

## Article

# Influence of Soil Quality on the Browsing Intensity of Ungulate Herbivores on Tree Species in European Forests

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**Abstract:** The impact of ungulate browsing on tree saplings has been found to have a negative effect on the regeneration of temperate forests. However, it remains ambiguous whether a relationship exists between browsing intensity and soil quality in natural forests. Therefore, we conducted a study in Roztoczańskie National Park to investigate the relationship between soil quality and browsing intensity for tree saplings. The aim was to gain a better understanding of how soil quality affects the browsing of ungulates on tree species. Baseline data (sapling height, basal diameter, crown length and width, browsed-shoot diameter, and soil samples) were collected from the 22 belt transects established in the permanent research plots. The soil quality index was calculated using physical and chemical soil properties. Twig dry mass was determined using allometric equations. Species relative density and browsing intensity were assessed through field measurements. Relationships between the variables were established using a linear regression model. The results suggest that browsing intensity is influenced by the gradient of the soil quality index and that it varies between tree species. Along the increasing soil quality gradient, tree species' relative density ( $p = 0.012$ ) and twig dry mass  $m^{-2}$  ( $p = 0.005$ ) significantly decreased for *A. pseudoplatanus*. In contrast, browsing intensity increased significantly with an increasing species relative density for *A. pseudoplatanus* ( $p = 0.00$ ) and *C. betulus* ( $p = 0.001$ ) and with an increasing twig dry mass for *F. sylvatica* ( $p = 0.034$ ) and *C. betulus* ( $p = 0.004$ ). Browsing intensity increased significantly with an increasing soil quality index for *F. sylvatica* ( $p = 0.027$ ) and decreased significantly for *A. pseudoplatanus* ( $p = 0.036$ ). Notably, there was a significant positive relationship between browsing intensity and species relative density and twig dry mass, indicating that ungulate browsing is concentrated where browsing is abundant. These results provide insights that can be used to improve management and conservation strategies to protect tree species vulnerable to ungulate herbivory.

**Keywords:** browsing; soil quality; species density; tree species; twig dry mass



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## 1. Introduction

The impact of ungulate herbivory on ecosystems has been an important ecological concern in Europe [1,2]. This is due to the fact that browsing by wild ungulates plays an important role in the regeneration of forests and the dynamics of tree stands [3–5]. In forests that have experienced natural disturbances, a high ungulate density significantly affects the frequency of browsing on young trees [6] and is often considered to be a threat to tree regeneration [7,8]. Ungulate browsers directly affect the survivorship and recruitment of tree saplings, which in turn can affect ecosystem function [9,10]. Furthermore, selective ungulate herbivory causes unpalatable, chemically defended plants to dominate the ecosystem [11].

Browsing intensity on tree saplings is determined by several factors, including the presence of forest gaps, tree composition, elevation, former management, and soil properties [12–14]. In particular, studies have shown that browsing intensity on specific tree species is indirectly impacted by the prevailing soil conditions [12]. Other reports suggest that soil quality may influence the response of plant communities to browsing by wild ungulates [15–17].

The logic in this regard is that soil is a center for the process of material and energy exchange and circulation in terrestrial ecosystems. It provides the water and nutrients necessary for plants to grow and develop, thus influencing tree regeneration [18,19].

Soil nutrient status is highly related to vegetation growth and plant diversity [20,21] and may also lead to a shift in community composition [22]. Thus, soil quality operates as a filter for the pool of species that can flourish in a specific location. For instance, poor soils may lead to lower quality and quantities of browse, which can, in turn, increase browsing intensity on individual plants [4,23]. Indirectly, soil conditions influence the share of various tree species in the forest canopy, thus altering light availability on the forest floor. Shade-tolerant tree species dominate the forest canopy in nutrient-rich ecosystems, allowing less light to reach the forest floor [24]. In contrast, shade-intolerant tree species usually form the canopy layer in poorer habitats, and the amount of light beneath their canopies is greater. As a result, forest floor vegetation in poorer habitats may be more productive and have higher biomass than that in richer environments [25,26], which, in turn, can affect ungulate browsing relations. Niche theory predicts that plant species are adapted for survival and growth in a particular environment and have different habitat preferences [27,28], and their variation is expected elsewhere.

Many studies have examined the effects of forest cover and specific tree species on soil properties [23,29–32]. Others have investigated the effects of ungulate browsing on soil properties in general [33] and on soil organic matter and nutrient cycling [34].

However, the effect of soil quality on the intensity of ungulate browsing on saplings in temperate forests has not been well studied and, where it has been studied, the reports have been inconsistent. There are conflicting results in the existing literature. While some studies have suggested that soil properties indirectly affect the amount of browsing on certain tree species, others have found no significant effects [6,18,35,36]. This discrepancy indicates that there is a gap in our knowledge of the precise mechanistic relationship between soil quality and browsing intensity by wild ungulates in natural forest ecosystems, and generalizations have remained elusive.

Thus, the novelty of this study lies in answering the following questions: (1) Does the impact of ungulate browsing on different tree species vary across a gradient of soil quality? (2) Does soil quality along with the species identity of a tree affect the intensity of browsing and reduce the risk of the elimination of palatable species due to ungulate browsing pressure? We used a novel approach to investigate the relationship between browsing intensity on tree seedlings and soil quality. Because this relationship was investigated in depth by assessing the measurable values of browse abundance, this study can be replicated on a large scale and used for generalizations. Answering these questions is also important to improve our understanding of the complex interactions between ungulate browsing and soil quality and inform practical efforts to manage and conserve natural ecosystems. To answer these questions, we formulated two hypotheses:

**Hypothesis 1 (H1).** *Ungulate browsing on tree saplings is less intense on fertile soils because of higher vegetation productivity and higher availability of fodder.*

**Hypothesis 2 (H2).** *In temperate forests, where light availability plays a major role in the development of ground vegetation, browsing on woody plants is more intense on fertile soils, because ground vegetation is sparse.*

## 2. Materials and Methods

### 2.1. Study Site Description

This research was carried out in Roztoczańskie National Park, situated in the Roztocze region of Poland, where more than 95% of the park's expanse is covered by forests. This park covers 8483 hectares and is divided into five strict protection zones. The park experiences an average yearly air temperature within the range of 7.4–7.5 °C, coupled with an annual precipitation of 600–650 mm [37]. The highest elevation in the region is 360 m above sea level.

Within the natural forest stands of Roztoczańskie National Park, the European beech (*Fagus sylvatica*) and Silver fir (*Abies alba*) are notably abundant tree species, regenerating naturally. European hornbeam (*Carpinus betulus*), Sycamore maple (*Acer pseudoplatanus*) and Rowan (*Sorbus aucuparia*) occur mostly as admixtures but are also present among the younger generations of trees [38]. Furthermore, this national park serves as a habitat for various herbivores, such as red deer, roe deer, and wild boar, as well as all the major carnivores characteristic of Central Europe. According to unpublished official data for the study area, in 2019, there were 380 red deer and 360 roe deer. In 2021, the number of red deer increased to 400, while the number of roe deer decreased to 277.

### 2.2. Study Design and Plot-Level-Data

A total of 22 belt transects were established in the years 2020–2022 to study the relationship between ungulate herbivores' browsing intensity on tree saplings and soil properties (Figure 1). Each transect had a width of 5 m and a length of 30 m. Within these designated areas, tree saplings ranging in height from 0.5 m to 3 m were measured. For each tree species, a maximum of 30 individual saplings (located closest to the long axis of the transect) were examined. Accordingly, a total of 1060 tree saplings of all species showing signs of recent (within a year) browsing were found in all transects. The measurements conducted on saplings included sapling height (cm), basal diameter (mm), diameter of the browsed shoot (mm), crown length (cm), and maximum crown width (cm). Furthermore, any visible signs of browsing, such as bite marks on the top and side branches of the saplings with a diameter greater than 1 mm, were recorded, with a maximum of 50 browsing signs being tallied for each sapling within a transect.

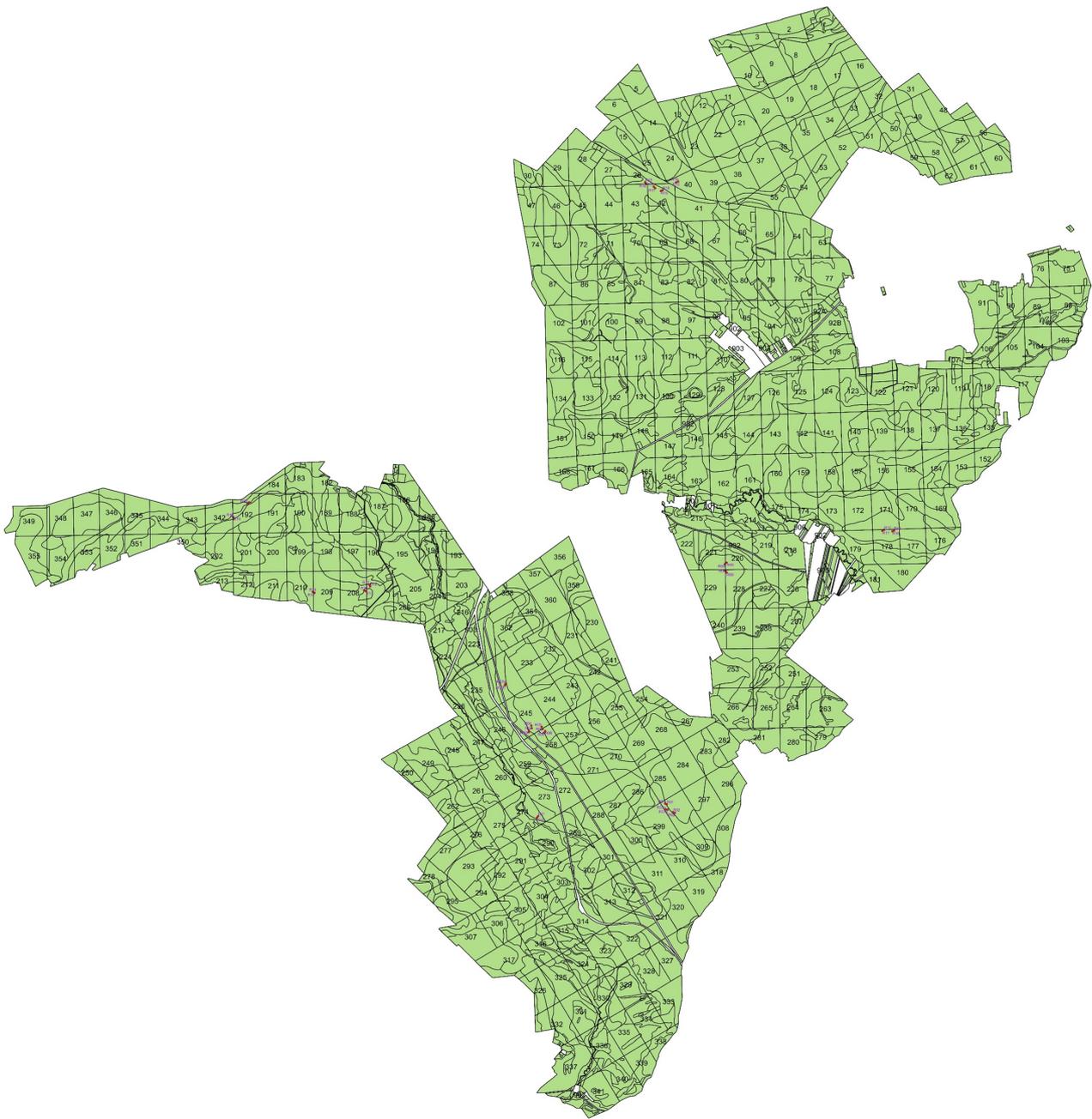
Concurrently, soil samples were collected from the same transects to investigate the correlation between soil properties and the browsing potential of various tree saplings from different species. For each transect, the parent material is similar. The general characteristics of the tested soils are mineral soils with light grain size (from loose sand to sandy loam). In each transect, two soil samples (one soil sample at each of the 15 m intervals along the 30 m belt transect) were taken. The soil on the forest floor contains a considerable amount of undecomposed and partially decomposed litter. Therefore, soil samples were taken after the litter cover had been removed. Due to the varying thickness of the soil horizons at different locations of a transect, samples were taken from the top 30 cm of soil depth, which included the A horizon. These individual samples were then combined to form a single representative aliquot.

### 2.3. Data Generation and Soil Lab Analysis

The species density was calculated by using the number of saplings and the transect area (30 m × 5 m). Then, the relative density was calculated by dividing each species' density by the sum of all species' densities per transect and multiplying the result by 100 (Equations (1) and (2)).

$$\text{Tree species density} \dots\dots\dots SD = \frac{n_i}{A} \quad (1)$$

$$\text{Tree species relative density} \dots\dots\dots RD = \frac{SD_i}{\sum SD_i} * 100 \quad (2)$$



**Figure 1.** The map of the transects located in the forest area in Roztoczańskie National Park. The red dots stands for the transects used for data collection in each of the permanent research plots.

SD stands for the species density,  $n_i$  is the number of individuals of the  $i$ -th species per transect,  $A$  is the transect area ( $150 \text{ m}^2$ ), and  $RD$  is the relative density of the  $i$ -th species per transect.

According to the results of our earlier studies, there are huge differences in the intensity of browsing among tree saplings. In some instances, we recorded up to fifty browsed shoots per sapling, while there were only single shoots that had been browsed in other cases. Therefore, we needed a quantitative measure of browsing intensity; we took into account both the number of browsed shoots and their thickness (as a proxy for their mass) and related these values to the sapling size (with the squared basal diameter of sapling serving as a proxy for the total dry mass of a plant).

Browsing intensity index (BI) was calculated using the following formula (Equation (3)).

$$\text{Browsing intensity index} \dots\dots\dots \text{BI} = \sum_{i=1}^N \frac{d_i^2}{D^2} \quad (3)$$

where *d* is the diameter of the browsed shoot (mm), *N* is the number of browsed shoots per plant, and *D* (mm) is the basal diameter of the tree sapling (mm). As a result, the sum of the BIs and mean BI for each species per transect were calculated.

The measurements taken for tree saplings, such as height (cm), basal diameter (mm), crown length (cm), and crown width (cm), were employed to compute the total dry mass of twigs for each species per transect and then per m<sup>2</sup>. This computation was carried out using newly established allometric equations specific to the particular tree species and study location [39].

The soil samples were subjected to laboratory analyses to determine factors such as soil textures, soil reaction, organic matter content (OC), and various soil chemical attributes like nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), and potassium (K) content. These analyses were conducted according to established soil laboratory procedures in the Geochemistry of Forest Environment and Reclaimed Areas (Department of Ecology and Silviculture) laboratory at the University of Agriculture in Krakow, Poland.

The soil samples were air-dried and sieved through a 2.0 mm sieve. The pH of the samples was measured in H<sub>2</sub>O (pHH<sub>2</sub>O) and a 1 M KCl solution (pHKCl) (soil/liquid ratio 1:5, *v/v*) using a digital pH meter (CPC-411, ELMETRON) at 20 °C. Exchangeable acidity (EA) was determined in 1 M of Ca(OAc)<sub>2</sub>; the basic exchangeable cations (Ca<sup>2+</sup>, Mg<sup>2+</sup>, K<sup>+</sup>, and Na<sup>+</sup>) were determined in 1 M of NH<sub>4</sub>Ac using ICP-OES (iCAP™ 6000 Series). The cation exchange capacity (CEC) was determined by calculating the sum of exchangeable cations and exchangeable acidity (EA). Organic carbon (OC) and total nitrogen (N) content were measured using a LECO TruMac® CNS analyzer. The percentage of base saturation (BS%) was computed by multiplying the sum of basic exchangeable cations by 100 and then dividing the resulting value by the cation exchange capacity (BS% = BEC \* 100/CEC). C:N ratio, and N<sup>2</sup>/C were calculated based on existing values. Soil texture was analyzed with a Fritsch GmbH Laser Particle Sizer ANALYSETTE 22. Bulk density was calculated based on the soil depth and organic carbon content, employing the formula developed by [40]:

$$\text{Bulk density of the soil} \dots\dots\dots D = 1.3773 * \text{Exp}(1)^{-0.0547*x}, \quad (4)$$

where *D* stands for the soil bulk density (g m<sup>-3</sup>), and *x* stands for the content of organic carbon (%).

Soil properties were then used to calculate the soil quality index (SQI). The method of calculating the SQI was developed for soil profiles that are 1.5 m deep. As our samples were taken from the upper 30 cm of the soil profile, the content of fine fractions (grains <0.02 mm), base cations (Ca, Mg, K, and Na), and soil acidity obtained from our analyses were then multiplied by 5 to make them comparable with the SQI values obtained based on regular soil profiles according to the approach described in [41].

The soil quality index was considered to be the main factor influencing the relative density of tree species and browse availability per m<sup>2</sup>. These relationships were thus, used to test the relationship between the soil quality index and the browsing intensity of tree saplings by ungulates. The SQI values were interpreted based on the descriptions (Table 1).

**Table 1.** The table describes soil quality index ranges, and the corresponding forest habitat types.

Soil Quality Range	Forest Habitat Type	Trophic Variety of Soil Subtype
SQI of 4 to 13	Coniferous forests	Dystrophic
SQI of 14 to 23	Mixed coniferous forests	Oligotrophic
SQI of 24 to 33	Mixed deciduous forests	Mesotrophic
SQI of 34 to 40	Deciduous forests	Eutrophic

## 2.4. Statistical Analysis

In order to draw conclusions on the relationship between browsing intensity and soil quality index, we used the relationship of relative density of tree species and twig dry mass (g) with soil quality index as important indicators. Therefore, tree species' relative density and twig dry mass (g) were fitted to the soil quality index across soil quality gradients one by one. These variables, which indicate the level of browse abundance, were then fitted to ungulate browsing intensity on the saplings. The relationship between the soil quality index and browsing intensity was analyzed by fitting the data with the linear model.

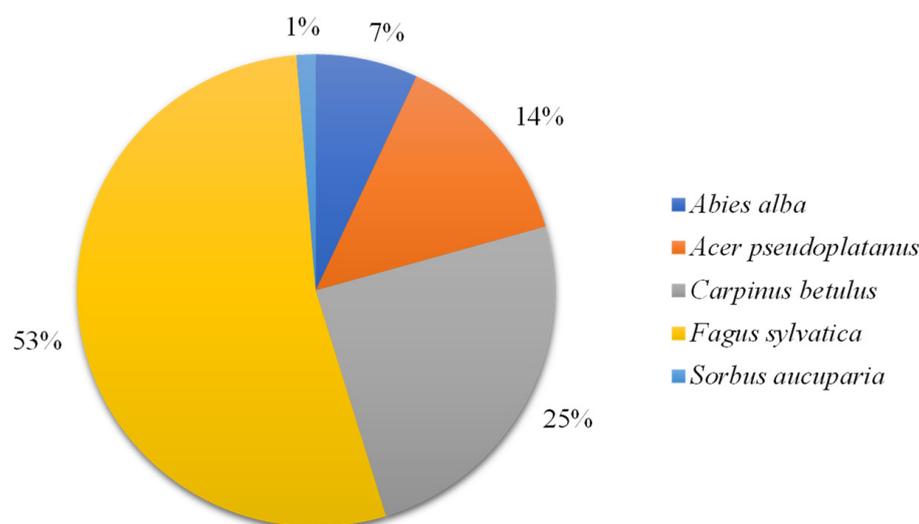
The linear regression model was used in this study because it makes it easier to interpret complex relationships and multiple comparisons. It is used to estimate the relationship between an independent variable and a dependent variable. This model has been applied in similar data analyses [32,34,42]. The linear model with the Ordinary Least Squares method was used based on the assumptions of a normal distribution, independence between variables, and equal variance across the regression line. Hence, the normality of the data was checked using the Shapiro–Wilk test, and for those variables that were not normally distributed, log transformation was conducted.

The goodness of fit of the regression was determined using beta coefficients as well as the adjusted  $R^2$ . To control for the family-wise error rate (FWER) when performing multiple comparisons, the Bonferroni correction was used, which adjusts the significance level ( $\alpha$ ). All of the statistical computations were executed using the R programming language (version R4.3.1).

## 3. Results

### 3.1. The Relative Proportion of Tree Species and Descriptive Summary of the Soil Properties

During the field measurements, several tree species were noted within the transects. However, we focused on five specific tree species that were abundant enough to permit statistical analyses: *A. alba*, *A. pseudoplatanus*, *C. betulus*, *F. sylvatica*, and *S. aucuparia*. Nevertheless, these species were not evenly distributed throughout the forest community; *F. sylvatica* (53%), *C. betulus* (25%), and *A. pseudoplatanus* (14%) were the predominant tree species in most of the transects (Figure 2).



**Figure 2.** Relative proportions of tree species among the surveyed saplings.

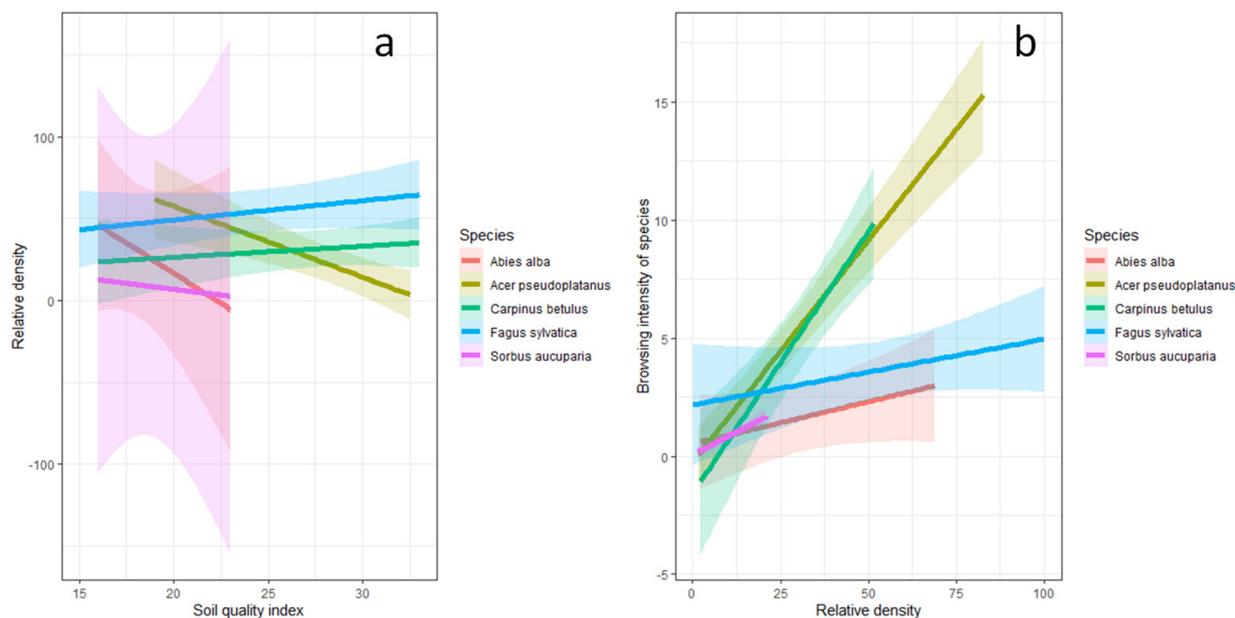
The ascertained soil properties (Table 2) were used to derive the soil quality index for our study plots. The table below also describes the chemical and physical properties of the soil in our study transects.

**Table 2.** A descriptive statistical summary regarding the soil. SE stands for standard error, SD stands for standard deviation, and var stands for sample variance.

Variable	Mean	SE	Med.	SD.	Var.	Kurtosis	Skewness	Range	Minimum	Maximum
pH_H <sub>2</sub> O	4.350	0.097	4.353	0.454	0.206	−0.691	0.183	1.640	3.545	5.185
pH_KCl	3.953	0.102	4.005	0.479	0.230	0.102	−0.168	2.005	2.860	4.865
Ca	3.424	0.657	2.409	3.080	9.485	1.386	1.476	10.406	0.383	10.789
K	0.300	0.045	0.243	0.212	0.045	−0.562	0.673	0.677	0.061	0.738
Mg	0.250	0.037	0.223	0.172	0.030	−0.070	0.998	0.555	0.058	0.613
Na	0.037	0.004	0.035	0.020	0.000	−0.451	0.785	0.064	0.017	0.081
BEC	4.012	0.725	3.035	3.399	11.556	1.097	1.374	11.387	0.525	11.912
EA	12.367	2.598	9.632	12.184	148.440	13.581	3.527	56.656	4.814	61.470
CEC	16.378	2.734	12.959	12.822	164.395	9.126	2.748	57.853	6.283	64.136
BS	22.767	2.955	22.042	13.858	192.056	−0.414	0.477	49.332	2.813	52.145
N	0.182	0.029	0.137	0.134	0.018	5.805	2.379	0.549	0.080	0.629
OC	3.201	0.770	2.010	3.613	13.056	7.982	2.879	14.561	1.181	15.742
C:N	13.852	0.745	12.987	3.493	12.202	3.221	1.822	13.312	10.206	23.518
N <sup>2</sup> :C	0.011	0.001	0.010	0.006	0.000	0.941	1.260	0.020	0.005	0.025
Sand	76.364	3.368	83.250	15.799	249.600	−1.592	−0.380	44.500	49.000	93.500
Silt	19.932	2.867	13.750	13.447	180.817	−1.495	0.428	39.000	5.500	44.500
Clay	3.705	0.517	3.000	2.423	5.873	−1.783	0.249	6.500	1.000	7.500

### 3.2. Relationship between Soil Quality Index, Tree Species Relative Density, and Browsing Intensity

The relationship between the soil quality index and the relative species density showed variation among tree species (Figure 3a). The relative densities of *F. sylvatica* and *C. betulus*, which were distributed across the whole range of habitats, tended to increase from poorer to richer soil quality. In contrast, the relative densities of *A. alba* and *S. aucuparia* tended to decrease and their distribution was restricted to locations with poor soil quality. However, neither of the aforementioned relationships were statistically significant. On the other hand, the relationship for *A. pseudoplatanus*, which was distributed from moderate to rich soils, was significantly decreased along the soil quality gradient with 95% confidence (Table 3(a)).



**Figure 3.** The relationship between soil quality and tree species relative density (a) and relative density and browsing intensity per species per transect (b).

**Table 3.** The relationship between soil quality and tree species relative density (a) and relative density and browsing intensity (b).

<b>(a) Species Relative Density Predicted Using the Soil Quality Index</b>							
Species	Explanatory Variable	Estimate	Std. Error	t Value	Pr (>  t )	Adj. p Value	Adj. R <sup>2</sup>
<i>A. pseudoplatanus</i>	(Intercept)	144.13	29.434	4.897	0.001 ***		0.6247
	Soil quality index	−4.328	1.03	−4.201	0.002 **	0.012 *	
<i>F. sylvatica</i>	(Intercept)	25.694	24.46	1.05	0.306		0.02297
	Soil quality index	1.178	0.964	1.222	0.236	1.000	
<i>S. aucuparia</i>	(Intercept)	35.756	43.235	0.827	0.56		−0.4333
	Soil quality index	−1.442	2.293	−0.629	0.643	1.000	
<i>C. betulus</i>	(Intercept)	12.849	25.602	0.502	0.626		−0.03806
	Soil quality index	0.679	0.908	0.748	0.47	1.000	
<i>A. alba</i>	(Intercept)	164.358	91.109	1.804	0.169		0.2315
	Soil quality index	−7.379	4.969	−1.485	0.234	1.000	

<b>(b) Browsing Intensity per Species per Transect Predicted Using Species Relative Density</b>							
Species	Explanatory Variable	Estimate	Std. Error	t Value	Pr (>  t )	Adj. p Value	Adj. R <sup>2</sup>
<i>A. pseudoplatanus</i>	(Intercept)	−0.239	0.538	−0.444	0.667		
	Species relative density	0.188	0.016	11.622	0.000 ***	0.000 ***	0.931
<i>F. sylvatica</i>	(Intercept)	2.179	1.227	1.776	0.091 .		
	Species relative density	0.028	0.02	1.4	0.177	0.884	0.044
<i>S. aucuparia</i>	(Intercept)	0.065	0.021	3.093	0.199		
	Species relative density	0.077	0.002	45.09	0.014 *	0.071	0.999
<i>C. betulus</i>	(Intercept)	−1.576	1.472	−1.071	0.307		
	Species relative density	0.222	0.041	5.424	0.000 ***	0.001 ***	0.703
<i>A. alba</i>	(Intercept)	0.521	0.652	0.799	0.482		
	Species relative density	0.036	0.015	2.306	0.104	0.522	0.519

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1.

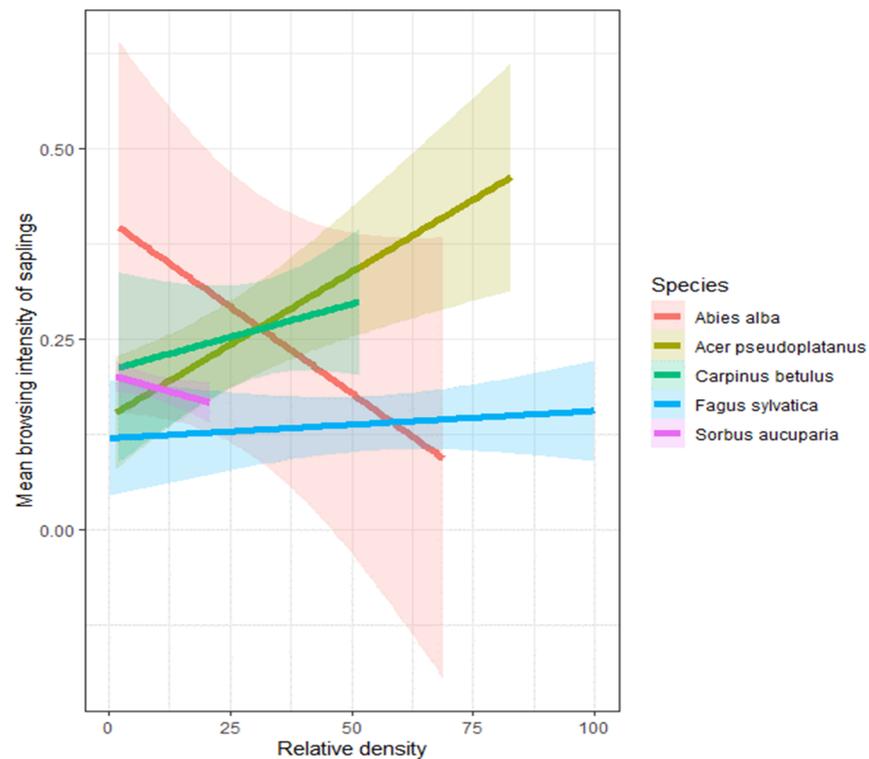
The relationship between the relative density of tree species and total browsing intensity per transect (Figure 3b) was strongly positive for *A. pseudoplatanus* and *C. betulus*, corresponding to a 99.9% confidence level, while that for *S. aucuparia* was significant at a 90% confidence level. For *F. sylvatica* and *A. alba*, on the other hand, browsing intensity did not change significantly with an increasing species relative density, although a high value of the adjusted R-squared (51.9%) indicates the better fit of the regression model in the case of *A. alba* (Table 3(b)).

The relationship between mean browsing intensity and the relative density of the species varied between tree species (Figure 4). Table 4 shows that there was a strong positive relationship between relative density and mean browsing intensity in the case of *A. pseudoplatanus*, whereas for *S. aucuparia* and *A. alba*, the relationship was negative and weakly significant, corresponding to a 90% confidence. However, according to the Bonferroni correction test for multiple comparisons, the relationship between relative density and mean browsing intensity of tree species was not significant for all species except *A. pseudoplatanus*.

**Table 4.** Relationship between a relative density of tree species and mean BI for a given species in a transect.

Species	Explanatory Variable	Estimate	Std. Error	t Value	Pr (>  t )	Adj. p Value	Adj R <sup>2</sup>
<i>A. pseudoplatanus</i>	(Intercept)	0.148	0.034	4.392	0.002 **		
	Species relative density	0.004	0.001	3.782	0.004 **	0.021 *	0.571
<i>F. sylvatica</i>	(Intercept)	0.12	0.036	3.293	0.004 **		
	Species relative density	0	0.001	0.611	0.548	1.000	−0.031
<i>S. aucuparia</i>	(Intercept)	0.203	0.002	115.76	0.006 **		
	Species relative density	−0.002	0	−12.34	0.052	0.257	0.987
<i>C. betulus</i>	(Intercept)	0.209	0.06	3.497	0.005 **		
	Species relative density	0.002	0.002	1.05	0.316	1.000	0.008
<i>A. alba</i>	(Intercept)	0.406	0.079	5.113	0.015 *		
	Species relative density	−0.005	0.002	−2.406	0.095	0.476	0.545

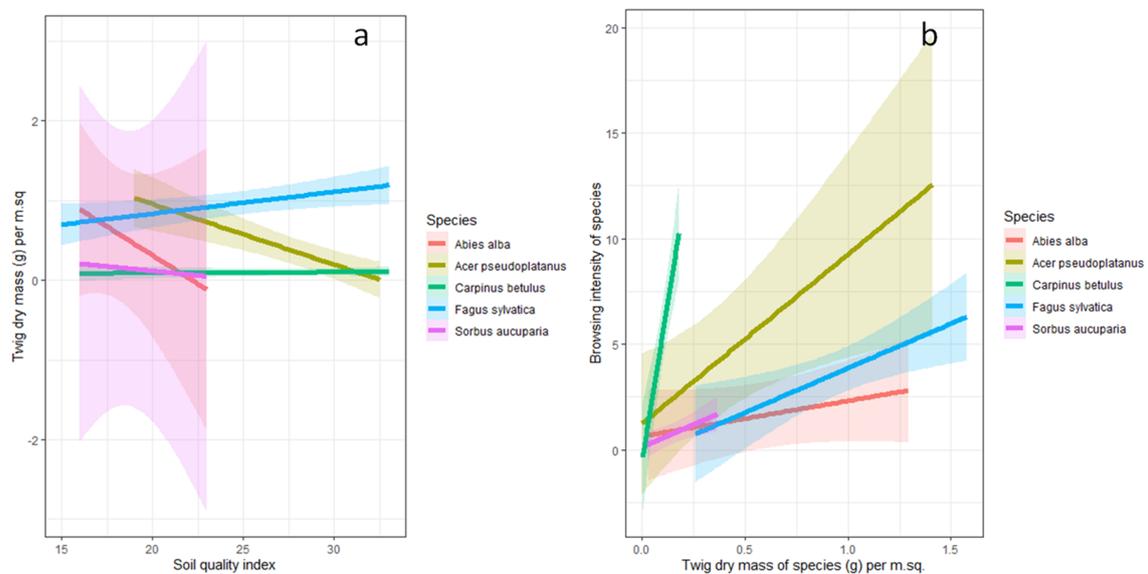
Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1.



**Figure 4.** The relationship between the relative density of species and the mean browsing intensity of species per transect.

### 3.3. The Relationship between Soil Quality Index, Twig Dry Mass and Browsing Intensity

The species-specific relationship between soil quality and the dry mass of twigs  $m^{-2}$  for *A. pseudoplatanus* was significantly negative at the 95% confidence level, while it was weakly positive at the 90% confidence level for *F. sylvatica* (Table 5(a)). For the rest of the species, the relationship was not statistically significant despite a rapid decrease along the soil quality gradient in the case of *A. alba* (Figure 5a).



**Figure 5.** The relationship between soil quality index and total twig dry mass of tree species  $m^{-2}$  (a) and between the total twig dry mass of tree species  $m^{-2}$  and browsing intensity on tree species (b).

**Table 5.** Statistical summary of the relationship between soil quality index and mean twig dry mass of tree species  $m^{-2}$  (a) and between mean twig dry mass of tree species  $m^{-2}$  and browsing intensity on tree species (b).

(a) Total Twig Dry Mass of Tree Species (g) $m^{-2}$ Explained by the Soil Quality Index							
Species	Explanatory Variable	Estimate	Std. Error	t Value	Pr (>  t )	Adj. p Value	Adj. R <sup>2</sup>
<i>A. pseudoplatanus</i>	(Intercept)	2.480	0.449	5.529	0.000 ***		0.6923
	Soil quality index	−0.076	0.016	−4.847	0.001 ***	0.005 **	
<i>F. sylvatica</i>	(Intercept)	0.289	0.271	1.065	0.300		0.2105
	Soil quality index	0.027	0.011	2.569	0.018 *	0.091	
<i>S. aucuparia</i>	(Intercept)	0.570	0.816	0.698	0.612		−0.5718
	Soil quality index	−0.023	0.043	−0.522	0.694	1.000	
<i>C. betulus</i>	(Intercept)	0.072	0.098	0.729	0.481		−0.0819
	Soil quality index	0.001	0.003	0.303	0.768	1.000	
<i>A. alba</i>	(Intercept)	3.197	1.867	1.712	0.185		0.2006
	Soil quality index	−0.144	0.102	−1.416	0.252	1.000	
(b) Browsing Intensity of Tree Species Explained by the Total Twig Dry Mass of Tree Species $m^{-2}$							
<i>A. pseudoplatanus</i>	(Intercept)	1.221	1.476	0.827	0.430		0.430
	Twig dry mass (g) $m^{-2}$	8.035	2.748	2.924	0.017 *	0.084	
<i>F. sylvatica</i>	(Intercept)	−0.362	1.434	−0.252	0.803		0.279
	Twig dry mass (g) $m^{-2}$	4.220	1.398	3.020	0.007 **	0.034 *	
<i>S. aucuparia</i>	(Intercept)	0.114	0.053	2.149	0.277		0.993
	Twig dry mass (g) $m^{-2}$	4.272	0.249	17.185	0.037 *	0.185	
<i>C. betulus</i>	(Intercept)	−0.646	1.215	−0.532	0.605		0.741
	Twig dry mass (g) $m^{-2}$	60.334	10.141	5.949	0.000 ***	0.004 ***	
<i>A. alba</i>	(Intercept)	0.631	0.692	0.912	0.429		0.429
	Twig dry mass (g) $m^{-2}$	1.682	0.840	2.002	0.139	0.695	

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1.

According to the adjusted  $p$ -values (Figure 5b), the browsing intensity of ungulates on the tree species increased significantly with an increasing twig dry mass  $m^{-2}$  for *F. sylvatica* and *C. betulus* at the 95% confidence level and at the 90% confidence level for *A. pseudoplatanus*. However, the relationship was not significant for *S. aucuparia* and *A. alba* (Table 5(b)).

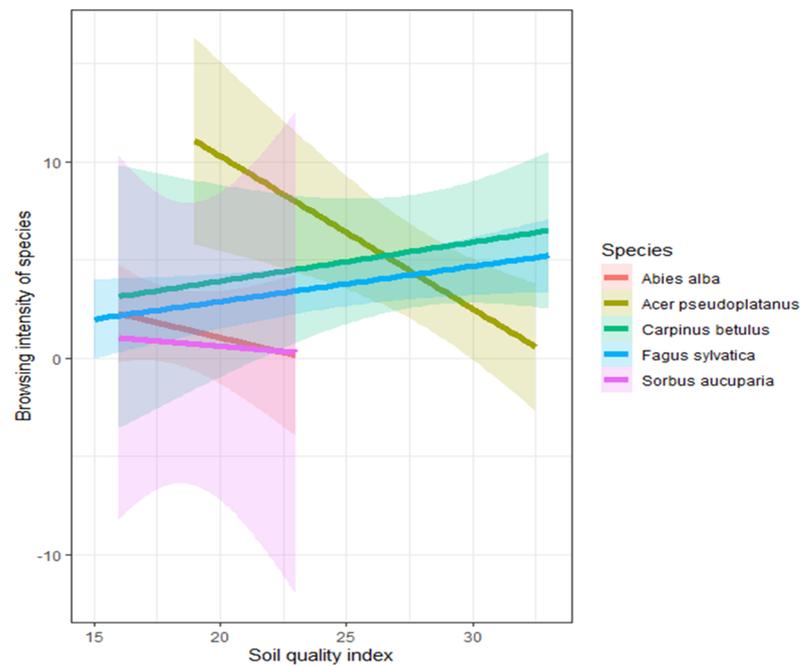
### 3.4. The Relationship between Soil Quality Index and Browsing Intensity

The results showed variation among the tree species regarding the relationship between the soil quality index and browsing intensity of the tree species (Figure 6). The browsing intensity for *A. pseudoplatanus* per transect significantly decreased along the gradient from moderate to richer soil quality, whereas in the case of *F. sylvatica*, it significantly increased. However, the relationship for the other species was weak and insignificant: positive in the case of *C. betulus* and negative in the case of *S. aucuparia* and *A. Alba* (Table 6).

**Table 6.** The relationship between soil quality index and browsing intensity of species per transect.

Species	Explanatory Variable	Estimate	Std. Error	t Value	Pr (>  t )	Adj. p Values	Adj. R <sup>2</sup>
<i>A. pseudoplatanus</i>	(Intercept)	25.845	6.429	4.02	0.003 **		
	Soil quality index	−0.778	0.225	−3.458	0.007 **	0.036 *	0.523
<i>F. sylvatica</i>	(Intercept)	−0.707	2.125	−0.332	0.743		
	Soil quality index	0.179	0.084	2.143	0.045 *	0.027 *	0.146
<i>S. aucuparia</i>	(Intercept)	2.75	3.381	0.813	0.565		
	Soil quality index	−0.107	0.179	−0.598	0.657	1.000	−0.473
<i>C. betulus</i>	(Intercept)	−0.024	6.611	−0.004	0.997		
	Soil quality index	0.198	0.234	0.843	0.417	1.000	−0.025
<i>A. alba</i>	(Intercept)	7.138	4.284	1.666	0.194		
	Soil quality index	−0.305	0.234	−1.304	0.283	1.000	0.149

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1.



**Figure 6.** Relationship between soil quality index and browsing intensity of tree species per transect.

#### 4. Discussion

##### 4.1. Relationship between Soil Quality Index, Tree Species Relative Density, and Browsing Intensity

Our results on the relationship between soil quality index and tree species' relative density showed different responses for different tree species along the soil quality gradients. The increasing tendency of species relative density for *F. sylvatica* and *C. betulus* and the decreasing tendency for *A. alba* and *S. aucuparia*, whose distributions were restricted to poor-quality soil, as well as to medium-to-richer-quality soil for *A. pseudoplatanus*, indicate that soil quality is one of the important factors determining the distribution and abundance of saplings for various tree species. This finding is consistent with a report stating that soil is positively correlated with vegetation richness in coniferous, mixed coniferous, and deciduous forests [42], indicating that soil directly determines the survival and growth of plant species. Similarly, there is some evidence of niche partitioning between silver fir and beech, suggesting that corresponding forests are likely to reach an alternative stable state dominated by beech within a few decades, although many processes may be masked by the avoidance strategy of *A. alba* [43].

The relationship between the relative density of tree species and browsing intensity of tree species per transect provides insight into browse abundance and ungulate attraction to available resources. Our results contrast with the findings in [44], in which it was reported that browsing intensity decreased with increasing winter food availability for deer, calculated as the number of available saplings. In our study, browsing intensity on *A. pseudoplatanus*, *C. betulus*, and *S. aucuparia* saplings increased significantly with an increasing relative density. Browsing intensity on *F. sylvatica* and *A. alba* showed a trend similar to the other species' trends, although the relationship was not statistically significant. This suggests that ungulate herbivores are likely to concentrate their foraging activities in areas with abundant resources, which may vary for different tree species as a function of soil quality. These findings are consistent with the report by [45], which stated that an abundance of browse allows ungulates to spend more time opportunistically foraging in places with ample food supply, thereby increasing the level of damage.

The current findings highlight that soil quality plays a fundamental role in determining the distribution and abundance of tree saplings, which, in turn, influence the browsing intensity for different tree species within their respective soil-quality niches. For example, the higher relative density of *A. pseudoplatanus* in the low–medium soil-quality ranges

is associated with increased browsing pressure, whereas it is lowest in the high soil-quality range.

#### 4.2. The Relationship between Soil Quality Index, Twig Dry Mass, and Browsing Intensity

Our findings show a general decrease in browse availability ( $\text{m}^{-2}$ ) along the soil quality gradient, although this relationship is not statistically significant. However, the relationship between soil quality index and browse availability varies between species. This is due to the tree species' habitat preferences in the forest ecosystem [25,42,46]. Accordingly, the browse availability for the two broadleaved species significantly increases for *F. sylvatica*, while for *C. betulus*, the increase along the soil quality gradient was not strongly significant. These two species are distributed over a broad range of soil quality levels and provide higher browse resources in places with higher soil quality. This finding is in agreement with reports by some authors [47,48].

In the case of *A. pseudoplatanus*, which was found in moderate-to-rich soils, a higher availability of browse was found in lower-quality soil, and it declined more rapidly in richer soils. This phenomenon may be due to an increase in competition between tree species and the lower light availability under canopies dominated by shade-tolerant trees in richer soils [49]. In full light, *A. pseudoplatanus* can out-compete beech, but under a dense canopy where light is limited, it can remain a small seedling with high survival and slow growth [50], resulting in low browse availability of this species.

The availability of browse from *A. alba* is limited to poor-to-medium soils. This browse exhibits a higher availability in the lower soil quality ranges, which then decreases with an increasing soil quality index. *S. aucuparia* also follows a similar trend, but the contribution of this species to browse is minimal within the same range of soil quality. This finding suggests that soil quality plays a crucial role in determining the distribution and abundance of browse in forest habitats through the shaping of species' ecological niches in temperate forests [47]. On the other hand, the lower impact of browsing on *A. alba* in nutrient-rich soils is a strong indication that this species is less abundant in fertile habitats, partly due to competition from shade-tolerant species, and this finding agrees with a report that light availability on the forest floor is associated with soil quality [25].

#### 4.3. The Relationship between Soil Quality Index and Browsing Intensity

The range of adaptation to different levels of soil quality varies among tree species. Out of the five tree species analyzed in our study, three (*F. sylvatica*, *C. betulus*, and *A. pseudoplatanus*) cover a broad range of soil quality levels, although *A. pseudoplatanus* does not occur in the poorest-quality soils. The other two species (*A. alba* and *S. aucuparia*) are confined to poorer- to medium-quality soils. This result corresponds to the ecological characteristics of these species [51] but also reflects their abundance within the study area.

The total browsing intensity per species per transect shows a significant negative correlation between the soil quality index and browsing intensity for *A. pseudoplatanus*. This finding indicates that *A. pseudoplatanus* saplings are not only more heavily browsed but also more abundant in habitats with moderate soil quality. As rapid canopy cover is partly explained by soil quality status, browsing intensity was higher under the more open canopies for *A. pseudoplatanus* [52]. The lower density of *A. pseudoplatanus* in transects with high soil quality is probably due to reduced light availability on the forest floor. In rich habitats, the canopy is often very dense and dominated by shade-tolerant species such as *F. sylvatica* and *C. betulus*, potentially leading to a lower density of *A. pseudoplatanus* in such areas. This explanation is supported by the relationship between soil quality, browse availability, and relative species densities revealed in our current study. As a result, following changes in browse access and species composition mediated by soil quality, browsing intensity on tree species gradually shifts from palatable species such as *A. pseudoplatanus* to less palatable species such as *F. sylvatica*.

The positive and statistically significant relationship between the soil quality index and the browsing intensity found for *F. sylvatica* may be due to the increased relative density

and twig dry mass (browse availability) of this species in the higher soil quality range. The relationship between the soil quality index and browsing intensity per species per transect is consistent with the results regarding species relative density and browse availability shown in Figures 3a and 5a. On the other hand, *F. sylvatica* and *C. betulus* saplings, two shade-tolerant broadleaved species, are abundant in all transects and increase in number with increasing soil quality. This reflects their preference for moderately rich and rich habitats. They are therefore at the forefront of heavy browsing, as their dominance in richer soils makes them the primary food source for ungulates.

Soil quality is a crucial environmental factor influencing the adaptation of *A. alba* in forest ecosystems and its subsequent browsing pressure with respect to ungulates [53]. In our case, the reduction in browsing intensity for this species in the richer soils is justified by the availability of browse from this species. The majority of *A. alba* saplings are found in poor habitats, although mature trees of the same species are also present as a small admixture in rich habitats. In the case of *A. alba*, which is a very shade-tolerant species, the lack of saplings in the richer habitats is probably unrelated to lower light intensities but is instead related to soil factors, possibly indirectly through interactions with fungi [54,55]. Research on the effect of microsites on *A. alba* survival, density, and ectomycorrhizal status has shown that habitat quality reinforces this interaction. Consequently, sites with an abundance of older regeneration had higher local stand density, lower canopy openness, and lower soil quality [56]. On the other hand, the narrow range of occupied habitats in the case of *S. aucuparia* can be partly explained by the low number of saplings in our sample (with only 12 individuals).

On the other hand, mean browsing pressure on *A. pseudoplatanus* increased significantly with an increasing relative density of the species, which was negatively correlated with the soil quality index. In medium-to-rich habitats, where the relative density of this species decreases, the mean browsing intensity significantly decreases. This may be related to the morphology of the species. *A. pseudoplatanus*, which has few lateral shoots and is even modified by competition in the richer habitats, does not provide much browse for ungulates in comparison to *F. sylvatica* and *C. betulus*, but it can survive under dense canopies [57].

## 5. Conclusions

In this study, we examined the relationship between soil quality and browsing intensity by analyzing the relationship between soil quality and tree species density, as well as soil quality and twig dry mass, which are indicators of browse availability. The findings confirm that ungulate browsing intensity on the tree species in temperate forests varies depending on the soil quality index. The relationship between the soil quality index and browsing intensity was not significant for *A. alba*, *C. betulus*, and *S. aucuparia*. Nevertheless, in the case of *A. pseudoplatanus*, this finding supports the original hypothesis that browsing intensity decreases with increasing soil quality. However, this phenomenon is not due to an increased productivity or abundance of food resources for this species. Rather, it was due to the soil quality limitations that hindered growth due to increased canopy closure. Similarly, for *F. sylvatica*, the results provided evidence for the second hypothesis, i.e., that browsing intensity significantly increases with increasing soil quality. The intensity of ungulate browsing on tree species is impacted by soil quality in a species-specific manner as different responses were found among tree species, while the pressure generally increases with increasing browse availability. Furthermore, the soil-quality-mediated changes in browse availability and species composition result in a gradual shift in browsing pressure from palatable tree species such as *A. pseudoplatanus* to those less palatable like *F. sylvatica*, thus allowing *A. pseudoplatanus* to survive and eventually recruit to the forest canopy.

Our method, in which quantitative values of browse are used to correlate browsing intensity with soil quality, is an objective and reliable approach that can be applied in large-scale studies. Additionally, the information in this research is vital for managing tree regeneration in natural forest ecosystems where ungulate herbivores interact with

tree recruitment. The relationship between soil quality, browse availability, and browsing intensity is an important consideration in guiding conservation efforts aimed at protecting against and mitigating the impact of ungulate herbivory on tree species. In addition, the results of this research may be useful in developing a conservation strategy, particularly in situations where the regeneration of certain tree species is limited by increasing pressure from wild ungulates in temperate forests.

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