Eidgenössische Technische Hochschule Zürich
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Debarking habits of *Bison bonasus* in the Wisent Thal Project

Master's Thesis

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Cover picture: Personal photograph of the bull and one of the two younger calves in the Wisent Thal Project. The picture was taken on the 08.11.2023.

Abstract

The Wisent Thal project aims to reintroduce the European bison in a commercially used forest in the Swiss Jura mountain-range. Bison strip the bark of trees for food in addition to herbaceous forage. This study was conducted to better understand this debarking behaviour in order to help assess the feasibility of the reintroduction. To find out which tree species and -diameters were selected for and which were avoided by the bison, Ivlev's modified electivity index was calculated and generalized linear mixed effects models were fit to the data. Additional predictors for debarking were calculated in a spatial analysis and tested in the models. The width and length of debarking wounds were modelled in a cumulative link mixed model and a linear mixed effects model respectively, to determine factors impacting debarking intensity. Six percent of all trees in the study area exhibited debarking wounds and were rarely completely girdled. I identified coniferous tree species to be avoided by the bison and broadleaved species to be positively selected for debarking, except for European beech, which was selected at random. Trees of smaller diameters were preferentially debarked, while trees with diameters over 36 cm were actively avoided. The models predicted trees to be debarked more often in areas where bison remained for longer periods of time and in areas with increased ground-cover of herbaceous plants. Broadleaved trees had significantly wider debarking wounds than beech trees and coniferous trees. Surprisingly, I observed that 45% of the debarked trees already showed signs of wound occlusion after about 5 months. Further inventories and analyses will need to be conducted to better inform whether the impact of debarking in the Wisent Thal project is within acceptable limits. This study contributes to the understanding of debarking behaviour of the European bison and may help stakeholders decide on the future course of the Wisent Thal project.

Keywords: *European bison, Switzerland, species conservation, bark stripping, tree species, tree size, resource selection, electivity index, mixed effects model*

Acronyms and abbreviations

AIC	Akaike Information Criterion
ANOVA	Analysis of Variance
CLMM	Cumulative Link Mixed Model
DBH	Diameter at Breast Height (130 cm above ground)
d_{dom}	Average diameter of the 100 thickest trees per hectare
df	Degrees of freedom
GLMM	Generalized Linear Mixed effects Model
GNSS	Global Navigation Satellite System
LMM	Linear Mixed effects Model
VIF	Variance Inflation Factor

B. freq.	Bison frequency
Deb.	Debarking
Dev. stage	Forest stand developmental stage
F. community	Forest community after Ellenberg and Klötzli, 1972
Inclin.	Inclination
Prox.	Spatial proximity to an object
Raspb. cover	Raspberry ground cover
Reg. comp.	Regeneration competition: Ground cover of vegetation that competes with tree regeneration
Std. error	Standard error
Stand str.	Forest stand structure
Stem dmg.	Non-bison related stem damage
Veg. sum	Vegetation sum: Sum of grass-, herb-, shrub-, regeneration-, bramble-, raspberry-, ground cover

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Chapter 1

Introduction

1.1 The status of the European bison

The European bison (*Bison bonasus*, Linnaeus, 1758) once colonised the majority of the European mainland but nearly went extinct due to habitat loss and over-hunting. (Krasińska and Krasiński, 2013; Pucek et al., 2003). By the end of World War I the last free-ranging population in the Bialowieza Forest (PL) went extinct and only 54 animals survived in captivity (Pucek et al., 2003). As of 2022 the number of European bison has surpassed 10'000 individuals worldwide, of which over 8'000 live free (Raczynski, 2022). In spite of this conservation success, the last surviving species of Europe's large grazers is still at risk of extinction (Kuemmerle et al., 2010): All pure-bred European bison are descendants of only 12 founder animals (Pucek et al., 2003). As a result of this genetic bottleneck the population has low genetic diversity, which leads to reduced reproduction rates and disease resistance (Pucek et al., 2003; Olech and Perzanowski, 2002). Pucek et al., 2003 formulated an action plan for the protection and management of the species: This conservation strategy includes the continuation of captive breeding and further reintroductions of free or semi-free ranging populations, with the overarching goal being the establishment of a network of meta-populations, and thereby ensuring genetic exchange among herds (Pucek et al., 2003; Kuemmerle et al., 2010).

1.2 The Wisent Thal project

The Wisent Thal project is a field experiment on the prospect of such a reintroduction of the European bison in the Swiss Jura mountain-range. Over a 10 year period, a bison herd of 5 to at maximum 25 individuals are to be living in an initially fenced-off area with mixed forests and meadows. The project aims to test if the European bison can survive as wild animals in the Jura mountains and if the cultivated landscape can withstand the potential impacts of the herd. Additionally, the local population is to be familiarized with the relatively unknown species. Provided the field experiment produces positive results, the project is to serve as a starting point for a reintroduction of the European bison in the Jura mountains. The project is divided into three phases: For the first phase in September 2022 the herd was released into the 50 ha fenced area, which is to be extended to over 100 ha for phase two in autumn 2024. For phase three after 2027 the project plans to remove the fences and let the animals roam semi-free under surveillance and accompanying scientific research (Projekt Wisent Thal, 2022). Taking the possible influence of the European bison on forest

landscapes into account (Kowalczyk et al., 2011), the long-term acceptance of the bison largely depends on the extent of damage on forest and agricultural land (Kupferschmid and Straub, 2022).

1.3 Review of the European bison's debarking behaviour

As a ruminant, the European bison is adapted to feed on a variety of vegetation found on the forest floor, in clearings, in meadows and the shrub layer, as well as leaves, sprouts and bark from trees (Krasińska and Krasiński, 2013). The bison's large body mass demands consumption of large quantities of food; thus, they are non-selective feeders (Krasińska and Krasiński, 2013; Pucek et al., 2003; Hofmann, 1989). Depending on the composition of the food, an adult European bison requires about 23 - 32 kg of fresh mass of food per day (Gębczyńska and Krasińska, 1972). If the diet consists largely of grass and hay instead of herbs, leaves and branches, the daily requirement can even range between 30 and 60 kg (Krasińska and Krasiński, 2013; Pucek et al., 2003). The European bison is morphophysiologically adapted to grazing (Hofmann, 1989; Mendoza and Palmqvist, 2008): Their diet is primarily composed of herbaceous plants and only about 10% consists of shoots from shrubs and trees, as well as tree-bark. This percentage can also increase during winter, when herbaceous plants are much less available (Pucek et al., 2003; Krasińska and Krasiński, 2013). Higher percentages have further been shown in a DNA metabarcoding diet analysis (Kowalczyk et al., 2019): The proportion of woody plants in the bison's diet reached 60%, whereby trees made up 30% of the diet. The consumption of woody plant parts is considered only supplementary (Borowski and Kossak, 1972; Gebczynska et al., 1991; Krasińska and Krasiński, 2013; Pucek et al., 2003).

Differing results regarding which tree species are preferred by the European bison can be found in the literature, depending, amongst other things, on what tree species were present in the study area, which method was used to quantify the consumption of woody plants or variability in bison behaviour. According to Borowski and Kossak, 1972, tree species most often debarked by the bison are pedunculate oak (*Quercus robur* L.), common hornbeam (*Carpinus betulus* L.), European ash (*Fraxinus excelsior* L.) and Norway spruce (*Picea abies* (L.) H.Karst.). Based on an analysis of fecal matter, Kowalczyk et al., 2011 found that Scots pine (*Pinus sylvestris* L.), willow (*Salix* sp.), birch (*Betula* sp.) and elm (*Ulmus* sp.) were most selected with regard to the tree species abundance while European ash, small-leaved lime (*Tilia cordata* Mill.) and Norway maple (*Acer platanoides* L.) were avoided. An analysis on damage reports from Baligrod forest district (southeastern Poland) revealed that coniferous species were more likely to be damaged than broadleaved species (Nieszała et al., 2022). Few studies mention European beech (*Fagus sylvatica* L.): Brender, 2015 report beech to be spared as opposed to other broadleaved species. On the other hand, beech have also been reported to be positively selected for (Dietrich and Möhring, 2013). With regard to tree size, bison have been reported to prefer young trees with a diameter below 30 cm (Dietrich and Möhring, 2013; Krasińska and Krasiński, 2013), or even below 15 cm (Borowski and Kossak, 1972; Brender, 2015).

Pucek et al., 2003 describe deciduous forests with mosaic-structures as the most suitable habitats, and also mention the importance of open areas (e.g. meadows and forest clearings). However, the European bison has also been described as adapted to open habitat, while forest habitat is sub-optimal (Kerley et al., 2012). Free ranging European bison in Lithuania, for example, spend most of their time in open or half-open areas (Balčiauskas, 1999). As with food selection, the selection of habitat can therefore be considered highly plastic (Lopucki et al., 2023; Pucek et al., 2003).

The selective browsing and debarking of ungulates can lead to shifts in competition between tree species and potentially the establishment success of certain species (Kupferschmid and Straub, 2022; Kupferschmid et al., 2019; Angst and Kupferschmid, 2023), which ultimately can shape vegetation patterns in forest ecosystems (Feher et al., 2016; Schulze et al., 2014). On a larger scale, megafauna such as the European bison are even considered landscape engineers, capable of promoting open and semi-open habitats by reducing vegetation (Malhi et al., 2016; Trepel et al., 2024). In commercial forests, of all the possible effects herbivores can have on the forest, browsing and debarking are most crucial (Dietrich and Möhring, 2013). Debarking can lead to reduced timber quality, a general decline in tree growth, the risk of stem breakage at the wound (possibly induced by decay), loss in tree vitality and finally death of the entire tree (Borkowski and Ukalski, 2012; Rößner et al., 2023; Welch and Scott, 2008). It follows that analyzing and quantifying the damage by the European bison on forests is pivotal for the long-term success of existing and future reintroduction programs. Results from the conservation program in the Rothaar-mountains in Germany have, for instance, shown that the total of debarking damage by the bison can be considered permissible (Siebert et al., 2021).

1.4 Study aim and hypotheses

The Wisent Thal project offers the opportunity to explore the debarking behaviour of the European bison in a commercially used mixed deciduous forest in Switzerland. By sampling trees in plots arranged on a grid, the abundance of tree species and the occurrence of debarking can be estimated. Besides debarking, complete girdling by debarking, stem fraying and rubbing by the bison can also be assessed. The aim of this study was to identify which tree species, and tree diameters were preferentially debarked by the bison during the first year of the project (i.e., phase one on the 50 ha area). This was achieved by calculating Ivlev's modified electivity index after Jacobs, 1974, as well as fitting generalized linear mixed effects models (GLMM). In addition, characteristics of the forest stand and ground vegetation layer can influence debarking. On the basis of a spatial analysis, spatial predictors were calculated for the models to detect possible underlying rules for the spatial distribution of debarked trees and if they were more concentrated in certain parts of the project area. The size of the debarking wounds can vary greatly, which has a strong influence on the silvicultural carrying capacity. Models were built to determine what causes some trees to be debarked more intensely than others. Since inventories with the same sample design were conducted in June and November 2023, I was able to compare the

results of both inventories and detect if there were any changes in the bison's debarking behaviour within the first year, and if debarking wounds already showed signs of occlusion. Specifically, the primary aim of this master's thesis is to address the following primary research questions:

Q_1: Which tree species and diameters are debarked most by the European bison?
Q_2: What location-specific characteristics have an impact on the occurrence of debarking?
Q_3: What impacts debarking intensity?

Based on literature research, I formulated a specific research hypothesis for each research question:

H_1: I expect beech trees to be avoided and coniferous species, such as Norway spruce and Scots pine, to be preferentially debarked by the European bison (Nieszała et al., 2022; Kowalczyk et al., 2011; Borkowski and Ukalski, 2012). I expect trees with a diameter at breast height (DBH) less than 30 cm to be debarked frequently and larger trees to be avoided (Dietrich and Möhring, 2013; Krasińska and Krasiński, 2013).

H_2: I expect trees to be debarked more often if they are within or in the vicinity of areas where the bison stay frequently: i) trees close to the forest edge (Kuemmerle et al., 2010), since the bison spend most time on meadows or open areas (Balčiauskas, 1999; Wołoszyn-Gałęza et al., 2016), ii) trees close to the bison's water sources and iii) trees further away from paths where human disturbance is higher (Schneider et al., 2013). Areas offering cover from disturbances and offer forage are expected to be more frequented by the bison and therefore have more debarked trees (Schneider et al., 2013). I also expect bison to prefer trees at lower inclinations (Kuemmerle et al., 2010).

H_3: I expect trees that are preferentially debarked according to H_1 and are situated in a convenient spot according to H_2 to be debarked more intensely than other trees.

Besides describing the debarking behaviour of the European bison herd in the Wisent Thal project, this study contributes to the understanding of debarking behaviour of European bison in general. The results of the models may also allow us to make predictions of where debarking wounds can be expected in future, and therefore help forest managers and the project management assess the risk as well as decide on possible counter measures. The decision on whether or not the fence surrounding the project area can be completely removed, and therefore allow the European bison to be reintroduced in the Jura mountains, will not be discussed here. However, the results of this thesis may support the decision making process, along with further findings from the accompanying scientific research and repeated inventories on debarking in the near future.

Chapter 2

Materials and methods

2.1 Study site and -subjects

The study was conducted on the 50 ha fenced area of the Wisent Thal project. It lies south of the hamlet Solmatt (47° 27' 70" N, 7° 54' 45" E) in the municipality of Welschenrohr-Gänsbrunnen SO (Figure 2.1). The site has a north/north-west exposition and lies at an elevation between 700 and 860 m a.s.l. The inclination ranges from near-flat meadows to almost vertical rock faces, with an average of over 18 degrees (Figure 2.4).

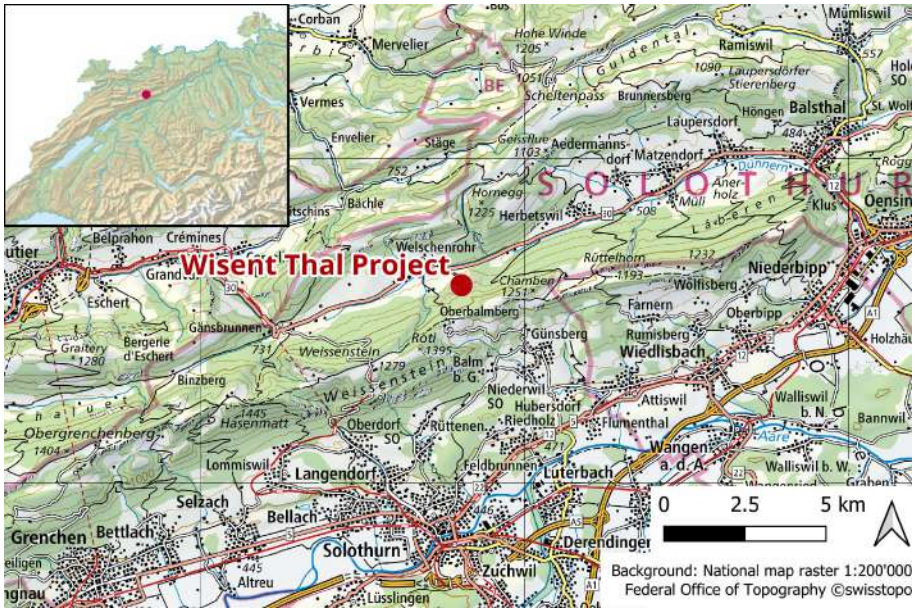

Figure 2.1: Map of Welschenrohr-Gänsbrunnen and the surrounding area with the location of the Wisent Thal project. The mini-map in the top-left corner shows northwestern Switzerland (©swisstopo).

Four separate meadows lie within the fenced-off study site and are thus inaccessible to nearby cattle. The fence built for the project is partly electric and partly a 2 m tall wire rope fence, through which wildlife up to the size of roe deer and wild boars can pass but the bison cannot (Projekt Wisent Thal, 2022). The site can be accessed through gates at all times, although visitors are told not to leave the gravel paths. 80 % of the area is forested (Projekt Wisent Thal, 2022) and belongs to one of the largest contiguous forests of Switzerland (Eidg. Forschungsanstalt für Wald, Schnee und Landschaft WSL,

2024). A preliminary evaluation of the initial situation of the Wisent Thal project revealed that the vertical forest stand structure was two-layered for the most part but single- and multi-layered stands were common as well (Kupferschmid and Straub, 2022). The forest stands are in various developmental stages: Pole timber (diameter of the 100 thickest trees per hectare (d_{dom}) = 12 - 30 cm), young timber (d_{dom} = 31 - 40 cm), medium timber (d_{dom} = 41 - 50 cm), old timber (d_{dom} > 50 cm) and uneven-aged, mixed stands occurred about equally often, while young growth (average tree height < 2 m) and thicket (d_{dom} < 12 cm) were rare. The vast majority of the forest on the site consists of the forest community *Cardamino-Fagetum typicum* (number 12a after Ellenberg and Klötzli, 1972) and is therefore dominated by European beech (Kupferschmid and Straub, 2022). Only a small area consists of *Abieti-Fagetum* variations: The occurrence of Norway spruce and to a lesser extent also of silver fir (*Abies alba* Mill.) is therefore mostly a result of forest management. During the course of the project, the forest is managed as usual by the forestry business of the Citizen's Community of Solothurn. The last forestry intervention took place in 2022: In three patches, on a total area of 1.8 ha, an estimated total of 310 solid cubic meters of wood were harvested (source: Otto Holzgang, Projekt Wisent Thal). No data was collected in those areas for this thesis.

The European bison herd in the Wisent Thal project consists of a 4 year old adult Bull, born in the wildlife park Bruderhaus in Winterthur, three adult cows at the ages of 4, 5 and 6 years, and a female calf of 1 year that all originate from the wildlife park of Zurich Langenberg. The bison were transferred from the wildlife park of Zurich Langenberg to an acclimatization enclosure within the present project area on the 15th of September, 2022. They had access to the entire 50 ha project area after the 3rd of November, 2022. In July 2023 a female and a male calf were born in the Wisent Thal project, increasing the herd size to 7 individuals at the time this was written (source: Otto Holzgang, Projekt Wisent Thal). The original 5 animals had never lived in freedom before, and thus had access to fodder at all times before the start of the project. The fodder consisted of hay, concentrate and softwood stems and -branches in addition to access to a small meadow. In the current project the bison had access to hay fodder only during winter. A drinking trough was placed next to the fodder station during winter and summer, when the stream within the project area runs dry.

2.2 Data collection

A debarking-inventory for trees larger than 2 m had already been conducted in June 2023 by Dr. Andrea D. Kupferschmid and her team. For this thesis a follow-up inventory has been carried out between the end of October until the beginning of December to study and quantify potential changes. The inventory was carried out in the same way as described in the unpublished WSL report of Kupferschmid et al., 2023b; the key points of the inventory are summarized in the following section.

Trees were sampled within plots that were set up for the evaluation of the initial situation on

the influence caused by wildlife within the area of the Wisent Thal project (Kupferschmid and Straub, 2022). The plots are arranged on a 50 x 50 m grid within the forest, excluding plots that would have lain on a path, a cliff, the fence, or the forest edge. Six plots that do not lie on the 50 x 50 m grid, but on the 25 x 25 m grid, were added additionally in the north-western part of the study site to avoid large gaps (See Figure 2.2).

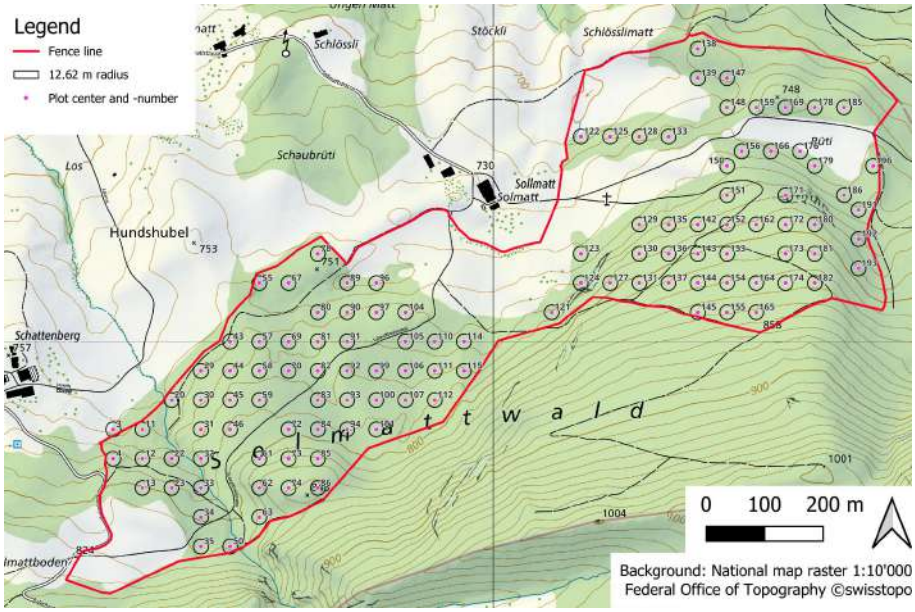

Figure 2.2: Map of the sample plots used for the tree debarking inventory in the first phase of the Wisent Thal project. Note that plot number 3 appears to be outside of the fence due to GNSS signal inaccuracies, when in reality it is entirely within the fenced study area.

For each plot, every tree taller than 2 m within a 50 m^2 circle (corresponds to a horizontal radius of 3.99 m from the plot center) was sampled; trees with a DBH smaller than 1 cm could thus be sampled as well. Trees shorter than 2 m were sampled for the initial inventory during 2019 and 2020 (Kupferschmid and Straub, 2022) and are not part of this analysis. Within a 200 m^2 circle around the plot center (horizontal radius of 7.98 m), trees with a DBH of 12 cm or more were sampled and trees with a DBH of 36 cm or more were sampled within a 500 m^2 circle (horizontal radius of 12.62 m). These three DBH ranges were thus used as DBH-classes in further analyses.

In June 2023, for every sampled tree the location was recorded by measuring the distance and azimuth to the plot center. The coordinates of the trees could be calculated by using the theoretical coordinates of the 50 x 50 m grid for each plot center; these coordinates were then used for the spatial analysis. In this first assessment, the status (alive or dead) and species was determined and the DBH was measured with a tree caliper. In June, it was also recorded if the stem exhibited non-bison-related damage, e.g. as a result of lumbering or rockfall, that has revealed the wood beneath the bark. In both inventories, to denote debarking caused by the bison, both the absolute length in cm and the relative

width were recorded. Debarking by bison is defined as gnawed- or pulled off pieces of bark, revealing the wood of the tree: As with other ungulates, bison strip bark from the bottom to the top, using their lower incisors, sometimes leaving bark strips dangling from the top of the wound and marks of their teeth on the exposed wood of the tree. The relative width of the wounds was sampled in categories as defined in the unpublished WSL report of Kupferschmid et al., 2023b and summarised in Table 2.1). The presence of signs of wound occlusion, i.e. the healing reaction of a tree to debarking were additionally recorded during the second inventory in November. The occlusion had to be apparent to the naked eye and therefore at least a few millimeters thick, to be recorded as such.

Table 2.1: Categories defined for the width of debarking wounds

Width	**Widest point of the wound in relation to the tree diameter/ circumference**
Small	Less than 1/3 of the diameter. For small trees also a bit more than 1/3, but then the length of the wound is less than 5 cm.
Medium	More than 1/3 but less than 2/3 of the diameter
Large	More than 2/3 of the diameter but less than 1/2 of the circumference
Very large	More than 1/2 of the circumference

Also recorded in both inventories was i) whether the tree had been girdled by the bison (the bark was removed all around the stem), ii) whether or not the tree had been frayed by the bison with his horns and iii) whether the tree had been used as a rubbing tree. A rubbing tree can be recognized by chipped off outer scales of the bark and hair from the bison's fur that got stuck in the bark as the bison rubbed it's torso against the tree.

2.3 Data preparation and grouping

Virtually all trees sampled during the first inventory were found again in the follow-up inventory. The 8 trees that could not be found were excluded from the analysis. 188 trees were sampled that were clearly dead but still standing. These trees were omitted as well since none of them showed debarking wounds; dead trees don't get debarked. Most of the dead trees were beech, spruce or silver fir and had a DBH < 5 cm. For the statistical analysis only the most frequent tree species were used. A total of 21 individual trees belonging to the following species were omitted from the statistical analysis, because their number was too small to make separate categories and none of them were debarked: European larch (*Larix decidua* Mill.), silver birch (Betula pendula Roth), wild cherry (*Prunus avium* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.), goat willow (*Salix caprea* L.), rowan (*Sorbus aucuparia* L.) and large-leaved lime (*Tilia platyphyllos* Scop.). Tree species of which more than 20 individuals were found - and thus statistically analysed - are European beech, silver fir, Norway spruce, Scots pine, European ash, sycamore maple

(*Acer pseudo-platanus* L.), whitebeam (*Sorbus aria* (L.) Crantz) and wych elm (*Ulmus glabra* Huds.). These 8 tree species will be referred to by only their genus name for the rest of this thesis.

Based on the results and the similarity between some of these species, tree species were grouped into "Coniferous", "Broadleaved" and "Fagus" for the models. The group "Coniferous" contains silver fir, Norway spruce and Scots pine, "Broadleaved" contains sycamore maple, European ash, whitebeam and wych elm, while European beech was kept separately.

2.4 Calculation of the Electivity Index

To study which tree species and which tree DBH classes are preferentially debarked by the bison, Ivlev's electivity index D, and the forage ratio Q (both modified by Jacobs, 1974) were calculated and compared:

$$D = \frac{r - p}{r + p - 2rp} \tag{2.1}$$

$$Q = \frac{r(1-p)}{p(1-r)} \tag{2.2}$$

Where r is the proportion of debarked trees of a given group i among the total number of debarked trees and p is the proportion of a given group i among the total number of trees:

$$r = \frac{number\ of\ debarked\ trees_{\mathrm{i}}}{total\ number\ of\ debarked\ trees} \tag{2.3}$$

$$p = \frac{number\ of\ trees_{\mathrm{i}}}{total\ number\ of\ trees} \tag{2.4}$$

However, using the sampled number of trees would not reflect reality due to the aforementioned sampling structure: Trees of the smallest DBH-class would be underrepresented and the other two groups would be overrepresented (see Figure 2.3). Consequently, the number of trees within each species and DBH-class, corresponding to the circles with an area of 50 m^2, 200 m^2 and 500 m^2, were converted to per hectare values. Only the number of trees per hectare of a given group reflects the true abundance of the group. As can be seen in Figure 2.3, the DBH distribution then follows a smooth negative exponential curve.

According to Jacobs, 1974, the modified electivity index D and the logarithm of the modified forage ratio, $log(Q)$ are related and both indicate food selection. D ranges from -1 (the strongest negative selection) to $+1$ (the strongest positive selection), while 0 indicates random selection. $log(Q)$ has an unlimited range in both directions and would therefore

be a more sensitive indicator for more extreme values ($log(Q) > \pm 1$) than D. Since none of the calculated values for $log(Q)$ exceeded ± 1, D is the more sensitive indicator for food selection. Therefore only the modified electivity index D will be presented in this case study.

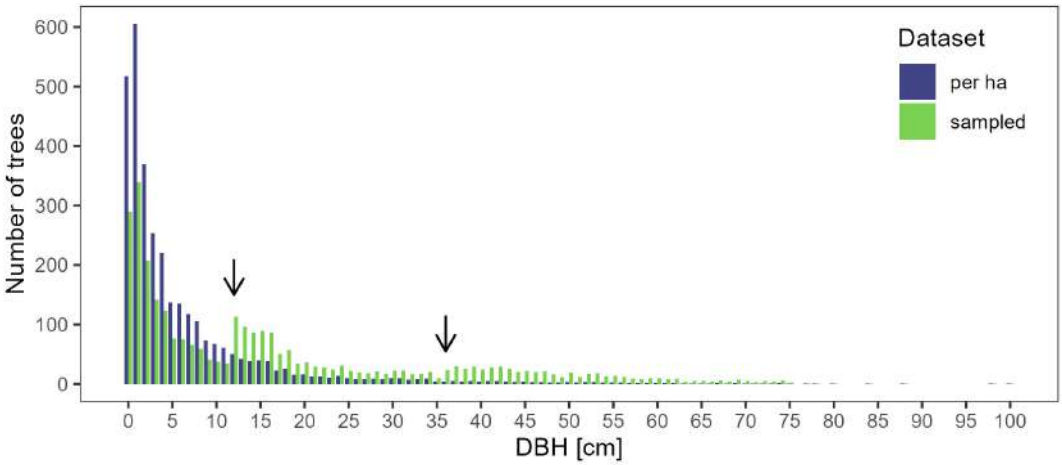

Figure 2.3: DBH distribution comparison between the sampled number of trees and the extrapolated per hectare values. The arrows indicate the thresholds between the three sampling circles.

2.5 Predictor calculation and Modelling

Models were built to study what factors influence the occurrence and extent of debarking in the study area. Three models were built using datasets with debarked- and non-debarked trees: One with the data from the inventory in November, one with data from June and a third where only trees that were debarked in between the June inventory and the November inventory were considered. Two models were built using a dataset with debarked trees only, to study what influences the length and width of debarking wounds. The following sub-chapters explain what predictor variables were used and how the models were built.

2.5.1 Spatial analysis

The inclination varies considerably over the study area and since the bison were more often seen on the near-flat meadows than in steep terrain during the debarking inventory, the inclination was used as a predictor for debarking in the models (Figure 2.4). Inclination was calculated using the Slope tool in QGIS (version 3.32.3-Lima) (QGIS Development Team, 2023) and the values were extracted for each tree at its location. The digital elevation model used for the calculation was the swissALTI^{3D} (Federal Office of Topography, ©swisstopo), which has a resolution of 0.5 m.

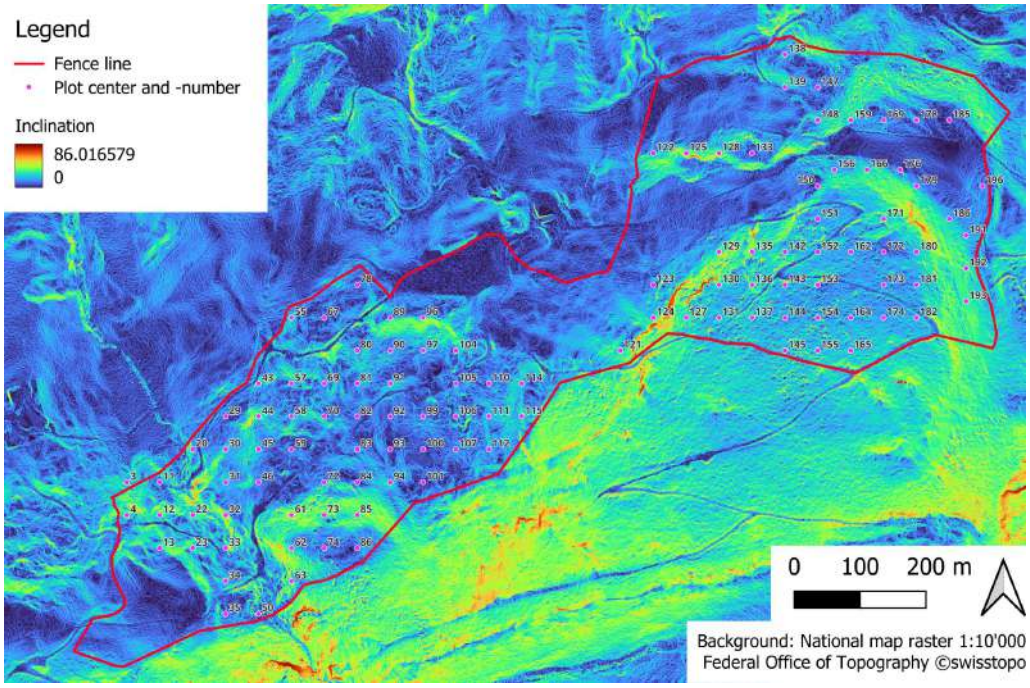

Figure 2.4: Map of the inclination in the study area. Values range from 0 to 86 degrees.

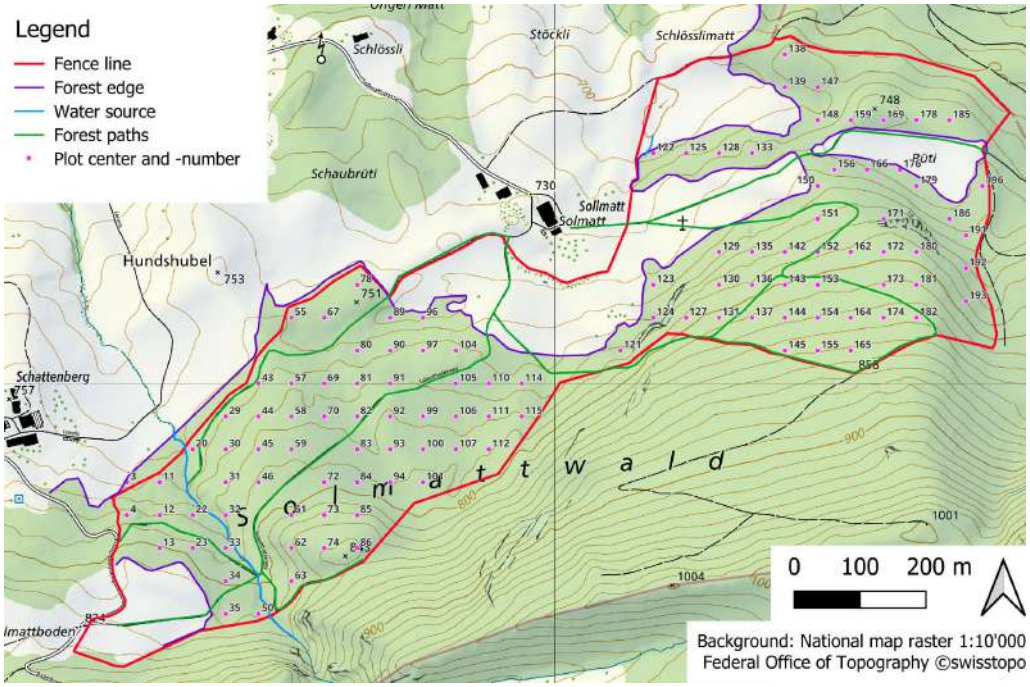

Figure 2.5: Map of the study area with drawn vectors on the forest edge, paths and water sources.

As explained in hypothesis H_2, trees further away from forest paths, closer to the forest edge and closer to water sources are hypothesized to be debarked more often. To test this in a model, the predictors “proximity to forest edge”, “- forest path”, "- water source" and “- stream”, as well as the “proximity to all”, which is the shortest distance to any of the aforementioned objects, were calculated. The stream passing through the study area was included in the water source predictor but also used separately to see if it makes a difference. After all, the stream might not provide water to the bison during dry periods in summer or freezing periods in winter. In QGIS, vectors were drawn on the forest edge towards the meadows, on the gravel- and unpaved forest-roads (width $>$ 2 m) and on the stream based on the Swiss national map 1:10’000 (Federal Office of Topography, ©swisstopo) (See Figure 2.5). A comparison with orthophotos (Federal Office of Topography, ©swisstopo) confirmed the accuracy of the national map. In addition to the stream, a natural spring in the north (close to plot number 122) as well as a watering trough placed by the ranger south of the farmstead Sollmatt, were considered water sources which constitute to the predictor "Proximity to water source". To calculate the proximity, the distance between each tree and the nearest point of a forest edge, forest path, stream or water source, as well as the distance to the nearest point of any of these layers, was calculated with the *v.distance* tool from the GRASS Plugin for QGIS (GRASS Development Team, 2022).

Considering that the forest edges are next to the meadows, they likely have low inclinations and a correlation between the inclination and proximity to a forest edge could be possible. This collinearity would violate the assumption of independent predictors for the models. However, Pearson’s correlation was -0.022 and -0.058 for both model-datasets, indicating no correlation between the two predictors.

The dominant female and another female of the bison herd wear collars which send GNSS signals at an hourly interval (data source: Position measurements, Wisent Thal project, 21.12.2023). The resulting GNSS positions of the herd from 03.11.2022 until 20.12.2023 (Figure 2.6) were used to calculate a density raster with the *Kernel Density Estimation* tool in QGIS for the model testing debarking until November (Figure 2.7). For the model testing debarking until June, GNSS positions from 03.11.2022 until 30.06.2023 and for the model testing only newly debarked trees between June and November, GNSS positions from 01.07.2023 to 20.12.2023 were used. For the kernel density estimation, a radius of 30 m was chosen, meaning that the influence area around a point has a radius of 30 m, which is in the same range as the GNSS signal accuracy. The maximum value of the resulting density raster per plot was used as the predictor "maximum bison frequency" in the models. The *Zonal Statistics* tool in QGIS was used to extract the maximum value within a radius of 12.62 m for each plot. This corresponds to the 500 m^2 circle in which trees were sampled. The mean bison frequency was calculated in the same manner. Figure 2.8 shows a visual representation of the maximum bison frequency until November. However, in the models the exact calculated values are used and not value classes. Plot number 130 does not have a bison frequency symbol, because the value is exactly zero. For the models, this zero was overwritten with the value 0.001, so that the predictor could be $\log_{10}$-transformed. Bison frequency maps for the models of the separate time spans can be seen in Appendix B.

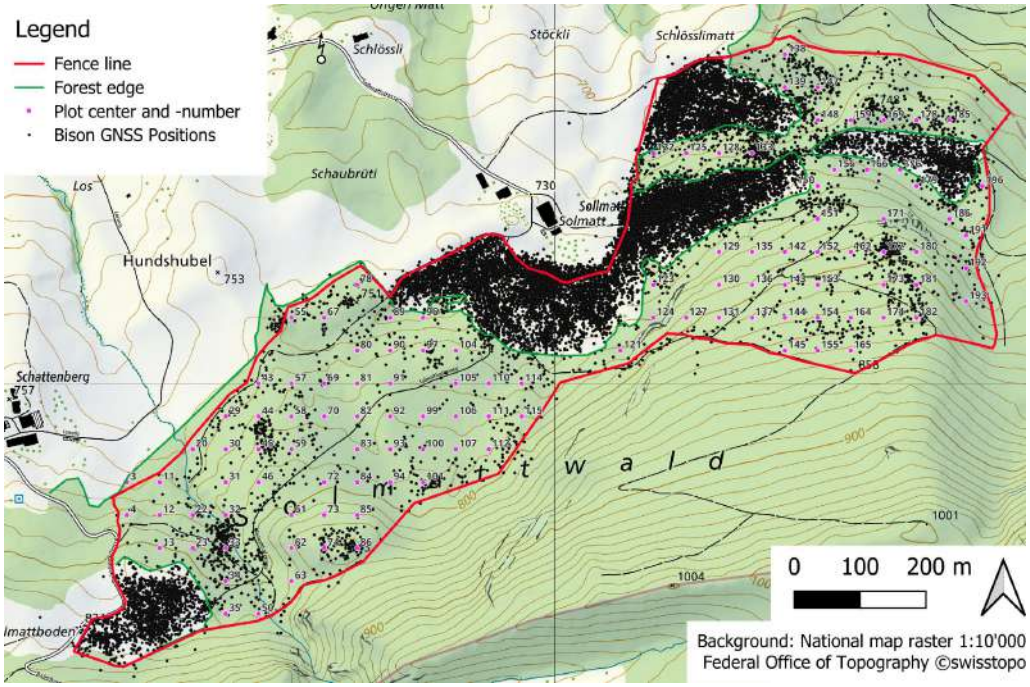

Figure 2.6: Bison GNSS signals recorded between 03.11.2022 and 20.12.2023.

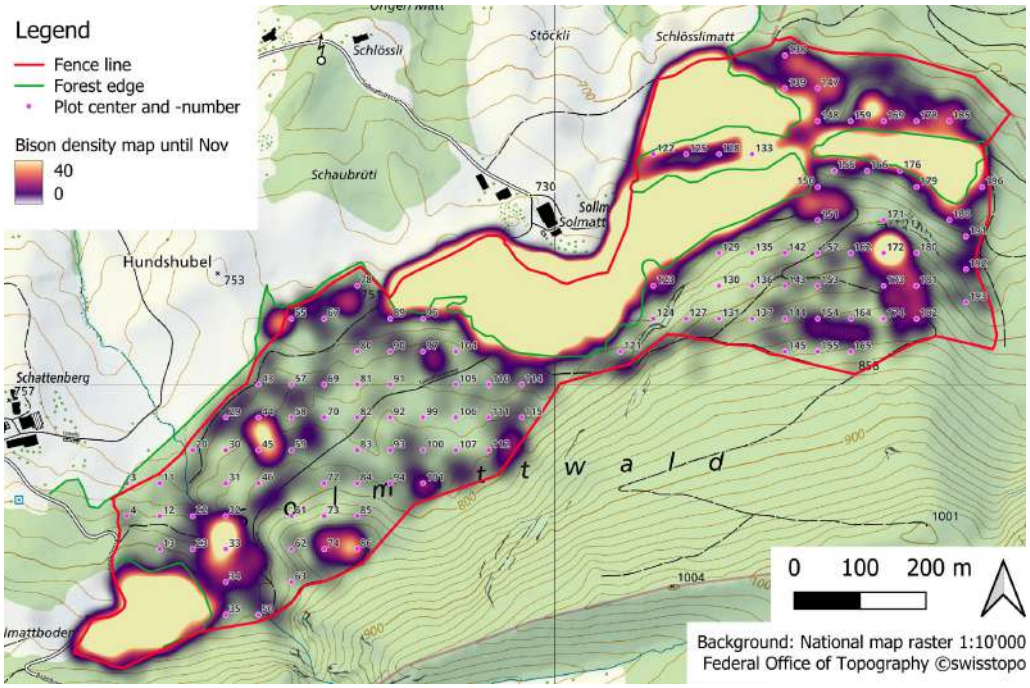

Figure 2.7: Bison density map between 03.11.2022 and 20.12.2023 calculated from the GNSS positions: The visualization is capped at values of 40 to emphasize bison density in the forest.

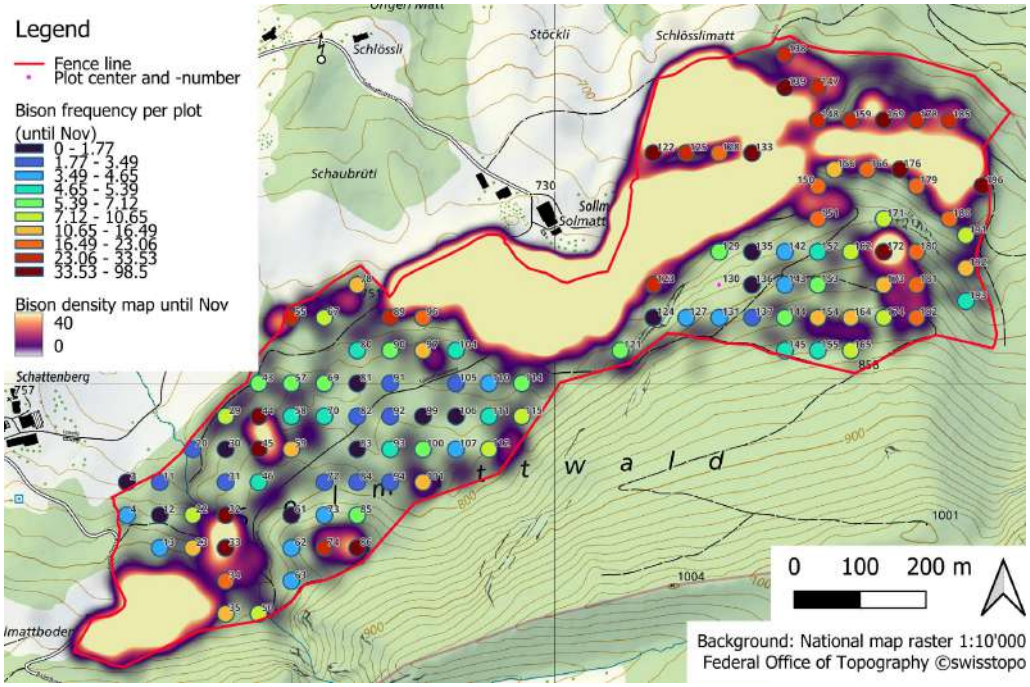

Figure 2.8: Map with the bison frequency calculated per plot for the inventory until November (i.e. 03.11.2022 till 20.12.2023). Black and blue dots indicate low presence of the bison within that plot and red dots indicate high presence.

2.5.2 Non-spatial predictors

Other predictors tested in the models are "species" and “species group” (described in chapter 2.3), non-bison related “stem damage” (described in chapter 2.2), and the DBH. To test during which season most trees were debarked, the predictor “debarking season” was calculated: If a tree exhibited a debarking wound in the inventory in November but had none in June, then the debarking happened in summer. If a tree exhibited a debarking wound in the inventory in June and the size did not increase in the inventory in November, then the debarking happened in winter. If a tree exhibited a debarking wound in the inventory in June and the size increased until the inventory in November, then the tree was debarked repeatedly. Thus, possible values for the debarking season are: “not debarked”, “summer debarking”, “winter debarking”, and “repeated debarking”. Note that the season definitions are not entirely accurate: Summer debarking also includes debarking that happened in fall until the inventory in November and winter debarking includes debarking that happened in spring and winter, because the herd had access to the entire study area since November 2022.

Furthermore, data was used from the preliminary evaluation of browsing influence (Kupferschmid and Straub, 2022): “Forest community” after Ellenberg and Klötzli, 1972, “forest

stand structure", "forest developmental stage", "regeneration competition" (ground-cover percentage of vegetation that competes with tree regeneration) as well as ground-cover percentage of grasses, herbs, shrubs, tree regeneration, brambles and raspberry bushes. The sum of these ground-cover percentages, excluding competing vegetation, amount to the predictor "vegetation sum". The percentage of ground showing tracks left by the bison was used as the predictor "footsteps". This information was available for each plot, meaning every tree within a plot had the same value. Details on these variables can be examined further in the aforementioned report.

2.5.3 Model building

The following analysis was performed using the statistical computing software R (version 4.3.0) (R Core Team, 2023). The R code and data are available separately to this thesis.

To study which predictors have an effect on whether or not trees are debarked and where they are debarked, three generalized linear mixed-effects models (GLMM) were built. The R package *glmmTMB* (Brooks et al., 2017) which uses a template model builder (TMB) was used. I specified the family function to be binomial and chose a logistic model link. The first model uses the full dataset until the debarking inventory in November. The second model uses the dataset until the debarking inventory in June, and thus only winter debarking. The third model considers all trees that were not debarked or debarked before June as not debarked; thus, only studying the effects on newly debarked trees from June to November (i.e. summer debarking). The target variable for all three models was binary: Trees were either debarked or not. To control for the nested structure of the datasets, the plot number, to which each tree belongs, was chosen as random effect. All models performed better with the random effect than without (see Appendix D). The DBH-class was added as a second random effect in the model studying debarked trees until June, to correct for the sampling structure as described in chapter 2.2. For the other models the DBH-class as random effect was omitted, because the models performed better without it.

All GLMM were built by following this procedure: A null-model with no predictors but with the random effect (the plots) was built as a reference. The predictor deemed most important was then added to the null model, and if the model performed better than the null model it was kept in the model structure. To compare the performance of models, an analysis of variance (ANOVA) was carried out and models having a p-value smaller than 0.01 were considered to be significantly better. In addition, the AIC (Akaike information criterion) values were used: Per additional degree of freedom (df) the difference in AIC (ΔAIC) had to be larger than 2 for the model to be considered better. Subsequently, the other predictors were added individually to the model structure and kept if the model performed better with than without them. All model selection tables can be found in Appendix D. In those Tables, the null model is highlighted in red and the best performing model in blue.

A residual analysis was performed with the R package *DHARMa* (Hartig, 2022) for the three selected GLMM. *DHARMa* simulates the residuals of the fitted models, which then

can be interpreted and tested with functions for over/underdispersion, outliers, zero-inflation and uniformity. To test for collinearity between model predictors, the function *check_ collinearity* from the R package *performance* (Lüdecke et al., 2021) was used. All model residual plots and the results of the collinearity tests can be seen in Appendix E.

To study which predictors have an effect on the width of the debarking wounds and where trees were debarked more intensely, a cumulative link mixed model (CLMM) was built, using the R package *ordinal* (Christensen, 2023). A CLMM was necessary because the target variable "debarking width" is categorical and ordinal: Possible values are "small", "medium", "large" and "very large", as described in chapter 2.2. All non-debarked trees were removed from the dataset. Therefore, the dataset from the inventory in November was used, which had more observations (156) than the inventory in June (76). As for the other models, the plot number was chosen as random effect. Due to the fact, that the dataset for the CLMM only contained 156 observations, the CLMM could not handle complex model structures with many predictors without being rank deficient or simply not converging. Consequently, every predictor was tested in a CLMM individually, and the predictors which had a significant effect on debarking width were combined in a final model in the end. Since a normal residual analysis was not possible for the CLMM and the residuals could not be simulated with *DHARMa*, only collinearity between model predictors were tested for, using the aforementioned *check_ collinearity* function (results see Appendix E).

To better support results from the CLMM a linear mixed-effects model (LMM) was built, using the R package *nlme* (Pinheiro and Bates, 2000), with "debarking length" as the continuous target variable. Because the length appeared to be exponentially distributed rather than normally distributed, the target variable debarking length had to be $\log_{10}$-transformed. After the transformation, low values still tended to be more frequent but the distribution looked better than without transformation. As for the CLMM, all non-debarked trees were removed from the dataset and the plot number was chosen as random effect. The model method was set to maximizing the log-likelihood so fixed effects could be compared. Because the LMM had the same dataset as the CLMM, the LMM was selected in the same manner: Predictors were tested individually, and the significant ones were added to a final model in the end. A residual analysis as well as a test for collinearity was performed for the LMM using base R functions (results see Appendix E).

Chapter 3

Results

The results are structured by the research questions: In Chapter 3.1, results of the descriptive analysis, electivity index calculation and the fitted GLMM will be presented and describe which tree species and tree diameters are preferentially debarked by the European bison. In Chapter 3.2 results of the methods described previously will be presented to describe where debarking occurred in the study area. In Chapter 3.3 the results of the models describing debarking intensity will be presented. Finally, in Chapter 3.4 additional findings in regard to wound occlusion and the occurrence of girdling, fraying and rubbing trees will be presented.

3.1 Selective behavior of the European Bison

3.1.1 Tree species preferentially debarked

Descriptive analysis results

During the inventory in June a total of 76 trees were recorded to be debarked (Table 3.1). Extrapolated to the entire study area and considering the sampling structure, 3.2% of all trees had debarking wounds in June. The number of debarked trees increased to 156 in the inventory in November (Table 3.1), which corresponds to 6.1% of all trees in the study area having debarking wounds.

Most debarked trees were beech trees; coniferous trees on the other hand were rarely debarked (Table 3.1 and Figure 3.1). The number of debarked trees per species until June did not increase to the same extent until the inventory in November. Beech, maple and elm had a much larger relative increase compared to ash and whitebeam; in fact, the number of debarked trees doubled for these species over a course of only about 5 months (Table 3.1). The table also shows that, in summer, more trees in total were debarked in a shorter period of time than in November: The Inventory in June spans about 7 months (November 2022 until beginning of June 2023), the inventory in November spans only about 5 months and the number of debarked trees increased by 105%.

Table 3.1: Number of sampled trees and number debarked thereof for both inventories, as well as the increase from June to November. Groups used for the analysis: Tree species and tree species group. *The group "Broadleaved" contains Acer, Fraxinus, Sorbus Ulmus and excludes Fagus.

	Total sampled	**Debarked until June**	**Debarked until Nov.**	**Increase**	**Increase [%]**
Total	2805	76	156	80	105%
Abies	395	3	4	1	33%
Picea	362	2	5	3	150%
Pinus	42	0	0	0	0%
Fagus	1849	50	113	63	126%
Acer	62	5	12	7	140%
Fraxinus	27	7	9	2	29%
Sorbus	32	6	7	1	17%
Ulmus	36	3	6	3	100%
Coniferous	799	5	9	4	80%
Broadleaved*	157	21	34	13	62%

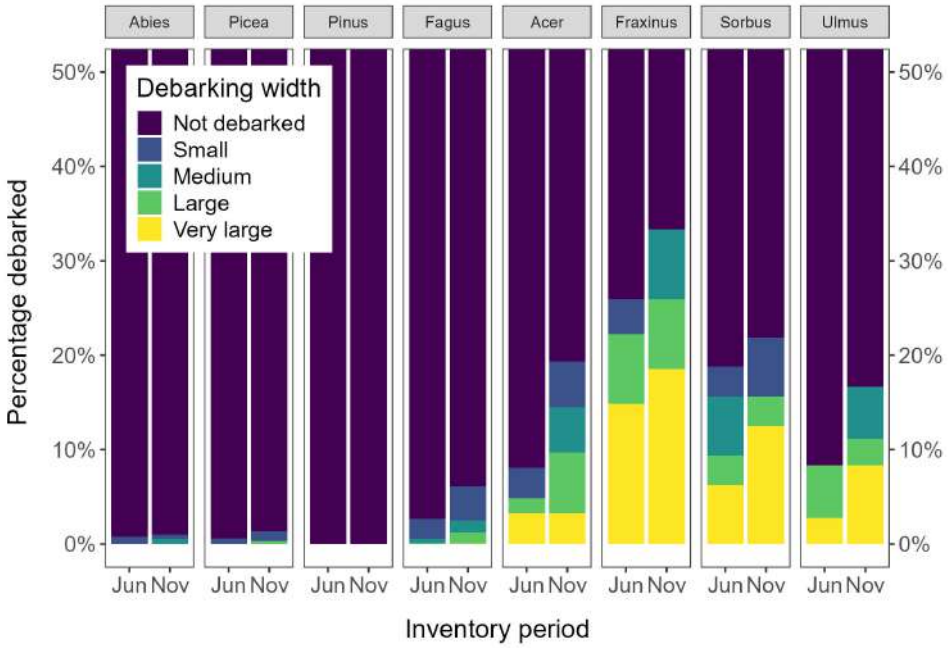

Figure 3.1: Comparison of the debarking width between species and the two debarking inventories; June and November. Sampled number per species can be seen in Table 3.1. Note that the scale only goes up to 50 %.

Even though fir and spruce were much more abundant than the broadleaved species (excluding beech) only about 1% showed debarking wounds, compared to the 10 - 30% of broadleaved tree species (Figure 3.1). Beech, the most abundant species, had an intermediate percentage of debarked trees. This further supports formation of the coniferous and broadleaved groups, and that beech was kept as a separate group from the other broadleaved species. It is striking, that only the broadleaved species have very large debarking wound widths, and the percentage of very large widths is usually higher than the percentage of small or medium debarking widths. Maple, having a smaller proportion of very large widths is the only exception within this group. On the other hand, Maple has one of the largest relative increase from June to November.

Regarding tree species distribution, the slope in the South on the eastern half of the study area is dominated by beech trees and the central plots on the western half have high proportions of coniferous trees (Figure 3.2). Broadleaved trees (excluding beech) are predominantly found in the North and South-East of the study area. Almost all plots are a mix between beech and coniferous species. Plots with high proportions of coniferous species have little or no debarked trees and this is shown in the inventory until June (Figure 3.3) but also until November (Figure 3.4). While plots with many debarked trees often have larger proportions of the broadleaved group, not all plots with a large proportion of broadleaved trees show high levels of debarking, e.g. plot number 13, 22, 61, 148 and 191 (plot numbers in Figure 2.5).

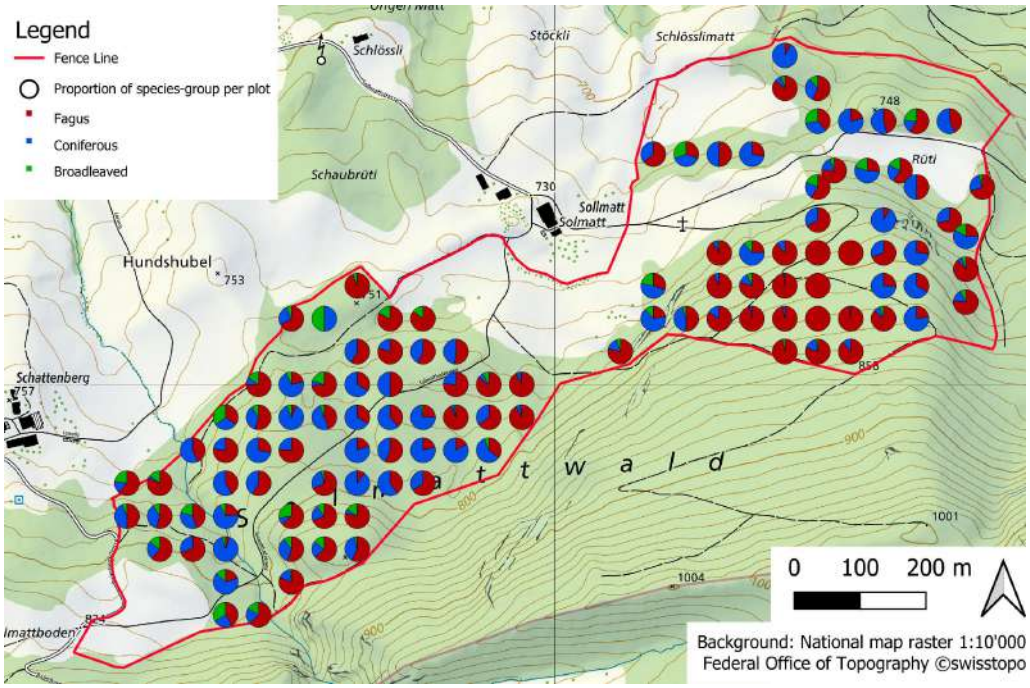

Figure 3.2: Map with the proportion of trees per plot belonging to one of the three species groups.

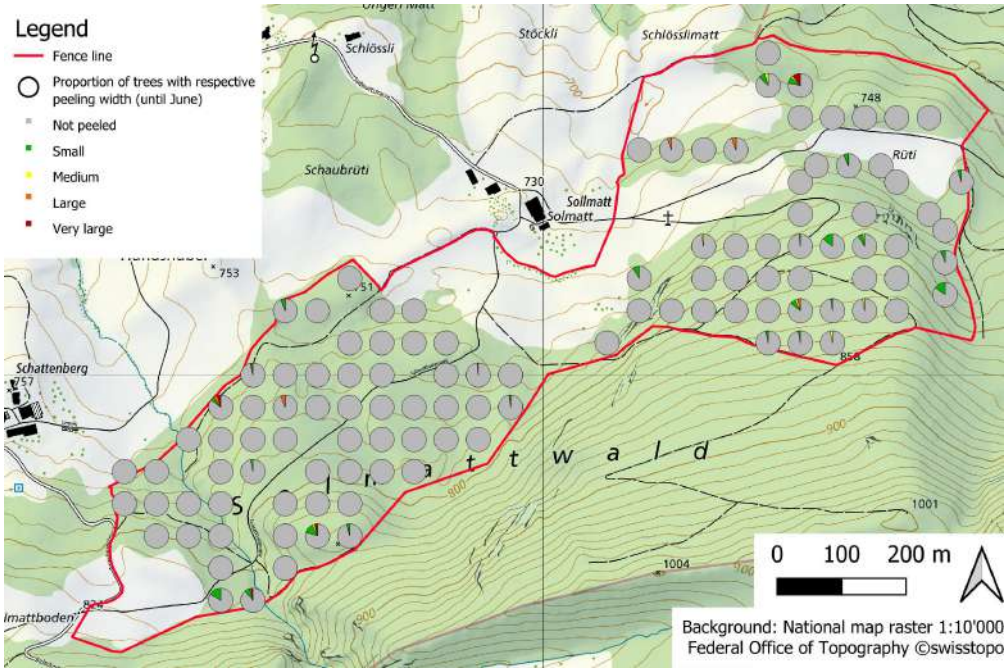

Figure 3.3: Map with the proportion of trees debarked per plot: Results from the inventory until June. A fully gray circle indicates that no tree was debarked in that plot during that inventory.

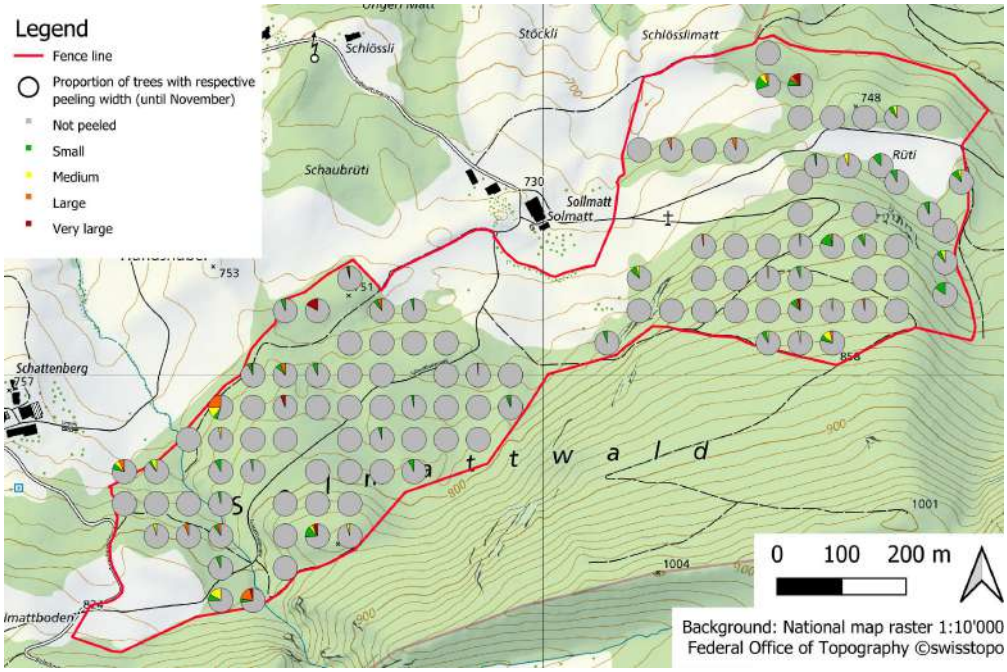

Figure 3.4: Map with the proportion of trees debarked per plot: Results from the inventory until November.

Electivity index for species

The modified electivity indices calculated for each tree species correspond to the percentage debarked as shown in Figure 3.1. That is, positive indices for the broadleaved species maple, ash, whitebeam and elm, while beech and the coniferous species silver fir, spruce and Scots pine had negative indices (Figure 3.5). The mod. electivity index for Scots pine is -1 (absolute avoidance) because none of the Scots pines exhibited debarking wounds. The modified electivity index of beech was slightly negative or close to zero, even though most debarked trees were beech trees; this is due to the fact that beech was the most abundant tree species in the study area. The differences between the calculated indices for the June and November inventory are generally small, except for silver fir. For all species except silver fir and sycamore maple, the index values are slightly closer to zero in November compared to June.

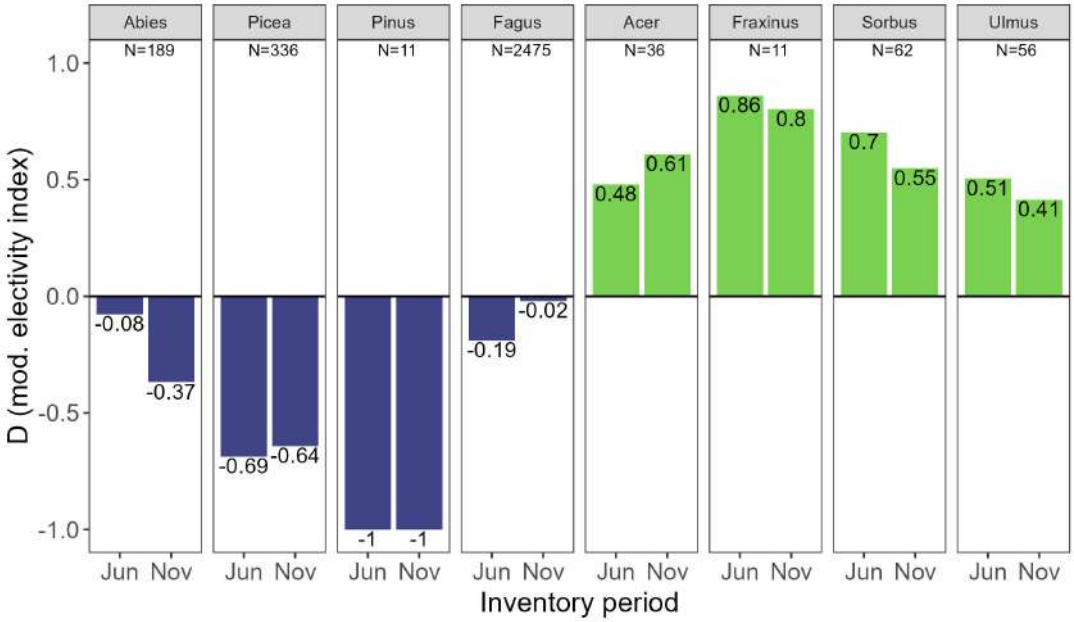

Figure 3.5: Modified electivity index calculated for each species and both inventories. The number of trees per species is extrapolated to per hectare values. A low index indicates avoidance, a high index indicates active selection, and a index around zero indicates random selection.

Debarking model for the whole year (until November)

At first, the predictor "species", where all 8 species were tested separately, was used in the GLMM until November (Table D.1 in Appendix D), which drastically increased model complexity by 7 degrees of freedom. Including species prevented the model from converging when more predictors were subsequently added. Since "species group" performed better

and was less complex (increase of only 2 df), the following models were only built using species group as a predictor. The final selected GLMM until November included species group, DBH, maximum bison frequency and herb cover (Table D.1 in Appendix D).

This model predicts large differences between the species groups: Coniferous trees were predicted to be debarked less than beech and broadleaved trees were predicted to be debarked more than beech (Table 3.2). It follows that coniferous trees were also predicted to be debarked less than broadleaved trees. The model estimates indicate that the species group has a stronger effect on debarking than the DBH, bison frequency and herb cover (all discussed in Chapters 3.1.2 and 3.2).

Models for debarking until June and June to November

The GLMM with the dataset until June (see Table 3.3 and Table D.2 in Appendix D) showed the same results for the species group but less pronounced: Coniferous trees were predicted to be debarked less than beech trees. However, this effect was only significant in tendency (on an alpha level = 0.05). Again, the species group broadleaved was predicted to be debarked more than beech trees. Results of the GLMM using only newly debarked trees from June to November are similar regarding the differences between the species groups (Table 3.4), but the estimates are lower for coniferous and broadleaved trees. This suggests that this model predicts beech trees to be debarked more in comparison to the other two groups. Compared to the other predictors in this model, the AIC was nevertheless reduced more by including the species group than by adding the other predictors, thus indicating a stronger effect of species group on debarking (Table D.3 in Appendix D). The final model until June included species group, DBH, maximum bison frequency and inclination (Table D.2 in Appendix D), while the model from June to November included the same predictors as the model until November (Table D.3 in Appendix D).

Table 3.2: Results of the selected GLMM with the dataset until November and the binary target variable "debarking". Significance levels are denoted as follows: $***$ indicates a p-value ≤ 0.001, $**$ indicates p ≤ 0.01 and $*$ indicates p ≤ 0.05. The reference for species group is Fagus.

	Estimate	Std. Error	Significance
(Intercept)	-4.280	0.318	***
Species group: Coniferous	-1.794	0.384	***
Species group: Broadleaved	1.251	0.275	***
DBH	0.071	0.020	***
DBH^2	-0.002	0.000	***
Max. B. freq	0.025	0.008	**
Herb cover	0.049	0.018	**

Random effect	Variance	Std. Error
(1 | Plot)	1.298	1.139

Table 3.3: Results of the selected GLMM with the dataset until June and the binary target variable "debarking". Significance levels explained in Table 3.2.

	Estimate	Std. Error	Significance
(Intercept)	-5.138	0.939	***
Species group: Coniferous	-1.240	0.506	*
Species group: Broadleaved	2.055	0.370	***
DBH	0.281	0.068	***
DBH^2	-0.008	0.002	***
Inclin.	-0.044	0.018	*
Max. B. freq	0.042	0.014	**

Random effect	Variance	Std. Error
(1 | Plot)	1.472	1.213
(1 | DBH class)	0.879	0.938

Table 3.4: Results of the selected GLMM with the dataset using only newly debarked trees from June to November and the binary target variable "debarking". Significance levels explained in Table 3.2.

Predictor	Estimate	Std. Error	Significance
(Intercept)	-4.512	0.321	***
Species group: Coniferous	-2.068	0.483	***
Species group: Broadleaved	0.851	0.311	**
DBH	0.067	0.021	**
DBH^2	-0.002	0.0004	***
Max B. freq.	0.055	0.017	**
Herb cover	0.053	0.017	**

Random effect	Variance	Std. Error
(1 | Plot)	1.030	1.015

3.1.2 Tree diameters preferentially debarked

Descriptive analysis

Note first that almost all whitebeam and elm trees and the majority of beech and spruce trees had a DBH < 12 cm (Figure A.2 in Appendix A). In contrast, ash, pine, and to a lesser extent also maple and fir, had very high proportions of trees with DBH > 12 cm.

Trees with a DBH larger than 36 cm were rarely debarked (Table 3.5 and Figure A.1 in Appendix A). Most debarked trees had a DBH of less than 12 cm, but the other two DBH classes had a larger relative increase from the first inventory in June to the inventory in November, most notably for the largest DBH class (Figure A.1 in Appendix A). All debarked trees with a DBH larger than 36 cm were either beech, maple or fir (Figure A.3 in Appendix A). All whitebeam and almost all elm trees and the majority of beech trees with debarking had a DBH < 12 cm. That is why the scaled number of trees per hectare was larger than the sampled number for these species in Figure A.2. Maple and ash, on the other hand, have very high proportions of debarked trees with DBH > 12 cm. This demonstrates, that the DBH classes are not clearly related to the species groups. Therefore, statements made about the species groups cannot automatically be related to statements about the DBH.

Table 3.5: DBH classes used for the analysis: Number of sampled trees and number debarked thereof for both inventories, as well as the increase from June to November.

	Total sampled	**Debarked until June**	**Debarked until Nov.**	**Increase**	**Increase [%]**
Total	2805	76	156	80	105%
DBH <12 cm	1338	52	95	43	83%
DBH 12-36 cm	956	22	52	30	136%
DBH >36 cm	511	2	9	7	350%

Trees with a DBH between 3 cm and 20 cm were debarked most (Figure 3.6). Interestingly, there appears to be two peaks of debarked trees in both periods: One at a DBH of about 7 cm, and another at a DBH of about 15 cm. As the DBH class threshold was at DBH $=$ 12, this is probably not an artefact of the sampling procedure. Trees with a DBH larger than 50 cm were almost never debarked and trees between DBH 25 and 50 only showed debarking wounds in the inventory of November.

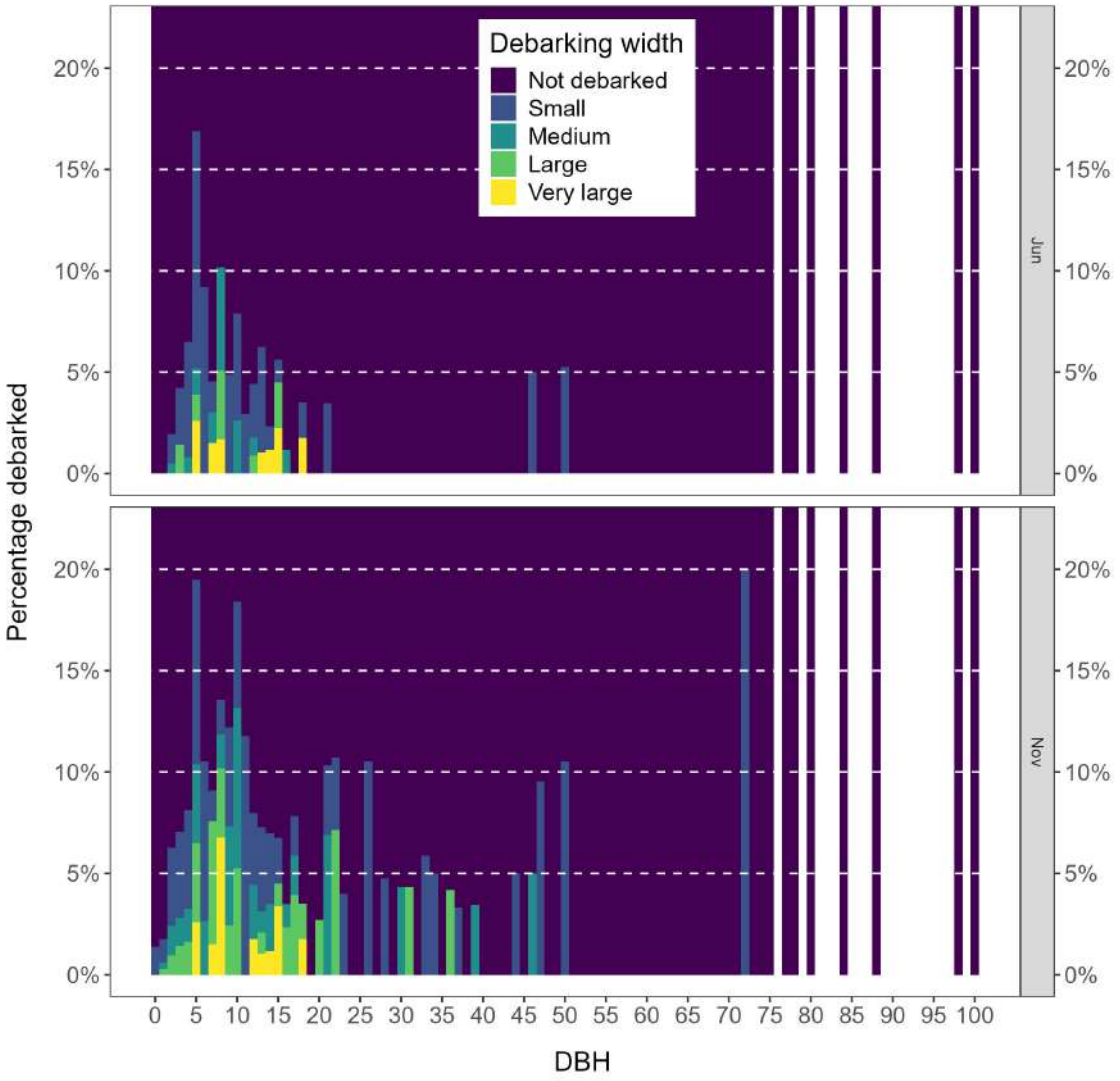

Figure 3.6: Percentage of debarked trees by DBH and debarking width. The upper plot shows results from the inventory in June and the lower plot from the inventory in November. Note that the scale only goes to 23 %. Since the data in this plot is not corrected for the sampling structure, the trees with DBH $>$ 12 cm are over-represented and the trees with DBH $<$ 12 cm are under-represented.

Electivity index for DBH

The modified electivity indices calculated for DBH classes are positive for trees with a DBH < 12 cm and negative for the two larger DBH classes (Figure 3.7). Except for trees with a DBH > 36 cm, the index values are relatively low and closer to zero than the electivity indices calculated for the tree species. Comparing the indices between the June and November inventories, it is evident that the index values are closer to zero for the November inventory period.

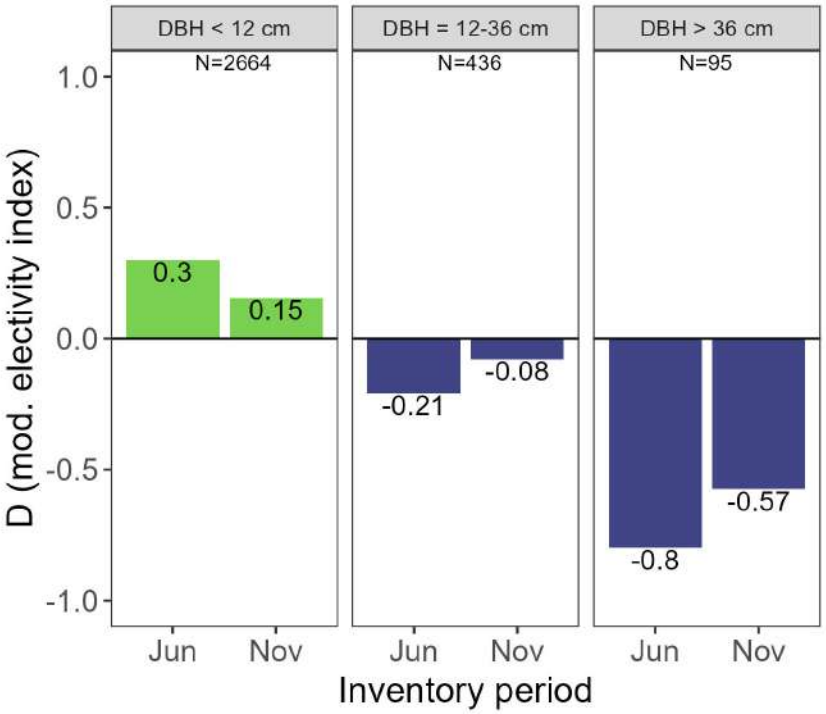

Figure 3.7: Modified electivity index calculated for each DBH class and both inventories. The number of trees per species is calculated per hectare. A low index indicates avoidance, a high index indicates active selection and a index around zero indicates random selection.

Debarking GLMM with DBH

Due to the fact that trees with a very small or large DBH were debarked less (Figure 3.6), the relationship between the DBH and whether or not trees were debarked was not linear. Therefore, the effect of the DBH on debarking alone was non-significant in the GLMM with the dataset until November (see Table D.1 in Appendix D). When including an interaction between the DBH and species group, meaning the model tests the DBH depending on the species group, the DBH terms were still non-significant. When adding DBH as quadratic term, however; DBH + DBH^2, the effects were highly significant. When

fitting a model with DBH^2 alone, the effect was significant but the model performance was worse than when DBH and DBH^2 were included. Therefore all three final GLMM contained the quadratic term DBH + DBH^2. As can be seen in the results of the selected GLMM until November (Table 3.2), the terms DBH + DBH^2 describe a downwards opened quadratic curve, where debarking increases from DBH = 0 cm to a maximum debarking probability at DBH $\approx$ 17.5 cm and then decreases to a minimum again at DBH $\approx$ 35 cm. Similarly, the results of the selected GLMM with the dataset until June in Table 3.3 show, that the terms DBH + DBH^2 describe a downwards opened quadratic curve with approximately the same minimum and maximum, but with an increased slope: Trees with a DBH $\approx$ 17.5 cm are more likely to get debarked by the bison according to this model with the dataset from June compared to the model with the dataset until November. For the GLMM using only newly debarked trees from June to November, the quadratic curve described by the DBH + DBH^2 terms (see Table 3.4) was almost identical to the one described for the entire period (i.e. Table 3.2).

3.2 Location-specific characteristics impacting debarking

3.2.1 Impact of spatial variables

Besides knowing what species and DBH classes the European bison debarked, it is important to find out where trees were debarked in the study area. The spatial distribution of the debarking widths can be seen in Figures 3.3 and 3.4. Already in June, debarked trees were recorded in plots far away from the meadows, as can be seen along the southern boundary of the study area. This phenomenon was even more apparent on the map with results from the inventory in November: most plots on the slope in the southern half on the eastern side have debarked trees. Looking at plots 139 and 147 (in the North-East) it is interesting to see that some plots displayed a sharp increase in debarking from June to November while neighbouring plots did not.

During the selection process for the GLMM with the dataset until November (see Table D.1 in Appendix D) and June to November (Table D.3 in Appendix D), I found that the inclination in the study area did not significantly impact the occurrence of debarking. In contrast, inclination was a significant predictor in the GLMM with the dataset until June (Table 3.3; p = 0.05), i.e., increasing inclination in the study area predicted a lower probability of debarking. Mean inclination was lower for debarked trees than non-debarked trees for both inventories, but the difference was more pronounced for the inventory in June (Figure A.5 in Appendix A).

None of the proximity predictors (i.e., proximity to the stream, -any water source, -paths, -forest edge and proximity to any of the aforementioned), had a significant effect on debarking in any of the three GLMM (see Tables D.1, D.2 and D.3 in Appendix D). For all three models both the mean and maximum bison frequency were significant predictors of debarking. However, maximum frequency always performed better in the ANOVA and was thus chosen for the final models. The distribution of the maximum bison frequency does

not fit the normal distribution but rather an exponential distribution. Neither a quadratic transformation nor any other transformation improved the model fit. A high bison frequency predicted increased debarking in all three GLMM (Tables 3.2, 3.3 and 3.4). The p-value was smaller than 0.01 for the GLMM until November and for the GLMM containing only newly debarked trees. For the model until June the p value for maximum bison frequency was smaller than 0.05. By plotting the data, a higher mean bison frequency for debarked compared to non-debarked trees was found for both inventories (Figure 2.8 in Appendix A).

3.2.2 Impact of variables within the forest stand

As mentioned, predictors related to the forest stand and vegetation layer were also tested in the GLMM. The predictor forest community was non-significant in the GLMM with the dataset until November and the dataset containing newly debarked trees between June and November (see Tables D.1 and D.3 in Appendix D). When the forest community was included as predictor in the GLMM until June the model did not converge. Forest stand structure and stand developmental stage were non-significant in the GLMM for all three datasets as well, but the model results for stand developmental stage in the GLMM for November show a larger standard error than the estimate, meaning this result needs to be taken with a grain of salt. This phenomenon can be explained by the fact that there are only three plots in the developmental stage thicket ($d_{dom} < 12$ cm): Slight variability in the plots with thicket stage in turn lead to large standard errors.

Further, the predictors grass-, shrub-, tree regeneration-, bramble-, raspberry- and regeneration competition cover could not significantly predict the occurrence of debarking. The predictors vegetation sum as well as herb cover (which is contained in the vegetation sum) had a significant effect on debarking for the GLMM with the dataset until November and the dataset containing newly debarked trees between June and November. However, the effect of herb cover was stronger and lead to a better model performance in the ANOVA. Thus, herb cover was used in the final models and the more general predictor vegetation sum was omitted. The results of these two final models (see Tables 3.2 and 3.4) show that an increased ground cover of herbs in a plot predicts increased debarking occurrence (significance level = 0.01). When plotting the data, I found plots with high ground cover percentages to have a higher percentage of debarked trees (Figure A.6 in Appendix A). For the GLMM with the dataset until June, neither the ground-cover percentage of herbs nor the sum of vegetation were significant (see Table 3.3 in Appendix D).

3.2.3 Debarking season and other tested predictors

Further predictors tested in the GLMM were occurrence of bison footsteps and non-bison related stem damage. As can be seen in the model selection tables D.1, D.2 and D.3 in Appendix D, none of these predictors had a significant effect on debarking occurrence. The model containing the predictor debarking season, which should test if more trees

were debarked in winter or in summer, did not converge, because non-debarked trees were present in both the predictor and the target variable. Nonetheless, more trees were debarked in summer than in winter (Figure A.7 in Appendix A). This result is more pronounced when considering the time spans covered by both inventories: Over the 7 months until the inventory in June, about 11 trees were debarked per month and over the 5 months until the inventory in November about 22 trees were debarked per month (including trees debarked repeatedly).

3.3 Impact on debarking intensity

3.3.1 Results from the descriptive analysis

In this chapter, results are shown regarding what influences the size of the debarking wounds. The size was described by the width and length of the wound. Debarking width and length are correlated: Wide debarking wounds are also longer on average (Figure 3.8).

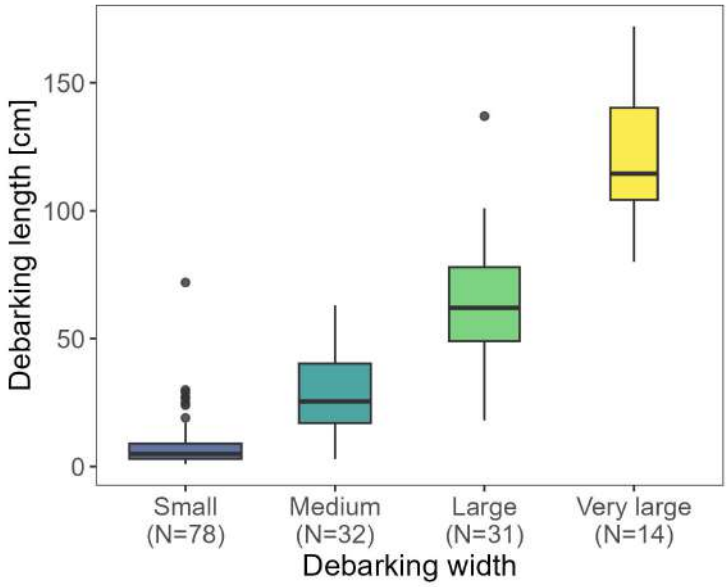

Figure 3.8: Boxplot showing the range and mean length of debarking wounds by width category. Boxplot width is proportional to the number of observations (N). Note that an outlier with a very large width and a length of 400 cm was omitted to better show differences in the low range.

The mean DBH is similar for all debarking width categories (Figure 3.9), though a slight tendency of an increasing DBH with increasing debarking width can be recognized. Interestingly, the variance decreases with increasing debarking width category. In addition,

the distribution of large and very large debarking widths per DBH is comparable to the distribution of small and medium widths.

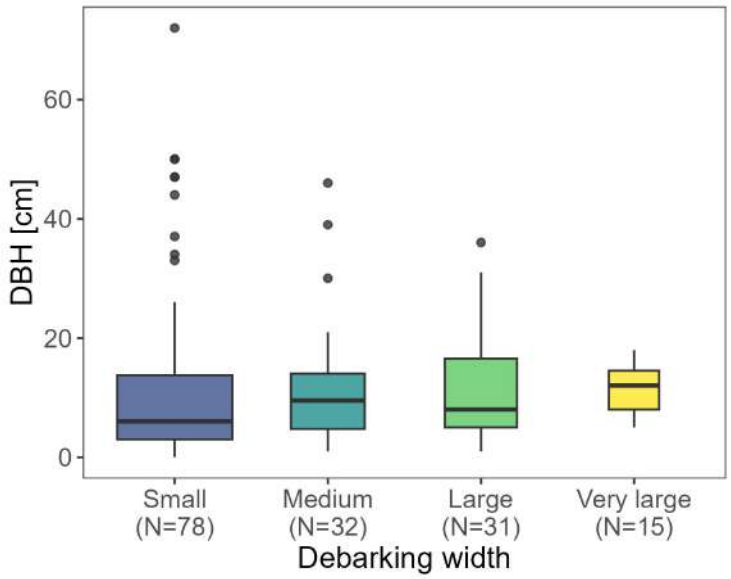

Figure 3.9: Boxplot of the DBH by debarking width. The box width is proportional to the number (N) of observations.

3.3.2 Results of the debarking width model

The selected CLMM with debarking width as target variable included debarking length, DBH and debarking season2 (debarked once or repeatedly) as predictors (Table D.4 in Appendix D). The model predicts a highly significant difference between all the debarking width categories (Table 3.6). The estimates show an especially large difference between large and very large debarking widths and a smaller difference between small and medium debarking widths. The length of debarking wounds turned out to be a significant predictor of debarking width in the CLMM (Table D.4 in Appendix D). Since debarking length was non-normally distributed, a $\log_{10}$ transformation was carried out for the debarking length. However, the ANOVA revealed that the model performed worse than with the non-transformed debarking width, so the predictor was kept non-transformed. The length of debarking wounds significantly and positively predicts wider wounds (Table 3.6).

The broadleaved group of the predictor species group had a significant effect on debarking width: The estimate was 2.51 ± 0.45 (p-value $= 2.37 \times 10^{-8}$), meaning that broadleaved trees had significantly wider debarking wounds than beech trees. The effect was non-significant for the coniferous species group. The CLMM did not converge when both the species group and debarking length were included in the model structure. As debarking length was the

better predictor, species group was not selected in the best model (Table D.4 in Appendix D).

The CLMM also did not converge when including the DBH as a quadratic term such as in the GLMM. The DBH alone, however, was a significant predictor. With an increasing DBH trees are predicted to have narrower wounds (Table 3.6; p = 0.05) .

Inclination had a significant (p-value = 0.038) effect on the debarking width, with an estimate of -0.047 ± 0.023, but only if the debarking length was included in the model. This means, that the variance in debarking width cannot be explained by inclination alone; only a part of the variance is explained by the inclination and most by debarking length. In the final CLMM with debarking length and DBH the predictor inclination had to be omitted because the model could not converge.

The predictors proximity to the stream, proximity to a water source and forest type could not be included in a CLMM without producing an error and were therefore omitted. Since no debarked tree was recorded to be within a plot where other vegetation competed with tree regeneration, this predictor could not be tested. Ground-cover percentage of tree regeneration itself could predict debarking width with an estimate of -0.04 ± 0.02 (p-value = 0.019), if debarking length was not included in the model. The predictor vegetation sum, which includes regeneration cover, was also significant (p = 0.05), again only if debarking length was not included in the model.

The debarking season had a highly significant effect on debarking width: Trees debarked in summer (-2.47 ± 0.52; p-value = 2.34×10^{-6}) and winter (-2.46 ± 0.56; p-value = 1.33×10^{-5}) had significantly narrower debarking wounds than trees that were debarked repeatedly. Thus, the predictor "debarking season2", which only distinguishes between the categories "debarked once" and "debarked repeatedly", had a better model fit than debarking season and a lower df. The results of the final CLMM (see Table 3.6) show that the wounds were wider if trees were debarked repeatedly instead of only once either in winter or summer.

3.3.3 Results of the debarking length model

The selected LMM with debarking length as target variable included debarking width, DBH and proximity to the nearest path as predictors (Table D.5 in Appendix D). The debarking width was a highly significant predictor for debarking length in the LMM analysis. Trees with larger debarking widths also had larger debarking lengths (see Table 3.7). So, for example, wounds with a medium width are longer than wounds with a small width, and the extent of this effect gets larger with increasing debarking width.

As with the CLMM, the broadleaved group of the predictor species group had a significant effect on debarking width (see Table D.5 in Appendix D): The estimate is 0.58 ± 0.11 (p-value $< 1 \times 10^{-4}$). However, when combined with debarking width, the effect of species group was non-significant, because it was masked by the effect of debarking width.

Out of all combinations with DBH and DBH^2, including the interaction of DBH and

Table 3.6: Results of the selected CLMM with the dataset until November and the categorical/ ordinal target variable "debarking width". The reference for "Debarking season2: Repeated" was "debarked once".

	Estimate	Std. Error	Significance
Small | Medium	2.889	0.657	***
Medium | Large	6.471	1.073	***
Large | Very large	13.397	2.094	***
Deb. length	0.133	0.018	***
DBH	-0.050	0.025	*
Deb. season2: Repeated	2.787	0.765	***

Random effect	Variance	Std. Error
(1 | Plot)	0.574	0.758

debarking width, the model with DBH alone performed best in the ANOVA. An increasing DBH significantly predicts longer debarking wounds (Table 3.7), as opposed to the CLMM for debarking width, where the opposite was found. However, the estimate is very low, meaning the impact on the debarking length is highly significant but small.

In contrast to the models built so far, the spatial predictor proximity to the nearest path had a significant effect on debarking length (Table 3.7), i.e., the model predicts that debarking wounds are longer if the tree is closer to a path. Again, the estimate is very low.

During model selection, the forest type "silver fir - beech forest with wood clubrush" (number 19 after Ellenberg and Klötzli, 1972) had a significant and positive effect on debarking wounds: The estimate is 0.58 ± 0.21 (p-value = 0.0075). No other forest type categories had a significant effect on debarking length, and the predictors effect was only significant if debarking width was not included in the model structure. Trees in a forest stand with a multilayered structure had significantly shorter wounds (estimate: -0.49 ± 0.16; p-value = 0.0035) than trees in a single-layered stand. The tendency is the same for trees in a two-layered stand, the effect was non-significant in this case, however. Similarly, trees in uneven-aged stands, which are often multilayered, also had significantly shorter wounds (estimate: -0.37 ± 0.16; p-value = 0.029) compared to trees in the developmental stage young growth (shorter than 2 m). However, models containing forest stand structure and -developmental stage performed worse than the final model (Table D.5 in Appendix D).

As in the CLMM, regeneration cover was significant (Table D.5 in Appendix D) with an estimate of -0.012 ± 0.004 (p-value = 0.0093), meaning debarking wounds were shorter when regeneration cover was high. This effect was non-significant when debarking width was included in the model structure as well.

Neither bison footsteps nor bison frequency significantly predicted debarking length. If debarking width was not included, debarking season2 was significant (Table D.5 in Appendix D): Wounds were significantly shorter when debarked once either in winter or summer, compared to when debarked repeatedly (estimate: 0.533 ± 0.116 (p-value $< 1 \times 10^{-4}$).

When building the final LMM with as many significant predictors as possible, the model structure with debarking width, DBH and the proximity to the nearest path performed best in the ANOVA.

Table 3.7: Results of the selected LMM with the dataset until November and the numerical target variable "debarking length".

	Estimate	Std. Error	Significance
(Intercept)	0.776	0.066	***
Deb. width: Medium	0.597	0.067	***
Deb. width: Large	1.001	0.069	***
Deb. width: Very large	1.384	0.090	***
DBH	0.008	0.002	***
Prox. path	-0.003	0.001	**

Random effect	Variance	Std. Error
(1 | Plot)	0.000	0.000

3.4 Additional results

3.4.1 Findings in regard to wound occlusion

Signs of wound occlusion were recorded during the inventory in November, which can give insights to the tree's vitality and help to determine if the approximate moment of debarking could be estimated by such an observation or not. Of the 156 debarked trees, 60% showed signs of occlusion and the debarking wounds of 5 more trees were partly occluded: Either because the tree was not vital enough to invest in new growth around all of the edges of the wound or because not enough time had elapsed yet, so that occlusion could have been visible on the entire border. About 75% of trees debarked at least once before June showed signs of wound occlusion. Often, slight signs of wound occlusion were already found in June, but the occlusion was especially clear in November (e.g., Figure 3.10). Other trees did not show any signs of wound occlusion, despite having been debarked before June, the tree still being alive at the time of the inventory and not being completely girdled by the bison (e.g. Figure C.1 in Appendix C). More interestingly, about 45% of all trees only debarked after the inventory in June already showed signs of wound occlusion, meaning these trees were able to react to debarking within less than 5 months. Figures C.2, C.3 and

C.4 in Appendix C show examples of strong wound occlusion on trees that were debarked after June.

Figure 3.10: Photographs of a debarking wound on a beech tree, once taken during the inventory in June (left), and once during the inventory in November (right). The marker-pole in the photograph has a total length of 1 m and each coloured section corresponds to exactly 10 cm. Tree ID: 2713, plot ID: 192.

3.4.2 Girdled-, frayed- and rubbing-trees

Trees were only rarely completely girdled by the European bison. During the first inventory in June, 3 trees were recorded to be girdled and in the second inventory in November this number increased to 5. Considering the sampling structure, this corresponds to 0.08% of trees in June and 0.11% of trees in November in the study area that were girdled. Girdled trees were either ash or elm trees with a DBH ranging from 5 cm to 18 cm. The debarking wounds were always more than 100 cm long and the length of the completely girdled section ranged from 2 cm to 156 cm. All girdled trees were still alive at the time of the inventory in November. Three of the girdled trees occurred in plot number 147 and the other two

were spread out in two other plots in the study area, which suggests that girdling occurs more concentrated in certain areas.

A total of 16 trees showed signs of fraying in either of the two inventories. Two thirds of frayed trees were spruce trees, and had a DBH of 7 cm or less. Fraying at the roots of the trees was only recorded twice in the inventory in June. This type of injury was not found again during the second inventory. None of the frayed trees simultaneously showed signs of fraying and debarking. Frayed trees were found more or less spread out over the study area, only one plot (number 172) contained three frayed trees, while all others only one.

Trees which were used by the bison as rubbing-trees numbered 5 during the inventory in June and increased to 34 in November. The average DBH of rubbing trees was 37 cm, and was larger than 12 cm in most cases. The vast majority of these trees were silver firs (65%), but Norway spruce and Scots pine were used as well and one tree was a sycamore maple. The rubbing did not remove the bark and therefore left the trees unscathed. Only one of the 34 rubbing trees was also debarked. Rubbing trees occurred clumped over the study area: Few plots contained rubbing trees and plots 133 and 86 contained most of them. Interestingly, three of the five rubbing trees recorded in June were not recorded as such again in the inventory in November.

Chapter 4

Discussion

The discussion is also structured by the research questions and hypotheses: First, Q_1 "Which tree species and -diameters are debarked most by the European bison?" will be discussed based on results from Chapter 3.1. Then Q_2 "What location-specific characteristics have an impact on the occurrence of debarking?" will be discussed based on the results of Chapter 3.2. Next Q_3 "What impacts debarking intensity?" will be discussed based on results presented in Chapter 3.3. After the research questions and hypotheses have been discussed, the consequences of debarking will be discussed based on literature research and findings from Chapter 3.4. Lastly, study limitations and an outlook for future research in the Wisent Thal project will be discussed.

4.1 Which trees are debarked most by the European bison?

Tree species preference

Knowing where damage can be expected once the bison herd ranges free in the Jura mountains is key for forest owners and -managers. The electivity indices calculated for each tree species clearly show that coniferous species were avoided and the broadleaved species were positively selected by the European bison in this study. I therefore reject my hypothesis $\mathbf{H_1}$, that coniferous species would be preferentially debarked. Especially Scots pine and Norway spruce were avoided, while silver fir was only actively avoided when considering the inventory until November. Silver fir altogether has indices closer to zero than expected and a large difference between both inventory periods. This can be explained by the fact that most silver firs have a large DBH (see Figure A.2 in Appendix A) and the number of individuals was scaled down when calculating per hectare numbers, which in turn made the index more prone to change if a few trees were debarked. The index values for beech trees were close to zero, which indicates that the selection of beech trees by *B. bonasus* is not active and positive but rather random and opportunistic. The index value of -0.19 for beech in June even indicates avoidance. My hypothesis $\mathbf{H_1}$, that beech would be avoided, was therefore only partly confirmed. These index results are also reflected in Figure 3.1 and further supported by the model results: The models predict broadleaved trees to be debarked more and coniferous trees to be debarked less than beech. A comparison of the electivity index values from the inventory in June with the inventory in November (see Figure 3.5) suggests that these preferences are stable and thus might not significantly change in the near future.

All tree species in the preferentially debarked broadleaved group are recommended, or at

least conditionally recommended tree species under climate change for the forest community *Cardamino-Fagetum typicum* (number 12a after Ellenberg and Klötzli, 1972) according to the Tree App (`www.tree-app.ch`). The bison's debarking habits therefore might at least partly impede the forest manager's goal to promote climate-adapted tree species and have an impact on the tree species diversity. Nevertheless, European beech is still a recommended species for the study site, and silver fir, as well as Scots pine, are conditionally recommended, so not all recommended tree species are preferentially debarked.

Under the assumption that some of the debarked trees will die in the future, the long term loss of certain tree species and a change in species composition in the forest could be another potential consequence of selective debarking (Gill, 1992; Feher et al., 2016). A shift or even a loss in species composition is possible if ungulates display selective behaviour for certain tree species Schulze et al. (2014). This effect is further exacerbated if the preferred tree species are already rare: Since the beginning of the 1970s the Dutch elm disease has been spreading out in Europe, affecting several Elm species including wych elm(Santini and Faccoli, 2015; Nierhaus-Wunderwald and Engesser, 2003). And since 2008 ash dieback has been present in Switzerland, severely impacting European ash (Carroll and Boa, 2024; Schlegel et al., 2018; Rigling et al., 2016). Considering that in this study over 30% of sampled ash trees exhibited debarking wounds and almost 20% showed very large debarking widths, as well as almost 20% of sampled elm trees showed debarking wounds (see Figure 3.1) after just one year of bison presence, a local loss of these species is conceivable.

However, the results regarding tree species preference are not supported by the findings of other research. Kowalczyk et al., 2011 calculated the modified electivity index by measuring the proportion of a given tree species in the diet of the bison in the forest stands of Bialowieza Primeval Forest: The index value for Scots pine is 0.97, demonstrating very strong positive selection, while I computed an index value of -1, demonstrating absolute avoidance. Similarly, opposing index values for European ash and maple were found (Kowalczyk et al., 2011), although the maple in this thesis is *Acer pseudoplatanus* compared to *Acer platanoides* in the Bialowieza study. The indices for Norway spruce and elm were in the same range. In contrast, Norway spruce was positively selected in a survey in the Rothaar mountains (Dietrich and Möhring, 2013) and even preferred over broadleaved species in a study on debarking intensity by the European bison in the Bieszczady Mountains. Nieszała et al., 2022 found higher frequencies of debarking in stands dominated by Norway spruce, silver fir or Scots pine compared to stands dominated by European beech or sycamore maple. Other studies have also mentioned Norway spruce and European ash to be amongst the most frequently debarked tree species (Borowski and Kossak, 1972; Wajdzik et al., 2011; Krasińska and Krasiński, 2013; Kibiša et al., 2017). Kibiša et al., 2017 reported spruce, pine and ash to be preferred and elm to be avoided, which contradicts my findings for the most part.

It is remarkable that only few of these studies reported European beech to be strongly selected or avoided by the bison; Brender, 2015 report beech to be spared as opposed to other broadleaved species. Dietrich and Möhring, 2013 shows positive selection for young

beech trees but negative selection for old beech trees. This somewhat supports my finding that beech trees are debarked at random by the European bison. Nonetheless, the opposing results found for the other tree species are unlikely to be due to methodological differences between the studies alone, which makes it difficult to generalize from my findings. That different groups of bison select different tree species based on the local availability of food (Kowalczyk et al., 2011) might be a possible explanation for these discrepancies. The European bison is generally considered to have a high plasticity in their feeding strategy (Kowalczyk et al., 2019; Hartvig et al., 2021; Pucek et al., 2003). The studied bison herds may simply have different preferences, which may even vary over time. It will be interesting to see if the bison's preferences for certain tree species change in the future course of the Wisent Thal project, especially once the fenced area is enlarged and they get access to new forest stands.

Diameter preference

Modified electivity indices calculated for DBH classes showed a general tendency of stronger avoidance with increasing DBH (see Figure 3.7): Trees with a DBH < 12 cm are positively selected, albeit only to a modest degree. Trees with a DBH between 12 and 36 cm are only somewhat avoided or randomly selected and trees with a DBH > 36 cm are strongly avoided (see also Figure 3.6). However, trees with a very low DBH have a lower percentage of debarked trees (Figure 3.6), suggesting a non-linear relationship. The model results confirm this, and based on the estimates predict trees with a DBH of about 17 to 18 cm to be debarked most, while trees with a DBH close to zero are predicted to be debarked as rarely as trees with a DBH > 35 cm. Gill, 1992 gives a good explanation for this phenomenon: "Damage can begin when the main stem becomes rigid and accessible and ends when the bark is too coarse, thick or difficult to remove." Generally, younger and smaller trees are more susceptible to debarking ungulates than older and larger trees (Dietrich and Möhring, 2013; Gill, 1992; Månsson and Jarnemo, 2013; Nieszała et al., 2022). Studies have shown diameters between 2 and 15 cm to be preferentially debarked (Brender, 2015; Borowski and Kossak, 1972). Krasińska and Krasiński, 2013 mention studies on bison debarking in Bialowieza Forest in Poland, where preferred diameters of 10 cm or less were found, but also diameters of 15 to 30 cm, depending on the tree species. Due to the low number of observations of debarked trees and different diameter distributions per species (Figures A.2 and A.3 in Appendix A), I was not able to find out if the diameters that were preferentially debarked depended on the species. While my results don't consistently pinpoint a certain DBH to be debarked most, I can safely say that diameters larger than 36 cm are avoided by the bison and only debarked rarely, meaning I can accept the second part of my hypothesis $\mathbf{H_1}$.

The findings regarding DBH preference have further implications for the bison's effect on the forest. The long term development of the forest is not at risk, as long as there are still sufficient small trees to replace the existing population of large trees (Rubin et al., 2006). Consequently, if the bison only debark, and in extension devalue or even kill a certain amount of trees with small diameters, the forest can still be regarded as structurally

sustainable, as forest managers would have to thin pole stage stands anyway. However, Siebert et al., 2021 mention a report where all age groups of beech exhibited debarking wounds by the European bison to similar extent. If the European bison were to debark trees of large diameter more often in the future of this project, instead of just exceptionally as it is today, the impact on the forest could be considered problematic (Siebert et al., 2021). Where the threshold exactly lies, and what debarking percentage per DBH class is too much, is still an open research question.

4.2 What spatial- and forest stand characteristics impact debarking frequency?

Looking at the spatial distribution of debarking occurrence (Figures 3.3 and 3.4), it is hard to make out any patterns or rules as to where debarking occurred and where it did not. While some plots certainly show a large proportion of debarked trees, they are not clumped in one area or limited to forest edges as hypothesized, but more or less scattered over the entire study area.

The European bison has been described to have a preference for open habitats such as meadows and forest glades (Balčiauskas, 1999; Wołoszyn-Gałęza et al., 2016; Kerley et al., 2012). In fact, the bison's GNSS signals in this study (see Figures 2.6 and 2.7) clearly show, that the bison mainly resides on the meadows, although hot-spots can be found within the forest as well. Thus, I assumed debarked trees to occur more in areas with higher bison frequency. This assumption seems to be correct as all three GLMM predicted increased debarking with increased bison frequency and the effect can also be seen when plotting the data directly (Figure A.4 in Appendix A). When comparing Figures 3.4 and 2.8, it is noticeable that plots with higher proportions of debarked trees usually also had a higher bison frequency value. However, bison frequency was not always higher in plots close to the forest edge, which is a possible explanation for why the proximity to a forest edge was not a significant predictor for debarking. The same goes for the other proximity predictors. When comparing the maps with debarking (Figure 3.4) and with vectors used for the proximity predictors (Figure 2.5) no pattern can be seen.

The proximity to forest paths was expected to be significant because of increased levels of disturbance, in turn leading to lower bison frequency (Schneider et al., 2013). But since some forest paths in Figure 2.5 are not frequently used by visitors, the predictor was flawed and therefore unsurprisingly insignificant. The proximity to water sources was an insignificant predictor of debarking occurrence as well, possibly because the stream and the natural spring did not contain water all year round, and because the watering trough was relatively far away from the forest (see Figure 2.5). The results of the GLMM for June in Table 3.3 demonstrated, that increasing inclination in the study area predicted a lower probability of debarking. Although only one of the selected GLMM revealed this correlation to be significant ($p \leq 0.05$), the effect can also be seen for November when plotting the data (Figure A.5 in Appendix A). This effect has also been found in other

scientific research (Kuemmerle et al., 2010; Bleyhl et al., 2015).

The predictor forest community was not important in this study, probably because most plots are of the type *Cardamino-Fagetum typicum* (number 12a after Ellenberg and Klötzli, 1972), and the herb- and tree species theoretically present in that community might not be there in reality. Once the project area is extended to 100 ha, more area will be of the *Abieti-Fagetum* forest communities and therefore greater differences in debarking are to be expected.

Areas with a high ground cover percentage of herbs have a higher percentage of debarked trees (Figure A.6 in Appendix A). The results of the GLMM until November and the the GLMM with the dataset containing newly debarked trees between June and November affirmed that trees are more likely to be debarked if the ground cover of herbs is increased. This confirms part of the hypothesis $\mathbf{H_2}$, that areas that offer forage have more debarked trees. European bison generally select for habitats with herbaceous vegetation (Kuemmerle et al., 2011) and herbs also make up a large part of their diet (Kowalczyk et al., 2019; Borowski and Kossak, 1972; Gebczynska et al., 1991; Hartvig et al., 2021). Hence, one can presume that the European bison will debark trees while foraging for herbs in the same area, thus saving energy and increasing food intake. Similarly, ungulate browsing has been shown to be increased if the ground cover of alternate food, such as blackberry and raspberry was higher (Kupferschmid et al., 2020). A possible reason that this effect was not significant for the GLMM with the dataset until June is that the herbaceous layer only developed in spring, and the bison debarked trees at random in winter.

Debarking has been described to be seasonal, whereby it is most common in late winter and early spring (Pucek et al., 2003), possibly because bark is one of the few sources of food available during that time (Krasińska and Krasiński, 2013). In the first year of the Wisent Thal project, however, twice as many trees were debarked per month in summer compared to winter. The low relative increase in debarking seen in Figure 3.1 is thus misleading. On the contrary, there is a distinct increase of the number of trees from winter to summer (Figure A.7 in Appendix A). The number of trees debarked repeatedly is also surprisingly high. The development of these trends in the course of the project will be important to determine the bison's impact on the forest.

4.3 What impacts debarking intensity?

Debarking intensity is important because larger wounds are more susceptible to decay development (Vasaitis et al., 2012; Welch and Scott, 2008), although it must be mentioned that susceptibility to infection depends on the species of the tree (Nieszała et al., 2022). Strong (in particular girdling) and repeated debarking also directly leads to increased tree mortality (Nagaike, 2020).

Broadleaved trees had significantly wider debarking wounds than beech trees and coniferous trees. In particular whitebeam and European elm are probably the tree species that are not just debarked more often, but also more heavily (larger width and larger length) than

coniferous tree species (Figure 3.1). Thus, the first part of the hypothesis $\mathbf{H_3}$, stating trees that are preferentially debarked according to $\mathbf{H_1}$ are debarked more intensely than other trees seems correct.

Gill, 1992 suggests debarking wounds to be larger on trees with larger diameter. However, I was not able to find clear evidence for this relationship. The estimates for the DBH show opposite tendencies in the models for debarking width and length. This might be due to the fact that the width was assessed relative to the DBH of the tree, but not for very small wounds (see Table 2.1). Figure 3.9 in Chapter 3.3.1 also shows no clear trend between DBH and debarking width. It could also be related to the fact that different tree species occur in different DBH and thus could have masked any DBH effect. Whitebeam and elm were almost exclusively found in the smallest DBH class, while pine, fir and ash had very high proportions of trees with DBH $>$ 12 cm (Figure A.2 in Appendix A).

Half of all debarked trees (78 out of 156) had a small debarking width, i.e. less than 1/3 of the diameter of the trees. Only 14 trees had a very large debarking width, i.e. more than half of the circumference, and very few (5 trees) were girdled. The trees in the larger width classes were thus probably too few to get models with satisfactory residual distributions, which also lead to non-convergence of more complex models. Nevertheless, trees closer to paths likely have longer wounds (Table 3.7). This is not reflected in the findings from Chapter 4.2 on the location of debarked trees. Hypothesis $\mathbf{H_3}$, stating that trees are debarked more intensely if situated at a convenient location according to $\mathbf{H_2}$, is therefore to be rejected until future analyses provide supporting evidence.

4.4 Rubbing, fraying and the consequences of debarking

Results from Chapter 3.4 suggest, that trees with a coarse bark were used as rubbing trees by the bison, which might explain why most were coniferous. The bark of beech is smooth compared to the three coniferous species found in the study area. Another reason for this preference could be that they like the smell of coniferous trees when rubbing against them. The average DBH of 37 cm for these trees suggest that they must be able to offer resistance to be rubbed against. European bison rub against trees to aid moulting of their winter coat (Kowalczyk and Plumb, 2020; Krasińska and Krasiński, 2013). It is therefore interesting to see the marked increase in rubbing trees found in June (5) to November (34): One would expect the bison to have already moulted by June. But since rubbing-trees are not always easy to spot, this increase may also be due to differences in data collection. Since the rubbing behaviour of the bison never removed the bark, it cannot be considered damage to the trees.

Fraying by the bison with their horns, however, certainly did remove the bark and therefore injured the affected trees. Antler fraying is a commonly known behaviour of the male red deer (*Cervus elaphus*, L.) and male roe deer (*Capreoulus capreolus*, L.) (Kupferschmid et al., 2023a) and can seriously damage the tree or even cause it to die off (Motta and Dotta, 1994; Gill, 1992). I have not found scientific literature on fraying wounds by the

European bison. Nevertheless, browsing and debarking have been reported to be more important than fraying (Dietrich and Möhring, 2013) and Siebert et al., 2021 even claim, that the European bison does not cause fraying wounds. In the inventories 10 times more trees exhibited debarking wounds than fraying wounds, which also supports the notion that fraying is only of minor importance.

After a tree has been debarked, there are several possible physiological consequences for the tree: A general decline in tree growth, the risk of stem breakage at the wound, a decrease in tree vitality and ultimately death of the entire tree (Borkowski and Ukalski, 2012; Rößner et al., 2023; Vasaitis et al., 2012). Welch and Scott, 2008 revealed that debarking can lead to adversely changed physical attributes of the timber. According to Feher et al., 2016, stem injuries generally become critical when the debarking wounds exceed 90% of the stem circumference, which was rarely the case in this study: Less than 10% of all debarking wounds exceeded 50% of the stem circumference. However, 3.2% of all debarked trees were completely girdled and after extrapolation I can say 0.11% of all trees in the study area were girdled. In the study of Akashi and Nakashizuka, 1999 trees died if girdled by sika deer (*Cervus nippon*, Temminck, 1838) and if debarking wounds exceeded 70% of the stem's circumference, most trees died as well. According to statements from Prof. Rohloff of the Institute of Forest Botany (University of Dresden) in Herbst and Finck, 2016, for beech trees with debarking wounds up to about 40% no consequences are expected because the tree can still redirect water and nutrients through the intact parts of the bark. For debarking wounds of 50 to 75% of the circumference, a measurable loss in crown vitality is to be expected and for wounds over 75% the tree's growth can be reduced by 25 to 50%. For wounds over 90% of the circumference severe subsequent damage and dieback of the tree can be expected.

In general, debarking wounds can serve as optimal entry points for infection by several fungi species (Vasiliauskas et al., 1996) and lead to stem rot and discoloration (Vasiliauskas and Stenlid, 1998; Welch and Scott, 2008). Welch and Scott, 2008 also demonstrated, that smaller wounds were less likely to exhibit discoloration and stem rot. Wound occlusion is important because it can prevent the establishment of an infection by decay fungi (Vasaitis et al., 2012; Vasiliauskas and Stenlid, 1998). This is especially true for small and fast healing wounds: The study of Vasaitis et al., 2012 on wound occlusion and decay in Norway spruce found that small wounds healed faster and the occurrence of wound decay increased with increasing width of the initial injury. In this study, about 45% of all trees debarked in between June and November already showed signs of wound occlusion and about 75% of trees debarked at least once before June showed signs of wound occlusion. Therefore, for some trees that were already debarked in June, no wound occlusion was visible while others already show signs of wound occlusion after less than 5 months. It follows that the reaction time to debarking differs greatly between trees. By simply noticing wound occlusion one can neither discern between first- and repeated debarking, nor make assumptions on the elapsed time since debarking. To determine the approximate date of debarking and properly analyze the temporal trend of debarking occurrence, it is necessary to conduct debarking inventories in regular intervals. The fast response of the trees to debarking

wounds demonstrates their vigor (Vasiliauskas and Stenlid, 1998) and in a broader sense a high productivity of the studied forest site. Therefore, for forest stands with less vigorous trees, the impact of debarking might be greater and cause more tree mortality than in the Wisent Thal project.

4.5 Study limitations and outlook

The spatial analysis in this thesis is limited due to the inaccuracy of the true location of the plots. The coordinates used for the spatial analysis are based on the theoretical location of the plots; they should lie on a 50 x 50 m grid. But during the inventory it became clear that the locations of these plots were sometimes off by 10-20 m. Therefore, the proximity predictors as well as the inclination predictor are not accurate. In order to obtain the true coordinates of the plot centers, it is advisable to use a more precise GNSS positioning instrument. After a subsequent recalculation of the coordinates of the trees as well as the spatial predictors, the impact of the spatial predictors might be stronger and more significant in the models.

Some of my predictors were limited by design. Proximity to the stream for example, because the stream likely does not provide water for the bison all year round. It was realized at a later stage that the north western forest edge cannot be accessed by the bison from outside because of the fence, only from the inside. After all, I hypothesized, that the bison would debark trees at the forest edge more, because they were so close to the meadows they graze.

Moreover, the definitions for the debarking seasons (winter and summer) were not accurate: Winter debarking encompasses trees debarked between November 2022 (release of the bison) until the inventory in June 2023, and summer debarking encompasses the shorter time period from June 2023 to November 2023. Perhaps future inventories could be timed better, but one must remember that an inventory takes about 6 weeks for one person alone to carry out and therefore will never be a precise capture of the situation during a single moment.

Future studies could also include predictors such as the location of birth of the bison within the study area. The bison herd resided in that area for longer periods during that time. As already mentioned, human disturbance (e.g. well frequented paths) could also be used as predictors for debarking. Wołoszyn-Gałęza et al., 2016 found European bison to avoid forests with full canopy cover. More importantly, increased occurrence of debarking was found in stands with more open canopies, such as wind-throw areas, because of a higher abundance of natural food such as herbs (Nieszała et al., 2022; Herbst and Finck, 2016; Schneider et al., 2013). Canopy cover could therefore be an important predictor of debarking in future models.

My findings on the impacts on debarking intensity are very limited, as already mentioned, likely due to the limited number of observations (156). In future inventories this number is likely to increase. Hopefully, then more robust results will be found regarding debarking

intensity. Theoretically, the closest debarked trees to the plot center were assessed in both inventories (maximum searching distance was 25 m), which in combination to the debarked trees in the plots would have considerably increased the number of observations. This data set should thus be included in further analyses of debarking intensity.

Another problem with debarking intensity is that the debarking width is relative to the DBH. The absolute width is important, since wounds of only 2-3 cm heal fast and wounds of 15 cm width might take many years to occlude, if they even occlude at all (Vasaitis et al., 2012). To study debarking intensity, it might therefore be better to approximate the maximum debarking width in centimetres from the DBH. However, this brings its own problems: The absolute width is rarely at a height of 130 cm, and debarking width classes encompass a range of values per class (the category "very large" ranges from 50–100% of the circumference). Nonetheless, it might be interesting to run models with maximal debarking area (width × length as a basic example) as a target variable. Measuring the width of the debarking directly in the field for each tree is, in contrast, very difficult as rarely was only one contiguous wound found (e.g. Figure C.4 in Appendix C).

Further studying the occlusion of wounds in future might deliver interesting results, such as an occlusion rate (how many millimeters wounds close per year) for vital and non-vital trees. This could be done by comparing photographs of debarking wounds, but then I would recommend taking higher resolution pictures in future. The rate of infection in wounds might also be interesting to study, if there is a method of measuring this that is not too invasive. Regardless, monitoring the health of debarked trees is key for future studies on debarking in the Wisent Thal project, as it is important to know how many debarked trees survive and recover in the long run. The occlusion rate and initial size of the wounds could serve as predictors of mortality in a future model. However, the death of a tree is usually a combination of many factors (Franklin et al., 1987; Waring, 1987), it would therefore be necessary to control for other possible causes of mortality such as drought, disease, bark beetle infestation and especially competition (Das et al., 2011). To calculate the competition index after Hegyi, 1974 the distance and DBH of competitor trees are necessary. The sampling design used for the two inventories so far might make this possible without much additional effort.

Chapter 5

Conclusions

In this study I carried out a debarking inventory to describe the debarking behaviour of the European bison in the Wisent Thal project. Ivlev's modified electivity index after Jacobs, 1974 and the results from the generalized linear mixed effects models all evidently demonstrate that silver fir, Norway spruce and Scots pine are avoided by the bison. European ash, sycamore maple, whitebeam and wych elm are positively selected for. European beech is selected at random by the bison. While these results are not well supported by other scientific studies, these findings nonetheless robustly describe the preferences of the herd in this project. Although about 6% of all trees in the study area exhibit debarking wounds, 30% and 20% of sampled ash and elm trees respectively were debarked after the first year of the project. Considering that ash and elm are already weakened and endangered by disease, I conclude that a local loss of these species in the future is likely. Furthermore, broadleaved trees had significantly wider debarking wounds than beech and coniferous trees. My finding that broadleaved trees are at a higher risk of debarking, and consequently devaluation, is especially important in the event of the herd being released and obtaining access to stands with high value timber. Indices and models consistently show that trees with diameters over 36 cm are avoided by the bison, while lower diameters are preferentially debarked. This is in line with most reports on debarking damage by the European bison (Krasińska and Krasiński, 2013; Nieszała et al., 2022). If the bison only debark small diameter trees, especially trees in the pole timber stage, then the forest structure is most likely sustainable in the long run, as these trees would have to be removed in forest thinnings anyway. These results might therefore help dispel beliefs of the European bison's destructive influence on forest landscapes (Kowalczyk et al., 2011). I was able to demonstrate that in areas where the bison remain for longer periods an increased number of debarked trees is to be expected. The map with GNSS positions of the bison indicated increased bison presence on the meadows and some forest edges, and some hot-spots are also found deeper within the forest. After all, debarking was scattered over the study area and not clumped or concentrated at forest edges. The trees' proximity to the forest edge, as well as forest paths and water sources, were not significant predictors for debarking. Two of my models predicted an increased number of debarked trees in areas with higher ground cover percentage of herbs, which make up a large part of the European bison's diet (Kowalczyk et al., 2019; Hartvig et al., 2021; Gebczynska et al., 1991; Borowski and Kossak, 1972). This implies that the bison debark trees while foraging for herbs in the same area, and also gives us insight into where debarking can be expected once the European bison acquire access to other forests. I was surprised to observe a high proportion of wound occlusion in debarked trees: 45% of trees debarked between June and November already showed signs of occlusion. Furthermore, small wounds were most common and

trees were rarely completely girdled. Considering that the risk of infection is higher and subsequent reduced vitality and growth or even death is more likely for large wound sizes (Welch and Scott, 2008; Herbst and Finck, 2016), consequential damage is likely to remain within reasonable limits if the average wound size does not increase in future.

Future studies on the debarking behaviour of the European bison in the Wisent Thal project should include canopy cover as predictor, as it was shown to be relevant (Nieszała et al., 2022; Herbst and Finck, 2016). Human disturbance was shown to influence their behaviour as well (Schneider et al., 2013) and would be an interesting predictor to test. If a spatial analysis is to be repeated, then remeasuring the coordinates of the plot-centers is advised, since I expect stronger results in the models with more accurate coordinates. Most importantly, future studies will have to assess the vitality and rate of mortality for debarked trees to quantify the impact of debarking on forest stands in the Wisent Thal project. With repeated inventories and the enlarged area in phase two of the project, the resulting larger datasets will lead to more robust results.

This study underlines the importance of quantifying and qualifying the occurrence of debarking and paves the way for future inventories in the Wisent Thal project. My findings contribute to the understanding of debarking behaviour of the European bison and may help stakeholders assess the feasibility of the reintroduction of the European bison in the Swiss Jura mountain range.

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Chapter 6

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Appendix A

Data plots

Appendix A contains additional plots that describe collected data and visualize correlations between variables that were shown in the model results.

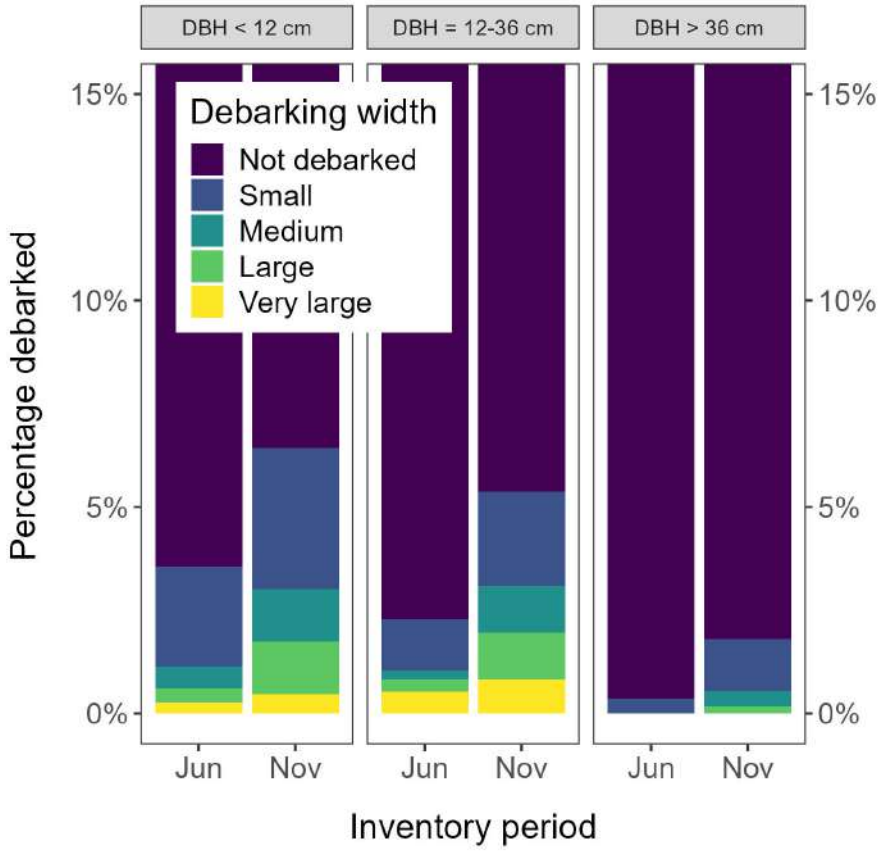

Figure A.1: Proportion of debarked trees grouped by DBH class; comparison between inventory periods until June and until November. Note that the scale only goes to 15%.

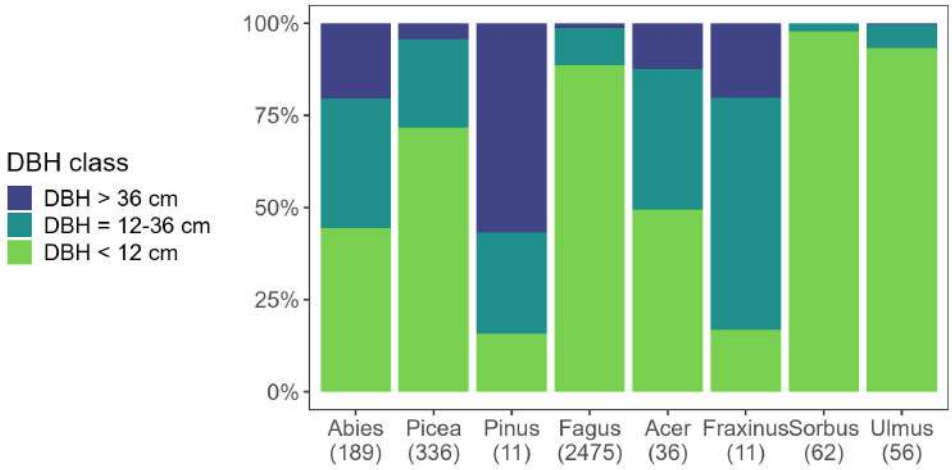

Figure A.2: Ratio between the three DBH classes for each tree species. To correct for the sampling structure the number of trees in each class have been scaled to per hectare values (values in brackets).

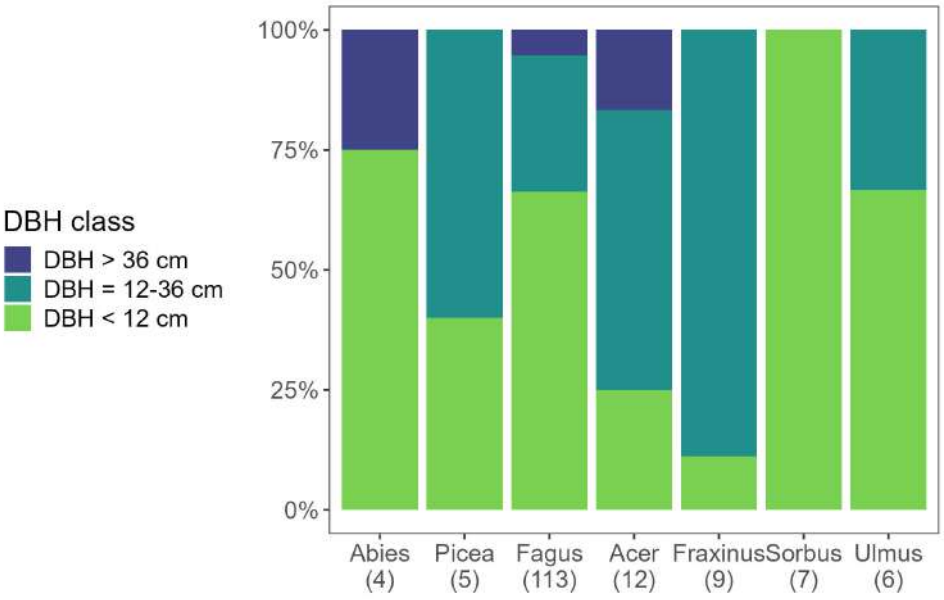

Figure A.3: DBH class distribution by species, but only including trees with debarking wounds. The total number of sampled trees with debarking wounds is specified in brackets. Note that *Pinus* is missing, since none of the sampled Scots pines showed debarking wounds.

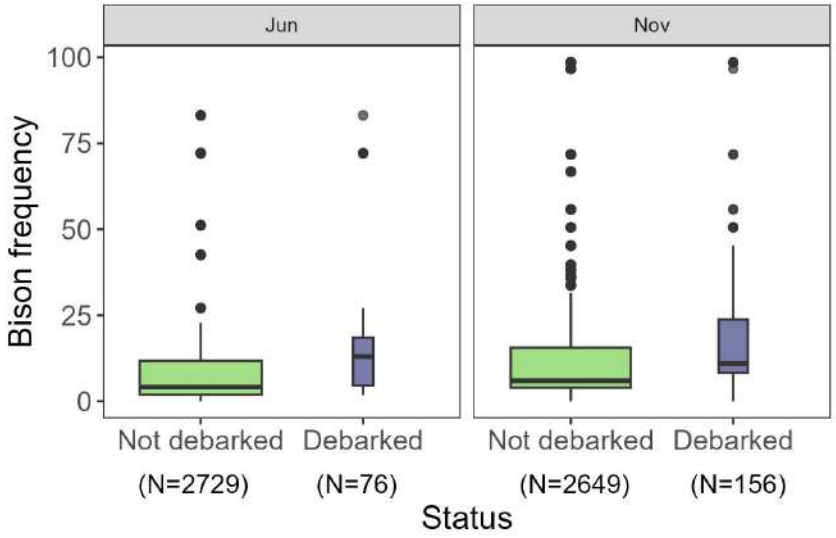

Figure A.4: Boxplot of the bison frequency for debarked and non-debarked trees for the inventory in June and November. The number of trees per group is displayed in brackets and the box-width is proportional to the number.

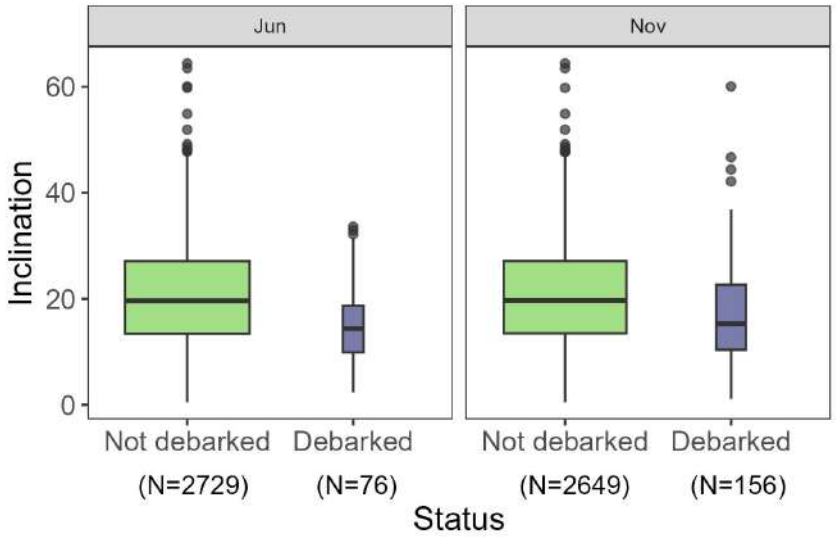

Figure A.5: Boxplot of the inclination for debarked and non-debarked trees for the inventory in June and November. The number of trees per group is displayed in brackets and the box-width is proportional to the number.

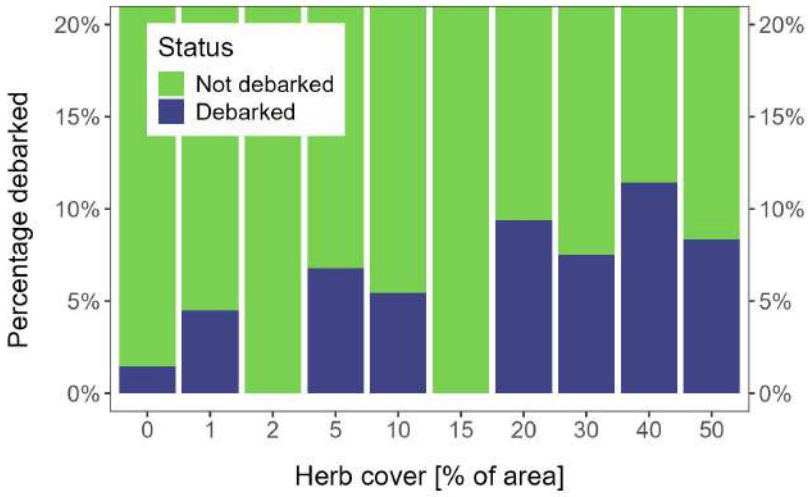

Figure A.6: Percentage of debarked trees in November for each herb cover category. Areas with a high ground cover percentage of herbs have a higher percentage of debarked trees. Note that the scale only goes to 20%.

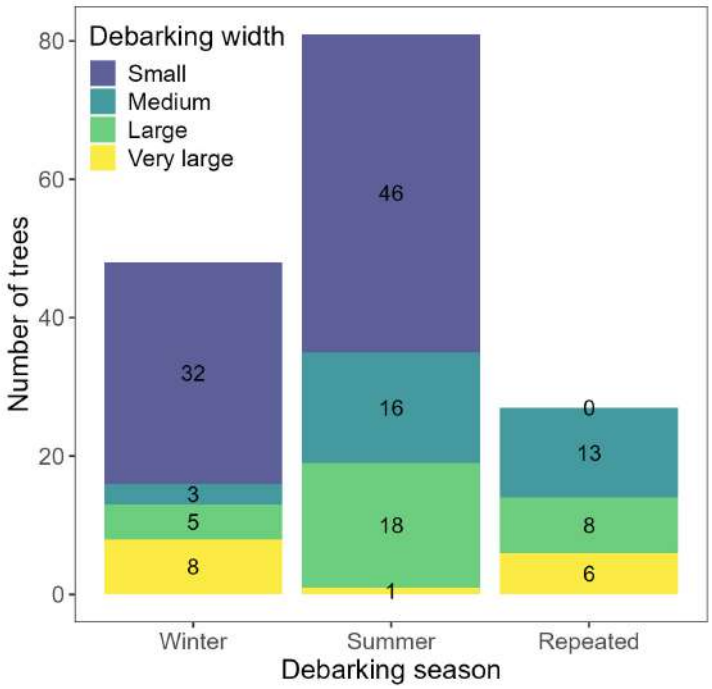

Figure A.7: Number of debarked trees by debarking width; comparison between trees that were only debarked once, either in Winter/Spring or Summer/Fall, and trees debarked repeatedly, at least once in both seasons.

Appendix B

Bison frequency maps

Appendix B contains maps with calculated bison frequency variables for the inventory period until June (Figure B.2) and for the period from June to November (Figure B.1), which was used for the CLMM and LMM. Black and blue dots indicate low occurrence of the bison within that plot and red dots indicate high occurrence. The visualization for the heat map in the background is capped at values of 40 to emphasize bison density in the forest.

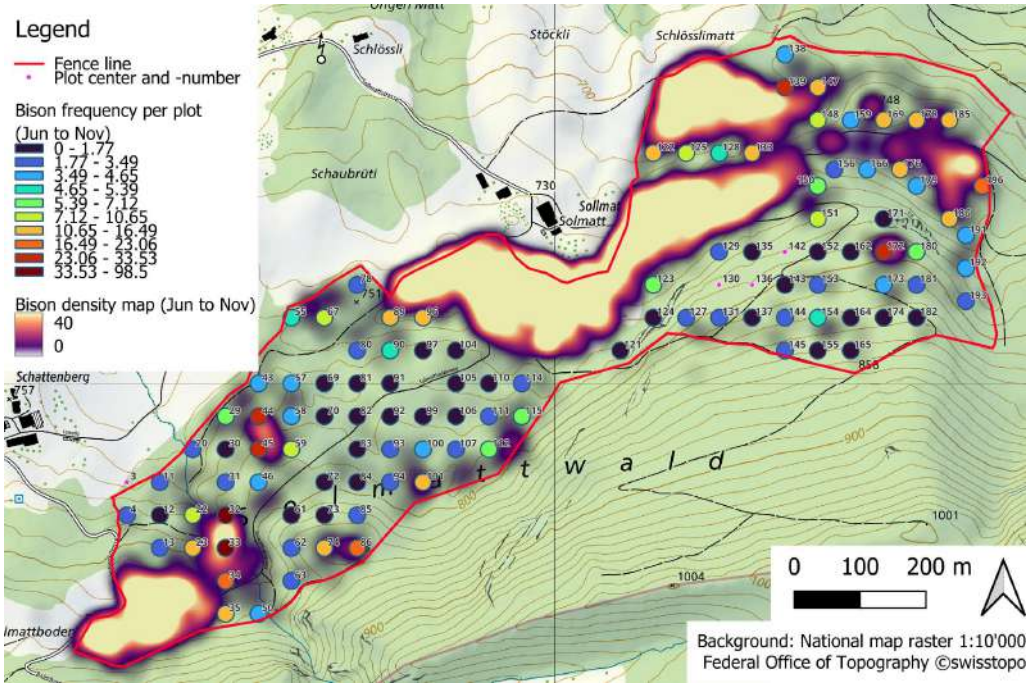

Figure B.1: Map with the bison frequency calculated per plot for the inventory period from June to November.

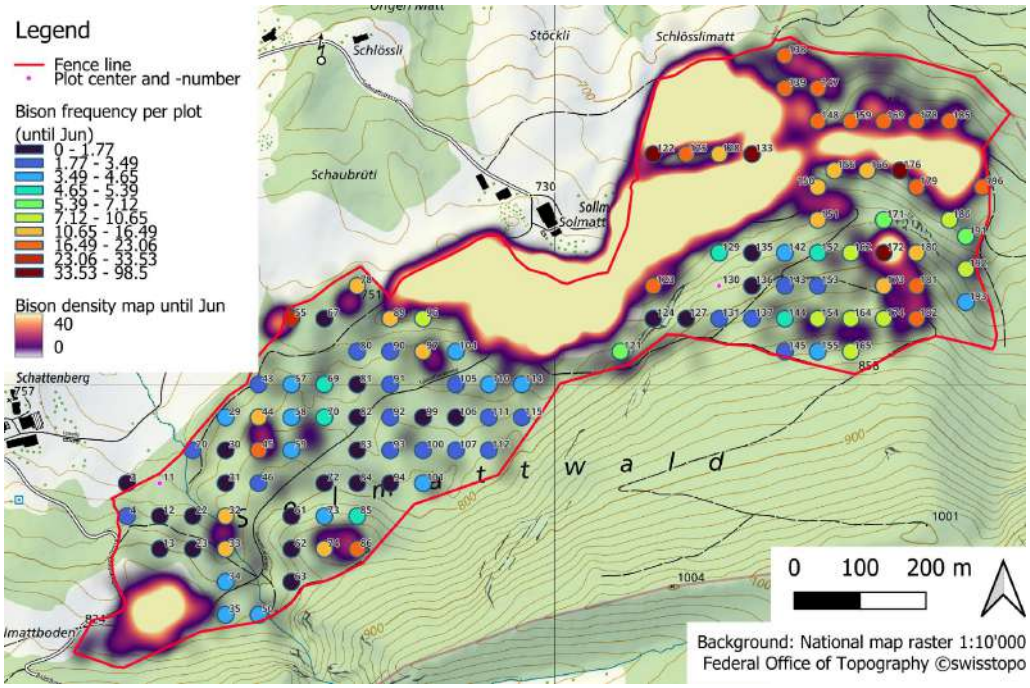

Figure B.2: Map with the bison frequency calculated per plot for the inventory until June.

Appendix C

Photographs of debarking wounds

Appendix C shows additional photographs of debarked trees. Figure C.1 is a comparison between photographs taken during both inventories: No wound occlusion can be seen. Figures C.2, C.3 and C.4 show occluding wounds of trees that were debarked between June and November. A red, or white section respectively, on the marker-pole in the photographs has a length of exactly 10 cm and the height of the pole is 1 m.

Figure C.1: Photographs of a debarking wound on an ash tree, first taken during the inventory in June (left), and again during the inventory in November (right). Notice, that the wound does not appear to occlude, even in November. Tree ID: 2014, Plot ID: 58.

Figure C.2: Photograph of a debarking wound on a beech tree taken during the inventory in November. In the inventory in June the tree was not recorded to be debarked. Tree ID: 1181, Plot ID: 176.

Figure C.3: Photograph of a debarking wound on a beech tree taken during the inventory in November. In the inventory in June the tree was not recorded to be debarked. Tree ID: 836, Plot ID: 74.

Figure C.4: Photograph of a debarking wound on a beech tree taken during the inventory in November. In the inventory in June the tree was not recorded to be debarked. Tree ID: 4, Plot ID: 78.

Appendix D

Model selection tables

Appendix D contains model selection tables, each with the model structure, degrees of freedom (df), AIC score and the difference in AIC (ΔAIC) to the model with lowest AIC. Tables D.1, D.2 and D.3 show all fitted GLMM with the dataset until November, until June and the dataset containing only newly peeled trees between June and November respectively. Table D.4 shows all fitted CLMM with debarking width as target variable and table D.5 shows all fitted LMM with debarking length as target variable.

Table D.1: Selection of the GLMM with the dataset until November and the binary target variable "debarking". The null model is highlighted in red and the selected model is highlighted in blue: Selected by AIC; ΔAIC > 2 per additional degree of freedom.

Model structure	df	AIC	ΔAIC
Species * (DBH + DBH^2) + (1 | Plot)	25	978.19	0
Species group + DBH + DBH^2 + Max B. freq. + Herb cover + (1 | Plot)	8	984.35	6.16
Species group + DBH + DBH^2 + Max B. freq. + Reg. comp. + (1 | Plot)	8	985.46	7.27
Species group + DBH + DBH^2 + Max B. freq. + Veg. sum + (1 | Plot)	8	987.37	9.18
Species group + DBH + DBH^2 + Max B. freq. + Footsteps + (1 | Plot)	8	989.72	11.53
Species group + DBH + DBH^2 + Max B. freq. + (1 | Plot)	7	989.91	11.72
Species group + DBH + DBH^2 + Max B. freq. + Reg. cover + (1 | Plot)	8	990.41	12.22
Species group + DBH + DBH^2 + Mean B. freq. + (1 | Plot)	7	991.07	12.88
Species group + DBH + DBH^2 + Max B. freq. + Grass cover + (1 | Plot)	8	991.87	13.68
Species group + DBH + DBH^2 + Max B. freq. + Shrub cover + (1 | Plot)	8	991.88	13.69
Species group + DBH + DBH^2 + Max B. freq. + Raspb. cover + (1 | Plot)	8	991.9	13.71
Species group + DBH + DBH^2 + Max B. freq. + Bramble cover + (1 | Plot)	8	991.91	13.71

Species group + DBH + DBH^2 + $\log_{10}$(Max B. freq.^{2}) + (1 | Plot)	7	993.35	15.16
Species group + DBH + DBH^2 + (1 | Plot) + (1 | DBH class)	7	996.1	17.91
Species group + DBH + DBH^2 + Prox. edge + (1 | Plot)	7	997.7	19.5
Species group + DBH + Max B. freq. + Herb cover + (1 | Plot)	7	998.04	19.85
Species group + DBH + DBH^2 + Inclin. + (1 | Plot)	7	998.56	20.37
Species group + DBH + DBH^2 + (1 | Plot)	6	998.92	20.73
Species group + DBH + DBH^2 + Prox. path + (1 | Plot)	7	999	20.81
Species group + DBH + DBH^2 + Prox. all + (1 | Plot)	7	999.72	21.53
Species group + DBH + DBH^2 + Stem dmg. + (1 | Plot)	7	1000.1	21.91
Species group + DBH + DBH^2 + Stand str. + (1 | Plot)	8	1000.84	22.65
Species group + DBH + DBH^2 + Prox. water + (1 | Plot)	7	1000.91	22.72
Species group + DBH + DBH^2 + Prox. stream + (1 | Plot)	7	1000.92	22.73
Species * DBH + (1 | Plot)	17	1001.26	23.07
Species group + DBH + DBH^2 + F. community + (1 | Plot)	14	1003.87	25.68
Species * DBH + (1 | Plot) + (1 | DBH class)	18	1004.95	26.76
Species group + DBH^2 + (1 | Plot)	5	1005.59	27.4
Species + DBH + DBH^2 + (1 | Plot)	11	1006.03	27.84
Species group + DBH + DBH^2 + Dev. stage + (1 | Plot)	11	1007.61	29.42
Species group * DBH + (1 | Plot)	7	1009.6	31.41
Species group + DBH + (1 | Plot)	5	1011.05	32.86
Species group + (1 | Plot)	4	1012.62	34.43
Species + DBH + (1 | Plot)	10	1017.86	39.67
Species + (1 | Plot)	9	1020.61	42.42
Species group + DBH + DBH^2 + Max B. freq. + Herb cover	7	1068.57	90.38
(1 | Plot)	2	1075.89	97.7
Species + DBH + DBH^2	10	1109.33	131.14

Table D.2: Selection of the GLMM with the dataset until June and the binary target variable "debarking". The null model is highlighted in red and the selected model is highlighted in blue: Selected by AIC; ΔAIC > 2 per additional degree of freedom.

Model structure	df	AIC	ΔAIC
Species group + DBH + DBH^2 + Inclin. + Max B. freq. + (1 | Plot) + (1 | DBH class)	9	540.9	0
Species group + DBH + DBH^2 + Inclin. + Max B. freq. + Reg. comp. + (1 | Plot)	9	544.09	3.2
Species group + DBH + DBH^2 + Inclin. + Max B. freq. + Footsteps + (1 | Plot)	9	544.49	3.59
Species group + DBH + DBH^2 + Inclin. + Max B. freq. + Shrub cover + (1 | Plot)	9	544.59	3.69
Species group + DBH + DBH^2 + Inclin. + Max B. freq. + (1 | Plot)	8	545.04	4.14
Species group + DBH + DBH^2 + Inclin. + Mean B. freq. + (1 | Plot)	8	545.63	4.73
Species group + DBH + DBH^2 + Inclin. + Max B. freq. + Herb cover + (1 | Plot)	9	545.88	4.98
Species group + DBH + DBH^2 + Inclin. + Max B. freq. + Grass cover + (1 | Plot)	9	546.7	5.8
Species group + DBH + DBH^2 + Inclin. + Max B. freq. + Raspb. cover + (1 | Plot)	9	546.74	5.84
Species group + DBH + DBH^2 + Inclin. + Max B. freq. + Veg. sum + (1 | Plot)	9	546.92	6.02
Species group + DBH + DBH^2 + Inclin. + Max B. freq. + Reg. cover + (1 | Plot)	9	547.01	6.11
Species group + DBH + DBH^2 + Inclin. + Max B. freq. + Bramble cover + (1 | Plot)	9	547.04	6.14
Species group + DBH + DBH^2 + Inclin. + Prox. stream + (1 | Plot)	8	549.39	8.49
Species group + DBH + DBH^2 + Inclin. + Prox. path + (1 | Plot)	8	550.52	9.62
Species group + DBH + DBH^2 + Inclin. + (1 | Plot)	7	551.17	10.27
Species group + DBH + DBH^2 + Inclin. + Prox. water + (1 | Plot)	8	551.73	10.83
Species group + DBH + DBH^2 + Inclin. + Prox. edge + (1 | Plot)	8	553.13	12.23
Species group + DBH + DBH^2 + Inclin. + Prox. all + (1 | Plot)	8	553.16	12.26

Species group + DBH + DBH^2 + Inclin. + Stand str. + (1 | Plot)	9	553.47	12.57
Species group + DBH + DBH^2 + (1 | Plot)	6	556.76	15.86
Species + DBH + DBH^2 + (1 | Plot)	11	556.9	16
Species group + DBH + DBH^2 + Inclin. + Dev. stage + (1 | Plot)	12	557.73	16.83
Species group + DBH + DBH^2 + Stem dmg. + (1 | Plot)	7	558.72	17.82
Species group + (1 | Plot)	4	574.82	33.92
Species + (1 | Plot)	9	579.68	38.78
(1 | Plot)	2	611.65	70.75

Table D.3: Selection of the GLMM using the dataset with only newly debarked trees from June to November and the binary target variable "debarking". The null model is highlighted in red and the selected model is highlighted in blue: Selected by AIC; ΔAIC > 2 per additional degree of freedom.

Model structure	df	AIC	ΔAIC
Species group + DBH + DBH^2 + Max B. freq. + Herb cover + (1 | Plot)	8	793.2	0
Species group + DBH + DBH^2 + Max B. freq. + Herb cover + (1 | Plot) + (1 | DBH class)	9	794.08	0.88
Species group + DBH + DBH^2 + Max B. freq. + Herb cover + Footsteps + (1 | Plot)	9	794.56	1.36
Species group + DBH + DBH^2 + Max B. freq. + Veg. sum + (1 | Plot)	8	796.7	3.5
Species group + DBH + DBH^2 + Max B. freq. + Reg. comp. + (1 | Plot)	8	796.74	3.54
Species group + DBH + DBH^2 + Max B. freq. + (1 | Plot)	7	800.12	6.92
Species group + DBH + DBH^2 + Herb cover + (1 | Plot)	7	800.69	7.49
Species group + DBH + DBH^2 + Max B. freq. + Reg. cover + (1 | Plot)	8	801.19	7.99
Species group + DBH + DBH^2 + Max B. freq. + Shrub cover + (1 | Plot)	8	801.74	8.54
Species group + DBH + DBH^2 + Mean B. freq. + (1 | Plot)	7	801.79	8.59
Species group + DBH + DBH^2 + Max B. freq. + Raspb. cover + (1 | Plot)	8	801.91	8.71
Species group + DBH + DBH^2 + Herb cover + (1 | Plot) + (1 | DBH class)	8	801.91	8.71
Species group + DBH + DBH^2 + Max B. freq. + Bramble cover + (1 | Plot)	8	802.08	8.88
Species group + DBH + DBH^2 + Max B. freq. + Grass cover + (1 | Plot)	8	802.11	8.91
Species group + DBH + DBH^2 + Prox. edge + (1 | Plot)	7	809.58	16.38
Species group + DBH + DBH^2 + Prox. all + (1 | Plot)	7	810.72	17.52
Species group + DBH + DBH^2 + (1 | Plot)	6	810.94	17.74
Species group + DBH + DBH^2 + Prox. path + (1 | Plot)	7	811.92	18.72
Species group + DBH + DBH^2 + Stand str. + (1 | Plot)	8	811.94	18.74
Species group + DBH + DBH^2 + Inclin. + (1 | Plot)	7	812.21	19.01
Species group + DBH + DBH^2 + Prox. stream + (1 | Plot)	7	812.3	19.09
Species group + DBH + DBH^2 + Stem dmg. + (1 | Plot)	7	812.5	19.3

Species group + DBH + DBH^2 + Prox. water + (1 | Plot)	7	812.75	19.55
Species group + (1 | Plot)	4	816.51	23.31
Species group + DBH + DBH^2 + Dev. stage + (1 | Plot)	11	818.98	25.78
Species + DBH + DBH^2 + (1 | Plot)	11	819.05	25.84
Species + (1 | Plot)	9	824.87	31.67
(1 | Plot)	2	854.8	61.6

Table D.4: Selection of the CLMM with the dataset until November and the categorical/ ordinal target variable "debarking width". The null model is highlighted in red and the selected model is highlighted in blue: Selected by AIC; ΔAIC > 2 per additional degree of freedom.

Model structure	df	AIC	ΔAIC
Deb. length * Deb. season + (1 | Plot)	9	160.16	0
Deb. length + DBH + Deb. season2 + (1 | Plot)	7	161.9	1.74
Deb. length + DBH + Deb. season + (1 | Plot)	8	162.27	2.11
Deb. length + DBH * Deb. season2 + (1 | Plot)	8	163.27	3.11
Deb. length + Deb. season + (1 | Plot)	7	165.72	5.55
Deb. length + DBH + (1 | Plot)	6	182.83	22.66
Deb. length + Inclin. + (1 | Plot)	6	185.61	25.45
Deb. length + Herb cover + (1 | Plot)	6	187.26	27.1
Deb. length + (1 | Plot)	5	188.12	27.96
Deb. length + Prox. path + (1 | Plot)	6	188.37	28.21
Deb. length + Veg. sum + (1 | Plot)	6	188.49	28.33
Deb. length + Bramble cover + (1 | Plot)	6	188.95	28.79
Deb. length + Reg. cover + (1 | Plot)	6	189.28	29.12
Deb. length + Footsteps + (1 | Plot)	6	189.43	29.26
Deb. length + Shrub cover + (1 | Plot)	6	189.59	29.43
Deb. length + Mean B. freq. + (1 | Plot)	6	189.78	29.62
Deb. length + Raspb. cover + (1 | Plot)	6	189.83	29.67
Deb. length + Prox. edge + (1 | Plot)	6	189.89	29.72
Deb. length + Grass cover + (1 | Plot)	6	189.95	29.79
Deb. length + Max B. freq. + (1 | Plot)	6	189.99	29.83
Deb. length + Stem dmg. + (1 | Plot)	6	190.05	29.89
Deb. length + Prox. all + (1 | Plot)	6	190.05	29.89
Deb. length + Stand str. + (1 | Plot)	7	191.61	31.45
log10(Deb. length^2) + (1 | Plot)	5	197.06	36.9
log10(Deb. length) + (1 | Plot)	5	197.06	36.9
log10(Deb. length) + $\log_{10}$(Deb. length^2) + (1 | Plot)	5	197.06	36.9
Species group + (1 | Plot)	6	348.65	188.49
Deb. season + (1 | Plot)	6	354.82	194.66
Reg. cover + (1 | Plot)	5	378.11	217.95
Veg. sum + (1 | Plot)	5	378.67	218.51
Stand str. + (1 | Plot)	6	380.74	220.57

(1 | Plot)	4	381.98	221.82
Herb cover + (1 | Plot)	5	382.87	222.71
Prox. edge + (1 | Plot)	5	383.11	222.95
Prox. all + (1 | Plot)	5	383.16	223
Inclin. + (1 | Plot)	5	383.26	223.1
Prox. path + (1 | Plot)	5	383.28	223.12
Stem dmg. + (1 | Plot)	5	383.43	223.26
Raspb. cover + (1 | Plot)	5	383.44	223.28
DBH + (1 | Plot)	5	383.53	223.37
Bramble cover + (1 | Plot)	5	383.57	223.41
Max B. freq. + (1 | Plot)	5	383.62	223.46
Shrub cover + (1 | Plot)	5	383.71	223.55
Grass cover + (1 | Plot)	5	383.96	223.8
Footsteps + (1 | Plot)	5	383.97	223.81
Mean B. freq. + (1 | Plot)	5	383.97	223.81
Dev. stage + (1 | Plot)	9	385.38	225.22

Table D.5: Selection of the LMM with the dataset until November and the numerical target variable "debarking length". The null model is highlighted in red and the selected model is highlighted in blue: Selected by AIC; ΔAIC > 2 per additional degree of freedom.

Model structure	df	AIC	ΔAIC
Deb. width + DBH + Prox. path + (1 | Plot)	8	96.84	0
Deb. width + DBH + Prox. path + Dev. stage + (1 | Plot)	13	96.97	0.14
Deb. width + DBH + DBH^2 + Prox. path + (1 | Plot)	9	97.59	0.76
Deb. width + DBH + Dev. stage + (1 | Plot)	12	97.76	0.92
Deb. width + DBH + Prox. path + Stand str. + (1 | Plot)	10	97.78	0.95
Deb. width + DBH + Prox. path + Species group + (1 | Plot)	10	100.7	3.87
Deb. width + DBH + (1 | Plot)	7	100.82	3.99
Deb. width + DBH + DBH^2 + (1 | Plot)	8	101.37	4.54
Deb. width + DBH^2 + (1 | Plot)	7	105.04	8.2
Deb. width * DBH + (1 | Plot)	10	105.93	9.09
Deb. width + Prox. path + (1 | Plot)	7	106.6	9.77
Deb. width + Max B. freq. + (1 | Plot)	7	109.75	12.92
Deb. width + Inclin. + (1 | Plot)	7	109.82	12.98
Deb. width + Stand str. + (1 | Plot)	8	109.9	13.06
Deb. width + (1 | Plot)	6	110.3	13.47
Deb. width + Dev. stage + (1 | Plot)	11	110.57	13.73
Deb. width + Reg. cover + (1 | Plot)	7	111.03	14.19
Deb. width + Shrub cover + (1 | Plot)	7	111.28	14.44
Deb. width + Mean B. freq. + (1 | Plot)	7	111.38	14.55
Deb. width + Prox. stream + (1 | Plot)	7	111.46	14.62
Deb. width + Herb cover + (1 | Plot)	7	111.63	14.8
Deb. width + Veg. sum + (1 | Plot)	7	111.85	15.02
Deb. width + Prox. water + (1 | Plot)	7	111.99	15.15
Deb. width + Bramble cover + (1 | Plot)	7	111.99	15.16
Deb. width + Stem dmg. + (1 | Plot)	7	112.09	15.26
Deb. width + Raspb. cover + (1 | Plot)	7	112.1	15.26
Deb. width + Prox. all + (1 | Plot)	7	112.18	15.35
Deb. width + Prox. edge + (1 | Plot)	7	112.23	15.4
Deb. width + Grass cover + (1 | Plot)	7	112.26	15.42
Deb. width + Footsteps + (1 | Plot)	7	112.28	15.45
Deb. width + Deb. season + (1 | Plot)	8	113.21	16.38

Deb. width + Species group + (1 | Plot)	8	114.1	17.26
Deb. width + F. community + (1 | Plot)	13	115.3	18.46
Species group + (1 | Plot)	5	261.24	164.4
Deb. season2 + (1 | Plot)	4	267.43	170.59
Deb. season + (1 | Plot)	5	269.43	172.59
Stand str. + (1 | Plot)	5	279.85	183.01
DBH + DBH^2 + (1 | Plot)	5	280.03	183.19
Reg. cover + (1 | Plot)	4	280.36	183.52
Prox. water + (1 | Plot)	4	281.42	184.59
Veg. sum + (1 | Plot)	4	282.38	185.55
Prox. path + (1 | Plot)	4	282.98	186.14
Prox. stream + (1 | Plot)	4	283.79	186.95
Max B. freq. + (1 | Plot)	4	285.02	188.19
F. community + (1 | Plot)	10	285.07	188.24
DBH + (1 | Plot)	4	285.21	188.37
Shrub cover + (1 | Plot)	4	285.78	188.94
Prox. all + (1 | Plot)	4	286.03	189.2
Raspb. cover + (1 | Plot)	4	286.38	189.54
Prox. edge + (1 | Plot)	4	286.45	189.61
Mean B. freq. + (1 | Plot)	4	286.5	189.67
Stem dmg. + (1 | Plot)	4	286.74	189.9
Herb cover + (1 | Plot)	4	286.77	189.94
DBH^2 + (1 | Plot)	4	286.8	189.97
Inclin. + (1 | Plot)	4	286.81	189.97
Bramble cover + (1 | Plot)	4	286.83	189.99
Footsteps + (1 | Plot)	4	286.83	190
Grass cover + (1 | Plot)	4	286.83	190
Dev. stage + (1 | Plot)	8	288.84	192
(1 | Plot)	2	394.03	297.2

Appendix E

Residual and collinearity analysis

Appendix E contains the plotted residuals of the selected models described in Chapters 3.1, 3.2 and 3.3. Figures E.1, E.2 and E.3 show plots with the simulated residuals for the GLMM with the dataset until November, until June and the dataset containing only newly peeled trees between June and November respectively. The KS test is a test for uniformity and deviation, n.s. means the deviation is non-significant. Figure E.4 shows plots with the residuals of the LMM with debarking length as target variable.

For the three selected GLMM, the distributions of observed and predicted quantiles match very well and the plots of simulated residuals against predicted values show an even distribution (Figures E.1, E.2 and E.3). All tests for uniformity, outliers, dispersion, quantile location and zero inflation were non-significant for all three GLMM.

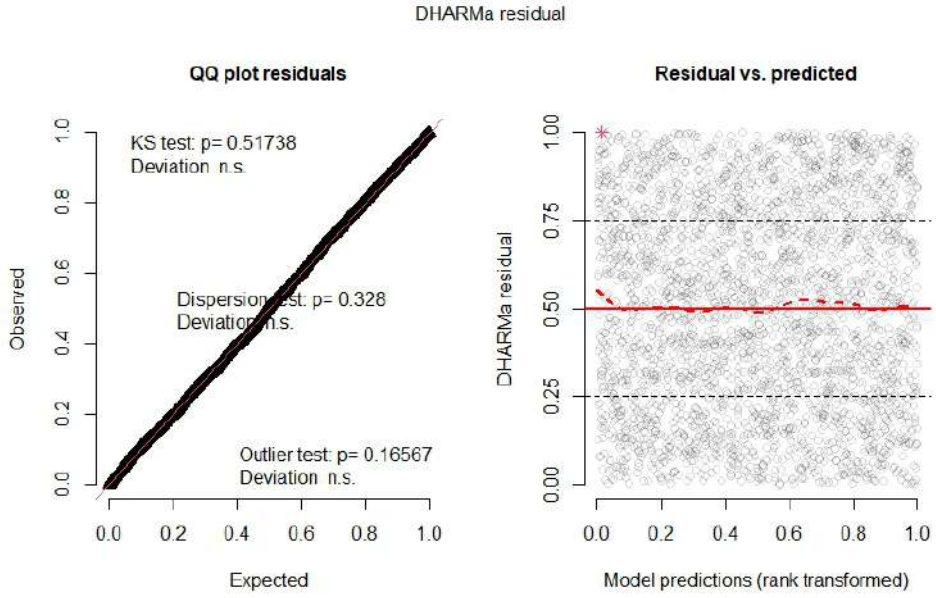

Figure E.1: Residual plots for the GLMM using the dataset until November.

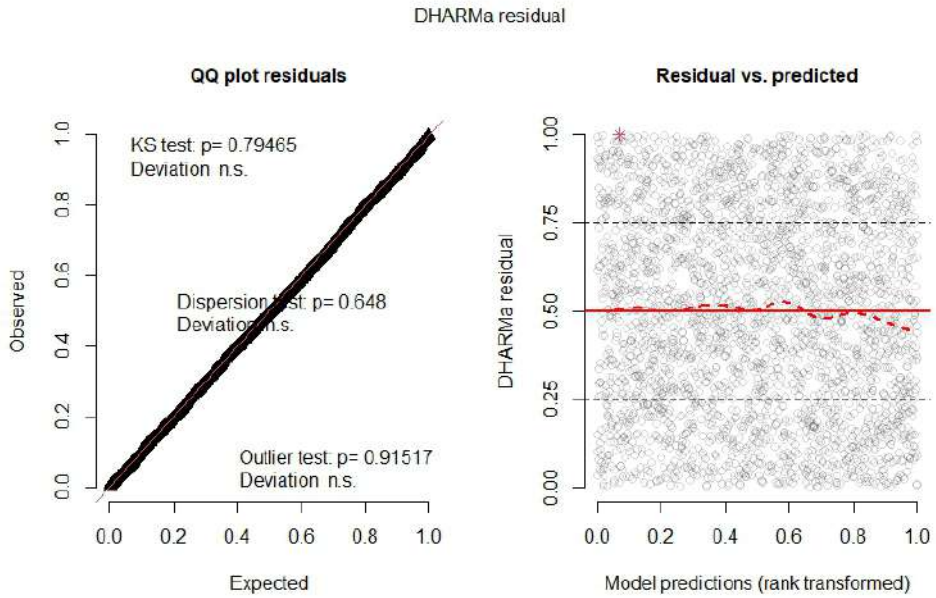

Figure E.2: Residual plots for the GLMM using the dataset until June.

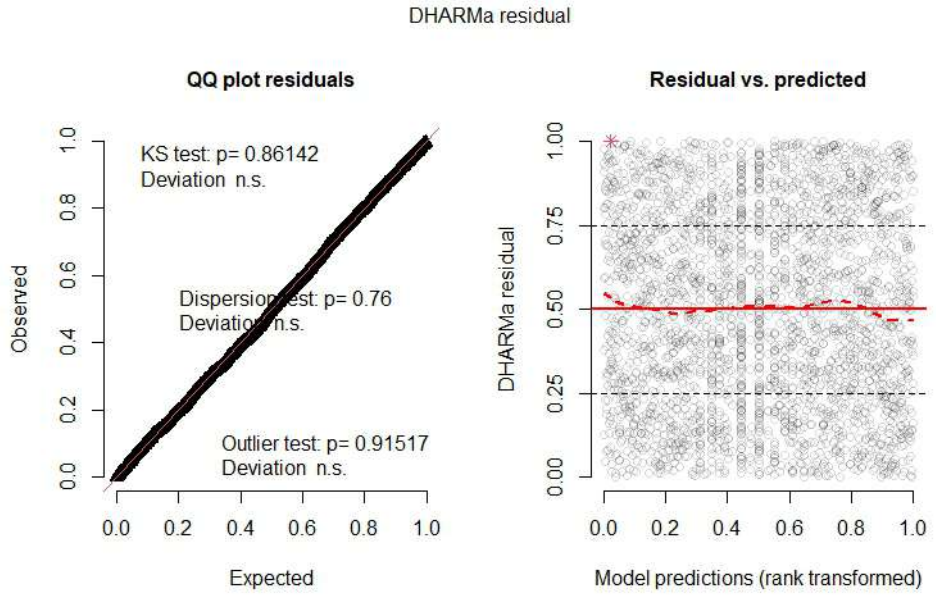

Figure E.3: Residual plots for the GLMM using the dataset with only newly debarked trees from June to November.

When analyzing collinearity between model predictors for the GLMM with the dataset until November, the function revealed very low correlation for species group, bison frequency and herb cover: The Variance Inflation Factor (VIF) was close to 1. For the DBH and DBH^2 a moderate correlation was found (VIF = 5.66 and 5.22 respectively). This makes sense, however, as the DBH^2 is based on the DBH. The same was found in the collinearity test for the GLMM until June: The VIF for species group, inclination and bison frequency were close to 1 and the VIF for the DBH terms were between 5 and 6. Also for the GLMM using only newly debarked trees from June to November the VIF for species group, bison frequency and herb cover were close to 1 while the VIF for the DBH terms were between 5 and 6.

As already mentioned in Chapter 2.5.3, residuals for the Cumulative Link Mixed Model could not be simulated or plotted and analyzed. The selected CLMM was tested for collinearity; unfortunately, the test revealed VIF values of 3.88 for debarking length, 7.3 for the DBH and 11.25 for debarking season 2. The VIF values were 3.51 and 3.2 for the DBH and debarking season 2 respectively, when debarking length was removed from the model, indicating the problem was due to the debarking length. Unfortunately, when the debarking length was $\log_{10}$-transformed the problem persisted. The Pearson correlation coefficient between the DBH and debarking length was 0.02, suggesting there is no linear relationship between the two predictors. I was therefore not able to find out why the VIF values were so high for this model.

The residuals for the selected LMM appear to be normally distributed (Figure E.4). However, the Q-Q Plot shows that the data quantiles do not correspond well to the normal quantiles on both ends of the distribution. The Tukey-Anscombe plot also shows heteroscedasticity: The variance of the residuals decreases with increasing fitted values. When analyzing collinearity between model predictors for the selected LMM, VIF values close to 1 were found for the model predictors debarking width, DBH and proximity to a path, indicating no collinearity for this model.

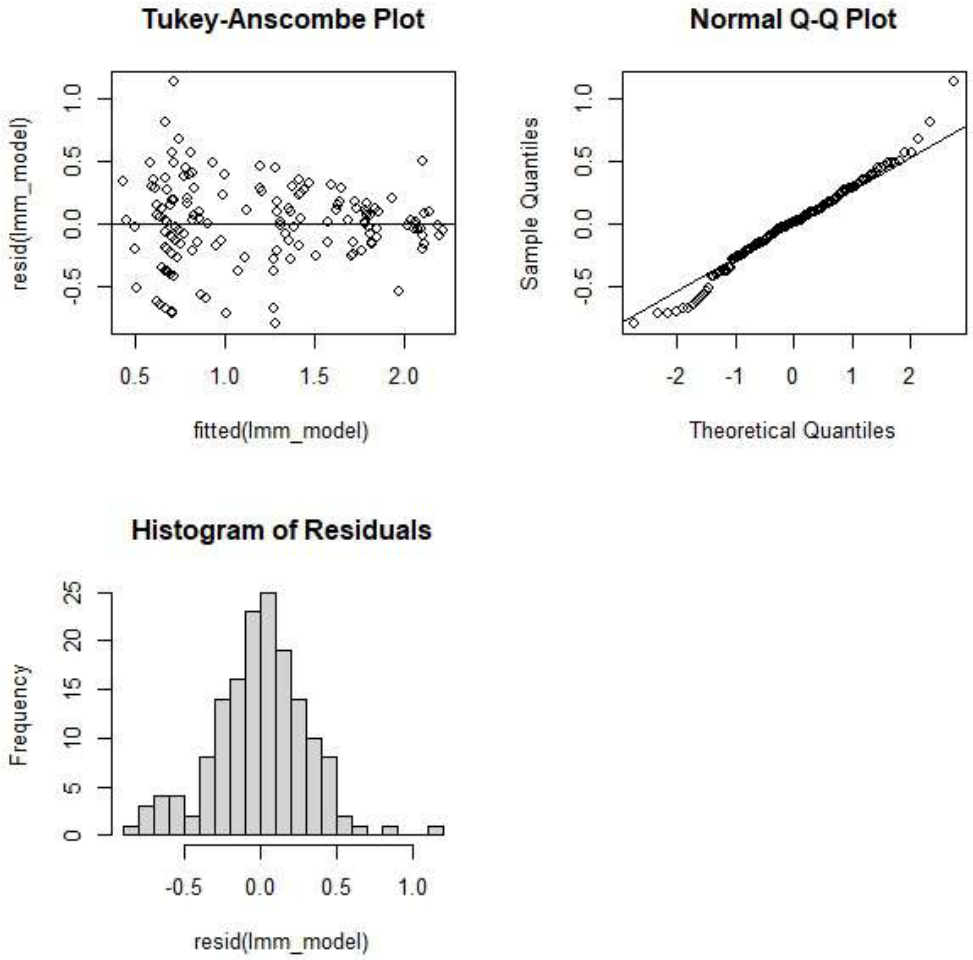

Figure E.4: Residual plots for the LMM using the dataset until November.

Appendix F

AI use statement and declaration of originality

Here, I specify the processes for which I utilized artificial intelligence (AI) tools and internet sources during the entire process leading to my master's thesis. At no point in my work have I used AI tools such as ChatGPT, Grammarly or DeepL. Instead I relied on online forums, Blogs and other website types for code debugging and translation: During the data analysis I used `stackoverflow.com`, `stackexchange.com`, `statology.org`, `gis.stackexchange.com` as well as `tex.stackexchange.com` for debugging, finding solutions for specific problems and learning about statistical methods. I also learned about statistical methods and how to use LaTeX on `youtube.com`. Since I am more fluent in German than in English, I used `dict.leo.org`, `translate.google.com` and `thesaurus.com` for translation as well as for finding synonyms to specific words.

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