# The influence of wild ungulates on forest regeneration in the Swiss National Park

Master thesis at
the Department of Environmental Sciences
Zoology
University of Basel

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2023

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## Summary

The browsing behavior of wild ungulates can have a profound effect on the structure and composition of forest stands. Due to the strict protection and absence of large predators, the density of wild ungulates including red deer (*Cervus elaphus*), ibex (*Capra ibex*), and chamois (*Rupicapra rupicapra*) is exceptionally high in the Swiss National Park (SNP). As part of a monitoring program of the SNP our study investigated the structure and composition of forest stands and aimed to identify factors that may influence the probability of browsing. We examined the 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 different topographic and location factors affected the probability of browsing on saplings of larch, cembra pine, and spruce. Despite the exceptional high density of wild ungulates, the number of saplings and young trees increased over the past 30 years. The probability of browsing on saplings is highest for larch between a height of 10 cm and 40 cm and rises with increasing elevation. Larch as the only deciduous conifer in our model has softer leaves and may therefore be preferred for browsing. In our study area, open grasslands are mainly located above the tree line. Favoring open grasslands as their foraging grounds, wild ungulates stay close to the tree line and retreat into the forest during disturbances, where they browse on saplings. This might explain the positive correlation between elevation and the probability of browsing. Exposition and slope as the other topographic factors of our model as well as the other location factors describing available food resources and disturbance by humans do not show a clear effect on the probability of browsing. Our study shed light on the browsing behavior and influence of wild ungulates on forest regeneration within a protected area of the SNP and is a base for further investigations of the foraging patterns of wild ungulates after the ecosystem interactions will be extended by the establishment of large predators.

## 1. Introduction

Large herbivores play an important role in the ecosystems of subalpine and boreal forest in Europe. They directly shape the landscape by trampling, dispersing seeds, fertilizing the soil and by reducing the growth and resource uptake of plants by grazing, browsing, stripping, and fraying (Hester et al., 2006). Due to a lack of predators and to active protection and promotion of certain ungulate species, the population of wild ungulates in Western Europe increased over the last few decades (Clutton-Brock et al., 2004; Côté et al., 2004; Ripple & Beschta, 2012).

Many previous studies have shown that ungulates have a profound impact on forest ecosystems and that browsing has a negative impact on forest regeneration (Charco et al., 2016; Côté et al., 2004;

Frerker et al., 2013; Nieszała et al., 2022; Ramirez et al., 2018; Rooney & Waller, 2003). Consequently, as the 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 the forests and their functions (Bundesamt für Umwelt, 2022; Putman et al., 2011).

In strictly protected areas like national parks, such management systems are mostly not applied, and apart from providing a natural habitat, forests mostly do not have a specific function. The Swiss National Park (SNP), established in 1914 in the canton of Grisons, is designated as one of the most strictly protected nature reserve in Central Europe (IUCN category Ia, i.e. Strict Nature Reserve). Part of this strict protection includes a general hunting ban, spatial limitation of visitors to trails, and time restriction of visiting hours to daytime and summer. 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 the 1920's and 1970's after the species had returned to the canton of Grisons from the Rätikon (Principality of Lichtenstein and Vorarlberg) in the second half of the 19th century (Haller, 2002). Next to roe deer (*Capreolus capreolus*), chamois (*Rupicapra rupicapra*) and ibex (*Capra ibex*), which represent the other native ungulate species in the subalpine and alpine region of the SNP, red deer has the largest population size. According to Côté et al. (2004), the impact of wild ungulates on forests increases with increasing density; this and other studies investigating such matters are mostly conducted in 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. Hence, since 1991 the SNP has collected forest inventory data once per decade, which include data on the number of saplings and on browsing of their apical shoot, as well as on young trees and the trunk damage inflicted by wild ungulates.

As part of the monitoring program of the SNP, our study investigated the influence of a high density of wild ungulates on the forest regeneration between 1991 and 2021 in Val Trupchun, a valley within the strictly protected area of the SNP. Hence, we examined the 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 1991, 2003, 2011, and 2021, to investigate a possible change in the numbers of saplings or young trees due to wild ungulates. If increasing density of wild ungulates is generally 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 within an area with a high density of wild ungulates is influenced by many factors and is therefore spatially not evenly distributed. On the landscape scale, topographic factors like elevation, exposition, and slope influence meteorological parameters such as solar radiation, temperature, precipitation, and snow cover that themselves have an influence on the spatial distribution of ungulates (Campbell et al., 2006; Heuze et al., 2005; Mysterud, 1999). On the local scale, the structure and composition of the surrounding vegetation are factors that affect the probability of browsing (Augustine & McNaughton, 1998). Additionally, not all tree species are preferred for browsing by ungulates (Gebert & Verheyden-Tixier, 2001).

Our study investigated the spatial heterogeneity of browsing events in Val Trupchun and aimed to identify factors that may influence the probability of browsing. Thus, we modelled how different topographic and location factors affected the probability of browsing on saplings of larch, cembra pine, and spruce.

## 2. Methods

### 2.1 Study area

The Swiss National Park (SNP) is located in the east of Switzerland in the Central Alps of the canton of Grisons (figure 1). Our study area Val Trupchun is a valley in the south-west of the park. Since the foundation of the SNP in 1914, its area is designated as the most strictly protected nature reserve in Central Europe by 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 picking or removal of natural objects, no entry in winter or during the night). Nevertheless, approximately 150'000 people visit the SNP annually, and around one quarter of the visitors hike in Val Trupchun.

At 21.56 km$^2$, Val Trupchun represents almost one eighth of the area of the SNP. It covers altitudes of 1800 to 2800 m a.s.l. and is characterized by an inner-alpine dry climate. Mean air temperatures are 11.5 °C ± 3.0 °C in summer and -6.1 °C ± 5.0 °C in winter, with an annual mean precipitation of 695.5 ± 120.6 mm (weather station in Samedan, 1708 m a.s.l., mean between 2012 and 2021, MeteoSwiss, 2022). The two sides of Val Trupchun differ in their climatic conditions and past land-use. The northeast-exposed slope was used for grazing until 1960 and was included into the area of the SNP in 1961. This slope lies in the shadow of the mountain flank. In contrast, the southwest-exposed slope is exposed to more solar radiation and has been part of the SNP since its foundation in 1914 (Parolini, 1995).

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, they are relatively uncommon in Val Trupchun. The upright mountain pine and mountain ash occur only rarely (Zoller, 1995).

The three wild ungulate species that principally roam the forests of Val Trupchun are red deer, which have the highest density at 21 individuals / km$^2$, followed by Alpine ibex at 7 individuals / km$^2$ and Alpine chamois at 6 individuals / km$^2$ in 2021 (ungulate observation data from the Swiss National Park, 2021). Apart from these three species, there are a low number of roe deer in Val Trupchun. Red deer undertake major seasonal migrations. During summer they stay in Val Trupchun and during winter they migrate out of the valley to surrounding areas at lower elevations (Haller, 2002).

### 2.2 Sampling design

The SNP has a monitoring program for collecting data on forest structure and regeneration, including counts of saplings and young trees (forest inventory data), counts of browsing events of saplings, and trunk damage on young trees inflicted by wild ungulates. In Val Trupchun, data are collected since 1991 once per decade in summer, using a standardized method that was defined and tested in 1991 and slightly adjusted for the following surveys in 2003 and 2011. Our study 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 by 100 m was laid over the map of Val Trupchun, and each intersection over forest area represented the center of a sampling plot (figure 1). The center of each plot was marked by an iron pole in the ground and a color marker on the nearest large tree. However, not all sampling plots were found each sampling year (table 1).

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) of heights between 0 cm and 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). We checked all saplings for a browsing event, defined as the apical shoot of the sapling being apparently bitten off by an ungulate. To determine such browsing events, we followed the instructions from Eiberle and Nigg (1987).

Within an 8-m radius from the plot center, we counted the young trees of the five most common tree species from a height of 130 cm and 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 had been used instead of the 8-m radius. 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. Therefore, we did not include data of the 8-m radius from 1991 in our study (table 3).

The radii of the plots were adapted to the slope of the terrain because the forest inventory data refer to the area of a flat map. For this, a horizontal projection of the terrain into the map plane was performed, using the formula by Kramer & Akça, 1982 (figure 2). In 1991, no adjustment to 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).

### 2.3 Development of the numbers of trees over time

The SNP provided the forest inventory data on saplings and young trees of the five most common tree species (larch, cembra pine, spruce, upright mountain pine, and mountain ash), as well as data on the proportion that had been browsed or damaged by wild ungulates for the years 1991, 2003 and 2011. In 2021, we collected the data following the same methodology as in 2003 and 2011. A summary of the deviations of the sampling design in 1991 from the standardized sampling design since 2003 and how deviations were addressed is in table 3.

To answer our research question regarding 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 was 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). For our visualization, we only used plots that were sampled in all sampling years (n = 168).

### 2.4 Factors affecting the probability of browsing

We calculated topographic values in ArcMap using a digital elevation model with a grid size of 2 m, provided by the SNP (Schweizerischer Nationalpark, 2011). These topographic values included elevation, slope, and aspect. We changed the unit of aspect from degree to *rad* and calculated the *sin* of the resulting values to receive 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" parameters (as opposed to "topographic" parameters described above) including distance to the next hiking trail, distance to the next meadow, tree species diversity, and the average developmental stage of the tree species of each sampling plot. For spatial calculations and visualizations, we used Esri® ArcMap™ from the program ArcGIS Desktop (10.8.0.12790).

For the distance to the next hiking trail, we calculated an approximation of the distance through the terrain from the plot center to the next hiking trail. For this, we used the digital elevation model and the hiking trail line feature provided by the SNP. With the tool “Extract Values to Points” and “Near” we determined the closest point on the hiking trail from the center of each sampling plot and their aerial distance. With the aerial distance and the elevation difference of the point on the hiking trail to the plot center, we calculated the length of the hypothenuse of this perpendicular triangle.

For the distance to the next meadow, we calculated the aerial distance of the plot center to the closest meadow with the tool “Near”. We used the data from the HABITALP project of the SNP that gave us the vegetation map of Val Trupchun including information on the location of meadows (Lotz, 2006).

For species diversity, we used the Shannon index for each plot, considering only the five tree species that were under investigation. We used the diversity function from the R package vegan (Oksanen et al., 2022), which calculates 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 the plot
$i$: tree species
$N$: total number of saplings of the five tree species within the plot
$n_i$: number of saplings belonging to tree species $i$ within the plot

For the average developmental stage, we calculated the mean developmental stage over all tree species that were found within each 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.

### 2.4.1 Statistical analysis

For statistical analysis, we used R 4.1.2 (R Development Core Team 2021) and R studio (2022.07.1 Build 554). In R we applied the packages tidyverse (Wickham et al., 2019), vegan (Oksanen et al., 2022), lme4 (Bates et al., 2015), blmeco (Korner-Nievergelt et al., 2015), and arm (Gelman & Su, 2021).

We used a binomial generalized linear mixed-effects model fit by maximum likelihood with the link function “logit” to estimate browsing probability. For this, we used the function glmer from the package lme4. Our response variable was binomial, i.e., whether a sapling was browsed or not. We included the forest inventory data of saplings and their browsing events of all four sampling years, including non-consecutive sampling (table 1, column: Total number of plots sampled). However, we excluded the tree species mountain ash and upright mountain pine, as well as developmental stage 1 because of small sample sizes (see figure 5). The topographic and location variables were included into the model as additional predictors, and the sampling year and the 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 rated 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. We used 2000 simulated random samples from the joint posterior distribution of the model parameters to describe parameter estimates and their uncertainty. We used the mean as point estimate and the 2.5 % and 97.5 % quantiles from the joint posterior distribution as lower and upper limits of the 95 % compatibility intervals (Amrhein & Greenland, 2022).

## 3. Results

### 3.1 Development of the numbers of trees over time

3.1.1 Overall development of the numbers of trees

Figure 3 shows a slight increase of the median in numbers of trees over the past 30 years, with a median of one sapling per sampling plot in 1991 and of four young trees in 2003, to a median of five saplings and five young trees per sampling plot in 2021. 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). During the last four sampling years, the sampling plots with Plot ID 132 and 3 (outliers in figure 3) were repeatedly among the sampling plots with the highest numbers of recorded saplings. Similarly, during the last three sampling years, the sampling plot with Plot ID 97 was repeatedly among the sampling plots with the highest numbers of recorded young trees.

3.1.2 Differences between slopes of the valley

Overall, the median of the number of saplings and young trees per sampling plot was higher on the northeast-exposed slope (median of saplings in: 1991 = 3, 2003 = 4, 2011 = 7, 2021 = 7; median of young trees in: 2003 = 4, 2011 = 4, 2021 = 6.5) than on the southwest-exposed slope (median of saplings in: 1991 = 0, 2003 = 0, 2011 = 0, 2021 = 0; median of young trees in: 2003 = 3, 2011 = 3, 2021 = 3) (figure 4). Moreover, in each sampling year, the sampling plots with most saplings or young trees were found on the northeast-exposed slope.

3.1.3 Differences between developmental stages

The number of upright mountain pines with a maximum of three individuals in developmental stage 4 and 7 and the number of mountain ash with a maximum of 39 individuals in developmental stage 3 were much smaller compared to spruce with a maximum of 143 individuals in developmental stage 7, cembra pine with a maximum of 300 individuals in developmental stage 3, and larch with a maximum of 889 individuals in developmental stage 7 (figure 5). The fewest individuals in all tree species were recorded within developmental stage 1 that includes germ buds. With six germ buds in 2021, cembra pine had the most germ buds recorded. Larch, cembra pine and spruce showed a peak around developmental stage 3 and in 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 and spruce. Most developmental stages of each tree species showed an increase in the number of trees over the past 30 years.

### 3.2 Factors affecting the probability of browsing

According to the binomial generalized linear mixed-effects model, the probability of browsing (PB) was higher for larch (PB: 0.15, compatibility interval (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 6, left, and appendix H). With a probability of browsing of 0.15 (CI: 0.096 – 0.22), the developmental stage 3 that includes saplings of 10 cm to 40 cm height had the highest probability of browsing (figure 6, right, and appendix H).

Among the predictors, the only clear effect on the probability of browsing was found for “elevation” (see figure 7 and appendix H): the higher the elevation of the location of a sapling, the higher was its probability of being browsed (min. elevation of 1835 m = PB: 0.049, CI: 0.021 – 0.12; max. elevation of 2225 = PB: 0.31, CI: 0.19 – 0.48). The interval estimates of the other predictors included both an increase and a decrease of the probability of browsing, leaving an effect of the predictors more unclear. The least ambiguous of those less clear predictors was "northness" that was negatively correlated with probability of browsing (northness of -1 [i.e., south-exposed sampling plots] = PB: 0.31, CI: 0.18 – 0.49; northness of 1 [i.e., north-exposed sampling plots] = PB: 0.12, CI: 0.079 – 0.19). "Eastness" showed an increasing (yet unclear) probability of browsing from west-exposed to east-exposed sampling plots (eastness of -1 [i.e., west-exposed sampling plots] = PB: 0.087, CI: 0.048 – 0.15; eastness of 1 [i.e., east-exposed sampling plots] = PB: 0.21, CI: 0.13 – 0.31). "Slope" showed a decrease in the probability of browsing, the steeper the area of the sampling plot was (min. slope of 16 % = PB: 0.19, CI: 0.10 – 0.35; max. slope of 138 % = PB: 0.093, CI: 0.033 – 0.22).

The least ambiguous "location" predictor was the distance to the next hiking trail, showing an increase in the probability of browsing the farther away a sampling plot was from a hiking trail (correlation coefficient to “elevation” of 0.74; min. distance of 2 m = PB: 0.12, CI: 0.068 – 0.20; max. distance of 583 m = PB: 0.21, CI: 0.099 – 0.41). Point estimates of the number of saplings per plot, average developmental stage, Shannon index, and the distance to the next meadow showed only slight negative correlations (appendix H).

# 4. Discussion

## 4.1 Development of the numbers of trees over time

### 4.1.1 Overall development of the numbers of trees

The increasing median of saplings and young trees per sampling plot over the last 30 years in figure 3 suggests that the potential of the forest to regenerate increased despite the continuously high density of wild ungulates (appendix A). This confirms the findings of Weppler and Sutter (2006) and Brüllhardt et al. (2015), the former investigated the forest regeneration in Val Trupchun between 1991 and 2003 and the latter investigated the forest regeneration between Val Trupchun and Il Fuorn in 2011. However, we do not have a control area for Val Trupchun with similar topographical and climatic conditions but without wild ungulates. Therefore, we cannot make a statement about the relative impact of wild ungulates on forest regeneration. Nevertheless, an exclusion experiment in Val Trupchun by Camenisch and Schütz (2000) showed that there were no 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.

Further, our results suggest that the highest potential for forest regeneration is at the edge of the forest or close to avalanche tracks. We see this in the location of our sampling plots with the highest number of saplings and young trees (appendix E). In comparison to inner parts of the forest, the edge of the forest or avalanche tracks provide more light for saplings and young trees (e.g., less competition), which benefits their growth (Kupferschmid et al., 2014). Nevertheless, the edge of the forest and avalanche tracks are exposed to more disturbances than the inner part of the forest, which may lead to a higher mortality rate of saplings and young trees.

### 4.1.2 Differences between slopes of the valley

The median of the number of saplings and young trees on the northwest-exposed slope was higher in each sampling year than on the southwest-exposed slope (figure 4). The difference in the number 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 (appendix B) resulting in distinct browsing and trunk-damage intensities (appendix C and D). 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 (appendix C) and trunk damage on young trees by wild ungulates (appendix D). Over all sampling years, however, the difference of the two slopes in their ratio of browsed saplings or damaged young trees is not higher than 6.78 % (appendix C, table 6 and appendix D, table 7). The small difference of the ratio of browsed saplings and damaged trees between the two slopes of the valley and the distinct spatial preference by wild ungulates of 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 (Kienast et al., 1999).

### 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 was described in the vegetation maps created by Zoller (1995). The exceptional high number of larches in developmental stage 7 with no corresponding high number of individuals in developmental stage 8 and 9 implies that larches have a higher mortality between developmental stage 7 and 8 than cembra pine and spruce. Whether this high mortality rate is due to a strong preference of wild ungulates for larch in developmental stage 7 for stripping and fraying is not clear.

## 4.2 Factors affecting the probability of browsing

As expected, larch showed the highest probability of browsing (figure 6, left). This preference of wild ungulates for larch may be due to the softness of the leaves. Because the larch is a deciduous conifer and thus grows new leaves each year, these leaves are softer than the leaves of the other two conifer species. A study conducted by Gebert & Verheyden-Tixier (2001) 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 of spruce over cembra pine. Leaves of cembra pine, though, are very stiff from the beginning.

The results of figure 6 (right) showed that there are differences in the probability of browsing between the developmental stages and that the probability of browsing is highest for developmental stage 3. Chamois, ibex, and reed deer are grazers and browsers and, therefore, have a mixed feeding type (Hofmann, 1989). This mixed feeding type opened an alternative food resource of another niche compared to grazers. Browsing of saplings between 10 cm and 40 cm height may be very convenient for ungulates, because they do not need to adjust the position of their head to a higher level while grazing. Hence, browsing saplings between 10 cm and 40 cm height may come with a lower energetic cost.

The only clear effect of topographic and location predictors on the probability of browsing was found for the predictor "elevation" (figure 7). Our result is consistent with the findings of Campbell et al. (2006) that elevation is an important predictor for browsing pressure and that the probability of browsing is positively correlated with elevation. In Val Trupchun, open grasslands are mainly located above the tree line (appendix F) and are the preferred foraging grounds for ungulates. Thus, such meadows are areas where we frequently observe wild ungulates (appendix B). 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 bark of saplings.

The effect of the distance to the next meadow is not as clear as the effect of elevation. This may be due to the rather high correlation between elevation and the distance to the next meadow (correlation coefficient -0.39, table 10 of appendix H).

Even though the highest density of ungulates and the highest abundance of saplings is found on the northeast-exposed slope (figure 4 and appendix B), the probability of browsing is 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 that prefer to stay on the southwest-exposed slopes during these seasons. During these cold seasons, red deer migrate out of the valley (Meyer & Filli, 2006; Rempfler, 2017) and the browsing behavior of the remaining ungulate species increases because food sources are scarce (Häsler & Senn, 2012).

The effect of eastness has a wide interval estimate, but most values in the interval suggest that probability of browsing increases with increasing eastness. This means that the more exposed a sampling plot is to the east, the higher is the probability that a sapling on such a sampling plot has been browsed. With the prevailing west-wind in summer (according to a weather station in Val Trupchun, mean wind direction in summer 2016 of winds >5 m/s: 264°, 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 the west-wind. Further, there seems to be a trend of a decreasing probability of browsing with increasing steepness of the sampling plot. Red deer, which make up for 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. However, we do not have data on the steepest terrains because they were too dangerous to sample, which may also affect our results.

Location factors that describe the food resources (number of saplings per plot, average developmental stage, and Shannon index) do not have a clear effect on the probability of browsing. However, the effect of the distance to the next hiking trail, which indicates the intensity of disturbance by humans, shows a trend that with increasing distance to the next hiking trail the probability of browsing increases. The rather small effect of human disturbances on the probability of browsing may occur because visitors to the SNP are not allowed to leave the hiking trails, thus human disturbances are spatially limited and regulated. Additionally, visitors to the SNP are only allowed to stay in the park during daytime. At dusk, night and dawn, there are no visitors in the SNP. Therefore, sampling plots close to the hiking trail could be browsed during visitor-free periods. Additionally, the study of Anderwald et al. (2021) analyzing fecal glucocorticoid metabolite levels of chamois and red deer in the SNP has shown that visitor densities do not manifest themselves as a particular stressor. Furthermore, the hiking trails are mainly located at the base of the valley and hence this predictor correlates strongly with elevation (correlation coefficient of 0.74). This strong correlation may influence the effect of the distance to the next hiking trail on the probability of browsing because part of its effect is explained by elevation.

## 5. Conclusion

The results of our study shed light on the browsing behavior and the influence of wild ungulates occurring in high densities on the 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 continued to be at a high level. Due to the migratory pattern of red deer, the highest density of wild ungulates is found in summer on the northeast-exposed slope at the end of the valley on open grassland. Despite the pressure of browsing, stripping, and fraying by wild ungulates in such high densities, the number of saplings and young trees increased over the past 30 years. The probability of browsing on saplings is highest for larch between a height of 10 cm and 40 cm and rises with increasing elevation. Our study is a base for further investigations of the foraging patterns of wild ungulates after the ecosystem interactions will be extended by the establishment of large predators.

## 6. Acknowledgements

I would like to express my gratitude to everyone who supported me during my Master's thesis. I am very grateful for the help, advice, and constructive input from my supervisors Valentin Amrhein, Pia Anderwald, and Sonja Wipf. Further, I thank Fränzi Korner-Nievergelt who guided me through the statistical analysis. I would also like to thank Julia Paterno and Anne-Catherine Gutzwiler who supported me at any time with different kinds of problems. Moreover, I am thankful to Dominic Leimgruber, Saskia Aeschbach, Erwan Zimmermann, Nadline Kjelsberg, Domenic Godly, Andrea Frischknecht, Seraina Campell, Sam Cruickshank, Aline Morger, Ursula Sterrer, Diego Walder, Lukas Henggeler, and Gian Paul Calonder for the help in the field. I thank Marco Vanoni, Jürg Hassler and Martin Brüllhardt for their advice. Finally, I'm grateful for many valuable ideas and support from Valentin Amrhein's research group at the University of Basel and various members of the Swiss National Park. Finally, I want to thank my partner, Alexander Shanmugam, who always supported me. This study was made possible by the financial support of the Swiss National Park and its research board (FOK SNP) at SCNat.

## Figures

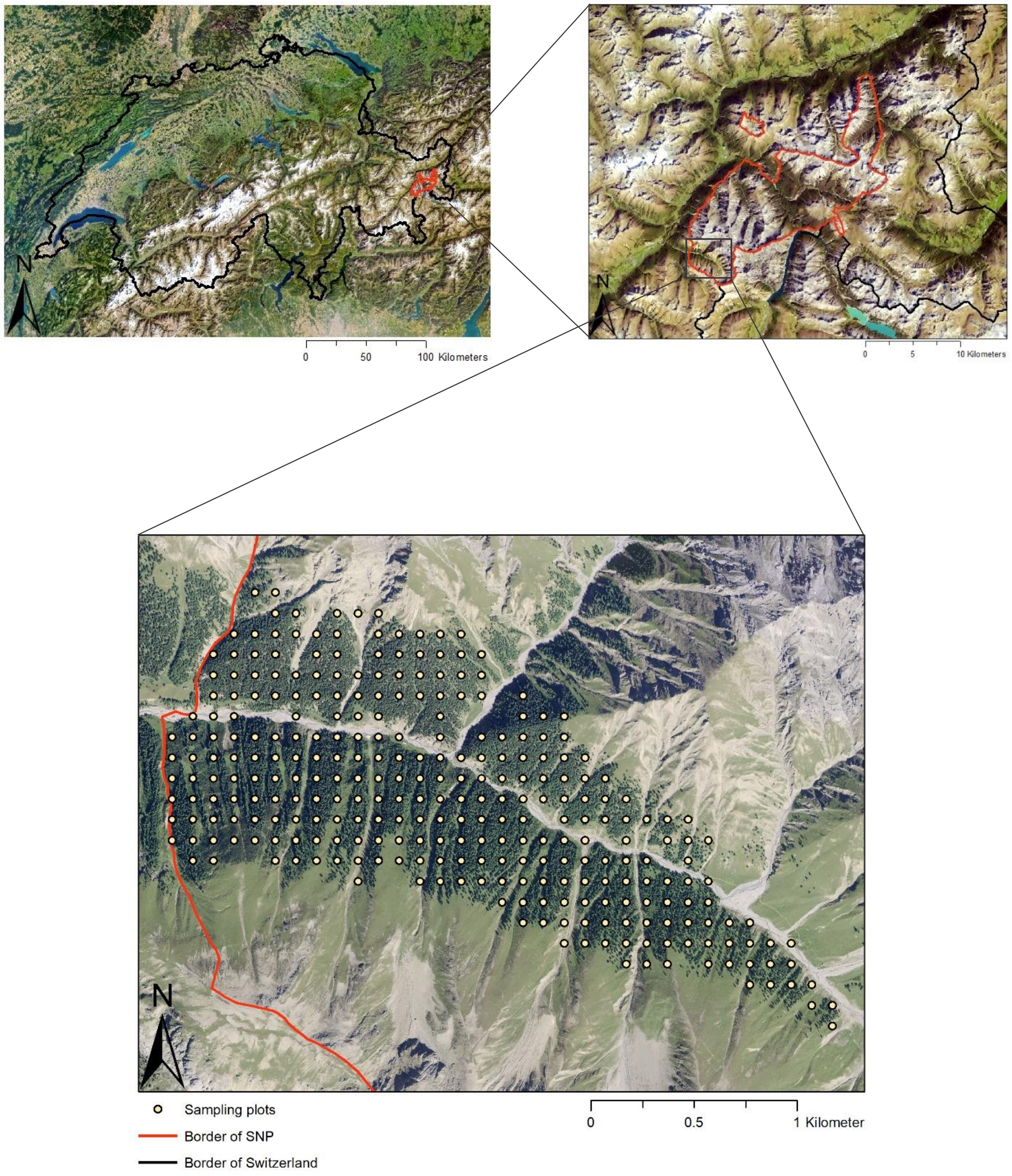
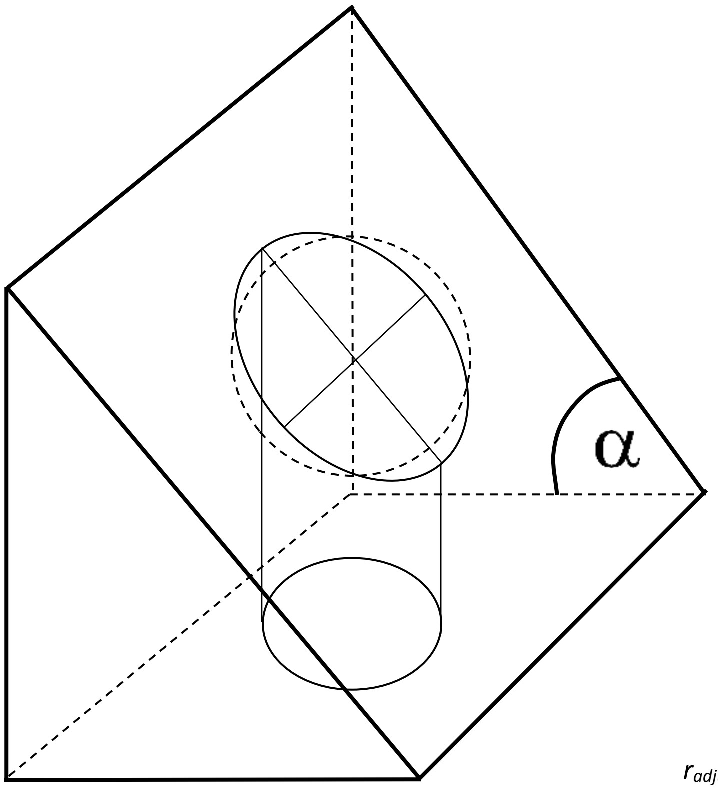


**Figure 1:** Study area in the Swiss National Park

The black line is the border of Switzerland. The red line is the border of the Swiss National Park, and the yellow dots are the sampling plots of this study.



$$r_{adjusted} = r/\sqrt{(\cos \alpha)}$$

**Figure 2:** Adaption of the horizontal radius to the slope

The adjustment of a horizontal circle to a certain slope gives an ellipse. For a more convenient measuring method in the field, the ellipse is converted into a circular area. For this, the slope (α) is measured in degrees. The adjusted radius of the circular area is calculated using the formula by Kramer & Akça (1982).

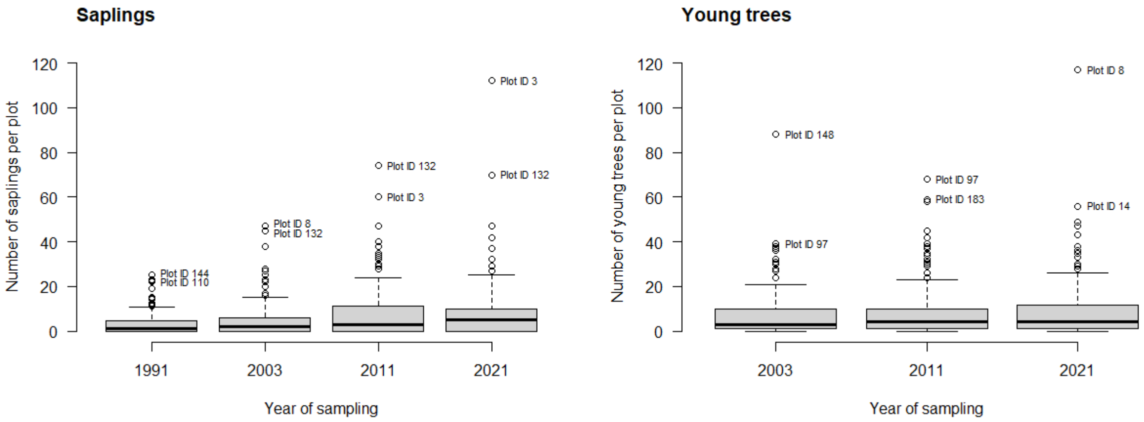


**Figure 3:** Number of saplings (left) and young trees (right) per sampling plot

Saplings include developmental stages 1 to 6, and young trees include developmental stages 7 to 9 (table 2). Medians are calculated per sampling plot including the forest inventory data of sampling plots that were surveyed in all four sampling years (n = 168). In each sampling year, the plot identification numbers (Plot ID) of the two sampling plots with the highest number of individuals are indicated. The sampling year 1991 is not included for young trees (table 3).

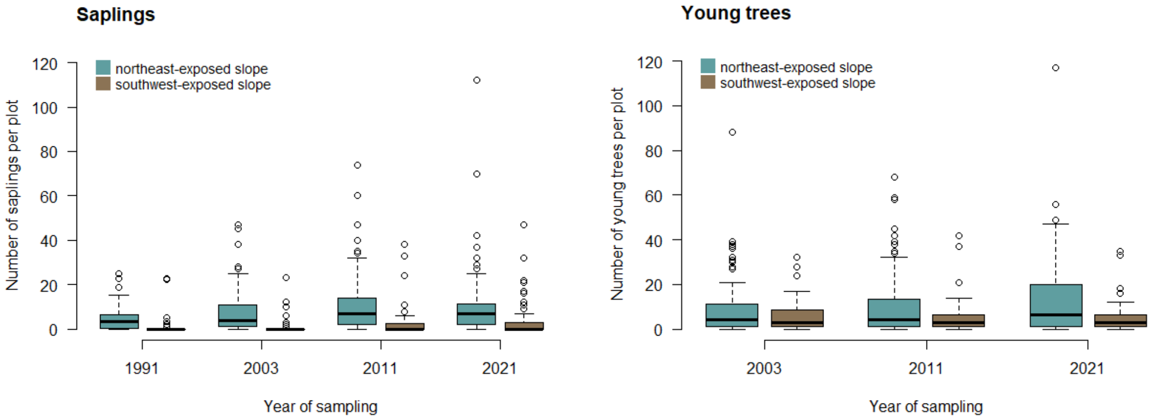


**Figure 4:** Number of saplings (left) and young trees (right) per sampling plot split by northeast-exposed (blue) and southwest-exposed slope (brown) of Val Trupchun

Saplings include developmental stages 1 to 6, and young trees include developmental stages 7 to 9 (table 2). Medians are calculated per sampling plot including the forest inventory data of sampling plots that were surveyed in all four sampling years (northeast-exposed slope: n = 108, southwest-exposed slope: n = 60). The sampling year 1991 is not included for young trees (table 3).

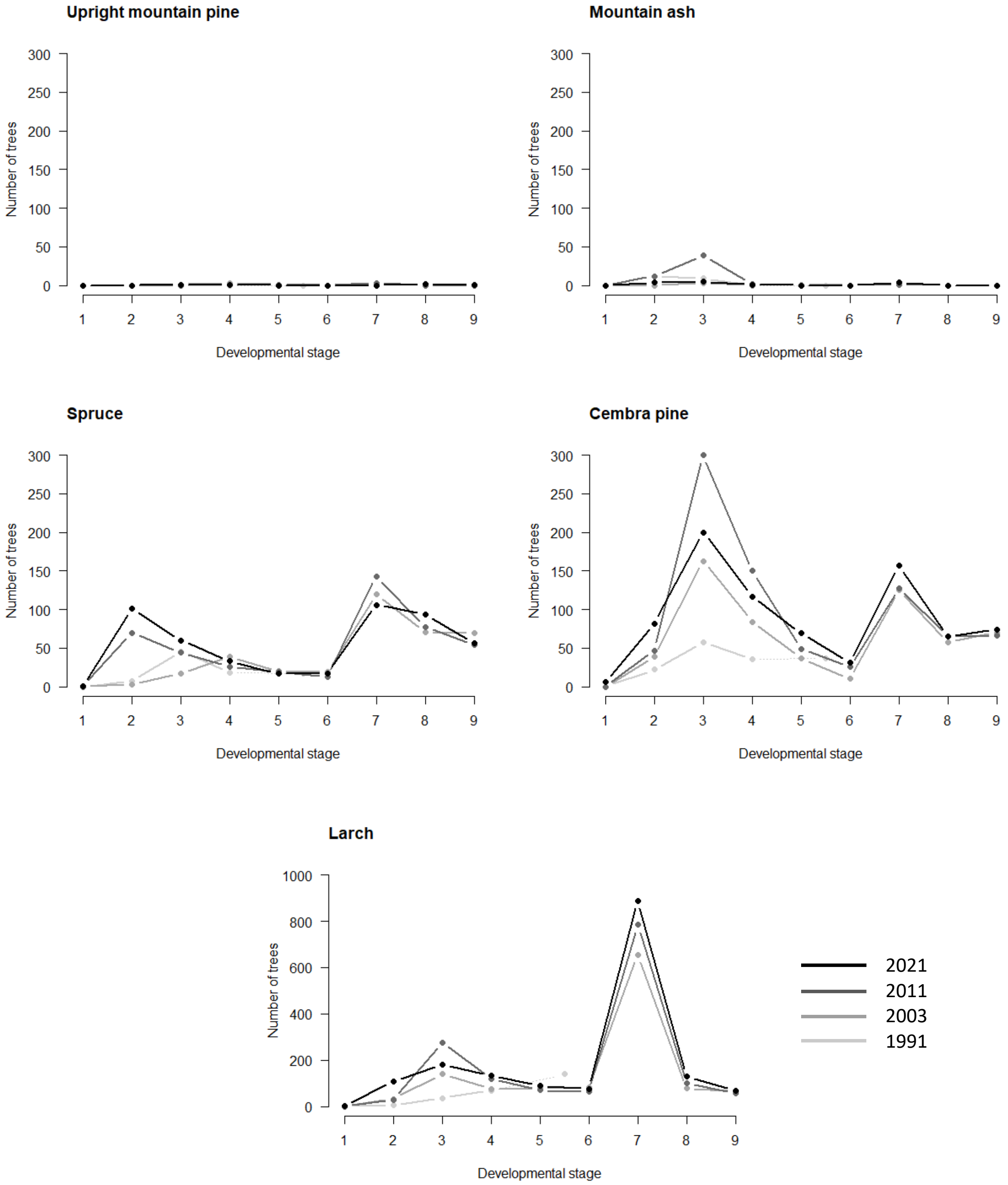


**Figure 5:** Development of the number of individuals within each developmental stage over the four sampling years for each tree species

The total number of saplings and young trees according to their developmental stage (table 2) per sampling year and tree species, using only sampling plots that were sampled in every sampling year (n = 168). Years are indicated as a grey gradient in chronological order (1991: light grey, 2021: black). The y-axis for larch ranges from 0 to 1000 and for the other tree species from 0 to 300. In 1991, the saplings from developmental stages 5 and 6 were combined into one developmental stage 5.5, represented by the dashed line. Data of developmental stages 7, 8 and 9 of the year 1991 are not considered (table 3).

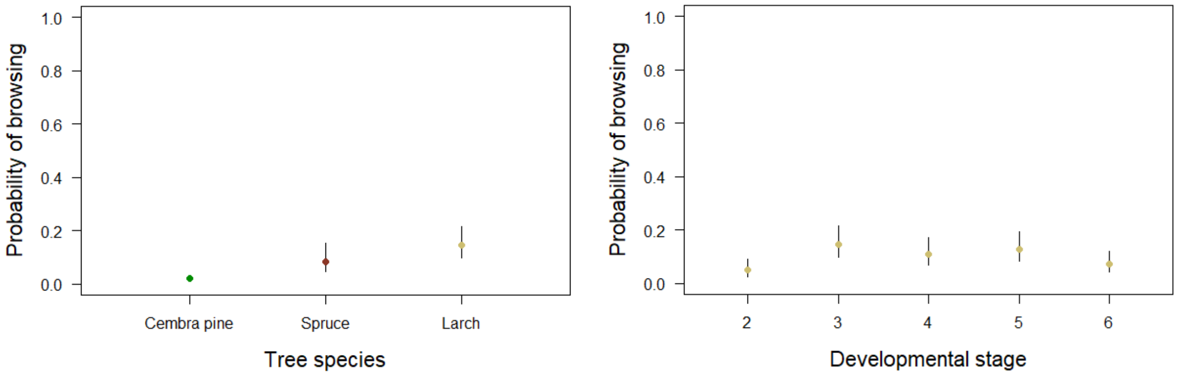


**Figure 6:** Probability of browsing per tree species (left) and per developmental stage (right)

The probability of browsing of cembra pine (green), spruce (brown) and larch (golden; left) in developmental stage 3 and the browsing probability of larch in developmental stage 2 to 5 (right; see table 2). The dots are point estimates and the black lines are 95 % compatibility intervals of the probability of browsing.

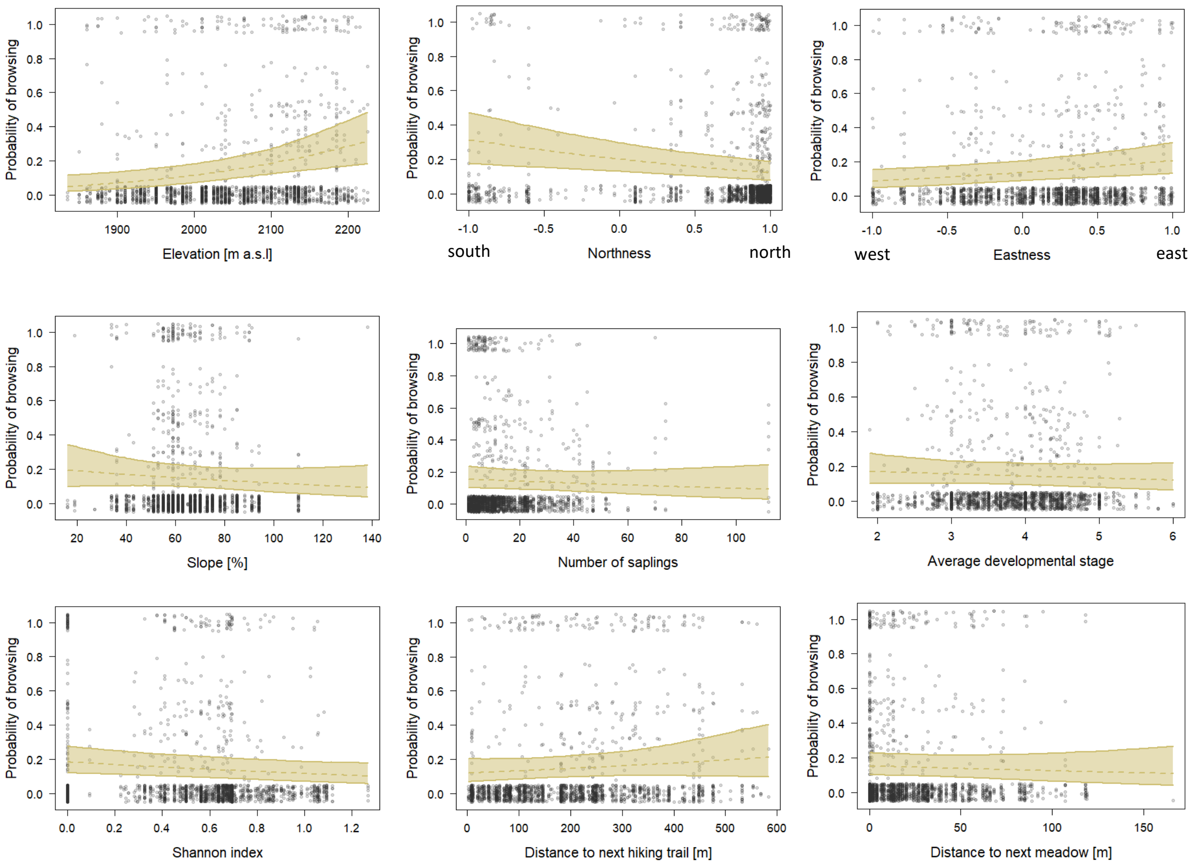


**Figure 7:** Topographic and location predictors and their influence on the probability of browsing

The probability of browsing for each topographic and location predictor based on the binomial generalized linear mixed-effects model. The dots represent the proportion of browsed trees of the same species, same developmental stage, within one plot, and one sampling year (n = 1808). 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 the other tree species and developmental stages would be parallel at different heights according to figure 6 (left and right).

# Tables

**Table 1:** Sample size per sampling year

| Year | Total number of plots sampled | | | Consecutive plots[1] 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 |

[1] plots that were surveyed in all previous sampling years

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

| **Developmental stages** | |
|---|---|
| Saplings | Height |
| 1 | Germ bud |
| 2 | 0 – 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 | Diameter |
| 7 | 130 cm height – 7.99 cm breast height diameter (BHD) |
| 8 | 8 – 15.99 cm BHD |
| 9 | 16 – 24 cm BHD |

**Table 3:** Differences of 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 count data from developmental stage 5 and 6 |

| **Count data of young trees** | | |
|---|---|---|
| Standardized Method | 1991 | Dealing with difference |
| Young trees and their trunk damage are 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 horizontal radius to the slope | No slope correction | Extrapolation of the count data to the radius that is slope-corrected and rounding to integers |

**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 a priori | Reason |
|---|---|---|
| Tree species | | From the literature, we know that wild ungulates have different preferences for spruce, and larch (Gill, 1992). |
| Cembra pine | Least browsed | |
| Spruce | Medium browsed | |
| Larch | Most browsed | |
| Developmental stage | Unclear | Wild ungulates might prefer some developmental stages over others. |
| Topography | | |
| Elevation | Positive | At high elevations, above the tree line, are meadows that are the preferred foraging grounds of wild ungulates. |
| Aspect | | |
| Eastness | Unclear | Sampling plots are differently exposed to wind due to their east-west exposition. |
| Northness | Positive | South-exposed sampling plots are exposed to high solar radiation which represents challenging conditions for ungulates in summer. |
| Slope | Negative | Red deer, which is the wild ungulate species with the highest density in Val Trupchun, are more adapted to flatter terrain. |
| Location factors per sampling plot | | |
| Total number of trees | Positive | A high number of trees 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. |
| Shannon index | Positive | A high diversity of saplings represents different important nutrients and minerals. |
| Distance to next hiking trail | Positive | Wild ungulates avoid human presence. |
| Distance to next meadow | Positive | Meadows are the main and preferred foraging grounds of wild ungulates. |

**Table 5:** Transformations of the predictors of the binomial generalized linear mixed-effects model

| Predictor | Data type | Unit | Transformation |
|---|---|---|---|
| Tree species | Factor | | - |
| Developmental stage | Ordered factor | | - |
| Topography | | | |
| Elevation | Numeric | m a.s.l. | Centered and scaled |
| Aspect | | | |
| Eastness | Numeric | | Centered and scaled |
| Northness | Numeric | | Centered and scaled |
| Slope | Numeric | % | Centered and scaled |
| Location | | | |
| Total number of trees | 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 |

## References

Amrhein, V., & Greenland, S. (2022). Discuss practical importance of results based on interval estimates and *p* -value functions, not only on point estimates and null *p* -values. *Journal of Information Technology*, *37*(3), 316–320. https://doi.org/10.1177/02683962221105904

Anderwald, P., Campell Andri, S., & Palme, R. (2021). Reflections of ecological differences? Stress responses of sympatric Alpine chamois and red deer to weather, forage quality, and human disturbance. *Ecology and Evolution*, *11*(22), 15740–15753. https://doi.org/10.1002/ece3.8235

Augustine, D. J., & McNaughton, S. J. (1998). Ungulate Effects on the Functional Species Composition of Plant Communities: Herbivore Selectivity and Plant Tolerance. *The Journal of Wildlife Management*, *62*(4), 1165. https://doi.org/10.2307/3801981

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). *Fitting Linear Mixed-Effects Models Using lme4*. *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Brüllhardt, M., Risch, A. C., Filli, F., Haller, R. M., & Schütz, M. (2015). Spatiotemporal dynamics of natural tree regeneration in unmanaged subalpine conifer forests with high wild ungulate densities. *Canadian Journal of Forest Research*, *45*(6), 607–614. https://doi.org/10.1139/cjfr-2014-0358

Bundesamt für Umwelt. (2022, November 15). *Waldfunktionen und Leistungen*. Waldzustand Und Waldfunktionen. https://www.bafu.admin.ch/bafu/de/home/themen/wald/fachinformationen/waldzustand-und-waldfunktionen.html

Camenisch, M., & Schütz, M. (2000). *Temporal and spatial variability of the vegetation in a four-year exclosure experiment in Val Trupchun (Swiss National Park)*. 24.

Campbell, T. A., Laseter, B. R., Ford, W. M., Odom, R. H., & Miller, K. V. (2006). Abiotic Factors Influencing Deer Browsing in West Virginia. *Northern Journal of Applied Forestry*, *23*(1), 20–26. https://doi.org/10.1093/njaf/23.1.20

Charco, J., Perea, R., Gil, L., & Nanos, N. (2016). Impact of deer rubbing on pine forests: Implications for conservation and management of Pinus pinaster populations. *European Journal of Forest Research*, *135*(4), 719–729. https://doi.org/10.1007/s10342-016-0967-6

Clutton-Brock, T. H., Coulson, T., & Milner, J. M. (2004). Red deer stocks in the Highlands of Scotland. *Nature*, *429*(6989), 261–262. https://doi.org/10.1038/429261a

Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., & Waller, D. M. (2004). Ecological Impacts of Deer Overabundance. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Eiberle, K., & Nigg, H. (1987). *Grundlagen zur Beurteilung des Wildverbisses im Gebirgswald* [Text/html,application/pdf,text/html]. https://doi.org/10.5169/SEALS-766065

Frerker, K., Sonnier, G., & Waller, D. M. (2013). Browsing rates and ratios provide reliable indices of ungulate impacts on forest plant communities. *Forest Ecology and Management*, *291*, 55–64. https://doi.org/10.1016/j.foreco.2012.11.041

Gebert, C., & Verheyden-Tixier, H. (2001). Variations of diet composition of Red Deer (Cervus elaphus L.) in Europe. *Mammal Review*, *31*(3–4), 189–201. https://doi.org/10.1111/j.1365-2907.2001.00090.x

Gelman, A., & Su, Y.-S. (2021). *arm: Data Analysis Using Regression and Multilevel/Hierarchical Models* (p. R package version 1.12-2). https://CRAN.R-project.org/package=arm

Gill, R. M. A. (1992). A Review of Damage by Mammals in North Temperate Forests: 1. Deer. *Forestry*, *65*(2), 145–169. https://doi.org/10.1093/forestry/65.2.145

Haller, H. (2002). *Der Rothirsch im Schweizerischen Nationalpark und dessen Umgebung*. 144.

Hester, A. J., Bergman, M., Iason, G. R., & Moen, J. (2006). Impacts of large herbivores on plant community structure and dynamics. In K. Danell, R. Bergström, P. Duncan, & J. Pastor (Eds.), *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* (1st ed., pp. 97–141). Cambridge University Press. https://doi.org/10.1017/CBO9780511617461.006

Heuze, P., Schnitzler, A., & Klein, F. (2005). Is browsing the major factor of silver fir decline in the Vosges Mountains of France? *Forest Ecology and Management*, *217*(2–3), 219–228. https://doi.org/10.1016/j.foreco.2005.06.003

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia*, *78*(4), 443–457. https://doi.org/10.1007/BF00378733

Kienast, F., Fritschi, J., Bissegger, M., & Abderhalden, W. (1999). Modeling successional patterns of high-elevation forests under changing herbivore pressure – responses at the landscape level. *Forest Ecology and Management*, *120*(1–3), 35–46. https://doi.org/10.1016/S0378-1127(98)00541-6

Korner-Nievergelt, F., Roth, T., von Felten, S., Guelat, J., Almasi, B., & Korner-Nievergelt, P. (2015). *Bayesian Data Analysis in Ecology using Linear Models with R, BUGS and Stan*. Elsevier.

Kupferschmid, A. D., Wasem, U., & Bugmann, H. (2014). Light availability and ungulate browsing determine growth, height and mortality of Abies alba saplings. *Forest Ecology and Management*, *318*, 359–369. https://doi.org/10.1016/j.foreco.2014.01.027

Meyer, D. L., & Filli, F. (2006). *Sommer- und Wintereinstandsgebiete von weiblichen Rothirschen Cervus elaphus im Schweizerischen Nationalpark*. 26.

Millhäusler, A., Anderwald, P., Haeni, M., & Haller, R. M. (2016). Publicity, economics and weather – Changes in visitor numbers to a European National Park over 8 years. *Journal of Outdoor Recreation and Tourism*, *16*, 50–57. https://doi.org/10.1016/j.jort.2016.09.005

Mysterud, A. (1999). Seasonal migration pattern and home range of roe deer ( *Capreolus capreolus* ) in an altitudinal gradient in southern Norway. *Journal of Zoology*, *247*(4), 479–486. https://doi.org/10.1111/j.1469-7998.1999.tb01011.x

Nieszała, A., Klich, D., Perzanowski, K., Januszczak, M., Wołoszyn-Gałęza, A., & Olech, W. (2022). Debarking intensity of European bison in the Bieszczady Mountains in relation to forest habitat features. *Forest Ecology and Management*, *508*, 120057. https://doi.org/10.1016/j.foreco.2022.120057

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., … Weedon, J. (2022). *vegan: Community Ecology Package* (p. R package version 2.6-2). https://CRAN.R-project.org/package=vegan

Parolini, J. D. (1995). *Zur Geschichte der Waldnutzung im Gebiet des heutigen Schweizerischen Nationalparks* [Doctoral Thesis, ETH Zurich]. https://doi.org/10.3929/ethz-a-001533724

Putman, R., Apollonio, M., & Reidar, A. (2011). *Ungulate Management in Europe: Problems and Practices*. Cambridge: Cambridge University Press.

Ramirez, J. I., Jansen, P. A., & Poorter, L. (2018). Effects of wild ungulates on the regeneration, structure and functioning of temperate forests: A semi-quantitative review. *Forest Ecology and Management*, *424*, 406–419. https://doi.org/10.1016/j.foreco.2018.05.016

Rempfler, T. (2017). Where do red deer come from and where do they go? *6th Symposium for Research in Protected Areas*, 2.

Ripple, W. J., & Beschta, R. L. (2012). Large predators limit herbivore densities in northern forest ecosystems. *European Journal of Wildlife Research*, *58*(4), 733–742. https://doi.org/10.1007/s10344-012-0623-5

Rooney, T. P., & Waller, D. M. (2003). Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management*, *181*(1–2), 165–176. https://doi.org/10.1016/S0378-1127(03)00130-0

Swiss National Park. (2009). *Location of Avalanches*. https://www.parcs.ch/snp/maindata/forest_avalanches_slf.htm

Weppler, T., & Suter, W. (2006). Forest regeneration at high densities of wild ungulates in Val Trupchun (Swiss National Park) between 1991/1992 and 2003,. *Ungulate research in the Swiss National Park, Nat.park-Forsch. Schweiz. 93. Research commission of the Swiss National Park, pp. 213–235.*, 29.

Wickham, H., Averick, M., Bryan, J., Chang, W., D’Agostino McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Lin Pedersen, T., Miller, E., Milton Bache, S., Müller, K., Ooms, J., Robinson, D., Paige Seidel, D., Spinu, V., … Yutani, H. (2019). *Welcome to the tidyverse*. *4*(43), 1686. https://doi.org/10.21105/joss.01686

Zoller, H. (1995). Vegetationskarte des Schweizerischen Nationalparks Erläuterungen. *Nationalpark-Forschung in der Schweiz*, *85*, 108.

# Appendix

## Appendix A

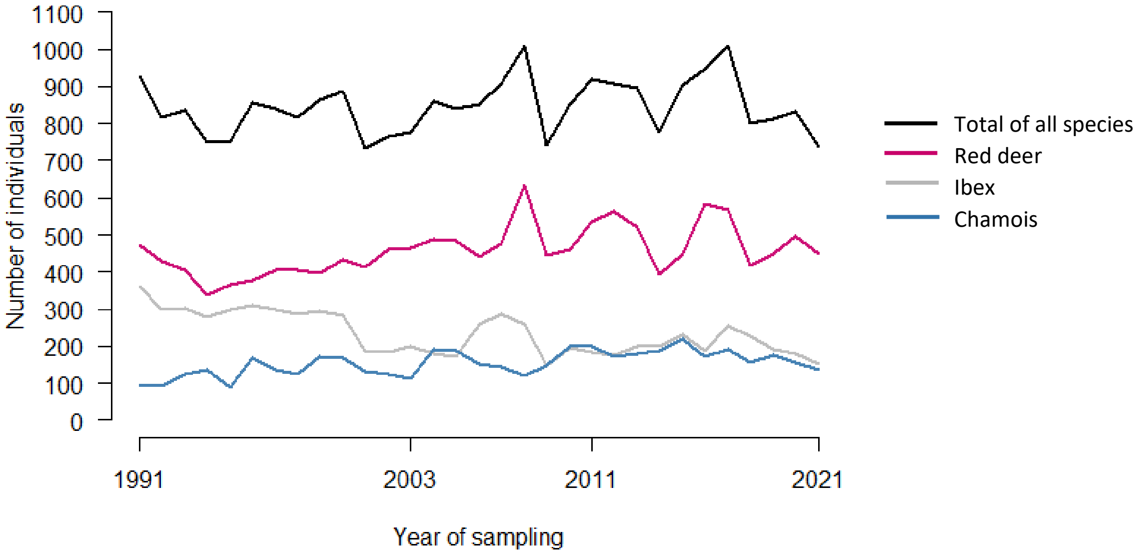


**Figure 8:** Development of the number of wild ungulates

Annual census counts of red deer (pink), ibex (grey) and chamois (blue) and the total number of all ungulate species (black) in Val Trupchun between 1991 and 2021 (data provided by the Swiss National Park; for a description of methodology, see Anderwald et al. 2015). The four sampling years of the monitoring program are indicated on the x-axis.

## Appendix B

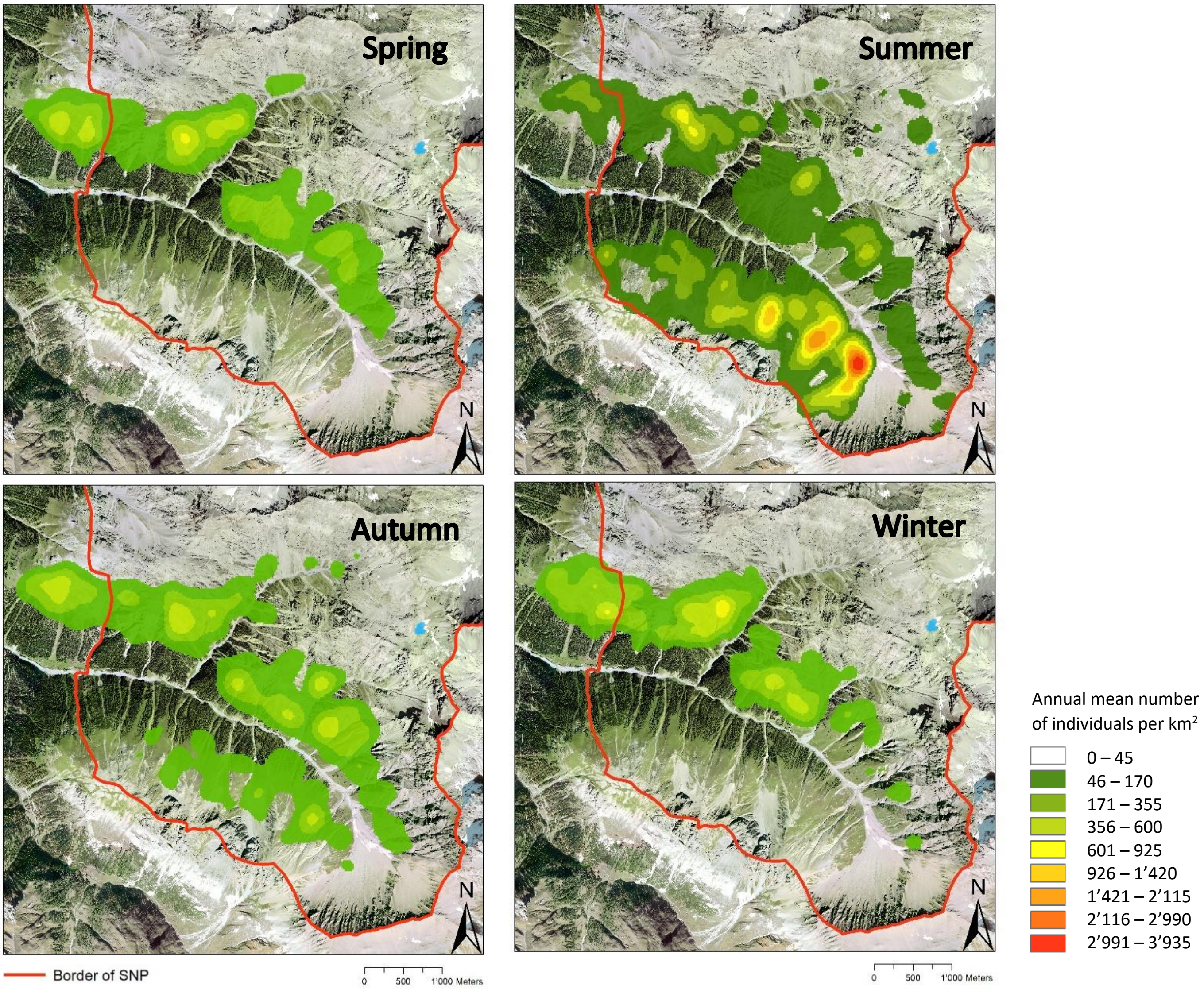


**Figure 9:** Spatial distribution of wild ungulates

Heatmap of the annual mean number of ungulates (red deer, chamois, and ibex) per km$^2$ per season, based on visual observation data from the SNP between 2012 and 2021 (data provided by the Swiss National Park; for a description of methodology, see Anderwald et al. 2015).

## Appendix C

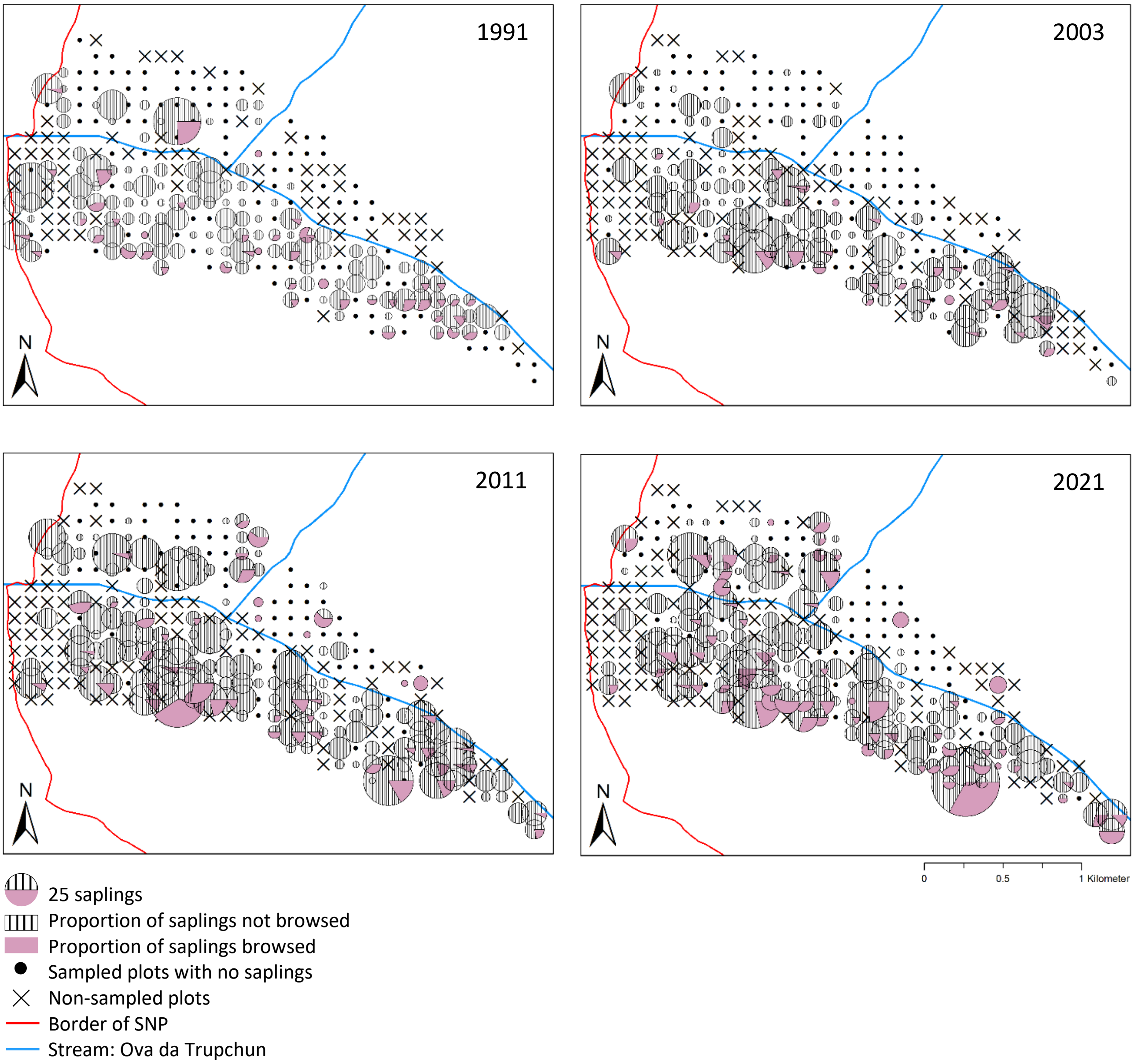


**Figure 10:** Spatial distribution of sampling plots and their number of saplings and proportion of saplings browsed

Distribution of sampling plots, numbers of saplings, and proportions of saplings that have been browsed over the four sampling years in Val Trupchun. Pie charts show sampling plots with saplings and the size of the charts represents the number of saplings. Striped patterns of the pie chart indicate saplings that have not been browsed, and pink colored areas indicate saplings that have been browsed. Dots are sampling plots without saplings and crosses are plots that were not sampled. The red line visualizes the border of the SNP and the blue line the stream that flows through Val Trupchun.

**Table 6:** Number of saplings and the number of saplings being browsed of all sampling plots (table 1, column: Total number of plots sampled) for each tree species in the according sampling year

| **Saplings** | | | | | |
|---|---|---|---|---|---|
| | | **Northeast-exposed slope** | | **Southwest-exposed slope** | |
| **Year** | **Tree species** | **Total individuals** | **Browsed individuals** | **Total individuals** | **Browsed individuals** |
| 1991 | Larch | 384 | 52 | 13 | 1 |
| | Cembra pine | 215 | 5 | 1 | 0 |
| | Spruce | 51 | 0 | 109 | 13 |
| | Mountain ash | 21 | 8 | 0 | 0 |
| | Upright mountain pine | 0 | 0 | 7 | 0 |
| | Total | 671 | 65 | 130 | 14 |
| | Ratio of browsed and total individuals in % | 9.69 % | | 10.77 % | |
| 2003 | Larch | 443 | 44 | 15 | 0 |
| | Cembra pine | 361 | 8 | 3 | 0 |
| | Spruce | 42 | 5 | 62 | 0 |
| | Mountain ash | 4 | 1 | 0 | 0 |
| | Upright mountain pine | 5 | 0 | 0 | 0 |
| | Total | 855 | 58 | 80 | 0 |
| | Ratio of browsed and total individuals in % | 6.78 % | | 0 % | |
| 2011 | Larch | 623 | 110 | 61 | 26 |
| | Cembra pine | 594 | 13 | 32 | 2 |
| | Spruce | 43 | 5 | 192 | 4 |
| | Mountain ash | 53 | 9 | 0 | 0 |
| | Upright mountain pine | 2 | 0 | 0 | 0 |
| | Total | 1315 | 137 | 285 | 32 |
| | Ratio of browsed and total individuals in % | 10.42 % | | 11.23 % | |
| 2021 | Larch | 637 | 171 | 84 | 29 |
| | Cembra pine | 591 | 19 | 15 | 1 |
| | Spruce | 72 | 3 | 202 | 27 |
| | Mountain ash | 10 | 0 | 0 | 0 |
| | Upright mountain pine | 1 | 0 | 1 | 0 |
| | Total | 1311 | 193 | 302 | 57 |
| | Ratio of browsed and total individuals in % | 14.72 % | | 18.87 % | |

## Appendix D

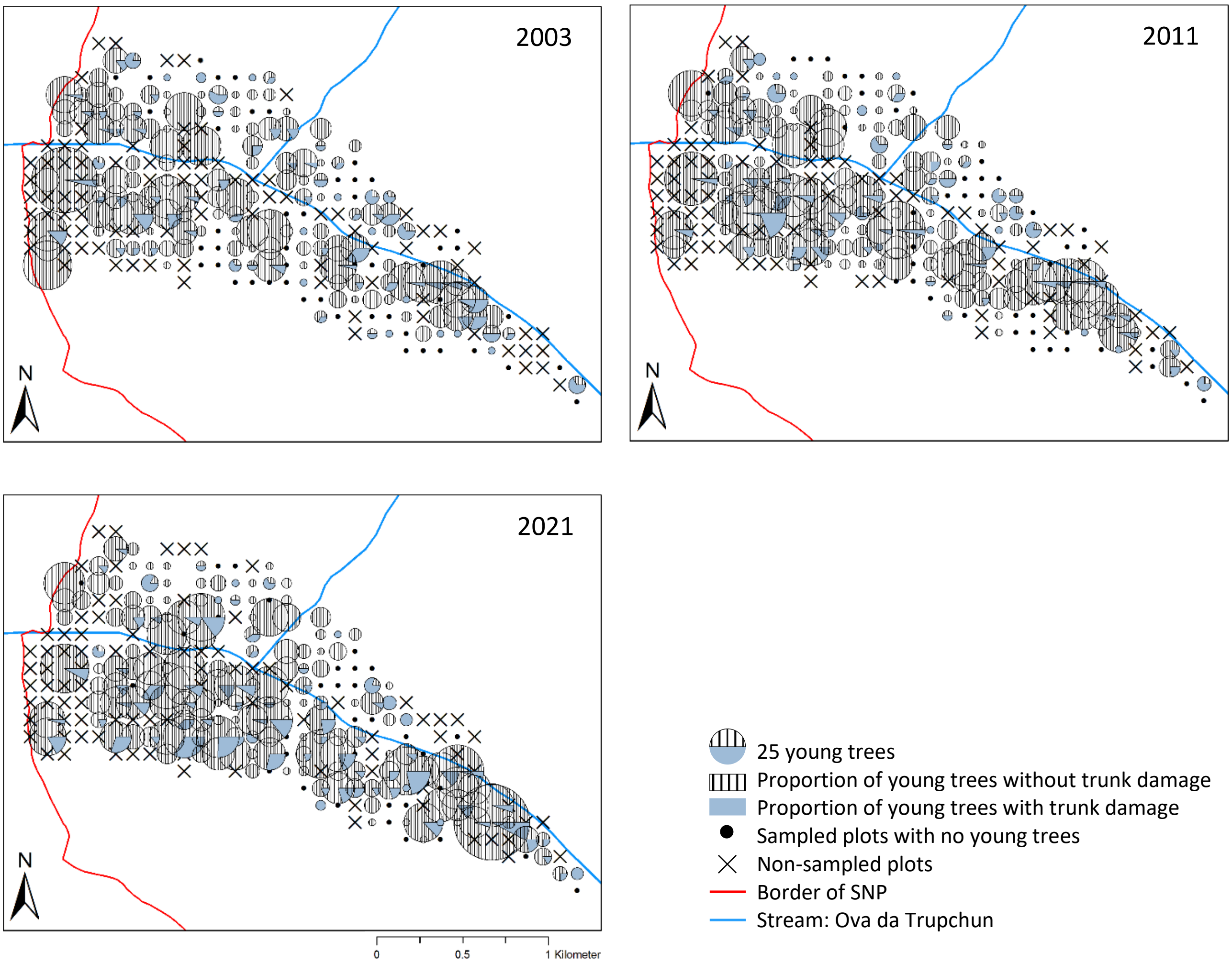


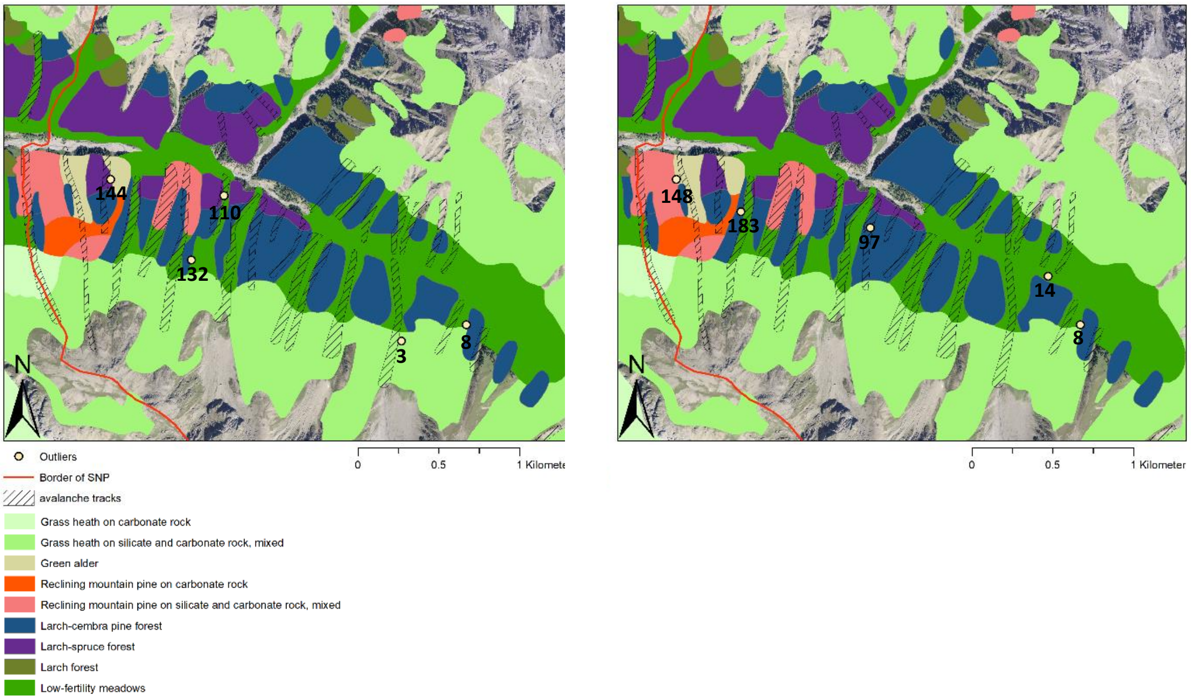
**Figure 11:** Spatial distribution of sampling plots and their number of young trees and proportion of young trees with trunk damage

Distribution of sampling plots, numbers of young trees, and proportions of young trees that show trunk damage by wild ungulates over three sampling years in Val Trupchun. Pie charts show plots with young trees and the size of the charts represents the number of young trees. Striped patterns of the pie chart indicate young trees with no damage to their trunks, and blue colored areas indicate young trees with damaged trunks. Dots are sampling plots without young trees and crosses are plots that were not sampled. The red line visualizes the border of the SNP and the blue line the stream that flows through Val Trupchun.

**Table 7:** Number of young trees and the number of young trees with damaged trunks of all sampling plots (table 1, column: Total number of plots sampled) for each tree species in the according sampling year

| **Young trees** | | | | | |
|---|---|---|---|---|---|
| | | **Northeast-exposed slope** | | **Southwest-exposed slope** | |
| **Year** | **Tree species** | **Total individuals** | **Individuals with trunk damage** | **Total individuals** | **Individuals with trunk damage** |
| 2003 | Larch | 769 | 53 | 125 | 12 |
| | Cembra pine | 171 | 19 | 110 | 31 |
| | Spruce | 85 | 12 | 228 | 11 |
| | Mountain ash | 1 | 0 | 0 | 0 |
| | Upright mountain pine | 2 | 0 | 0 | 0 |
| | Total | 1028 | 84 | 463 | 54 |
| | Ratio of damaged and total individuals in % | 8.17 % | | 11.66 % | |
| 2011 | Larch | 918 | 41 | 103 | 8 |
| | Cembra pine | 198 | 37 | 104 | 31 |
| | Spruce | 117 | 10 | 241 | 14 |
| | Mountain ash | 1 | 0 | 0 | 0 |
| | Upright mountain pine | 3 | 0 | 0 | 0 |
| | Total | 1237 | 88 | 448 | 53 |
| | Ratio of damaged and total individuals in % | 7.11 % | | 11.83 % | |
| 2021 | Larch | 1195 | 103 | 125 | 4 |
| | Cembra pine | 260 | 46 | 81 | 23 |
| | Spruce | 116 | 13 | 226 | 15 |
| | Mountain ash | 4 | 0 | 0 | 0 |
| | Upright mountain pine | 0 | 0 | 3 | 1 |
| | Total | 1575 | 162 | 435 | 43 |
| | Ratio of damaged and total individuals in % | 10.29 % | | 9.89 % | |

## Appendix E



**Saplings**

**Young trees**

**Figure 12:** Spatial location of largest two outliers of each sampling year for saplings (left) and young trees (right, see figure 3)

The outliers are indicated with yellow dots and the according identification number of the sampling plot. Additionally, a layer of categorizations of the forests and meadows has been laid over the valley (Zoller, 1995). The hatched shapes indicate avalanche tracks (Swiss National Park, 2009). The red line visualizes the border of the SNP.

## Appendix F

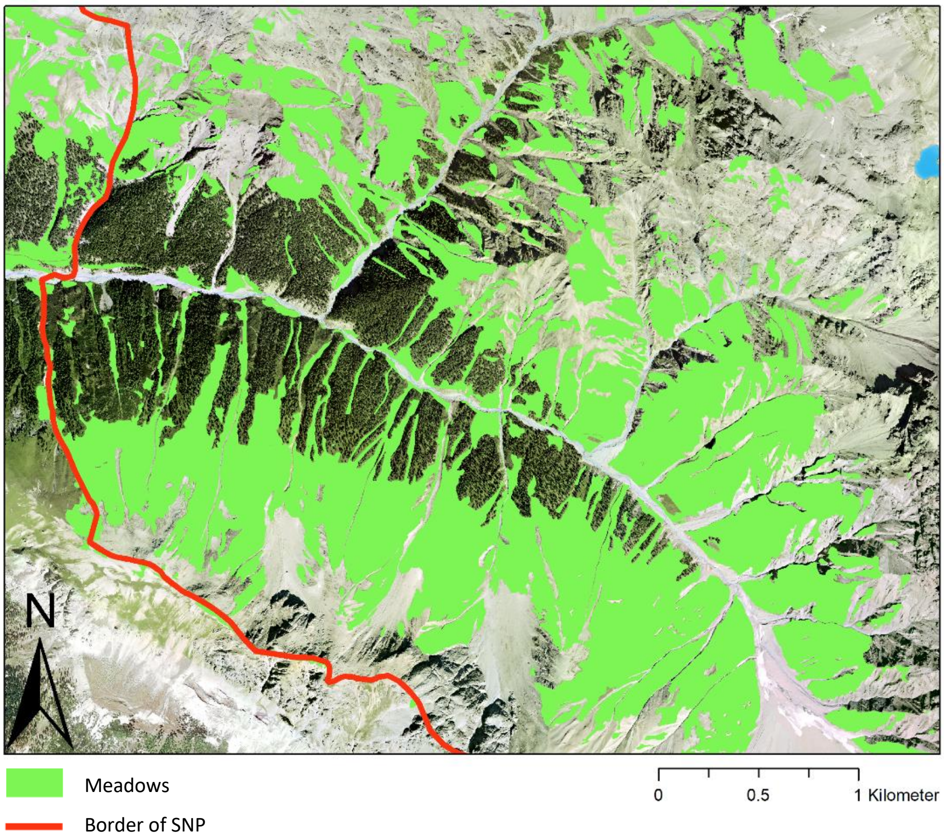


**Figure 13:** Spatial location of meadows in Val Trupchun

The green colored areas are meadows. The red line visualizes the border of the SNP (Lotz, 2006).

## Appendix G

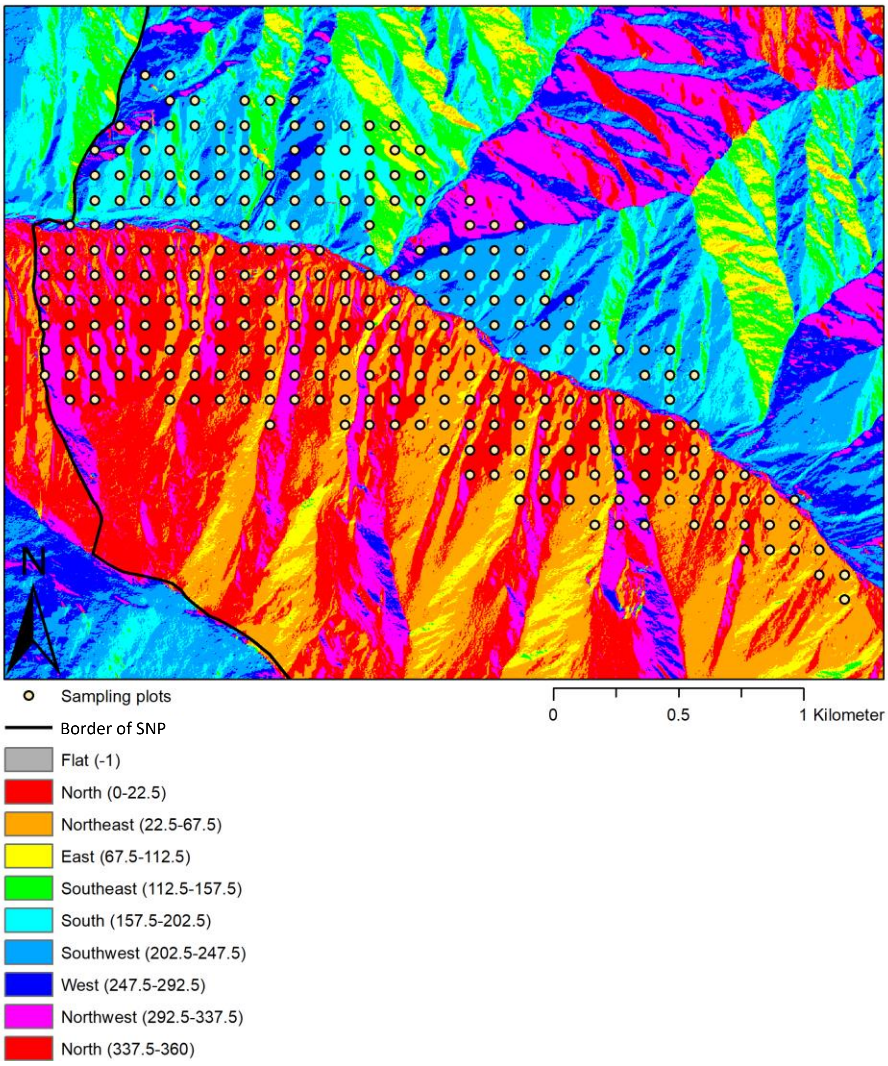


**Figure 14:** Exposition of the slopes in Val Trupchun

The exposition of the slopes of the valley are indicated with different colors according to the legend. In brackets are the span of degree values corresponding to the exposition. The yellow dots represent the center of the sampling plots, and the black line visualizes the border of the SNP.

## Appendix H

**Table 8:** Overview of estimated model variables of the fixed and random effects

The suffix ".z" of the variables indicates that they were centered and scaled, and transformations are indicated with their function. Mean, 2.5% quantile and 97.5% quantile are based on 2000 samples drawn from the joint posterior distribution. n = 1808

| **Fixed effects** | | | |
|---|---|---|---|
| **Explanatory variable** | **Mean** | **2.5 % quantile** | **97.5 % quantile** |
| Intercept | -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 | -0.074 | -0.23 | 0.077 |
| Shannon index.z | -0.17 | -0.34 | 0.0045 |
| Average developmental stage.z | -0.074 | -0.25 | 0.091 |
| Elevation.z | 0.51 | 0.21 | 0.80 |
| Slope.z | -0.10 | -0.28 | 0.085 |
| log(Dist. to next hiking trail).z | 0.16 | -0.11 | 0.44 |
| log(Dist. to next meadow+1).z | -0.064 | -0.25 | 0.12 |
| Eastness.z | 0.24 | 0.075 | 0.40 |
| Norrthness.z | -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 |

**Table 9:** Point estimate and 95 % compatibility interval of the predictors of the binomial generalized linear mixed-effects model

| Predictor | Point estimate | 95 % compatibility interval | |
|---|---|---|---|
| | | Lower | Upper |
| Tree species[1] | | | |
| Larch | 0.15 | 0.096 | 0.22 |
| Spruce | 0.084 | 0.046 | 0.15 |
| Cembra pine | 0.019 | 0.011 | 0.033 |
| Developmental stage[2] | | | |
| 2 | 0.049 | 0.026 | 0.091 |
| 3 | 0.15 | 0.096 | 0.22 |
| 4 | 0.11 | 0.070 | 0.17 |
| 5 | 0.13 | 0.080 | 0.19 |
| 6 | 0.072 | 0.041 | 0.12 |
| Elevation[3] | | | |
| min.: 1835 m.a.s.l | 0.049 | 0.021 | 0.12 |
| max.: 2225 m.a.s.l | 0.31 | 0.19 | 0.48 |
| Northness[3] | | | |
| -1 (south) | 0.31 | 0.18 | 0.49 |
| 1 (north) | 0.12 | 0.079 | 0.19 |
| Eastness[3] | | | |
| -1 (west) | 0.087 | 0.048 | 0.15 |
| 1 (east) | 0.21 | 0.13 | 0.31 |
| Slope[3] | | | |
| min.: 16 % | 0.19 | 0.10 | 0.35 |
| max.: 138 % | 0.093 | 0.033 | 0.22 |
| Number of saplings[3] | | | |
| min.: 1 | 0.15 | 0.098 | 0.23 |
| max.: 112 | 0.092 | 0.032 | 0.25 |
| Average developmental stage[3] | | | |
| min.: 1.89 | 0.17 | 0.099 | 0.28 |
| max.: 6 | 0.12 | 0.060 | 0.22 |
| Shannon index[3] | | | |
| min.: 0 | 0.18 | 0.12 | 0.28 |
| max.: 1.27 | 0.10 | 0.056 | 0.18 |
| Distance to next hiking trail[3] | | | |
| min.: 2 m | 0.12 | 0.068 | 0.20 |
| max.: 583 m | 0.21 | 0.099 | 0.41 |
| Distance to next meadow[3] | | | |
| min.: 0 m | 0.15 | 0.098 | 0.23 |
| max.: 166 m | 0.11 | 0.038 | 0.27 |

[1] The point estimates and 95 % compatibility intervals refer to developmental stage 3.
[2] The point estimates and 95 % compatibility intervals refer to larch.
[3] The point estimates and 95 % compatibility intervals refer to larch in developmental stage 3.

**Table 10:** Correlation coefficient of the untransformed model predictors, calculated with the Pearson correlation

| | Tree species | Dev. stage | Elev. | North. | East. | Slope | Num. of saplings | Av. dev. stage | Shannon index | Dis. to hiking trail | Dis. to meadow |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Tree species | 1 | | | | | | | | | | |
| Developmental stage | 0.11 | 1 | | | | | | | | | |
| Elevation | -0.041 | 0.017 | 1 | | | | | | | | |
| Northness | -0.14 | 0.16 | 0.33 | 1 | | | | | | | |
| Eastness | -0.050 | 0.084 | 0.069 | 0.11 | 1 | | | | | | |
| Slope | -0.0062 | -0.019 | 0.088 | -0.0065 | -0.0047 | 1 | | | | | |
| Number of saplings | 0.0062 | 0.0052 | 0.076 | 0.014 | -0.15 | 0.036 | 1 | | | | |
| Average developmental stage | 0.013 | 0.54 | 0.029 | 0.23 | 0.14 | -0.064 | -0.073 | 1 | | | |
| Shannon index | -0.032 | 0.024 | -0.097 | 0.29 | 0.16 | 0.064 | 0.20 | -0.025 | 1 | | |
| Distance to next hiking trail | 0.0053 | -0.078 | 0.74 | 0.045 | -0.15 | 0.052 | 0.19 | -0.12 | -0.11 | 1 | |
| Distance to next meadow | 0.061 | -0.14 | -0.39 | -0.26 | -0.26 | -0.040 | -0.17 | -0.20 | -0.11 | -0.12 | 1 |