

Wisent browsing is not additive but compensatory to roe deer and chamois in the Swiss Jura

Andrea Doris Kupferschmid

Swiss Federal Research Institute WSL, Forest Resources and Management, Switzerland

Abstract: The reintroduction of the wisent (*Bison bonasus*) raises questions about its additional impact on tree regeneration. The aim of this study was to investigate direct and indirect effects of a new wisent presence in a mixed beech forest in the Swiss Jura, which is native habitat for roe deer and chamois.

In 112 systematically established survey plots, the two nearest saplings per height class and tree species were examined for browsing, antler rubbing, and stem breakage. Surveys were conducted before (2019 and 2020) and after (2023 and 2024) the introduction of wisents into the enclosure (September 2022). The fences were accessible to roe deer and chamois at all times. GLMMs were used for analysis.

Fewer saplings were browsed in winters with wisents than in winters without them, but those that were browsed were subjected to more intense browsing. An exception was beech, for which winter browsing increased in the years with wisents. The highest summer browsing was recorded during fence construction. While stem breakage increased, fraying on spruce and fir trees decreased after wisent presence.

Thus, browsing by wisents partially compensated for browsing by roe deer and chamois and reduced fraying marks. The increased browsing intensity could be due to the larger bite size of wisents compared with both native ungulates. The increase in stem breakage indicates additional mechanical impacts that go beyond classic ungulate browsing.

Keywords: tree regeneration, ungulate browsing, game damage, European bison

Introduction

Wild ungulates, such as roe deer (*Capreolus capreolus* L.), chamois (*Rupicapra rupicapra* L.), red deer (*Cervus elaphus* L.), wild boars (*Sus scrofa* L.), and European bison (wisent, *Bison bonasus* L.), feed, among other things, on the shoots of young trees (Gebert, Verheyden-Tixier 2001; Kowalczyk *et al.* 2011; Tixier, Duncan 1996). Ungulates selectively browse individual tree species and therefore influence the growth of young trees differently depending on the

species (Angst, Kupferschmid 2023). This can lead to shifts in the competitive structure among tree species and alter the establishment success of individual species (Krueger *et al.* 2009).

When new animal species disperse into an area or are actively introduced by humans, additional effects may occur. Changes in the behavior of animals previously inhabiting the area are often observed. The more similar the foraging of the species is, the more likely such indirect effects are to occur (Filella *et al.* 2024). This can result in significantly more browsing damage, even though the newly arrived or introduced species itself is very rare and causes hardly any browsing damage. For example, the few red deer that have migrated into the Längwald forest have, on the one hand, led to more frequent marks of antler rubbing at their daytime resting sites (Kupferschmid *et al.* 2023), and on the other hand, have also led to increased browsing by roe deer (Mengotti 2023).

In the Swiss Jura, the Wisent-Thal Project is investigating the feasibility of reintroducing European bison to Switzerland, particularly regarding the coexistence of humans and wisents. This area differs from other Western European habitats of wisents in several key aspects: i) a highly small-scaled landscape with an interweaving of forested and open areas, ii) a forest landscape characterized predominantly by mixed forests managed with continuous cover forestry, with species-rich natural regeneration and a near-total absence of monocultures, and iii) a comparatively high level of human use, as the enclosure is freely accessible and both forestry operations and hunting of other wild ungulates take place within the enclosure. This combination of habitat structure and land-use context could significantly influence the spatial and foraging behavior of the wisents and other wild ungulates, and thus also the frequency of browsing.

This report examines the influence of wisents on tree regeneration using the k-tree method (Huber *et al.* 2015; Kupferschmid, Gmür 2020). This method is particularly well suited not only for objectively determining browsing frequency but also for recording other characteristics, such as browsing intensity at different times of the year, as well as marks of antler rubbing and other stem damage (Angst, Kupferschmid 2023; Kupferschmid *et al.* 2019). Because browsing can vary from year to year due to weather conditions and to the foraging patterns and habitat selection of wild ungulates, annual variability is to be expected. For this reason, two browsing surveys were conducted before fence construction, and two additional surveys were carried out after the wisents were introduced.

The main research question was whether the additional presence of wisents is associated with changes in browsing and antler-rubbing frequency, as

well as in the intensity of terminal shoot browsing. The significantly larger, more grass-eating wisents, compared with roe deer and chamois (Hofmann 1989), could dominate foraging in the meadows, thereby causing the other ungulates to increasingly shift to foraging in the forest. As a result, browsing and fraying on young trees could also increase indirectly.

Methods

Study site

The study area is located in the Swiss Jura (47° 16' 33" N, 7° 32' 40" E) at an elevation of 700–860 m above sea level on predominantly north-facing slopes. A 50-ha enclosure was established between spring and summer 2022 to investigate the coexistence of humans and European bison in the small-scale landscape of the Swiss Jura. The enclosure comprises approximately 13 ha of agriculturally used meadows and pastures, as well as 37 ha of forest. The forests predominantly belong to the Cardamino-Fagetum typicum site type on calcareous soil.

On September 15, 2022, five wisents were released into the enclosure (three cows and one calf from the “Wildnispark Zürich Langenberg” in Switzerland, and one bull from the “Wildpark Bruderhaus” near Winterthur, Switzerland). In 2023, two calves were born; in 2024, three; and in 2025, another two, bringing the herd size to a maximum of 11 animals. This corresponded to an initial density of 10 and later 22 animals per 100 ha. Two European bison were equipped with GPS collars that transmitted their locations hourly. On average, the European bison spent about 18% of their time in the forest, with the percentage being lower in summer (about 12.5%) than in winter (about 23%; internal report from the Wisent Thal Project). In winter, hay was provided on a meadow south of the Sollmatt, at the edge of the enclosure. There was also a permanent watering station there.

The fence was designed to allow free passage of native mammal species, including ungulates, hares, and lynx. Roe deer (*Capreolus capreolus* L.), chamois (*Rupicapra rupicapra* L.), and wild boars (*Sus scrofa* L.) were regularly observed in the enclosed area before and after fence construction, although wild boar activity had decreased significantly after the fence was built in 2022 (Weber 2026). Mean detections per 100 camera-trap days (eight camera traps) were 11.41 ± 2.93 for roe deer during 2019–2021 (before wisent presence) and 7.18 ± 3.90 during 2023–2025 (with wisents). The corresponding values for chamois were 0.46 ± 0.29 and 0.19 ± 0.06 , respectively. These declines were statistically insignificant (Weber 2026). Hunting for roe deer and chamois

continued within the enclosure, albeit on a reduced scale (personal information from hunters to Otto Holzgang).

Browsing and antler rubbing inventory

A systematic grid of 112 sample plots was established in the forested area and permanently marked (Kupferschmid, Straub 2022). Fieldwork was conducted in May of 2019, 2020, 2023, and 2024, that is, twice before the wisent arrived and twice after. In each sample plot, specific data were recorded, including slope inclination, stand structure (single-, two-, or multi-layered), development stage, and shading during the vegetation season. In addition, within a radius of 5 m around the center of each sample plot, the cover of grasses, herbs, shrubs, and tree regeneration was estimated (for detailed instructions, see the appendix in Kupferschmid, Straub 2022). After the wisent were introduced, the percentage of the area used by them as resting areas was also recorded within the 5 m radius.

Data on tree regeneration were collected using the k-tree method, with $k = 2$ for each tree species and height class (HC). Six height classes were considered: HC0: <10 cm tree height, HC1: 10–39.5 cm, HC2: 40–69.5 cm, HC3: 70–99.5 cm, HC4: 100–129.5 cm, and HC5: 130–200 cm. This results in a theoretical maximum of 6 height classes $\times$ 2 nearest saplings $\times$ 112 sample plots = 1344 saplings per tree species. Deciduous trees were searched for within a maximum distance of 5 m, while evergreen conifers were searched for within 10 m, as the latter are more easily identified in the forest.

For each sapling, tree height and terminal shoot length were measured, and terminal shoot browsing strength was recorded separately by season (summer and winter). The categories of browsing strength (also called within-tree browsing intensity, Kupferschmid 2018) were “not browsed or damaged,” “lightly browsed,” “heavily browsed” (more than half of the terminal shoot missing), and “other damage,” such as no leader shoot, dry, frost, or insect damage. In addition, antler rubbing (i.e., fraying) and lateral shoot browsing were assessed. Additional observations such as stem breakage were noted in the comments (Kupferschmid, Straub 2022). Summer and winter browsing were distinguished based on the degree of lignification of the shoot at the time of browsing. Accordingly, the events classified as summer browsing in the spring 2023 inventory occurred in summer 2022 before the wisent were introduced in September 2022.

Statistical Analysis

For the analyses, the binary variables “summer browsing” and “winter browsing” were defined for each year. Saplings with light or heavy browsing were assigned a value of 1, while all others were assigned a value of 0 (including those with other damage to the terminal shoot).

To analyze the occurrence of summer and winter browsing, generalized linear mixed-effects models (GLMMs) with a logit link were estimated using the `glmer` function from the `lme4` package (Bates *et al.* 2015). Plot was used as a random effect to account for spatial effects. Either survey year as a factor (2019, 2020, 2023, and 2024) or the presence of wisents – distinguishing between surveys without (2019 and 2020) and with wisents (2023 and 2024) – was included in the models as a fixed effect. Survey year explained the data significantly better than the variable “with/without wisent”: the Akaike Information Criterion (AIC; Stauffer 2008) was significantly lower with one additional degree of freedom. Therefore, all subsequent models were calculated using survey year as the explanatory variable.

The models were run either with all tree species classified into four groups or only with the most common tree species as fixed effects. The tree species groups were based on browsing susceptibility according to Fehr *et al.* (2019) and the distinction between deciduous and coniferous trees (Table 1). For each of the most common tree species, at least 30 saplings were recorded per year (Table 1). The most common species were beech (*Fagus sylvatica*), spruce (*Picea abies*), maple (*Acer pseudoplatanus*), fir (*Abies alba*), ash (*Fraxinus excelsior*), elm (*Ulmus glabra*), whitebeam (*Sorbus aria*), and cherry (*Prunus avium*).

Additional site variables, as well as tree height, were tested individually against the baseline models (survey year + species or species group + random plot effect). Variables that led to a reduction in AIC of more than 2 units per additional degree of freedom compared to the baseline model were tested against the baseline model using the likelihood ratio test (ANOVA). Variables that met both selection criteria (AIC reduction and $p < 0.01$ in LRT) were included in a comprehensive model for further analysis. Post hoc tests based on estimated marginal means were performed using the R package `emmeans` 2.0.2 (Lenth, Piaskowski 2026) to test for differences between levels of factors with more than two levels ($p < 0.05$). Model diagnostics included a test for collinearity (using the `checkCollinearity` function from the `performance` package; Lüdtke *et al.* 2011) as well as a residual analysis using the `DHARMa` package (tests for uniformity, outliers, dispersion, and quantiles; Hartig 2022).

For the browsed trees, a GLMM with a binomial error distribution was estimated to analyze the strength of browsing, with light browsing coded as 0 and heavy browsing as 1. Due to the small number of browsed spruce trees ($n = 26$), the analyses were conducted excluding the category “insensitive conifers.” Additional site variables were not considered.

GLMMs were also performed to analyze the frequency of antler rubbing. The methodology was essentially the same as that used to analyze the occurrence of browsing. However, due to the smaller number of trees with marks of antler rubbing, only baseline models with tree species groups were estimated, and no additional site variables were included. Only descriptive analyses were performed for stem breaks.

Results

Over the four surveyed years, a similar number of saplings per tree species was recorded in the 112 sample plots (Tabl. 1). As expected, the populations varied due to (i) newly germinating seedlings that survived the winter, (ii) growth into higher classes, and (iii) exceeding the 2-meter threshold of the highest class. The rarer a tree species was, the more pronounced these annual fluctuations tended to be. Overall, however, no systematic pattern emerged that would indicate a decline in individual tree species since the arrival of the wisents.

Occurrence of browsing in winter

Fir, elm, whitebeam, and cherry trees were browsed significantly more frequently than maple, ash, and beech, which in turn were browsed more frequently than spruce (Fig. 1). Across all species, the years 2019 and 2024 had higher winter browsing frequencies than 2020, which in turn had higher frequencies than 2023.

In 2019, fir showed significantly higher winter browsing than in all other years, and values in 2020 were higher than in 2023. Overall, winter browsing on fir was higher before the introduction of wisents than during their presence (Fig. 1). Cherry trees were browsed more frequently in winter in 2019 than in 2023 and 2024. Beech trees, by contrast, showed the opposite pattern, with the highest winter browsing occurring in 2024. Spruce and maple trees showed no significant differences between years. Winter browsing on whitebeam was less frequent in 2023 than in all three other years. The same was true for ash, where winter browsing was lower in 2023 than in 2019 and 2020, and for elm, which showed lower values in 2023 than in 2019 and 2024. Overall, the first

Table 1: Number of saplings per tree species and year, as well as the percentage of saplings with summer and winter browsing. Browsing susceptibility (S/I) with S = sensitive and I = insensitive. Foliage type (D/C) with D = deciduous trees and C = coniferous trees. Species are ranked according to their main occurrence. For rare tree species, the percentage values should be interpreted with caution due to the small sample size and are therefore shown in italics.

Species			Number of trees				Summer browsing [%]				Winer browsing [%]			
Name	S/I	D/C	2019	2020	2023	2024	2019	2020	2023	2024	2019	2020	2023	2024
<i>Fagus sylvatica</i>	I	D	604	591	594	600	3.0	0.8	3.2	1.3	4.6	2.4	4.2	11.7
<i>Picea abies</i>	I	C	569	608	572	550	0.2	0.0	0.5	0.7	2.5	0.3	0.9	0.9
<i>Acer pseudoplatanus</i>	S	D	374	386	370	336	11.0	3.4	9.7	1.5	7.0	7.5	4.6	6.5
<i>Abies alba</i>	S	C	299	336	340	342	0.3	1.8	5.3	2.0	27.4	13.7	6.5	9.1
<i>Fraxinus excelsior</i>	S	D	240	285	287	271	23.8	7.4	9.4	1.5	7.9	7.4	2.1	5.9
<i>Ulmus glabra</i>	S	D	128	112	117	116	10.9	9.8	21.4	2.6	21.1	17.0	7.7	20.7
<i>Sorbus aria</i>	S	D	83	102	65	67	6.0	11.8	29.2	3.0	21.7	17.6	3.1	25.4
<i>Prunus avium</i>	S	D	40	37	31	45	17.5	0.0	6.5	8.9	37.5	18.9	3.2	13.3
<i>Sorbus aucuparia</i>	S	D	12	21	25	16	0.0	9.5	20.0	6.3	16.7	23.8	12.0	31.3
<i>Tilia spp.</i>	I	D	12	13	13	13	41.7	0.0	30.8	0.0	8.3	0.0	0.0	15.4
<i>Quercus petraea</i>	S	D	1	6	5	23	0.0	0.0	0.0	8.7	0.0	16.7	0.0	4.3
<i>Carpinus betulus</i>	I	D		8	2	11		0.0	0.0	9.1		0.0	0.0	0.0
<i>Taxus baccata</i>	S	C	2	4	1	2	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0
<i>Pinus sylvestris</i>	I	C	1	2	1	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Betula spp.</i>	I	D	1	1	2		0.0	0.0	0.0		0.0	0.0	0.0	
<i>Salix spp.</i>	I	D	2	2			50.0	0.0			0.0	50.0		
<i>Larix decidua</i>	I	C				1				0.0				0.0
<i>Pyrus pyraeaster</i>	S	D				1				0.0				100.0
All species			2368	2514	2425	2395								

winter with European bison (2022/2023) showed lower levels of winter browsing for most deciduous tree species than the other winters studied (Fig. 1).

The proportion of European bison resting areas was the only site-specific variable that explained winter browsing in addition to the baseline model (AIC 4302.2 vs. 4314.1; $p < 0.001$). The relationship was positive (odds ratio 1.065 ± 0.017).

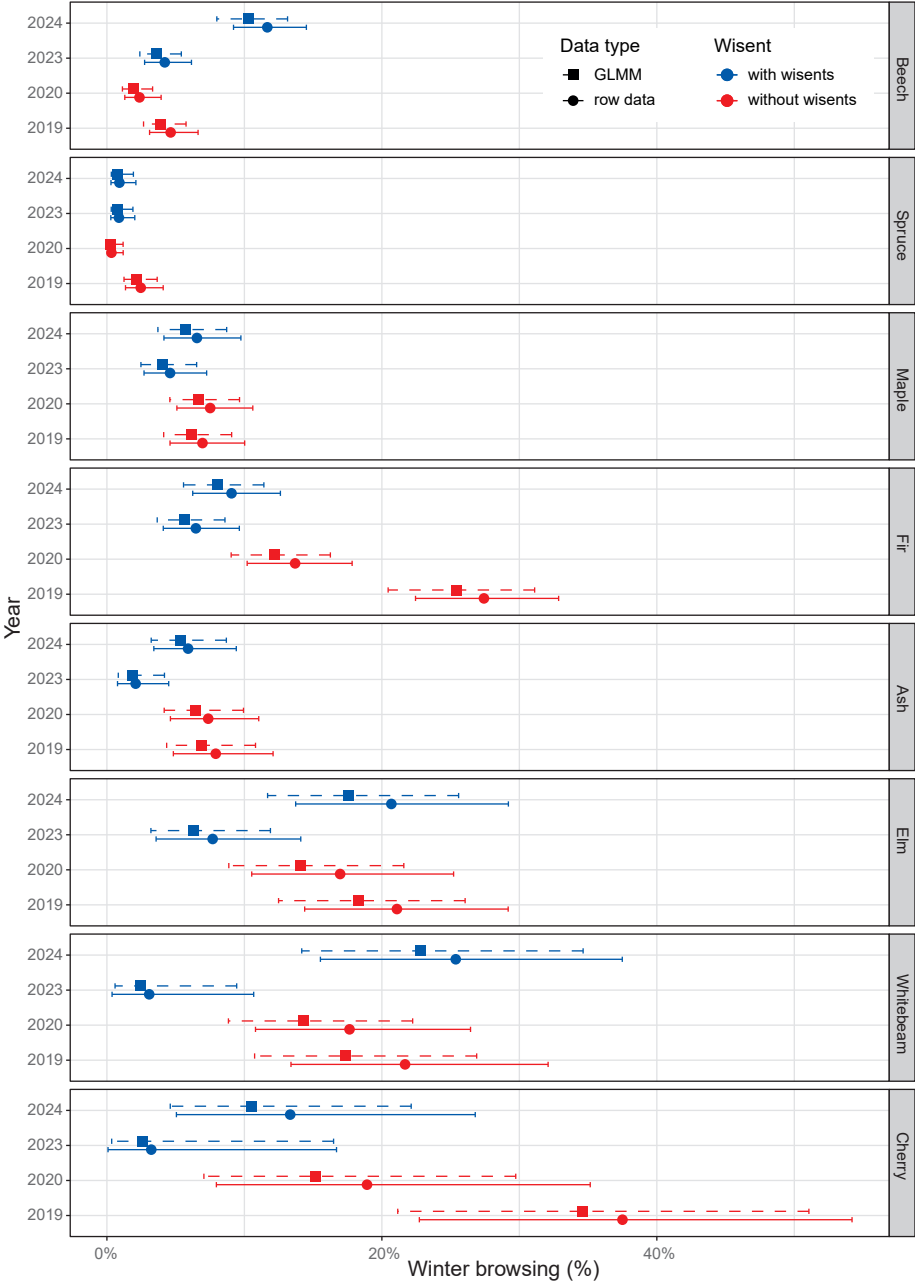


Figure 1: Proportion of saplings with winter browsing by tree species and survey year. Predicted values from the GLMM (winter browsing ~ tree species * year + (1 | plot number)) are shown as squares with dashed lines. The raw data are shown as circles with solid lines directly below. Colors distinguish survey years before the wisent arrived (red) from years with wisents (blue).

Occurrence of browsing in summer

It should be emphasized that the summer browsing on the terminal shoot formed in 2022—which was recorded retrospectively in the spring of 2023—took place before the wisents arrived.

Spruce also showed the lowest browsing in summer (Fig. 2). Beech and fir exhibited lower summer browsing than maple, ash, elm, and whitebeam. Maple exhibited lower summer browsing damage than ash but did not differ from elm and whitebeam. Due to the large variation, cherry differed only from spruce. Across all species, the years 2019 and 2023 had higher summer browsing than 2020, which in turn had higher browsing than 2024.

For beech, summer browsing was lower in the 2020 survey than in 2023 (Fig. 2). For maple, the 2020 and 2024 survey years showed lower summer browsing than 2019 and 2023. For fir, the only difference was between the survey years 2019 and 2023, with higher browsing in 2023. Ash showed the highest summer browsing in 2019, while 2020 and 2023 had lower values; the lowest summer browsing occurred in 2024, which represents the first full summer with wisents. For elm, summer browsing was higher in 2023 than in 2024. Whitebeam showed higher summer browsing in 2023 than in the other years. No significant differences between years were observed for cherry and spruce. Overall, for most sensitive tree species, the summer of 2022 (survey year 2023), that is, the summer immediately prior to the introduction of the wisents in September 2022, exhibited higher browsing levels compared to the other summers (Fig. 2).

Browsing strength

Most trees in all tree species groups and individual species showed no signs of browsing damage (Tabl. 1). This was true for all years and seasons (Fig. 3). A total of 686 instances of winter browsing were recorded during the four winters, of which 467 were light and 219 were heavy terminal shoot browsing.

However, the intensity of winter browsing varied between years and tree species groups (Fig. 3). In 2019 and 2020, less severe winter browsing was observed than in 2024. Furthermore, winter browsing was less severe in 2019 than in 2023. Deciduous trees exhibited lower overall levels of winter browsing than sensitive conifers.

Another notable observation was the high proportion of beech trees with other types of damage to their terminal shoots, particularly in 2019 (Fig. 3). These were predominantly dried-out terminal shoots.

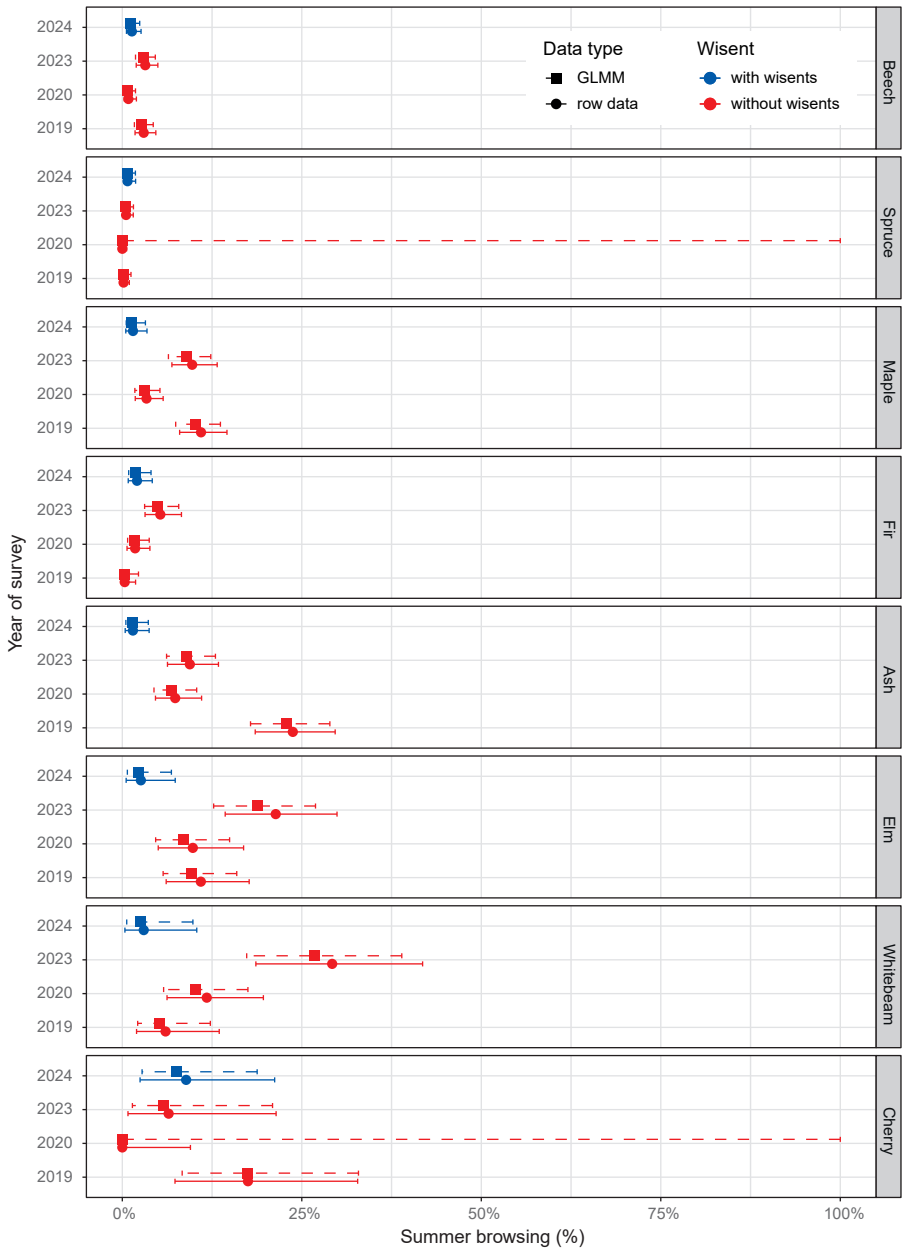


Figure 2: Proportion of saplings with summer browsing by tree species and survey year. Predicted values from the GLMM (summer browsing ~ tree species * year + (1 | plot number)) are shown as squares with dashed lines. The raw data are shown as circles with solid lines directly below. Red marks the years of the spring survey with summer browsing prior to the arrival of the wisent; blue marks the year with wisent presence. The wisents were introduced in September 2022, so the summer browsing recorded retrospectively in the 2023 survey occurred before that date and is therefore shown in red.

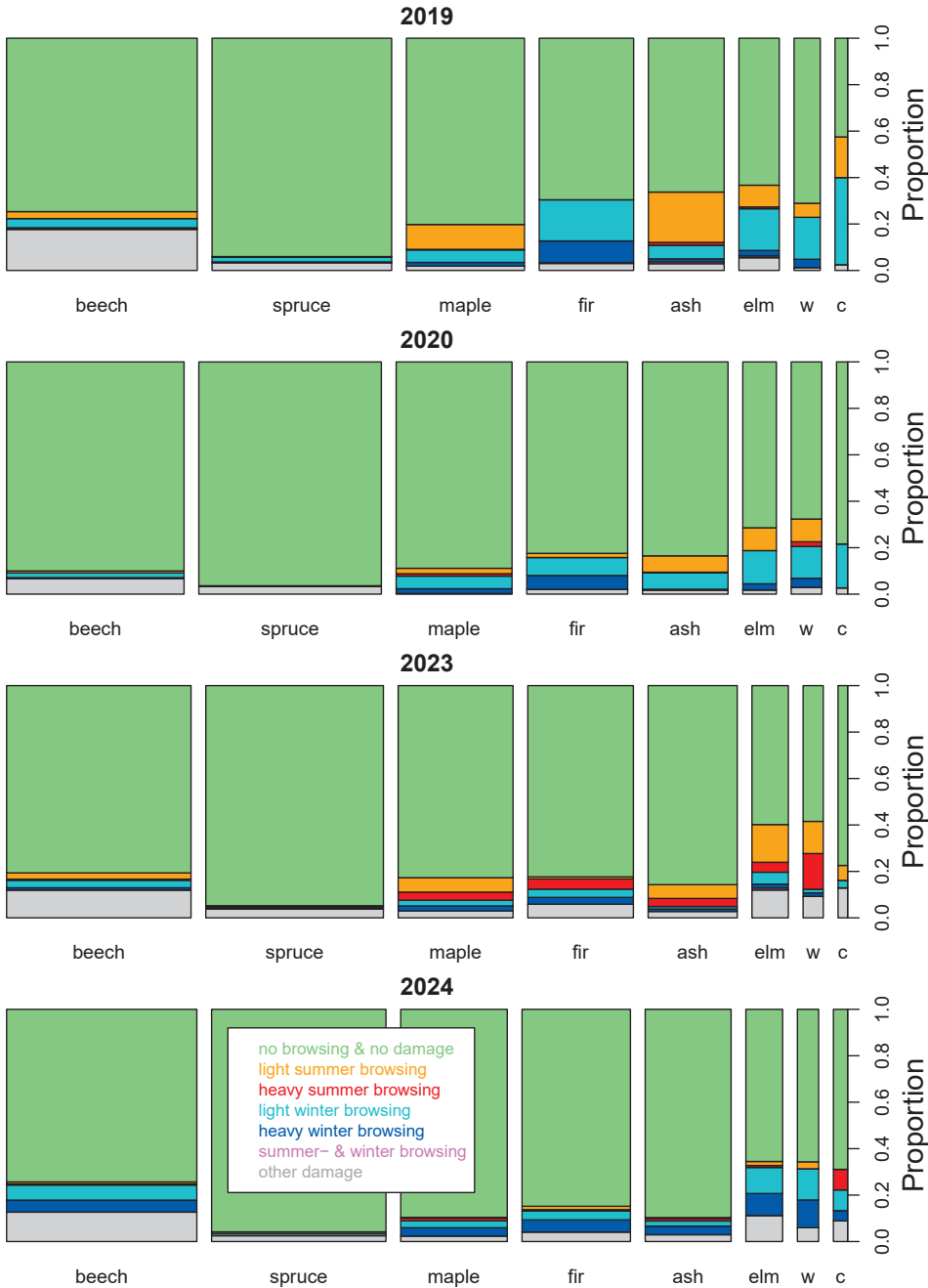


Figure 3: Browsing season: Proportion of k-saplings by tree species and survey year in the different browsing categories. Only common tree species are shown. Bar width indicates the number of saplings per year (see Table 1 for comparison). W = whitebeam (*Sorbus aria*), C = cherry (*Prunus avium*).

Antler rubbing

In addition to browsing, saplings were assessed for signs of antler rubbing. In total, seven of the eight common tree species, or seven of the 18 recorded species, exhibited trunk injuries caused by antlers (Tabl. 2). Spruce was the most frequently affected species (Tabl. 2), and thus the group of insensitive conifer species. No antler-rubbed whitebeam or rare tree species were recorded in the sample plots (thus subsumed as rare species in Tabl. 2).

Table 2: Number of saplings with marks of antler rubbing per species and survey year, as well as the percentage (%) of saplings with antler rubbing.

Species	Number of trees with rubbing				Percentage with rubbing [%]			
	2019	2020	2023	2024	2019	2020	2023	2024
beech	3	7	1	0	0.50	1.18	0.17	0.00
spruce	16	10	4	6	2.81	1.64	0.70	1.09
maple	2	0	0	0	0.53	0.00	0.00	0.00
fir	3	4	1	0	1.00	1.19	0.29	0.00
ash	0	1	0	1	0.00	0.35	0.00	0.37
elm	0	1	0	1	0.00	0.89	0.00	0.86
whitebeam	0	0	0	0	0.00	0.00	0.00	0.00
cherry	0	0	1	0	0.00	0.00	3.23	0.00
rare species	0	0	0	0	0.00	0.00	0.00	0.00
Total	24	23	7	8	1.01	0.91	0.29	0.33

A total of 62 saplings with antler rubbing were found across the four survey years, with the vast majority occurring in the first two years (24 and 23, pieces respectively; Tabl. 2). Consequently, the GLMM including the wisent presence variable performed significantly better than the model using survey year (AIC 3.82 lower with 2 fewer degrees of freedom). The modelled probability of antler rubbing marks was 0.18% in years with wisents and 0.55% in years without wisents. Post hoc comparisons on the response scale showed a predicted probability that was 0.38 percentage points lower in years with wisents. The odds of antler rubbing marks were approximately 3.15 times higher in years without wisents than in years with wisents ($OR = e^{1.147} \approx 3.15$).

Stem breakage

Stem breakage was noted in the comments. In each of the first two years before the introduction of the wisent, only one tree with a trunk break was recorded (a beech in 2019, a maple in 2020). In 2024, however, 59 trees were affected, representing 2.5% of all trees surveyed (Tabl. 3). Most trunk breaks

were observed in beech trees, both in absolute numbers and as a percentage. However, the latter applies only when focusing on the common tree species (Tabl. 3). Hornbeam (*Carpinus betulus*) and rowan (*Sorbus aucuparia*) were rarely present (Tabl. 1), so it is unclear how reliable the results on stem breakage are for these species (Tabl. 3).

Table 3: Number of saplings with stem breakage in the survey of 2024 by species, as well as the percentage (%) of saplings with breakage in 2024. For the number of trees, see Table 1.

Species	Number	Percentage [%]
<i>Fagus sylvatica</i>	39	6.50
<i>Picea abies</i>	4	0.73
<i>Acer pseudoplatanus</i>	2	0.60
<i>Abies alba</i>	4	1.17
<i>Fraxinus excelsior</i>	2	0.74
<i>Ulmus glabra</i>	2	1.72
<i>Sorbus aria</i>	0	0.00
<i>Prunus avium</i>	1	2.22
<i>Sorbus aucuparia</i>	2	12.50
<i>Tilia spp.</i>	0	0.00
<i>Quercus petraea</i>	0	0.00
<i>Carpinus betulus</i>	3	27.27
<i>Taxus baccata</i>	0	0.00
<i>Pinus sylvestris</i>	0	0.00
<i>Larix decidua</i>	0	0.00
<i>Pyrus pyraeaster</i>	0	0.00
Total	59	2.46

Stem breakage was particularly prevalent in the taller height classes; for example, 6% of trees in HC5 (130 to 200 cm tree height) were affected. The proportion of trunk breaks increased in an approximately linear fashion with height class: 0.34% in HC0, 1.26% in HC1, 3.40% in HC2, 4.24% in HC3, 5.42% in HC4, and 6.01% in HC5.

Discussion

The impact of browsing depends on several factors, including browsing frequency, the intensity of terminal shoot browsing, and regeneration density (Kupferschmid *et al.* 2019). Winter browsing was higher in the two years without wisents, while browsing intensity was lower. This suggests that browsing by wisents is not additive to browsing by roe deer and chamois in the Sollmatt Forest in Switzerland.

When considering individual winters rather than aggregated time periods, differences between years with the same wisent presence (2019 vs. 2020 and 2023 vs. 2024) were greater than those between years with different wisent presence. Summer browsing peaked in 2022, coinciding with fence construction and thus prior to the arrival of the wisents.

According to the eight camera traps installed in the Sollmatt Forest, roe deer and the much rarer chamois have shown statistically insignificant declines in activity density since 2022 compared to previous years (roe deer: 11.41 ± 2.93 events per 100 camera trap days (2019–2021) vs. 7.18 ± 3.90 (2023–2025); chamois: 0.46 ± 0.29 vs. 0.19 ± 0.06 ; cf. Weber 2026). Fence construction in the summer of 2022 may have influenced the behavior of native ungulates and, to a lesser extent, the number of individuals using the area.

A potential numerical decline in roe deer and chamois could explain the decrease in winter browsing since wisent introduction. The increased summer browsing in 2022, on the other hand, can be explained by behavioral changes in the existing ungulates, although it remains unclear whether these changes involve spatiotemporal shifts, alterations in feeding behavior, or a temporary confinement of ungulates within the enclosure during fence construction. However, the results do not support the hypothesis that wisents have increased overall browsing.

Remarkable, however, was the increase in beech browsing, while other tree species, as described above, showed a decline. In the Białowieska Forest, hornbeam, which dominates the understory there, was particularly frequently browsed (Kowalczyk *et al.* 2019).

Other studies show that wisents have little direct effect on tree regeneration. In the Rothaar Mountains, a declining trend in the proportion of browsed beech and spruce plants was also observed, while regeneration densities remained constant (Dietrich, Möhring 2013). Similarly, data from the Carpathians during a snow-covered period show that, despite a high proportion of woody plant consumption (46.8%), only a very small portion of this (1.1%) was attributable to browsing (Baraniewicz, Perzanowski 2015).

Changes in behavior, shifts in species composition, or a combination of both could also explain the increase in browsing intensity in the Sollmatt Forest. The animals (though it remains unclear whether they were roe deer, chamois, or wisents) browsed fewer saplings but did so more intensely. In survey plots with wisent resting areas, slightly more saplings were browsed in winter, suggesting a compensatory effect of wisent browsing relative to that of roe deer and chamois. In cases where wisents directly contributed to browsing, the increased browsing intensity could be explained by their larger mouth and bite size, as larger herbivores have larger bite sizes (Shipley *et*

al. 1999). The overall impact of browsing on tree regeneration is unlikely to have changed significantly in the Sollmatt Forest (for an impact assessment in years before wisent introduction, see Kupferschmid and Straub 2022).

However, the results from Sollmatt refer only to 112 survey plots in forest stands; forest edges were not included. Since wisents spent most of their time (82%) in open areas, a greater impact can be assumed there. Studies from the Białowieża Forest show that European bison reduce both the density and volume of woody vegetation in forest meadows (Kowalczyk *et al.* 2021). In this way, they can help keep habitats open. Kozorez (2016) consequently concludes that the restoration of forest meadows depends more on herbivores such as wisents than on selective feeders such as roe deer. Eight-year biodiversity studies on the island of Bornholm in Denmark show an increase in vascular plant species diversity, primarily in favor of grasses and in open oak forests (Gottlieb *et al.* 2024). Closed beech forests, on the other hand, remained unaffected by such effects (Gottlieb *et al.* 2024). Similarly, during the comparatively short study period, no change in the number of regenerating tree species has been observed to date in the Sollmatt beech forest.

Comparative studies from Spain show that when coexisting with red deer, wisents rely more heavily on grasses and shrubs than red deer (Filella *et al.* 2024). The proportion of woody vegetation was 81% for red deer, compared to 52% for wisents. In contrast, studies by Gebert and Verheyden (2001) across a wide variety of habitats showed that grasses generally make up about one-third of the red deer diet. Under sympatric conditions – as was the case in Spain – red deer probably switch to other resources. This is likely to be even more pronounced in roe deer, as they consume significantly less grass than red deer (Tixier, Duncan 1996). Chamois are likely to retreat to steeper terrain or higher-elevation areas.

The wisent exhibits a high degree of flexibility in its feeding habits, particularly on a seasonal basis (Kowalczyk *et al.* 2019). In the study area, it is unclear to what extent this affects browsing.

Since the arrival of the wisents, the proportion of stem breakage among young trees has increased. From the Carpathians it is known that fallen trees and branches are frequently utilized by wisents. In this context, gnawing (12.6%) contributes significantly more to food intake than browsing (1.1%), while bark stripping dominates (86.3%) (Baraniewicz, Perzanowski 2015).

It is also worth noting that marks of antler rubbing on spruce and fir have become significantly less common since the wisent arrived at the Sollmatt. Since fraying is primarily carried out by male cervids and depends heavily on their spatial behavior and habitat use (Ramos *et al.* 2006), this could indicate changes in the spatial use patterns of roe deer since the introduction of wisents.

Conclusions

Because of the short study duration, conclusions regarding long-term effects on forest structure, biodiversity, and regeneration dynamics remain limited. Changes in the density, behavior, and species composition of the native ungulate community may also have contributed to the observed browsing patterns. Furthermore, additional changes in the coexistence of wisents and native ungulates cannot be excluded as the system continues to develop. Consequently, the conclusions presented here should be interpreted as reflecting the current stage following reintroduction.

Within these limitations, the direct and indirect effects of wisents on browsing and tree regeneration in the closed beech forest of Sollmatt were small or possibly compensatory. Since wisents were not associated with an overall increase in browsing, the extent of the browsing impact they cause in the forest within the enclosure can currently be considered economically acceptable.

However, an increase in stem breakage and bark stripping suggests that wisents' use of the woodlands differs in some respects from that of the wild ungulates already present. At the same time, the findings – including, for example, reduced antler rubbing – suggest that the presence of wisents has influenced the behavior and spatial use of roe deer and chamois.

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Zgryzanie przez żubry jest kompensacją dla żerowania sarny i kozicy w Jurze Szwajcarskiej

Streszczenie: Wsiedlenie żubra rodzi pytania o jego dodatkowy wpływ na regenerację drzew. Celem pracy było zbadanie bezpośrednich i pośrednich skutków obecności żubra w mieszanym lesie bukowym w Jurze Szwajcarskiej, siedlisku saren i kozic. Na 112 powierzchniach zbadano dwa drzewa w każdej klasie wysokości i gatunku pod kątem zgryzania, ocierania porożem/rogami i łamania pni. Badania przeprowadzono przed (2019 i 2020) i po (2023 i 2024) wprowadzeniu żubrów do zagrody (wrzesień 2022). Ogródenia zagrody nie stanowiły przeszkody dla saren i kozic. Do analizy wykorzystano metodę GLMM. Mniej młodych drzew było zgryzanych zimą z żubrami niż zimą bez nich, ale te zgryzane miały intensywniejsze uszkodzenia. Wyjątkiem był buk, którego zimowe zgryzanie wzrosło po pojawieniu się żubrów. Najwyższe zgryzanie latem odnotowano podczas budowy ogrodzenia. Podczas gdy liczba wyłamań pni wzrosła, strzępienie świerków i jodeł zmniejszyło się po wsiedleniu żubrów. Zatem zgryzanie przez żubry częściowo rekompensowało zgryzanie przez sarny i kozice oraz zmniejszało ślady strzępienia. Zwiększona intensywność zgryzania może wynikać z większego rozmiaru ugryzień żubrów w porównaniu z oboma rodzimymi kopytnymi. Wzrost liczby pęknięć łodyg wskazuje na dodatkowe oddziaływanie mechaniczne wykraczające poza typowe działania zwierząt kopytnych.
