

## Article

# The Influence of Wild Ungulates on Forest Regeneration in an Alpine National Park

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**Abstract:** The browsing of wild ungulates can have profound effects on the structure and composition of forests. In the Swiss National Park, the density of wild ungulates, including red deer (*Cervus elaphus*), ibex (*Capra ibex*), and chamois (*Rupicapra rupicapra*), is exceptionally high due to strict protection and the absence of large predators. We examined count data of larch (*Larix decidua*), cembra pine (*Pinus cembra*), spruce (*Picea abies*), upright mountain pine (*Pinus mugo* subsp. *uncinata*), and mountain ash (*Sorbus aucuparia*) of four sampling years between 1991 and 2021, and modelled how topographic and location factors affected the probability of browsing on saplings of larch, cembra pine, and spruce. Despite the high density of wild ungulates, the number of saplings and young trees has increased over the past 30 years. The probability of browsing on saplings was highest for larch at a height of 10–40 cm and increased with increasing elevation. In our study area, open grasslands are mainly located above the tree line, which might explain the positive correlation between elevation and the probability of browsing. Further, the probability of browsing was related to exposition and slope, diversity of tree species, and disturbance by humans. It appears that in the investigated part of the Swiss National Park, the potential of the forest to regenerate has increased despite the high densities of wild ungulates.

**Keywords:** browsing; alpine forest; elevation; tree rejuvenation; ungulate management; protected area



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## 1. Introduction

Large herbivores play an important role in the ecosystems of subalpine and boreal forests. They directly shape the landscape by trampling, dispersing seeds, fertilizing the soil, and reducing the growth and resource uptake of plants by grazing, browsing, stripping, and fraying [1]. Due to a lack of predators and to active protection and promotion of certain ungulate species, the population of wild ungulates in Western Europe has increased over the last few decades [2–4].

The size and direction of the effects of browsing by wild ungulates on forest attributes may vary depending on multiple factors [5,6]. Many studies, however, have shown that ungulates have a strong impact on forest ecosystems and that browsing can negatively affect forest regeneration [3,6–10]. Consequently, as European populations of ungulates have grown, so have concerns of foresters and the public about the impact of such a high density of wild ungulates on forests and their capability to regenerate. As a response, in many countries, management systems were introduced by the government to lower the number of wild ungulates and to protect forests and their functions [11,12].

In strictly protected areas such as national parks, ungulate populations are usually not managed. For example, the Swiss National Park (SNP) was established in 1914 in the canton of Grisons and is one of the most strictly protected nature reserves in Central Europe (IUCN category Ia, i.e., Strict Nature Reserve). Protection includes a general ban on hunting

and restricting access by visitors to public trails, daytime hours, and summer months. This high level of protection and the absence of large predators led to an exponential increase of red deer (*Cervus elaphus*) in the SNP between 1920 and 1980 after red deer had returned to the canton of Grisons from the Rätikon (principality of Lichtenstein and Vorarlberg) in the second half of the 19th century [13]. Moreover, red deer populations have remained high after 1980 (at about 21 individuals per km<sup>2</sup> in our study area; see Methods section). In addition to red deer, Alpine ibex (*Capra ibex*), Alpine chamois (*Rupicapra rupicapra*), and roe deer (*Capreolus capreolus*; at low densities) occur in the study area.

According to Côté et al. [3], the impact of wild ungulates on forests increases with increasing density. However, Côté et al. and other studies investigated mostly areas with management systems for wild ungulates. To examine the influence of wild ungulates in an area with no management of their population sizes, the SNP established a monitoring program on forest regeneration. Since 1991, forest inventory data have been collected once per decade, including data on the number of saplings and on browsing of their apical shoot, as well as on young trees and trunk damage inflicted by wild ungulates.

As part of the monitoring program, the present study investigated the long-term influence of wild ungulates occurring at high densities on forest regeneration between 1991 and 2021 in Val Trupchun, a valley within the strictly protected area of the SNP. We analyzed temporal trends in the number of saplings and young trees of larch (*Larix decidua*), cembra pine (*Pinus cembra*), spruce (*Picea abies*), upright mountain pine (*Pinus mugo* subsp. *uncinata*), and mountain ash (*Sorbus aucuparia*) from surveys conducted in 1991, 2003, 2011, and 2021. If an increasing or constantly high density of wild ungulates is correlated with increasing damage to saplings and young trees, we expect a decrease in the number of saplings and young trees over time.

The browsing pressure by wild ungulates is usually influenced by many factors and is, therefore, spatially not evenly distributed. For example, at the landscape scale, topographic factors such as elevation, exposition, and slope can influence meteorological parameters such as solar radiation, temperature, precipitation, and snow cover, which themselves have an influence on the spatial distribution of ungulates [14–16]. At the local scale, the structure and composition of the surrounding vegetation can affect the probability of browsing [17]. Additionally, not all tree species are preferred for browsing by ungulates [18].

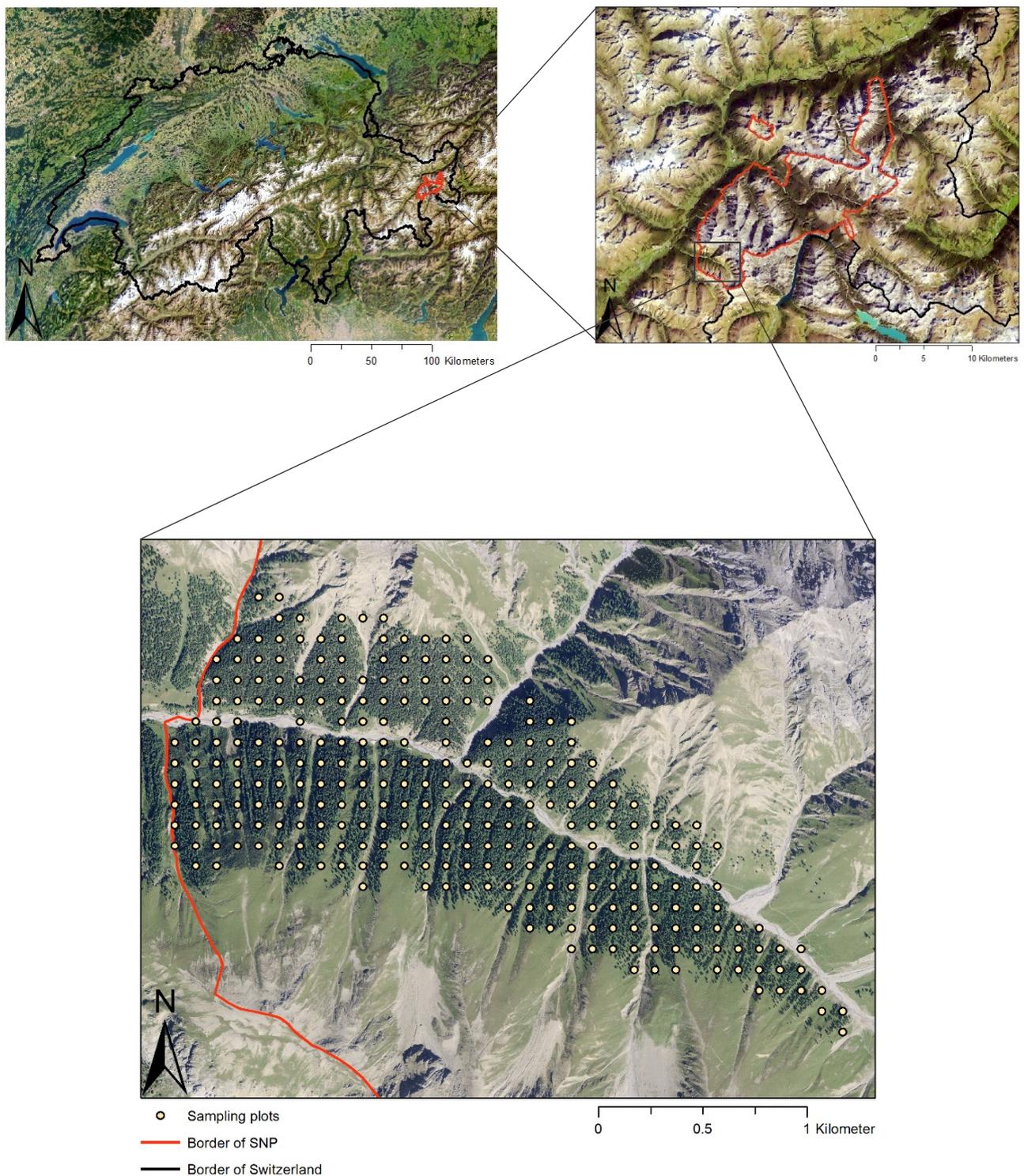
We thus investigated the spatial heterogeneity of browsing events in Val Trupchun and aimed to identify factors that may influence the probability of browsing, by modelling how topographic and location factors affected the probability of browsing on saplings of larch, cembra pine, and spruce.

## 2. Methods

### 2.1. Study Area

Founded in 1914, the Swiss National Park (SNP) is located in the east of Switzerland, in the canton of Grisons in the Central Alps (Figure 1). Due to the large elevational range from the montane to the nival belt (1380 to 3174 m a.s.l.), to the varied geology and geomorphology and the unhindered course of natural disturbances, the Swiss National Park consists of a rich mosaic of different habitat types and succession stages and contains relatively high biodiversity. As an example, about half of all Swiss diurnal lepidoptera species are found here, corresponding to a quarter of all European taxa [19].

The area of the SNP is designated as the most strictly protected nature reserve in Central Europe by the standards of the International Union for Conservation of Nature (IUCN). Human activities are thus restricted to a minimum (i.e., hiking only on marked trails, no dogs, no removal of natural objects, and no entry in winter or during the night). Nevertheless, up to 150,000 people visit the SNP per year, and around one-quarter of those visitors hike in Val Trupchun, a valley in the southwest of the park that represents our study area (Figure 1).



**Figure 1.** Study area in the Swiss National Park. The black line is the border of Switzerland, the red line is the border of the Swiss National Park, and the yellow dots are sampling plots used in this study. Background maps ©swisstopo.

At 21.56 km<sup>2</sup>, Val Trupchun represents almost one-eighth of the area of the SNP. It covers elevations of 1800 to 2800 m a.s.l. and is characterized by an inner-alpine dry climate. Mean ( $\pm$ SD) air temperatures are 11.5 °C  $\pm$  3.0 °C in summer and  $-6.1$  °C  $\pm$  5.0 °C in winter, with an annual mean precipitation of 695.5  $\pm$  120.6 mm (as measured at the weather station in Samedan, at 1708 m a.s.l., between 2012 and 2021 by MeteoSwiss [20]). The

two slopes of Val Trupchun differ in their climatic conditions and past land use. The northeast-exposed slope was used for grazing until 1960 and was added to the protected area of the SNP in 1961. This slope lies in the shadow of the mountain flank. By contrast, the southwestern slope is exposed to more solar radiation and has been part of the SNP since its foundation in 1914 [21].

The five most common tree species in Val Trupchun are larch, cembra pine, spruce, upright mountain pine, and mountain ash. However, the forests mainly consist of larch and cembra pine. Because spruce is only found in shady and humid locations, it is relatively uncommon in Val Trupchun. Likewise, upright mountain pine and mountain ash occur only rarely [22].

The three common wild ungulate species that roam the forests of Val Trupchun are red deer, which have the highest density at 21 individuals/km<sup>2</sup>, followed by Alpine ibex at 7 individuals/km<sup>2</sup> and Alpine chamois at 6 individuals/km<sup>2</sup> in 2021 (ungulate observation data from the Swiss National Park, 2021; Supplementary Material, Figure S1. For a description of methodology, see Anderwald et al. [23]). Apart from these three species, there are a small number of roe deer in Val Trupchun. Red deer undertake major seasonal migrations: in summer, they stay in Val Trupchun; in autumn, they migrate out of the valley to spend the winter in surrounding areas at lower elevations [13].

## 2.2. Sampling Design

The SNP runs a monitoring program for collecting data on forest structure and regeneration, including counts of saplings and young trees, counts of browsing events of saplings, and trunk damage on young trees inflicted by wild ungulates. In Val Trupchun, data have been collected since 1991 once per decade in summer, using a standardized method that was defined and tested in 1991 and was slightly adjusted for the surveys in 2003 and 2011. Our data collection from 2021 is part of this monitoring program.

The sampling design included 292 permanent sampling plots: for the first survey in 1991, a grid of 100 × 100 m was laid over the map of Val Trupchun, and each intersection over the forest area represented the center of a sampling plot (Figure 1). The center of each plot was marked with an iron pole in the ground and a color marker on the nearest large tree. However, not all sampling plots were found in each sampling year (Table 1).

**Table 1.** Sample sizes per sampling year.

Year	Total Number of Plots Sampled			Consecutive Plots <sup>1</sup> from All Previous Years		
	Plots on Northeast-Exposed Slope	Plots on Southwest-Exposed Slope	Total	Plots on Northeast-Exposed Slope	Plots on Southwest-Exposed Slope	Total
1991	153	74	227	153	74	227
2003	122	83	205	120	67	187
2011	120	87	207	111	66	177
2021	123	79	202	108	60	168

<sup>1</sup> Plots that were surveyed in all previous sampling years.

Within a 4 m radius from the plot center, we counted saplings of the five most common tree species (larch, cembra pine, spruce, upright mountain pine, and mountain ash) with heights of 0–130 cm and assigned them to one of six developmental stages (Table 2). In 1991, developmental stages 5 and 6 were combined into one developmental stage (Table 3). In addition, we assigned all saplings within the 4 m radius as browsed or not browsed, and a browsing event was defined as the apical shoot of the sapling having been bitten off by an ungulate [24].

**Table 2.** Developmental stages of saplings and young trees.

Developmental Stages	
Saplings	Height
1	Germ bud
2	–9.99 cm
3	10–39.99 cm
4	40–69.99 cm
5	70–99.99 cm
6	100–129.99 cm
Young trees (>130 cm height)	Breast-height diameter
7	–7.99 cm
8	8–15.99 cm
9	16–24 cm

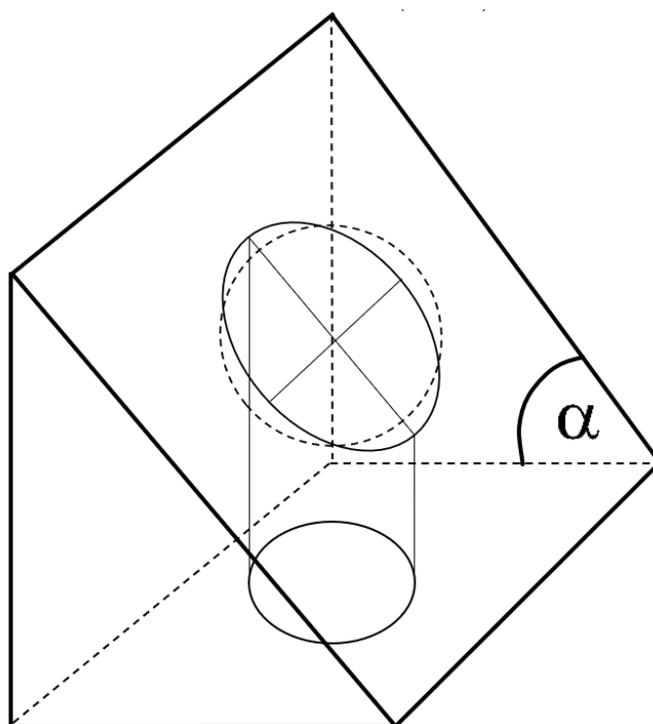
**Table 3.** Differences in sampling design in 1991 and how they were addressed in the visualizations.

Developmental Stages		
Standardized Method	1991	Dealing with difference
See Table 2	Developmental stages 5 and 6 were combined into one developmental stage	Visualization of a developmental stage 5.5 that includes the number of trees from developmental stages 5 and 6
Count data of young trees		
Standardized Method	1991	Dealing with difference
Young trees and their trunk damage were assessed within an 8 m radius	Young trees and their trunk damage were assessed within a 4 m radius	Exclusion of the data on young trees and trunk damage collected in 1991
Slope correction		
Standardized Method	1991	Dealing with difference
Adaption of the radius to the slope to obtain a consistent horizontal radius of 4 m or 8 m	No slope correction	Extrapolation of the counted number of trees to the radius that is slope-corrected

Within an 8 m radius from the plot center, we counted young trees (height > 130 cm) of the five most common tree species up to a breast-height diameter of 24 cm and assigned them to their corresponding developmental stage (Table 2). Additionally, we recorded trunk damage resulting from rubbing, stripping, and fraying by ungulates. In 1991, a 4 m radius was used instead of the 8 m radius. However, we refrained from extrapolating the data from 1991 to an 8 m radius, because such an extrapolation would have created too much uncertainty due to the large effect of local conditions on the number of trees. We therefore did not include data on the 8 m radius from 1991 in our study (Table 3).

The radii of the plots were adapted to the slope of the terrain by performing a horizontal projection of the terrain into the map plane, using the formula by Kramer and Akça [25] (Figure 2). However, in 1991, no such adjustment to the slope had been performed. We therefore extrapolated the counted saplings within the 4 m radius of 1991 to the radius after slope correction (Table 3).

To allow comparisons of densities with other studies, we extrapolated all count data to the number of saplings or young trees per hectare (ha).



**Figure 2.** Adjustment of a horizontal circle to a slope gives an ellipse. For more convenient data collection in the field, the ellipse was converted to a circular area. The slope ( $\alpha$ ) was measured in degrees, and the adjusted radius of the circular area was calculated using the following formula by Kramer and Akça [25]:  $r_{adjusted} = r / \sqrt{\cos \alpha}$ .

### 2.3. Development of the Numbers of Trees over Time

To investigate the influence of an increasing density of ungulates on forest development, we focused on three different aspects:

- Development of the numbers of saplings and young trees of the five most common tree species between 1991 and 2021;
- Development of the numbers of saplings and young trees of the five most common tree species between 1991 and 2021 on the two slopes of Val Trupchun;
- Development of the numbers of individuals within each developmental stage per tree species between 1991 and 2021.

Even though a standardized sampling method has been followed since 2003, we had to consider that not all plots were found and sampled in each sampling year, leading to different sample sizes per year (Table 1). Therefore, for our analysis, we used only plots that were sampled in all sampling years ( $n = 168$  plots).

To measure annual trends in the number of trees per plot and the difference between the slopes, we used negative binomial mixed models with the logarithm as a link function, plot identification number as a random factor, year as a numeric predictor for getting an average annual trend, and year and slope as categorical predictors for getting an average difference between the slopes. We fitted the model using Hamiltonian Monte Carlo as implemented in Stan [26], assessed via the interface rstanarm [27] from R 2.4.1 [28]. The mean, 2.5% and 97.5% quantiles of 4000 random values of the posterior distributions were used as point estimates and 95% compatibility intervals (CI), respectively.

### 2.4. Factors Possibly Affecting the Probability of Browsing

For spatial calculations and visualizations, we used Esri® ArcMap™ from the program ArcGIS Desktop, version 10.8.0.12790, Redlands, California. We calculated topographic values using a digital elevation model with a grid size of 2 m, created and provided by

the SNP. Slope and aspect were calculated with the Surface Tool of the Spatial Analyst Extension. We changed the unit of aspect from degree to *rad* and calculated the *sin* of the resulting values to obtain a measure for eastness, representing the east–west gradient (with east-exposed sampling plots = 1, and west-exposed sampling plots = −1). Northness, representing the north–south gradient (with north-exposed sampling plots = 1, and south-exposed sampling plots = −1), was calculated by applying the *cos* function to the same values.

We then calculated different location factors (Table 4), including distance to the next hiking trail, distance to the next meadow (both obtained from the HABITALP dataset [29]), species diversity of saplings, and the average developmental stage of the saplings of each tree species for each 4 m sampling plot.

For the distance to the next hiking trail, we calculated an approximation of the distance through the terrain from the plot center to the closest point of the next hiking trail, using aerial distances on the map and elevation differences obtained from the digital elevation model provided by the SNP. Distance through the terrain was calculated as the length of the hypotenuse of a perpendicular triangle with aerial distance and the elevation difference.

For the distance to the next meadow, we calculated the aerial distance of the plot center to the closest meadow, using data from the HABITALP project of the SNP with vegetation maps of Val Trupchun, including information on the location of meadows [29].

For quantifying the species diversity of the tree species, we used the Shannon index for each plot, considering only the saplings of the five tree species under investigation. We used the diversity function from the R package *vegan* [30], calculating the Shannon index as follows:

$$H' = -\sum_i^S p_i \times \ln(p_i) \text{ with } p_i = \frac{n_i}{N}$$

- *S*: total number of tree species within saplings of the plot;
- *i*: tree species of the saplings;
- *N*: total number of saplings of the five tree species within the plot;
- *n<sub>i</sub>*: number of saplings belonging to tree species *i* within the plot.

For the average developmental stage of the saplings, we calculated the mean developmental stage over all the tree species that were found within each 4 m sampling plot.

All variables with their influence on the browsing probability that we expected *a priori*, as well as the reasoning behind that expectation, are shown in Table 4.

**Table 4.** Predictors of the probability of browsing and the correlation expected *a priori*, as well as the reasoning behind that expectation.

Predictor	Correlation Expected <i>a priori</i>	Reason
Cembra pine Spruce Larch	Least browsed Medium browsed Most browsed	From the literature, we know that wild ungulates have different preferences for spruce and larch [31].
Developmental stage	Unclear	Wild ungulates might prefer some developmental stages over others [32].
<i>Topography</i>		
Elevation	Positive [14]	Meadows, which are the preferred foraging grounds of wild ungulates, are mostly at high elevations above the tree line. Sampling plots are differently exposed to wind due to their east-west exposition.
Eastness	Unclear	South-exposed sampling plots are exposed to high solar radiation, meaning challenging conditions for ungulates in summer [33].
Northness	Positive	Red deer, the ungulate species with the highest density in Val Trupchun, are better adapted to flatter terrain [34].
Slope	Negative	

Table 4. Cont.

Predictor	Correlation Expected <i>a priori</i>	Reason
<i>Location factors for 4 m sampling plot</i>		
Total number of saplings	Positive	A high number of saplings represent extensive foraging grounds for wild ungulates.
Average developmental stage	Unclear	The developmental stage of the surrounding saplings may have an influence on the browsing probability [35].
Shannon index	Positive	A high diversity of saplings may represent a resource of different nutrients and minerals.
Distance to next hiking trail	Positive	Wild ungulates avoid human presence.
Distance to next meadow	Unclear	Meadows are the main and preferred foraging grounds of wild ungulates [18].

We used a binomial generalized linear mixed-effects model with the link function logit to estimate browsing probability, using the function `glmer` from the package `lme4`. Our response variable was binomial, i.e., it was the number of browsed saplings of a tree species among the total number of saplings of the same species. We included data on saplings and their browsing events from all four sampling years and from all 4 m sampling plots (Table 1). However, we excluded the tree species mountain ash and upright mountain pine, as well as developmental stage 1, because of small sample sizes. Topographic and location variables were included in the model as additional predictors, and the sampling year and plot identification number were used as random factors.

Before we fitted the model, we transformed some numeric predictors and then centered and scaled all numeric predictors (Table 5). After comparing the fitted values from our model with our data, we judged the model fit as appropriate. We checked our model for overdispersion by comparing residual deviance with residual degrees of freedom and by using the function `dispersion_glmer` from the package `blmeco` [36]. We also checked for spatial correlation in the residuals using a semi-variogram and by displaying the residuals on a map (“bubble plot”). We did not include interactions because of two main reasons: First, we did not have *a priori* hypotheses that would require to be analyzed using interactions (see Table 4). Second, the study was designed as a monitoring project, i.e., it was not designed to investigate interactions.

We used the R-package `arm` [37] to generate 2000 random values from the joint posterior distribution of the model parameters. We used the mean as a point estimate and the 2.5% and 97.5% quantiles from the joint posterior distribution as lower and upper limits of 95% compatibility intervals (CI) [38].

**Table 5.** Transformations of the predictors of the binomial generalized linear mixed-effects model. For scaling, the values were divided by the standard deviation (given in Table 6), so that the standard deviation of the resulting variable was 1.

Predictor	Data Type	Unit	Transformation
Tree species	Factor		-
Developmental stage	Ordered factor		-
<i>Topography</i>			
Elevation	Numeric	m a.s.l.	Centered and scaled
Eastness	Numeric		Centered and scaled
Northness	Numeric		Centered and scaled
Slope	Numeric	%	Centered and scaled
<i>Location factors for 4 m sampling plot</i>			
Total number of saplings	Numeric		log-transformed, centered and scaled
Average developmental stage	Numeric		Centered and scaled
Shannon index	Numeric		Centered and scaled
Distance to next hiking trail	Numeric	m	log-transformed, centered and scaled
Distance to next meadow	Numeric	m	log(+1)-transformed, centered and scaled

**Table 6.** Parameter estimates of the mixed binomial model for browsing probability. The suffix “.z” of the variables indicates that they were centered and scaled, and transformations are indicated by their function. For the scaled variables, the standard deviation of the variable before scaling is indicated in squared brackets. Means and 2.5% and 97.5% quantiles are based on 2000 samples drawn from the joint posterior distribution. The sample size is  $n = 1808$  data points (browsed saplings of the same tree species in the same developmental stage per sampling plot and sampling year).

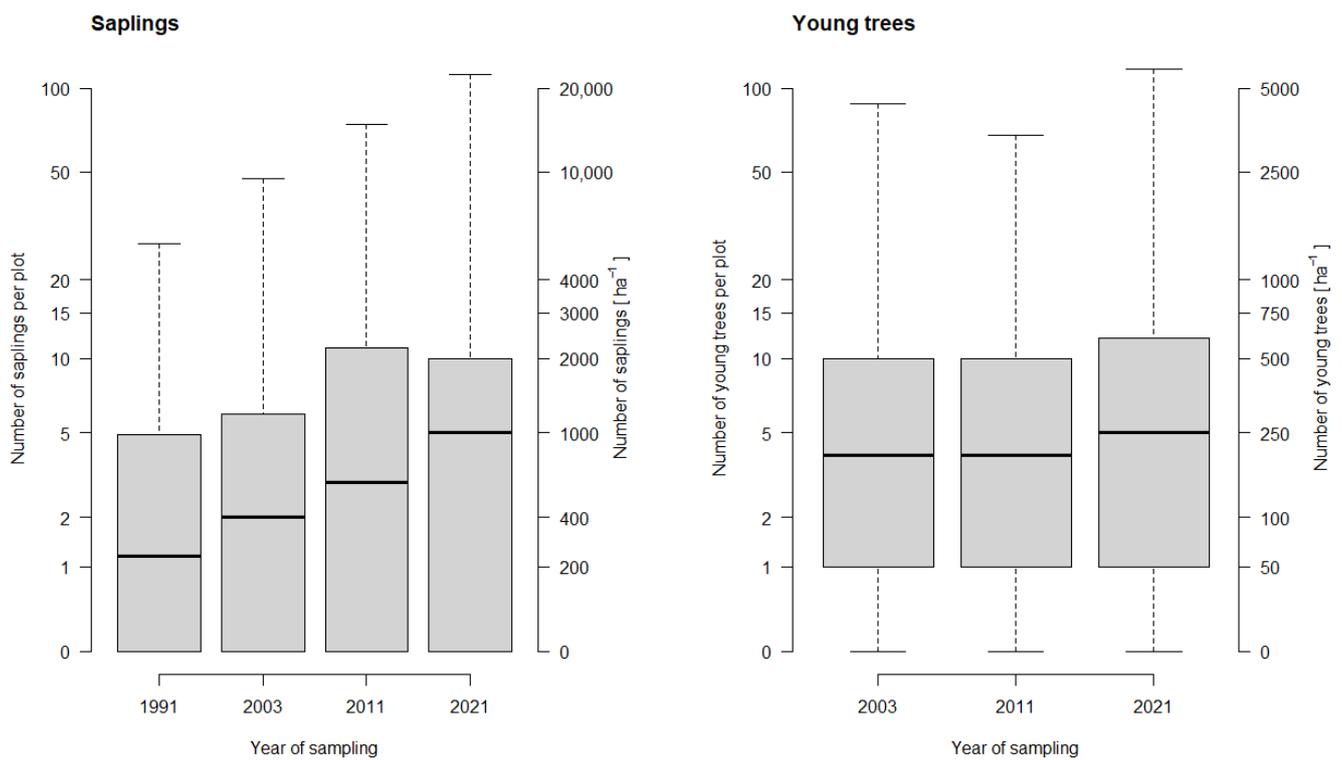
Fixed Effects			
Explanatory Variable	Mean	95% Compatibility Interval	
		2.5% Quantile	97.5% Quantile
Intercept (developmental stage 2 of cembra pine)	−5.13	−5.86	−4.44
Spruce	1.53	0.93	2.15
Larch	2.15	1.82	2.50
Developmental stage 3	1.19	0.69	1.66
Developmental stage 4	0.87	0.35	1.42
Developmental stage 5	1.02	0.46	1.59
Developmental stage 6	0.41	−0.22	1.049
log(Number of saplings).z [0.98]	−0.074	−0.23	0.077
Shannon index.z [0.31]	−0.17	−0.34	0.0045
Average developmental stage.z [0.86]	−0.074	−0.25	0.091
Elevation.z [91 m]	0.51	0.21	0.80
Slope.z [14.6%]	−0.10	−0.28	0.085
log(Dist. to next hiking trail).z [1.1 ln(meter)]	0.16	−0.11	0.44
log(Dist. to next meadow + 1).z [1.6 ln(meter)]	−0.064	−0.25	0.12
Eastness.z [0.48]	0.24	0.075	0.40
Northness.z [0.57]	−0.34	−0.54	−0.14
Random Effects			
Variables	Groups	Variance	Standard Deviation
Plot ID	197	0.44	0.67
Year	4	0.18	0.42

### 3. Results

#### 3.1. Development of the Numbers of Trees over Time

##### 3.1.1. Overall Development of the Number of Trees

The number of saplings and young trees increased in Val Trupchun over the past 30 years, with a median of 233 saplings per hectare in 1991 and 995 in 2021, and 199 young trees per hectare in 2003 and 249 in 2021 (Figure 3). The number of saplings increased annually (i.e., not per decade, but from year to year) with a factor of 1.033 (95% CI: 1.026–1.040) and the number of young trees increased annually with a factor of 1.012 (95% CI: 1.005–1.019). Additionally, the number of sampling plots on which no trees were recorded decreased both for saplings (1991 = 75, 2003 = 64, 2011 = 50, 2021 = 48) and young trees (2003 = 32, 2011 = 25, 2021 = 22).



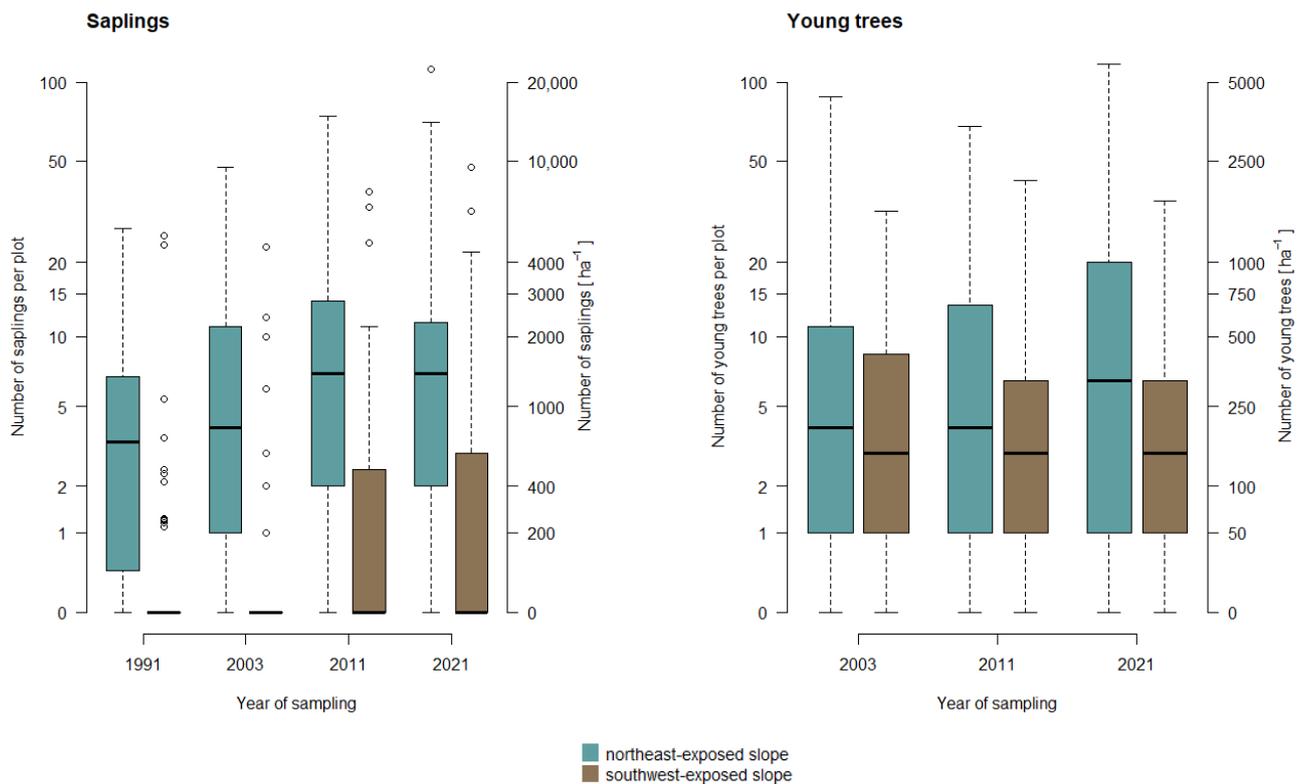
**Figure 3.** The number of saplings (left) and of young trees (right). The left *y*-axis represents the count data, and the right *y*-axis the count data extrapolated to the hectare. Saplings include developmental stages 1 to 6, and young trees include developmental stages 7 to 9 (Table 2). Data are from  $n = 168$  sampling plots that were sampled in each sampling year. Boxes show medians and interquartile ranges, whiskers are observations within 1.5 times the interquartile range.

### 3.1.2. Differences between Opposite Slopes of the Valley

Overall, the median of the number of saplings and young trees per hectare was higher on the northeast-exposed slope (median of 674 saplings per hectare in 1991 and 1393 in 2021, and of 199 young trees per hectare in 2003 and 323 in 2021) than on the southwest-exposed slope (Figure 4). On average, the number of saplings on the northeast-exposed slope was 10.12 (95% CI: 6.16–17.41) times higher than on southwest-exposed slopes. In addition, the number of young trees on the northeast-exposed slope was 1.572 (95% CI: 0.978–2.508) times higher than on the southwest-exposed slope.

### 3.1.3. Differences between Developmental Stages

Overall densities of upright mountain pine and mountain ash were much smaller than in spruce, larch, and cembra pine (Figure 5). In all five tree species, the fewest individuals were recorded in developmental stage 1 (germ buds). Most germ buds were found in the cembra pine (an average of 7.1 germ buds per hectare in 2021). All tree species showed a peak in the numbers of saplings around developmental stage 3 and of young trees around developmental stage 7. The number of larches in developmental stage 7 was exceptionally high. Despite this peak, there was not a much higher number of larches in developmental stages 8 and 9, compared with cembra pine. Most developmental stages of each tree species showed an increase in the number of trees over the past 30 years (see also Section 3.1.1).



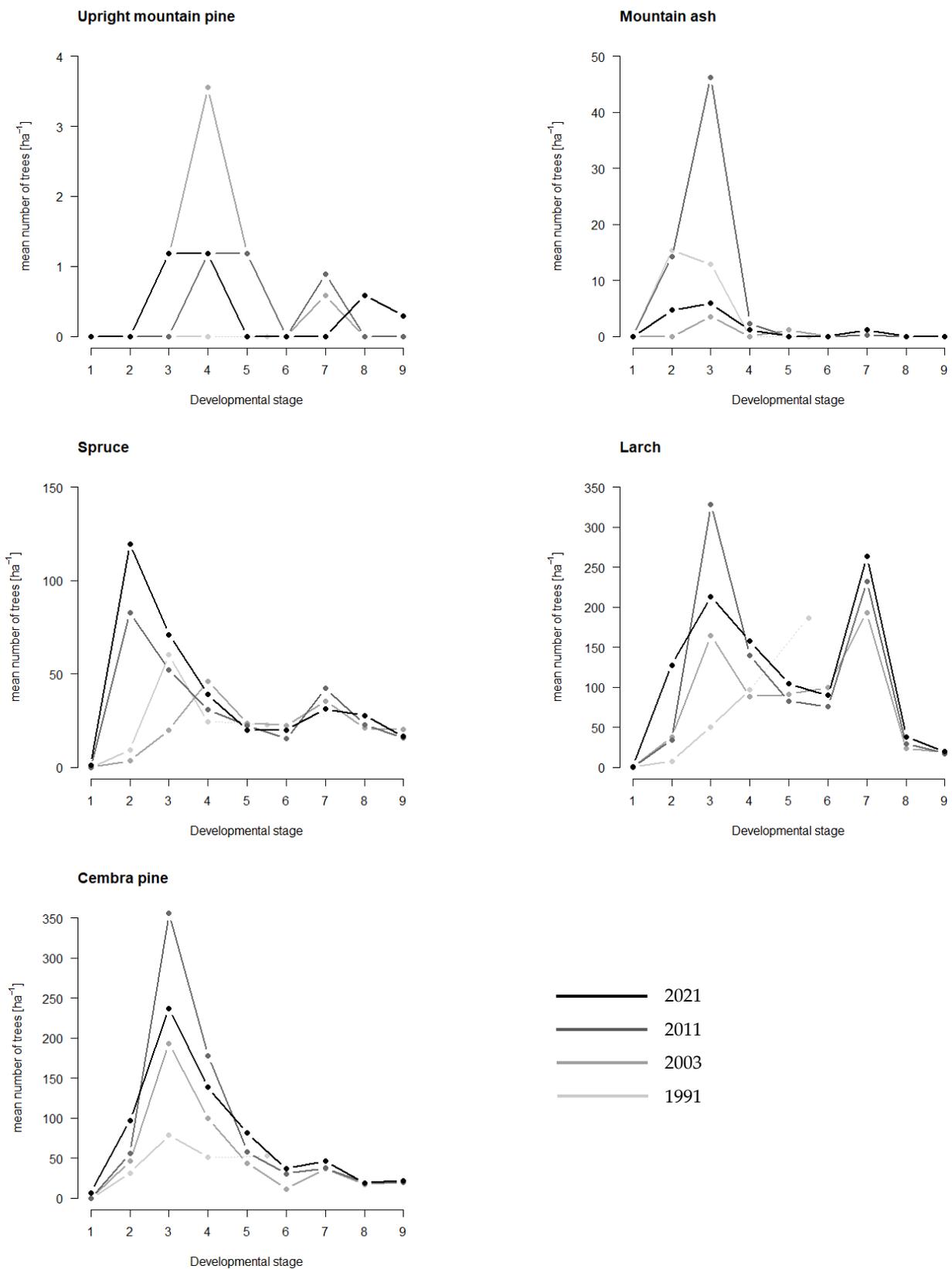
**Figure 4.** The number of saplings (left) and young trees (right) on the northeast-exposed (blue) and southwest-exposed slope (brown) of Val Trupchun. The left  $y$ -axis represents the count data, and the right  $y$ -axis the count data extrapolated to the hectare. Saplings include developmental stages 1 to 6, and young trees include developmental stages 7 to 9 (Table 2). Data are from sampling plots that were sampled in each sampling year (northeast-exposed slope:  $n = 108$  plots, southwest-exposed slope:  $n = 60$  plots). Boxes show medians and interquartile ranges, whiskers are observations within 1.5 times the interquartile range, circles are outliers.

### 3.2. Factors Affecting the Probability of Browsing

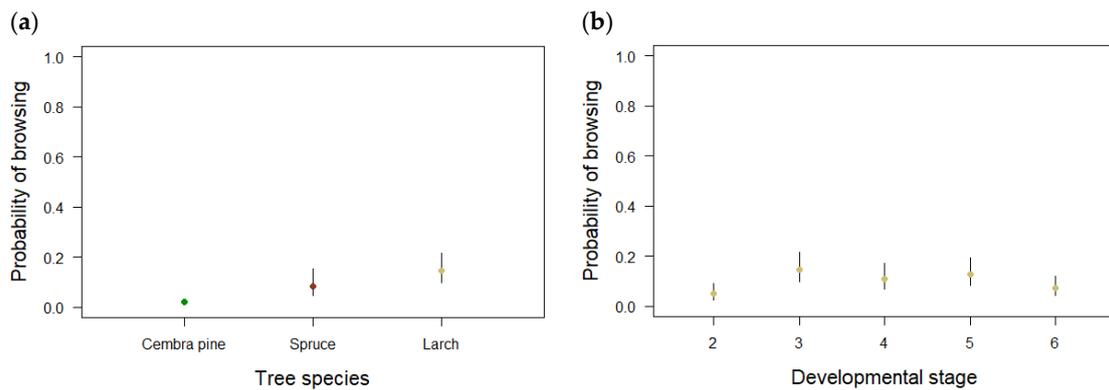
According to the binomial generalized linear mixed-effects model on sapling data from the 4 m sampling plots (Tables 6 and S1), the probability of browsing (PB) on saplings was higher for larch (PB: 0.15, 95% CI: 0.096–0.22) than for spruce (PB: 0.084, CI: 0.046–0.15) and cembra pine (PB: 0.019, CI: 0.011–0.033; see Figure 6a and Table S1). With a probability of browsing of 0.15 (CI: 0.096–0.22), developmental stage three, which includes saplings of 10–40 cm in height, had the highest probability of browsing (Figure 6b and Table S1).

Among the environmental predictors of browsing on saplings, the strongest effect (the largest coefficient) was found for elevation (Table 6, Figure 7): the odds of being browsed increased by a factor of 1.8 (95% CI: 1.3–2.4) per 100 m increase in elevation (numbers are exponentiated scaled (to 100 m) coefficients from Table 6).

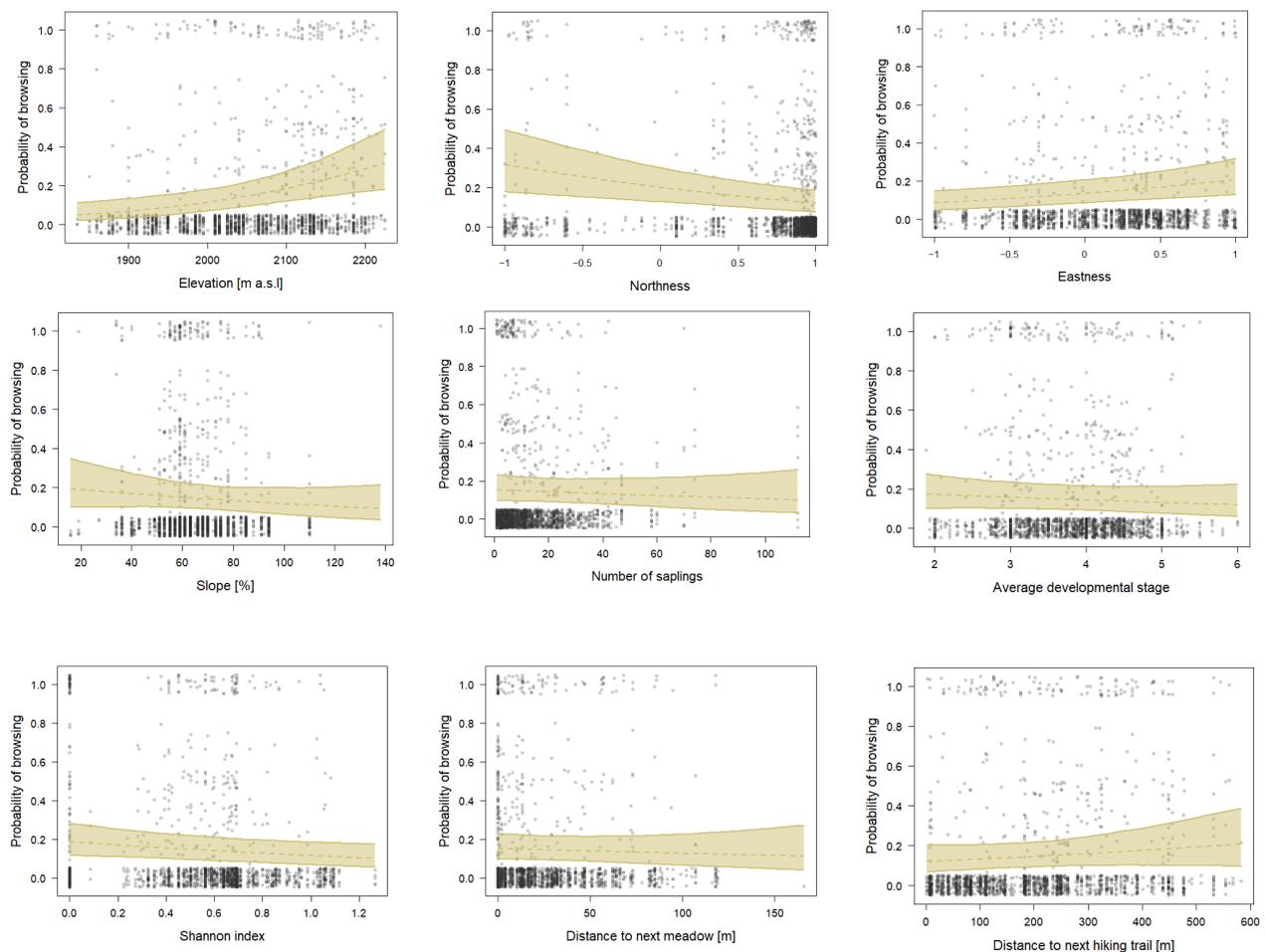
Browsing probabilities further differed among expositions (second-largest coefficients in Table 6), with the lowest browsing probabilities in west-exposed sampling plots (0.09; CI 0.05–0.15) and highest browsing probabilities on south-exposed plots (0.31; 0.19–0.48; Figure 7, Table S1). Further, the average probability of browsing decreased with increasing slope at the sampling plot: the odds of being browsed decreased by a factor of 0.93 (95% CI: 0.83–1.06) per 10% slope increase (minimum slope of 16% = PB: 0.19, CI: 0.10–0.35; maximum slope of 138% = PB: 0.093, CI: 0.033–0.22).



**Figure 5.** The mean number of saplings and young trees combined per hectare according to developmental stage (Table 2) and sampling year. Data are from  $n = 168$  sampling plots that were sampled in each sampling year. Saplings from developmental stages 5 and 6 in 1991 were combined into one developmental stage 5.5, represented by the dashed line. Further, data on developmental stages 7, 8, and 9 in the year 1991 were not included (see Table 3).



**Figure 6.** (a): Probability of browsing of saplings of cembra pine (green), spruce (brown), and larch (golden) in developmental stage 3 (point estimates for the other developmental stages would be parallel according to (b)). (b): Probability of browsing of larch in developmental stages 2 to 6 (estimates of the other tree species would be parallel according to (a)). Black lines are 95% compatibility intervals [38].



**Figure 7.** The probability of browsing of saplings for each topographic and location predictor, based on the binomial generalized linear mixed-effects model. Dots represent the proportion of browsed saplings of the same tree species in the same developmental stage per sampling plot and sampling year ( $n = 1808$  dots). Shaded areas are 95% compatibility intervals of the probability of browsing for larches in developmental stage 3, taking the other predictors into account. The point estimates and compatibility intervals of cembra pine and spruce and their developmental stages would be parallel at different heights according to Figure 6a,b.

The odds of being browsed decreased by a factor of 0.58 (95% CI: 0.34–1.01) per one unit increase of the Shannon index. Browsing probability increased the farther away a sampling plot was from a hiking trail (minimum distance of 2 m = PB: 0.12, CI: 0.068–0.20; maximum distance of 583 m = PB: 0.21, CI: 0.099–0.41), but estimated effect sizes had large uncertainty. The relations of browsing probability with the number of saplings per plot, their average developmental stage, and the distance to the next meadow remained largely unclear (Tables 6 and S1).

## 4. Discussion

### 4.1. Development of the Numbers of Trees over Time

#### 4.1.1. Overall Development of the Numbers of Trees

The Swiss National Park has an exceptionally high density of wild ungulates. For example, the density of red deer in Val Trupchun at about 21 individuals/km<sup>2</sup> is very high compared to other regions in Switzerland and neighboring countries [13] and has remained consistently high in the last decades (ungulate observation data from the Swiss National Park, 2021; Figure S1). Nonetheless, the increasing numbers of saplings and young trees per sampling plot over the last 30 years (Figure 3) suggests that the potential of the forest to regenerate has increased despite consistently high densities of wild ungulates. This confirms the findings of Weppeler and Suter [39], who investigated forest regeneration in Val Trupchun between 1991 and 2003, and of Brüllhardt et al. [40], who investigated forest regeneration between Val Trupchun and Il Fuorn in 2011. However, we do not have a control area with similar topographic and climatic conditions but without wild ungulates; therefore, the absolute impact of wild ungulates on forest regeneration remains unclear. Nevertheless, an exclusion experiment in Val Trupchun by Camenisch and Schütz [41] found that there were no obvious divergent trends in forest regeneration between enclosures and control areas. Therefore, our results are consistent with earlier studies in Val Trupchun, suggesting that the forest in this valley is able to regenerate despite the high density of wild ungulates. Indeed, the forest of Val Trupchun may still have the potential to expand because the northeast-exposed slope of the valley was used for grazing until 1960, and the forest of the whole valley shows evidence of logging up to the 19th century [21].

#### 4.1.2. Differences between Opposite Slopes of the Valley

In each sampling year, the median of the numbers of saplings and young trees per hectare on the northeast-exposed slope was higher than on the southwest-exposed slope (Figure 4). This difference in the numbers of saplings and young trees between the two slopes of the valley might be due to different climatic conditions and different spatial distributions of wild ungulates (Figure S2), resulting in distinct browsing and trunk-damage intensities (Figures S3 and S4). The high solar radiation on the southwest-exposed slope leads to a thinner snow cover in winter, to an earlier melting of the snow cover during spring, and to a drier climate during summer, compared to the northwest-exposed slope. This dry climate during summer may have a negative impact on the development of saplings and young trees. In each sampling year, both slopes showed events of browsing on saplings (Figure S3) and trunk damage on young trees (Figure S4) by wild ungulates. The small difference in the ratio of browsed saplings and damaged trees between the two slopes of the valley (Tables S3 and S4) and the distinct spatial preference by wild ungulates for the northeast-exposed slope supports our suggestion that the presence of ungulates is not the main reason for the difference in the number of saplings and young trees, but that it is a combination of the presence of ungulates and climatic conditions and probably also other environmental factors [42].

#### 4.1.3. Differences between Developmental Stages

Our results in Figure 5 show that upright mountain pine and mountain ash are rather uncommon in Val Trupchun. The most abundant tree species is larch, followed by cembra pine and spruce, as described in the vegetation maps created by Zoller [22]. Larch is a light-

demanding pioneer species that needs bare soil to regenerate and therefore benefits from disturbances such as heavy browsing, landslides, and avalanches [43]. The exceptionally high number of larches in developmental stage 7, with no corresponding high number of individuals in developmental stages 8 and 9, implies that larches have higher mortality between developmental stages 7 and 8 than cembra pine and spruce. It is currently unclear whether this high mortality rate is due to a strong preference of wild ungulates for larch in developmental stage 7 for stripping and fraying.

#### 4.2. Factors Affecting the Probability of Browsing

As expected, larch showed the highest probability of being browsed (Figure 6a). This preference of wild ungulates for larch may be due to the softness of the leaves. Because larch is a deciduous conifer and thus grows new leaves each year, they are softer than the leaves of the other two conifer species. A study conducted by Gebert and Verheyden-Tixier [18] about the dietary composition of red deer in Europe is consistent with our finding that deciduous trees are preferred by wild ungulates. Newly grown shoots of spruce are also soft, which may explain the preference for spruce over cembra pine. In contrast, the leaves of cembra pine are very stiff from the beginning.

The predictor with the strongest relation to the probability of browsing was elevation. This result is consistent with the findings of Campbell et al. [14], who showed that elevation was an important predictor for browsing pressure and that the probability of browsing was higher at higher elevations. In Val Trupchun, open grasslands are mainly located above the tree line (Figure S5) and are the preferred foraging grounds for ungulates. Thus, such meadows are areas where we frequently observe wild ungulates (Figure S2). When ungulates are disturbed during foraging, e.g., due to bad weather, they retreat into the forest to find shelter. However, they will preferably stay close to their foraging grounds and thus close to the tree line. Because there are fewer opportunities to feed on herbs and grasses in the forest, it is likely that ungulates increase their consumption of shoots and the bark of saplings.

Even though the highest density of ungulates and the highest abundance of saplings were found on the northeast-exposed slope (Figures 4 and S3), the probability of browsing was higher on the southwest-exposed slope. This result suggests that much of the browsing on the southwest-exposed slope does not occur in summer when wild ungulates occur at their highest densities in Val Trupchun due to the presence of red deer, but mainly during autumn, winter, and spring, caused by chamois and ibex preferring to stay on the southwest-exposed slopes during these seasons. During the cold seasons, red deer migrate out of the valley [44,45], and browsing by the remaining two ungulate species increases because food sources are scarce [46].

We found the lowest browsing probabilities in west-exposed sampling plots. With the prevailing westerly winds in summer (according to the weather station in Val Trupchun, mean wind direction in summer 2016 of winds  $> 5$  m/s:  $264^\circ$ ; data from Swiss National Park), the wind is channeled through the valley from west to east. Therefore, west-exposed sampling plots may have harsher conditions for ungulates than east-exposed sampling plots that are protected from westerly winds. Further, the probability of browsing decreased with increasing slope (steepness) at the sampling plot. Red deer, which have the highest density of wild ungulates, are not as well adapted to steep terrains as chamois and ibex. Therefore, they may avoid such places for browsing and stay closer to flatter areas.

The probability of browsing decreased with increasing Shannon index, meaning that each tree species was browsed less if there were other tree species present. Further, the probability of browsing may increase with increasing distance to the next hiking trail. However, such effect of human disturbance on the probability of browsing may be rather small because visitors to the SNP are not allowed to leave the hiking trails; thus, human disturbance is spatially limited and regulated. Additionally, visitors to the SNP are only allowed to stay in the park during the daytime. Therefore, sampling plots close to the hiking trail could be browsed during visitor-free periods at dusk, night, and dawn. Additionally,

Anderwald et al. [33] analyzed fecal glucocorticoid metabolite levels of chamois and red deer in the SNP and found that visitor densities were apparently not a strong stressor.

## 5. Conclusions

The results of our study shed light on the browsing behavior and the influence of wild ungulates occurring at high densities on forest regeneration within a strictly protected area of the Swiss National Park. Over the past 30 years, the number of wild ungulates in Val Trupchun has been consistently high. Due to the seasonal migrations of red deer, the highest density of wild ungulates occurs on the northeast-exposed slope at the end of the valley on open grassland in summer. Despite the pressure of browsing, stripping, and fraying by wild ungulates at such high densities, the numbers of saplings and young trees have increased over the past 30 years. The probability of browsing on saplings was highest for larch at a height of 10–40 cm and increased, for example, with increasing elevation. We hope that our study can serve as a basis for further investigations of the foraging patterns of wild ungulates and their influence on forest regeneration after ecosystem interactions are extended by the establishment of large predators such as wolves [47].

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f14061272/s1>, Figure S1: Development of the number of wild ungulates; Figure S2: Heatmap of the annual mean number of ungulates; Figure S3: Distribution of sampling plots, numbers of saplings, and proportions of saplings that have been browsed; Figure S4: Distribution of sampling plots, numbers of young trees, and proportions of young trees that show trunk damage by wild ungulates; Figure S5: Location of meadows in Val Trupchun; Table S1: Estimated browsing probabilities for the different tree species and developmental stages; Table S2: Pearson correlation coefficients of the untransformed model predictors; Table S3: Total numbers of saplings and numbers of saplings being browsed; Table S4: Total numbers of young trees and numbers of young trees with damaged trunks.

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