests. Continuous cover forestry is also practised on a smaller scale, and there are also forests not used for timber production. A catastrophic abiotic natural disturbance (ice-break) occurred in December 2014. It affected the study areas on a landscape level: ca. 1100 ha of forest stands were uprooted, and 1500 ha suffered crown loss within our study area in the Börzsöny Mts. [32]. The forests of the Mátra Mts. were similarly severely affected, but we do not have quantitative data on the extent. The Aggtelek Mts. were not damaged.

The estimated population density and composition of ungulates differ in the three study areas. We used data from the National Game Management Database (NGMD) [33] to calculate population density for our study areas (Table 2). However, these calculations are not entirely reliable due to the lack of information on the distribution within Game Management Regions (GMRs) and habitat use of the population caused by habitat fragmentation [3]. A study found that the simulated red deer population size between 1969 and 1989 was 40%–60% higher than officially reported data [34]. We believe that a similar underestimation is possible for all populations of the examined ungulate species. Moreover, we are unable to demonstrate an explicit trend for the study areas since there have been changes in the regulatory system during our data collection period, and the GMRs had different boundaries previously. Similarly to the national data shown in Table 1, an upward trend can also be observed here [26].

Table 2. Calculated ungulate population density (ind./km^2) in 2017 within the Game Management Regions (GMRs), which include our study areas [33]. The Börzsöny-Gödöllő GMR includes Börzsöny Mts. (study area share: 12.7%); the Bükk GMR includes Mátra Mts. (study area share: 2.9%); the Cserehát-Aggtelek GMR includes Aggtelek Mts. (study area share: 4.3%).

Ungulate Species	Population Density (ind./km^2) in Game Management Regions		
	Börzsöny-Gödöllő GMR	Bükk GMR	Cserehát-Aggtelek GMR
Red deer (*Cervus elaphus* L.)	2.0	1.7	1.5
European fallow deer (*Dama dama* L.) *	0.3	0.1	0.0
Roe deer (*Capreolus capreolus* L.)	3.0	2.4	2.6
European mouflon (*Ovis aries musimon* Pall.) *	0.4	0.5	0.0 *
Wild boar (*Sus scrofa* L.)	2.1	1.5	1.7

* According to our experience, at least some individuals live in the area.

Generally, red deer and wild boar dominate, and roe deer are marginal everywhere. The mouflon is mainly overabundant in southern parts of the Börzsöny and Mátra Mts. There are no fallow deer in the Aggtelek Mts.; they appear sporadically in the Mátra and Börzsöny Mts.

2.2. Data

Field surveys were carried out in these three Hungarian mountain areas during the vegetation periods of 2014, 2015, and 2016 in the frame of the SCP project. Data collection was carried out mainly in circular plots of 500 m^2 (Figure 3) along a grid of 50, 70, or 100 m resolution. Data collected at the plot level were as follows: main category (regenerating–young–mature stands), canopy closure, tree species composition within diameter classes, standing and lying deadwood, herbaceous plants (with particular emphasis on disturbance indicating nitrophilous herbs), tree-related microhabitats, severity and type of soil disturbance, and rock cover. The subplot is a smaller concentric sampling unit (30 m^2) (Figure 3). In the subplot, the following variables were recorded: shrub cover and composition, cover of low (0–0.5 m) and high (0.5–2.5 m) regeneration, species composition, and browsing intensity. In this study, only the most important components of the protocol are highlighted; the full list and detailed methodology are available in our article [27]. The variables used for this paper are presented in more detail.

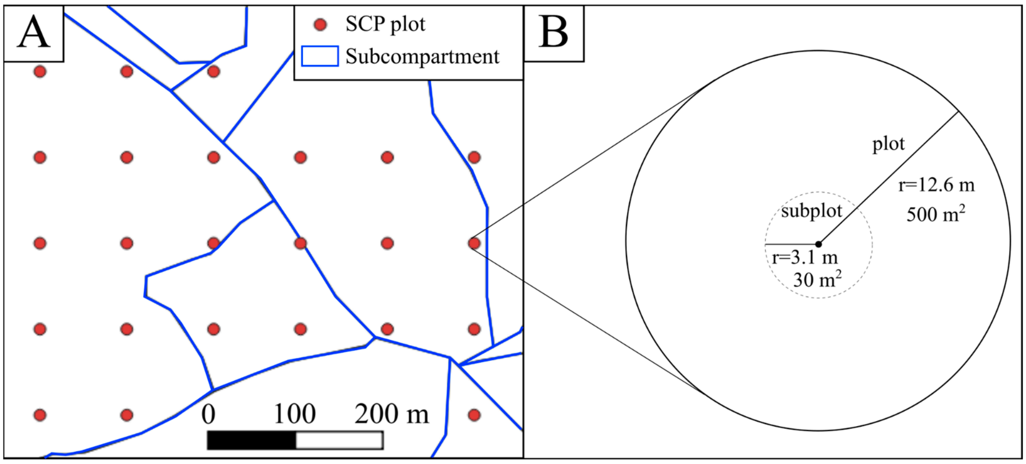

Figure 3. Structure of the SCP (Swiss Contribution Project) sampling units. (**A**) The polygons show forest subcompartments, the spatial units of the National Forestry Database (NFD), and the circular units, which are the SCP plots along a 100 m grid. (**B**) The structure of a plot and a subplot. The data originates from these different sampling units; see text for details.

A plot was considered a mature forest stand if the canopy closure of trees higher than 5 m was at least 20%.

The canopy closure was determined by visual estimation, with 5% accuracy for trees higher than 2.5 m; shrub species were not taken into account.

The cover values (*CV*) of the herbaceous plants, soil disturbance, rocks, and tree regeneration were recorded in uneven interval categories. The herbaceous cover was recorded on an ordinal scale ($CV \leq 1\%$, $1\% < CV \leq 5\%$, $5\% < CV \leq 20\%$, $20\% < CV \leq 50\%$, $50\% < CV$). For plots with a cover higher than 5%, dominant (relative cover above 20%) herbaceous species and the relative importance of native nitrophilous disturbance indicators were also recorded.

We recorded the degree of soil disturbance using an ordinal scale ($CV \leq 1\%$, $1\% < CV \leq 5\%$, $5\% < CV \leq 20\%$, $20\% < CV \leq 50\%$, $50\% < CV$). We distinguished the type of disturbance according to whether it was induced by wheel, skidding, ungulates, or other causes (e.g., uprooted tree). The factors causing soil disturbance had to be selected based on multiple choices. Soil disturbance by ungulates meant primarily the rooting of the wild boar and, in a smaller proportion, the presence of wallows, game trails, soil erosion, and acorn scraping [35].

The degree of rock cover was also recorded on a different ordinal scale ($CV \leq 5\%$, $5\% < CV \leq 20\%$, $20\% < CV \leq 50\%$, $50\% < CV$).

The cover of low and high tree regeneration (subplot) was recorded separately, also on an ordinal scale ($CV \leq 1\%$, $1\% < CV \leq 5\%$, $5\% < CV \leq 20\%$, $20\% < CV \leq 50\%$, $50\% < CV$). We used the most characteristic type of 6 possible categories for characterising browsing intensity within the subplot. We considered the regeneration to be "unbrowsed" if neither the terminal nor the side shoots of the last 2–3 years were browsed. The regeneration was categorised as "slightly browsed" where only the terminal shoots were browsed. It was "heavily browsed" if all shoots had been regularly browsed, but the plant was not deformed. The regeneration was classified as "bonsai-like" if the shoot system was distorted by repeated, intense browsing. "Inconclusive" value was given if the regeneration consisted of new, not yet browsable seedlings, e.g., first-year seedlings with cotyledons. In addition, the "NA" category is also possible, in which case the browsing is not interpretable because there was no regeneration in the subplot. The average/dominant browsing intensity of the regeneration in the 30 m^2 subplot was recorded (e.g., if 70% of the individuals were heavily browsed and 30% were slightly browsed, overall, they were considered highly browsed, or if 40% were unbrowsed, 20% were slightly browsed, and 40% were heavily browsed, then overall they were classified as slightly browsed). If the cover of the high regeneration exceeded 5%, browsing intensity was applied to this height class only; otherwise, it was determined for the entire regeneration. The measurement was made by visual estimation from the centre of the subplot. This variable expresses the browsing and grazing of all the presented ungulates (Tables 1 and 2).

We needed data on stand age for our analyses, and this was not recorded in the SCP survey; therefore, we had to retrieve it from an external data source. The National Forestry Database (NFD) contains data for all forests in Hungary [36]. The units of the NFD are forest subcompartments, which are delimited by climatic, habitat, stand, and administrative characteristics (Figure 3). The subcompartments vary in size (a few hectares on average). Age data per tree cohorts (all the trees, which are different in some parameter—species, DBH, age) are included in the NFD for each subcompartment. We defined the stand age for forest subcompartments by the age of the upper (dominant) canopy (excluding the age of the retention trees from the analysis). For each SCP plot, the age of the dominant cohort of the forest subcompartment was assigned as additional data.

As additional data, we used slope steepness derived from a Digital Elevation Model (DEM) prepared by Zsolt Pataki during the SCP project. This dataset has a spatial resolution of 5 m; therefore, the slope data were averaged to the SCP plot level.

2.3. Data Analysis

Only plots classified as mature stands were considered for our analyses (N = 56,774 plots). We examined frequency distributions for variables related to ungulate pressure (soil disturbance, browsing, cover of regeneration).

We made an attempt to define favourable habitat and vegetation conditions under which (in the absence of ungulate pressure) we would expect abundant regeneration. Soil disturbance was excluded as it is directly indicating ungulate pressure. Shrub cover and nitrophilous herbaceous cover are also not considered further, as they are likely to be indirectly influenced by the ungulates. We defined the favourable conditions for regeneration as follows: mature stands with an average slope steepness < 25 degrees, rock cover $\leq$ 50%, stand age > 50 years, and canopy closure between 20 and 80%. After simultaneous filtering of all variables, N = 10,423 plots were classified as favourable for regeneration. All the other plots (N = 46,351) were classified as unfavourable for regeneration due to the presence of one (or more) of the non-ideal factors. The frequency of regeneration cover categories was compared between plots with favourable and unfavourable conditions. Finally, the relationship between the regeneration cover and the soil disturbance categories was investigated only within the plots with favourable conditions for the regeneration. In this case, we used non-parametric Kruskal–Wallis and Dunn post-hoc tests to look for potential differences. Statistical analyses were performed using the R 4.0.4 software [37] base and 'dunn.test' [38] packages.

3. Results

Figure 4 shows the frequency distributions of the indicators related to ungulate pressure.

Figure 4A shows that 49% of the subplots did not have low regeneration, and 70% did not have high regeneration at all. The 1% < $CV \leq$ 5% category is the second most common in both cases. Cumulatively, 84% and 85% of the subplots had $\leq$ 5% cover of low and high regeneration, respectively. Figure 4B shows that in almost all cases, the surveyors identified the causes of major soil disturbance as (partially) ungulate-caused. This is not an exclusive categorisation. There may be other agents causing soil disturbance. Intensive soil disturbance is typical for the sampling areas.

Most frequently, the regeneration was heavily browsed (Figure 4C). If there was any regeneration, 62% was intensively browsed.

We assumed that the widespread lack of tree regeneration is (at least partly) caused by ungulates.

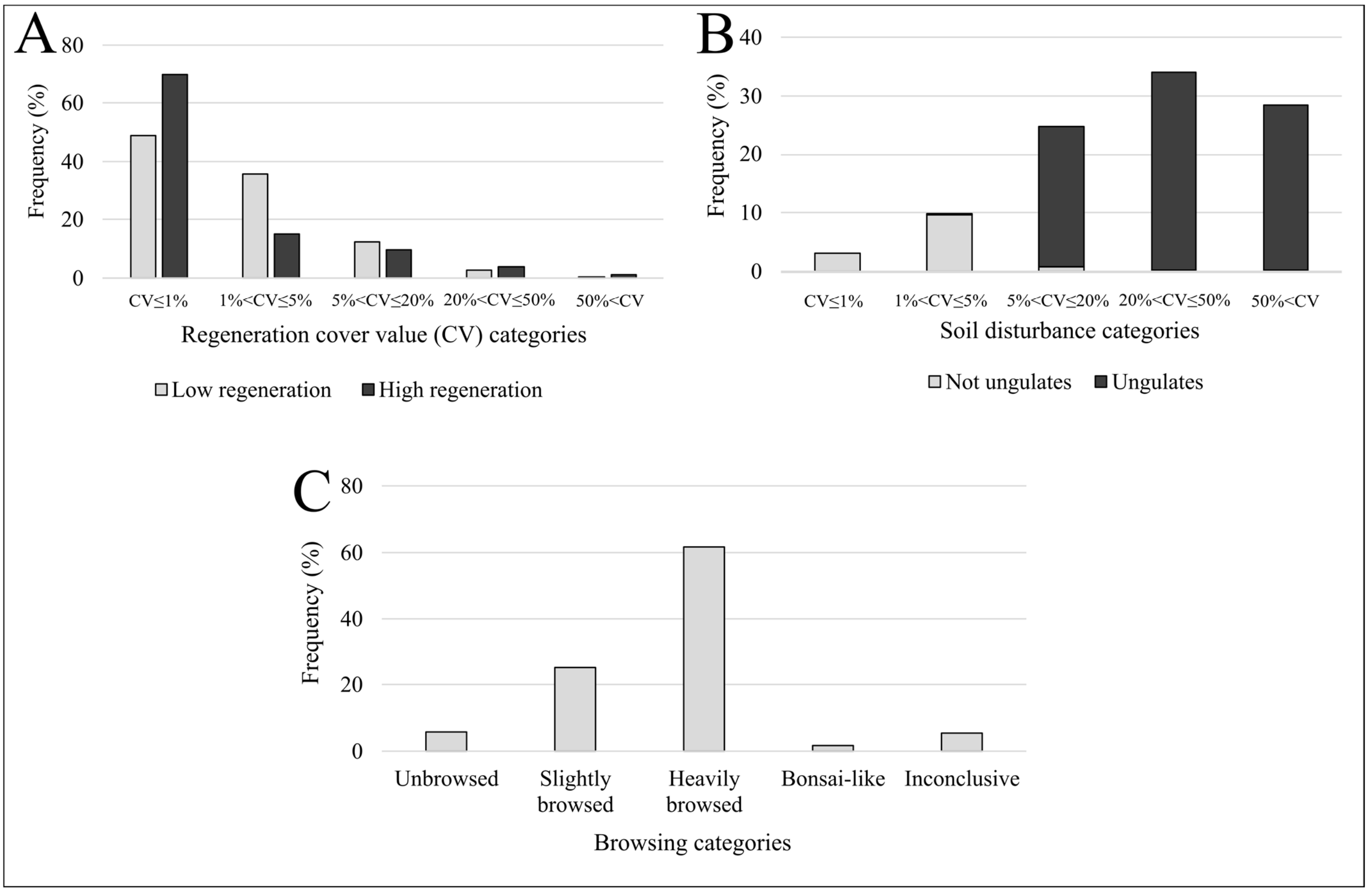

Figure 4. Frequency distributions of variables related to ungulate pressure. (**A**) Frequency distributions of the cover of low (<0.5 m) and high (0.5–2.5 m) regeneration categories (*N* = 56,774). (**B**) Frequency distributions of ungulate and non-ungulate induced soil disturbance categories (*N* = 56,774). (**C**) Frequency distributions of browsing intensity categories (*N* = 33,071). In (**C**), we do not show the cases of browsing not recorded due to lack of regeneration (NA category); only the distribution of browsed regeneration of subplots with 1% < cover of regeneration is shown here.

Figure 5 shows the frequency distributions of cover categories for low and high regeneration within the groups classified as favourable and unfavourable for regeneration.

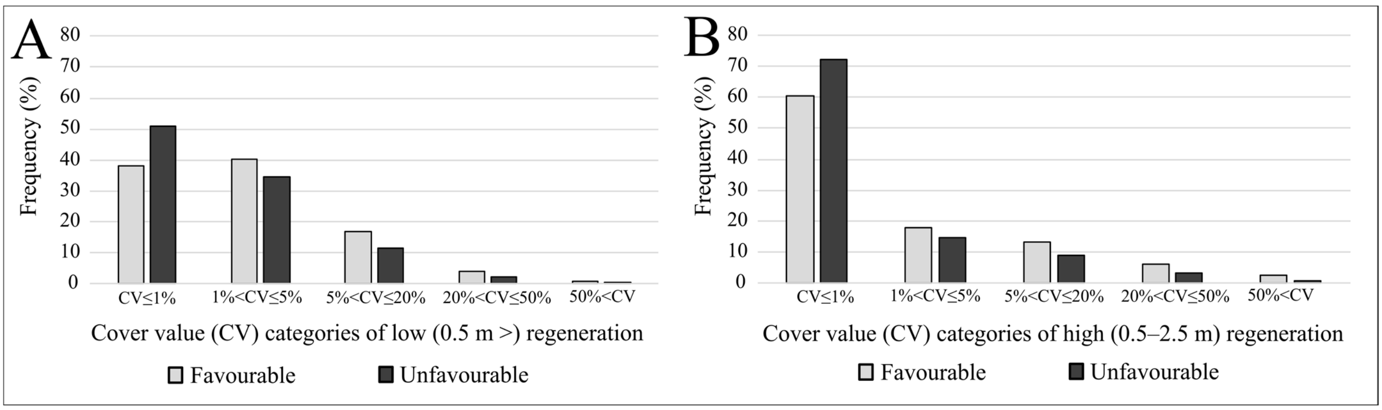

Figure 5. Comparison of the cover of low (<0.5 m; (**A**)) and high (0.5–2.5 m; (**B**)) regeneration under favourable (*N* = 10,423) and unfavourable (*N* = 46,351) conditions.

The comparison shows a slightly higher frequency of higher levels of cover of regeneration in the locations considered favourable (Figure 5). The total absence of regeneration had a higher frequency under unfavourable conditions. When looking at the results in absolute terms, 38% of the subplots surveyed did not have low, and 60% did not have high regeneration under favourable conditions. Regarding the cover of low regeneration (Figure 5A) under favourable conditions, $1\% < CV \leq 5\%$ had the highest frequency, which can be considered a low value. Our other direct indicator of the ungulate pressure besides the browsing is soil disturbance. Thus, it is worth investigating its relationship with the cover of regeneration under favourable conditions. Considering the preliminary distributions (Figure 5), it is worthwhile to form three merged groups of cover value categories for easier comparison: $CV \leq 1\%$, $1\% < CV \leq 5\%$, and $5\% < CV$. The distributions of the soil disturbance data were compared within these three groups. The results of the Kruskal–Wallis test showed that there was a significant difference between the soil disturbance values of both the cover of low ($\chi^2 = 38.72$; df = 2; $p < 0.001$) and high ($\chi^2 = 30.06$; df = 2; $p < 0.001$) regeneration groups. The results of Dunn's post-hoc test showed that in both cases, the frequency of soil disturbance categories with 5% < cover of regeneration was significantly different from the other two regeneration cover value groups (Table 3). The high coefficient values mean higher mean values, which indicate that the mean soil disturbance values were higher for the $CV \leq 1\%$, $1\% < CV \leq 5\%$ categories of regeneration. Differences between the cover groups of regeneration are shown in Figure 6.

Table 3. Significance matrices of Dunn's post-hoc tests calculated for soil disturbance data in the cover categories of low (<0.5 m) and high (0.5–2.5 m) regeneration.

	Low (<0.5 m) Regeneration			**High (0.5–2.5 m) Regeneration**		
Cover Value (*CV*) Categories	$CV \leq 1\%$	$1\% < CV \leq 5\%$	$5\% < CV$	$CV \leq 1\%$	$1\% < CV \leq 5\%$	$5\% < CV$
$CV \leq 1\%$						
$1\% < CV \leq 5\%$	$p = 0.28$ $d = -0.57$			$p = 0.17$ $d = -0.95$		
$5\% < CV$	$p < 0.001$ $d = 5.34$	$p < 0.001$ $d = 5.89$		$p < 0.001$ $d = 4.76$	$p < 0.001$ $d = 4.41$	

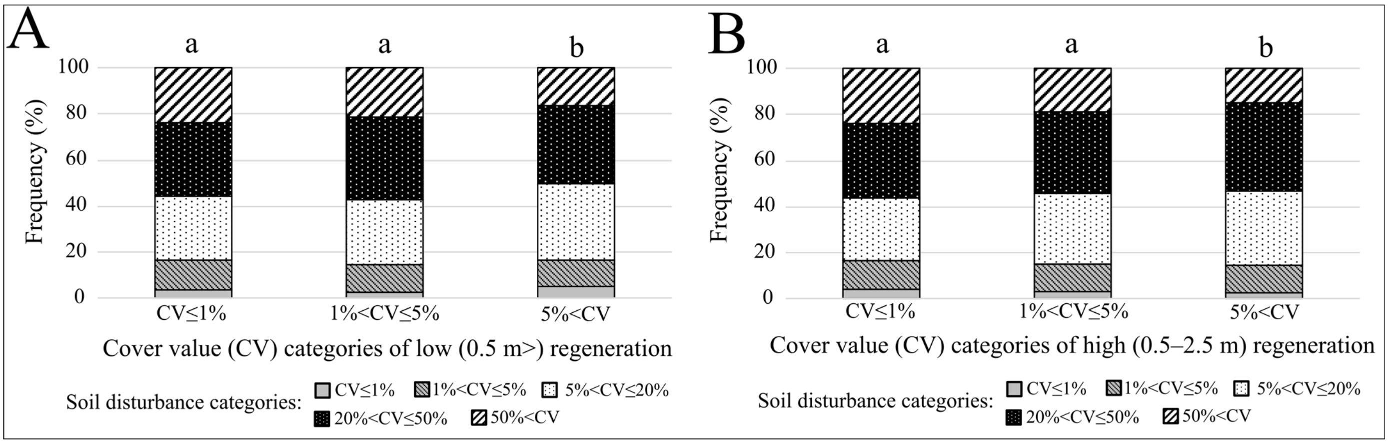

Figure 6. Cover categories of low (<0.5 m; (**A**)) and high (0.5–2.5 m; (**B**)) regeneration depending on soil disturbance under favourable conditions for them. The case numbers of the cover categories of low regeneration: $N_{CV \leq 1\%}$: 3978; $N_{1\% < CV \leq 5\%}$: 4192; $N_{5\% < CV}$: 2253. The case numbers of the cover categories of high regeneration: $N_{CV \leq 1\%}$: 6305; $N_{1\% < CV \leq 5\%}$: 1848; $N_{5\% < CV}$: 2270. Each column shows the soil disturbance distribution in each cover category of regeneration. The results of Dunn's post-hoc tests are shown in letters on the top of the columns.

There is no noticeable difference in the frequencies of soil disturbance values between the cover of regeneration groups, as represented in Figure 6. The most severe soil disturbance category (50% < *CV*) occurred less frequently with 5% < cover of regeneration in both cases, and a slight decline in the frequency of soil disturbance greater than 50% was observed with an increase in cover of regeneration.

4. Discussion

4.1. Frequency Distributions

Indicators directly (soil disturbance, browsing) and indirectly (low abundance of regeneration) related to ungulates indicate extremely high ungulate pressure (Figure 1). Based on the frequency distributions, we considered both direct indicators equally important and serious influencing factors since both browsing [4,39] and soil disturbance [40] can significantly alter vegetation over large areas. Concurrent with our data collection, a survey with a different method was conducted in an overlapping area in the Mátra Mts. to assess ungulate pressure at a regional scale [21]. They suggest two possible reasons for the missing understory: forest management practices and/or earlier, much greater ungulate pressure. They and others (e.g., [25]) also suggest this is a local rather than a regional problem. Furthermore, their study was carried out before the mentioned ice break event; therefore, their data originates from more dense forest stands. We have shown the same absence and pressure in several regions [41], in several stand types [42], under the authority of different forest managers and forestry companies. Therefore, we consider ungulate impacts to be widespread. We obtained this result despite the expected increase in the regeneration cover after the ice break.

4.2. The Lack of the Regeneration

To investigate the effect of ungulates on regeneration, we excluded sampling sites with conditions that were otherwise unsuitable for regeneration. To this end, we isolated sites with ideal conditions for regeneration. Among the explanatory variables, we excluded shrub and (nitrophilous) herbaceous cover indicators because a relationship with the ungulate effect was suspected. The relationship between nitrophilous herbaceous plants and soil disturbance has been shown in our previous work on the effects of the ice break in this region [43]. In the present study, this can be interpreted with the difference that ungulates specifically caused the soil disturbance. Shrubs can protect regeneration from browsing [44] but can also compete with it [45]. The intensity of browsing on the shrubs was not recorded. Even if this had been included, it is possible that we would have obtained a result showing even more intensive browsing. Soil disturbance is directly related to ungulate pressure, so this variable was also omitted from the criteria of favourable circumstances. The other variables and thresholds used to describe the favourable habitat and vegetation conditions for the regeneration were partially based on expert judgement, as it is difficult to know how much cover of regeneration is expected in forests under age-class forest management at a certain point. In addition, the effects of biotic and abiotic damages that can set back regeneration and periodic mast production should also be considered for this type of assessment. The mentioned effects typically occur at smaller spatial scales. However, our results are the same in three distant regions.

There were no significant differences in the distribution categories of regeneration cover between plots with favourable and unfavourable conditions (Figure 5). Thus, the lack of regeneration in the area cannot be attributed to other local habitat or vegetation factors. Additionally, we observed direct and intensive signs of ungulate pressure (such as browsing and soil disturbance) in the area. Therefore, we believe that ungulates are causing the lack of regeneration. This is further supported by the finding that the greater the level of soil disruption (caused by ungulates), the more likely a reduced cover of regeneration (Table 2, Figure 6). Ungulates can disrupt the soil by trampling, leaving traces that are challenging to detect over time. A thorough examination of this phenomenon would provide a more comprehensive understanding of the direct impact of ungulate pressure. Significant regeneration was confined to a limited number of locations (Figures 4A and 5B), so we can infer that the study areas were subject to uninterrupted, sustained, and high-intensity pressure from ungulate activity.

Our research has demonstrated that ungulate pressure can be so significant on a regional scale that it can result in an almost complete absence of regeneration. It should be noted that such intensive ungulate pressure has contributed to the natural pre-human forested landscape, but only in concentrated small areas [44]. Ungulates can cause the complete destruction of regeneration in several ways, including uprooting saplings during browsing [46], resulting in distorted and unviable individuals that eventually die due to continuous repeated browsing [1,47] and foraging on acorns [2,35,48]. In addition, soil disturbance caused by wild boars can reduce the cover of the regeneration layer by up to 80% [40].

Other authors also showed that the signs of strong ungulate pressure, in addition to the browsing of the regeneration and the shrubs, include the complete absence of the understory vegetation [1]. All plants within the reach of the ungulates can be damaged (Figure 1), and in the long term, the disappearance of some DBH classes can be observed. A good historical example of this is the Žofínský Prales virgin forest, a game reserve for almost 100 years with very high game density [49]. As a result, some DBH classes are missing from the stand. The lack of regeneration can be counterbalanced in commercial forests, as the ungulates can be excluded by a fence during the regenerating phase. However, ungulates can cause severe conservation damage in reserves, long untouched forests, and other protected areas (unless they are effectively fenced). If an area is under a similar level of high ungulate pressure, despite the physical protection of large amounts of dead wood [50], a decrease in the species diversity of the regeneration is expected [51] due to the browsing preference for admixing tree species [18,46,52].

4.3. Population Density

It has to be highlighted that our data are from the period before the African Swine Fever (ASF) epidemic. Since the outbreak of the epidemic in 2018, infected wild boars have been continuously found among dead and hunted individuals [53]. The death of ca. 12,500 individuals so far has resulted in an actual decrease in the population in recent years [54].

Population density data from our study areas (Table 2) are probably seriously under-estimated due to methodological bias and a local or even regional spatial aggregation of ungulates.

One author has shown a red deer population calculation failure in Hungary due to methodological bias [34]. Due to the distortion of the official reports, the management plans are also inadequate. As a result, the expected mitigation in population growth has not been achieved in Hungary over the past 30 years. This draws attention to the unreliability of traditional estimation methods (e.g., winter track-counting, drive count, etc.), and we recommend the widespread use of more reliable ones. For example, there is great potential in camera traps, but their application still requires further research. Trapping rates can be used to detect unmarked animals (e.g., ungulates) [55], but the reappearance of individuals before the camera could be a challenging problem for population estimation calculations, which require different models that include these distortion factors [56]. We agree with the authors who suggest that the monitoring system should be carefully chosen with simultaneous consideration of the resources and the properties of the environment to be surveyed [57], in addition to the expected reliability. Another possible suggestion is to monitor population size indirectly using pressure-related indicators together with habitat characteristics and resource availability.

Our assumption on spatial aggregation is also supported by recent data from the literature, where the total density of ungulates was estimated at 8.2 ind./km^2 in the Mátra Mts. [21], which is much higher than our calculations. This aggregation phenomenon has already been recognised [3], and some authors do not even consider the population density to be a suitable metric for ungulate pressure prediction [1,10]; nevertheless, it provides a basis for comparison.

According to a study, 2.3 red deer, 4.3 wild boar, or 10.2 roe deer per km^2 negatively affect the regeneration in temperate forests globally [3]. According to the NGMD, this result is still approaching the average 2.0 red deer per km^2 density, referring to the GMR, including the Börzsöny Mts. Our other calculated values are lower than the thresholds found in the literature. According to another study, lethal browsing can appear above 3 ungulates per km^2 [11]. Even though the predictions made for alpine coniferous forests involved relatively lower resource availability in this research, with the underestimated average of 7.1 ungulates per km^2, the expected lethality of the regeneration would be around 15% in our study areas.

4.4. Interplay between Natural Disturbances, Forest Management and Ungulate Effects

Very limited information is available about the complex interactions of high ungulate pressure and large-scale disturbances [4,58]. Forest management practice influences forests to become more susceptible to natural disturbances if they are managed under age-class forestry with a uniform shelterwood system [59]. Due to the opening canopy after the ice break, we expected a high cover of the low regeneration layer (due to the higher frequency of lower canopy closure values), but our results (Figure 4) did not support this, probably because of the suppression by ungulates.

There is an interaction between the severity of ungulate pressure and forest management practices, as the homogenising intention of age-class forest management leaves little room for admixed species. Where palatable species are available, the density of ungulates is locally higher, indirectly putting pressure on non-preferred species [12]. Our results suggest that if preferred food is unavailable, ungulates can browse economically important species more intensively because they have no other choice. More shade-tolerant species occur in the understory of the even-aged forests with high canopy closure. These slow-growing species are more sensitive to browsing, especially if it is repeated over many years [18]. With artificial regeneration, lower sapling densities can be achieved than under natural conditions, but the density resulting from each is less than from methods that provide continuous forest cover [60].

This suggests that the correct application of uneven-age, continuous cover forestry and other close-to-nature forest management methods may be able to mitigate the effects of ungulate pressure effectively. This can only be achieved if—as the first step—the ungulate population is successfully reduced. The transition to close-to-nature forest management methods is impossible as long as ungulate pressure is so intense due to the even-age characteristics of these forests. Some studies suggest that periodic fluctuations in the ungulate population offer opportunities for regeneration to recover even after their overall suppression (e.g., [61]). However, these results originate from the Białowieża Primeval Forest, which has much more natural characteristics than managed commercial forests. The general conclusion seems to be that even with a low ungulate density, the forest, which was previously exposed to a high level of ungulate pressure, is unable to recover its original state by itself [9,62]. Accordingly, further restoration and protection interventions may be necessary, such as providing seed sources and the protection and plantation of palatable species.

4.5. Close-to-Nature Game Management

The concept of close-to-nature game management has been developed; however, practical implementation requires more time. Close-to-nature game management occurs in natural habitats where native species coexist harmoniously with the environment. Hunting and feeding are solely aimed at game protection purposes. The population of ungulates in game management that adhere to a close-to-nature approach should correspond with the near-natural forest and close-to-nature forest management techniques [63]. Under a good and adaptive management system, ungulate populations could be beneficial too [64]. Even according to the Forest Act of Hungary, it would not be possible to maintain a game population of a size that would endanger biological processes [65], so the efforts to drastically reduce the number of ungulates could be justified by law. The acceptable density of ungulate populations for both forests and agricultural areas remains undefined [25].

The management of ungulates in Europe requires integrated frameworks owing to variations in political and socio-economic history, legislation and hunting practices among different countries [66]. To achieve this, representatives from various fields, including ecologists, veterinarians, managers, sociologists and decision-makers, should collaboratively review and modify regulations [7]. Our findings necessitate a prompt decrease in ungulate abundance to manage populations similar to those found in nature. Additionally, we advocate for the implementation of close-to-nature forest management techniques as extensively as possible. The significant problems and damages caused to forest management and nature conservation by an excessive number of ungulates also bring economic problems.

5. Conclusions

Our research demonstrates that the lack of regeneration can serve as an indirect indicator of ungulate pressure, in addition to direct indicators such as soil disturbance and browsing. The very low abundance of regeneration, even under favourable conditions, indicates this pressure. This effect can be observed both locally and regionally. Our findings signify an extensive presence of ungulates in the study areas, which is a widespread phenomenon throughout the country. The frequent absence of high regeneration suppresses forest regeneration potential for years due to the long-lasting extreme ungulate pressure. Our work aims to draw attention to this phenomenon, which can occur not only in Hungary but also elsewhere. Future research could include additional study areas in the country and should investigate the relationship of such ungulate pressure with natural disturbances and exclude SCP plots surveyed within ungulate exclusion fences from the analyses.

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