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Resilience of Alpine *Salix* shrubs to Changes in Browsing Pressure

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Naturforvaltning

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Cover picture: Salix shrubs at the study area close to Minnestølen in the municipality of Hol (Marlene Palm, 2019)

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Marlene Palm

Abstract

Browsing by large herbivores has the potential to inhibit climate-driven shrub expansion. How resilient shrubs are to a change in herbivory, however, is not fully understood.

In this study, I want to examine how *Salix* growth and shoot density respond to a change in browsing pressure along an elevational gradient. For fourteen years, the study site has been divided into fenced areas with different sheep densities (0, 25 and 80 sheep per km^2). Before and after this period the entire area had a sheep density around 25 sheep per km^2. In 2019, three years after the fences were taken down, I measured shoot density, height and stem diameter of *Salix* shrubs. I compared this data to data sampled in 2010, while the fences were still erect. I expected that the differences in shrub density and growth due to different sheep densities in the enclosures, had already disappeared in 2019.

Shoot density was increasing with elevation in enclosures without sheep in 2010, while it was decreasing in the other enclosures. This difference was still observed in 2019. Shrubs were generally smaller and had thicker stems in 2019 compared to 2010. The differences in height and stem diameter after 8 years with different sheep densities in the enclosures were still present in 2019. Compared to 2010, however, in there were changes in height to stem diameter ratio. In 2010, shrubs in the unbrowsed enclosures had a greater height to stem diameter ratio than shrubs in the other enclosures. In 2019, height to stem diameter ratio was the same for all shrubs, regardless of the sheep density they were exposed to when the fences were erect.

Salix shrubs seemed to quickly adapt their growth pattern to the reintroduction of low sheep density after the enclosures were removed. For shoot density, height and stem diameter, the differences resulting from different sheep densities in the enclosures remained in 2019. This indicates that three seasons with initial low grazing regime are not enough to reverse the changes caused by fourteen years with altered sheep density.

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Introduction

Ecosystems are usually in stable states where environmental conditions and relations between organisms are balanced. There is, however, variation and fluctuations around a stable state. Hence, if the system gets out of balance, it can handle the disruption and gradually returns to its initial state. This ability of an ecosystem to absorb disturbances and maintain relationships within the system even though some conditions may change, is called ecological resilience (Holling, 1973; Gunderson, 2000). Systems that return quickly to their initial state have a higher resilience than systems with longer recovery time. If a system is interrupted by a disturbance that exceeds its resilience, then it can shift to another regime from where it cannot regain its initial stable state (Scheffer & Carpenter, 2003). Hence, the changes after such disturbance are irreversible even if the disturbance ceases.

Global warming acts as a disturbance and is associated with environmental changes around the world (IPCC, 2014). The growth of shrubs is positively correlated with temperature (Pajunen, 2009). Thus, a warming climate in alpine regions facilitates a shift of shrublines into higher elevations (Körner, 2012; Hallinger et al., 2010). Shrublines represent the elevational range limit of erect shrubs. Volden (2018) found that shrub encroachment precedes treeline shifts, so that present shrublines potentially indicate the location of future treelines. A shift of shrublines into alpine ecosystems reduces the extent of these ecosystems. Shrub encroachment has been studied in several ecosystems (Naito & Cairns, 2011) and can have consequences for both structure and function of the system (Eldridge et al., 2011). Shrub expansion may influence species composition (Ims & Henden, 2012) and animal behavior (Wheeler & Hik, 2014). It can also enable positive feedback chains where increased shrub cover biomass may lead to increased accumulation of litter and snow. This in turn facilitates soil warming (Bonfils et al., 2012; Loranty & Goetz, 2012). Hence, shrub expansion may influence the microclimate in a way that promotes vegetation growth.

Climatic factors are not the only drivers of shrub growth. Local agents such as avalanches, soil conditions, geographic location and herbivory also influence shrubs (Körner, 2012; Mienna et al., 2020a, Yu et al., 2017). Browsing by large herbivores has generally a strong impact on ecosystems. It involves nutritional and physical modifications due to selective biomass removal, nutrient addition, as well as trampling and subsequent soil compression (Norderhaug et al., 1999). Both climate warming and herbivory may have a greater impact on shrubs than on other functional groups (Yu et al., 2017). Browsing can potentially strengthen the resilience of shrub-dominated tundra to warming because the removal of biomass weakens the positive feedback chain triggered by an increase of biomass (Kaarlejärvi et al., 2015). Furthermore, herbivory can moderate and counteract the effects of warming on vegetation by inhibiting the expansion of deciduous shrubs (Olofsson et al., 2009; Post & Pedersen, 2008). Evergreen shrubs, however, have potentially more secondary compounds to protect themselves against browsing, which gives them an advantage in the presence of herbivores (Vowles et al., 2017; but see Olofsson et al. (2009) for contrasting results). Effects of the interaction between browsing and warming seem to vary not only with shrub species but also with herbivore species and herbivory density (Christie et al., 2015). *Salix* shrubs are known to be very tolerant to browsing and respond to biomass removal with compensatory growth of shoots (Danell et al., 1994). Nevertheless, Christie et al. (2014) observed that browsing also inhibits shrub reproduction and growth due to the removal of vegetative buds. Because *Salix* shrubs reproduce primarily vegetatively (Elven & Fremstad, 2018), herbivory can impact their expansion despite growth compensation.

There are other factors that also determine *Salix* shrub expansion in alpine areas. Speed et al. (2013) observed that while sheep browsing moderates shrub expansion at high elevation, this is not the case at low elevation. There, sheep removal inhibits shrub growth due to the subsequent competition with field layer vegetation. This stands in contrast to the results from Løkken et al. (2019) who found an increase of shrub height and cover following sheep removal. This shows that plant-herbivore interactions in connection with a warmer climate are complex and local conditions must be considered.

Because of their potential impact, when introduced to a system, herbivores can be a great disturbance. There are, however, areas with a long history of herbivory where the vegetation is adapted to grazing and browsing, and large herbivores play a key role in maintaining the structure and function of those ecosystems (Bruteig et al., 2003). In those cases, the termination of herbivory or a change in herbivore density i.e., grazing and browsing pressure, would be a disturbance for the system. In Norway, ca. 50 % of the land area consists of alpine and arctic habitats (Bruteig et al., 2003) and is not suitable for agriculture. Thus, for the last 6000 years, it has been of great value to hold livestock and let it graze freely on alpine rangeland during the summer. That made it possible to generate food on this land (Kvamme et al., 1999). Especially, sheep have a key role and make up the majority of livestock in Norway. Since the middle of the 19th century, livestock holding has been changing in number and composition. While the number of free grazing cattle, horses and goats has decreased on a national scale, the number of sheep has been stable (Austrheim et al., 2008). However, this development varies regionally. In Norwegian lowlands, livestock grazing has declined, supposedly due to a change from extensive to intensive livestock farming with reduced grazing on outlying land (Speed et al., 2019). Whereas, in mountain regions general livestock abundance decline was minor, and the number of sheep slightly increased (Speed et al., 2019).

Sheep graze primarily on grass and herbaceous plants, but they also browse on leaves of woody plants like *Salix* shrubs. According to Rekdal (2001a) the leaves of *Salix glauca*, *Salix lanata* and *Salix phylicifolia* are popular forage among sheep. Although the foliage of *Salix glauca* contains bitter compounds, it is not recorded that this species is preferred less than the others (Rekdal, 2001a). *Salix* shrubs are an important part of the lower alpine ecosystem and can play a significant role in maintaining biological diversity. Besides cervides and livestock, mountain hare (*Lepus timidus*) and birds use *Salix* shrubs as forage source in Scandinavia (Elven & Fremstad, 2018). The willow ptarmigan (*Lagopus lagopus*) for example, depends on shrubs for protection (Christie et al., 2015). Their chicks live on insects in the thickets and as adults the willow ptarmigan feed on catkins (Hjeljord, 2008).

This study investigates the resilience of alpine *Salix* shrubs to a change in browsing pressure along an elevational gradient. The study area is an experimental site where the effect of different sheep densities is studied. For fourteen years, the site was divided into fenced areas with three different sheep densities. Before and after this experiment there was a low grazing pressure in the whole area. This results in three different grazing pressure developments (Figure 1):

1) no change in sheep density (control treatment **ϴ**),
2) increase in sheep density after establishing enclosures followed by a decrease in sheep density after fences were taken down (treatment **Λ**), and
3) decrease in sheep density after establishment of enclosures and a subsequent increase in sheep density with termination of controlled grazing experiment (treatment V).

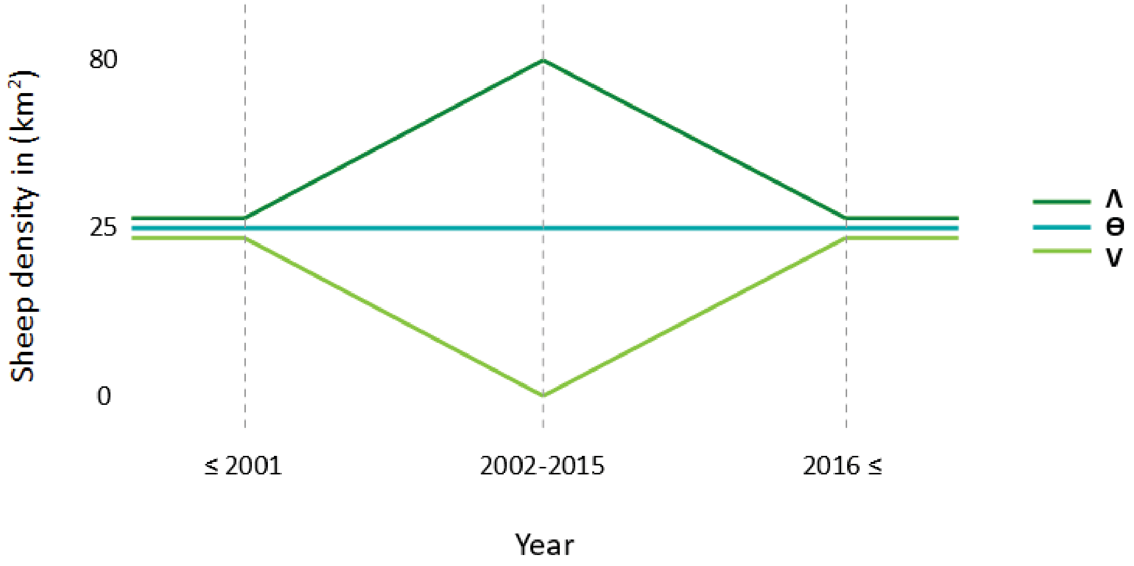

Figure 1*: Development of sheep density for the three treatments (****Λ****,* ***ϴ****,* ***V****) before (≤ 2001), during (2002-2015) and after (2016 ≤) controlled grazing experiment. All treatments had a sheep density of 25 sheep per km^2 both before enclosures were established and after fences were taken down. Control treatment* ***ϴ*** *had this density consistently also while fences were up. Within the enclosures of treatment* ***Λ*** *there were 80 sheep per km^2. Under* ***V*** *treatment sheep were excluded from the enclosure. Sheep density numbers are approximated. (Adapted from Mienna et al., 2020b).*

After fences were taken down in 2016 and until I performed the field sampling in 2019, there were three seasons in which browsing pressure was at the initial low level in the entire studyarea. The aim of this study is to examine how *Salix* growth and shoot density respond along an elevational gradient to:

1) a change from no browsing when fences were erect to low browsing pressure after they were removed (treatment **V**) and

2) a change from heavy browsing when fences were erect to low browsing pressure after they were removed (treatment **Λ**).

Hence, I am comparing data for shoot density, height and stem diameter that I collected in 2019 with data recorded in 2010 while fences were still erect (Speed et al., 2013). This data will give information about the change in shrub growth pattern and distribution during this period.

For shoot density, Speed et al. (2013) found an interaction between sheep density and elevation. When unbrowsed (treatment **V**), shoot density was high in high elevations and low in low elevations, i.e., increasing number of shoots with elevation. Whereas, at high sheep density (treatment **Λ**) there were more shrubs at low elevation than at high elevation. Speed et al. (2013) also found that *Salix* shoots were tallest and had a larger stem diameter at high sheep density (treatment **Λ**) as opposed to unbrowsed enclosures (treatment **V**). The height-diameter ratio was higher without sheep than at high sheep density.

With this background I seek to answer the following questions:

1) Are three seasons with the initial low browsing pressure enough to reverse the changes long-term sheep density manipulation had on Salix shrub density and growth?

2) Do the shrubs' responses to the re-established initial browsing pressure depend on which manipulated sheep density they were exposed to while the fences were erect?

3) Do the shrubs' responses to the re-established initial browsing pressure vary with elevation?

Generally, since *Salix* shrubs are relatively fast growing, I expect that the differences in growth and shoot density between different grazing pressure in 2010, are no longer visible in 2019. Since the sheep density in treatment **Ө** did not change over the years, it represents the initial state and I expect that treatment **V** and **Λ** will develop toward it.

More specifically, I assume the following:

1) Shoot density

I predict that in treatment **V** there are more shoots at low elevations and less in high elevations in 2019 than in 2010. The increase from no to low sheep density can lead to a reduction of herbaceous plants and, thus, facilitate recruitment of new *Salix* shoots.

2) Stem diameter and height

I assume a larger stem diameter and shrub height in 2019 across all treatments and elevations because of natural growth, but I expect more diameter and height growth in treatment **V** for the differences between the treatments to disappear.

3) Height to stem diameter ratio

In 2019, I expect height to diameter ratio to be lower in treatment **V** and higher in treatment **Λ**, as opposed to 2010.

Materials and Method

Study area

The study area is located in the municipality of Hol, northwest in Viken county, in southern Norway (60° 40’ - 60° 45’ N, 7° 55’ - 8° 00’ Ø). Hol lies in the western part of Hallingdal, a u-shaped valley surrounded by high mountains. The climate in this area is sub-continental with an average summer temperature of 7.9 °C, an average annual temperature and precipitation of -1.6 °C and 1430 mm (Speed et al., 2013a). As other Norwegian alpine municipalities, Hol has a long history of livestock grazing, and although the total grazing pressure of large herbivores in this area decreased between 1949 and 1999, the grazing pressure of sheep increased in the same period (measured as metabolic biomass per km^2; Austrheim et al., 2008). Every year in late June, sheep are released and can graze freely until early September, usually with a density of 10 to 25 sheep per km^2.

The controlled grazing experiment was conducted on a south facing slope in the alpine treeline ecotone where primarily mountain birch (*Betula pubescens tortuosa*) forms the treeline. The study area has an elevational range from 1050 to 1300 m a. s. l. and is crossed by several streams. The vegetation type which can be found especially along those streams is called tall herb meadow. It makes up 7.1 % of the experimental site and is the most productive vegetation type in alpine regions (Rekdal, 2001b). It is there *Salix* thickets can be found. The dominating vegetation type, however, is dwarf shrub heaths (51 %) followed by lichen ridges (17 %) and snow beds (12 %) (Rekdal, 2001b).

Salix glauca and *S. lapponum* are the most typical species of *Salix* shrubs in Norwegian mountain landscapes. They have a broad range and thrive in several different vegetation types. *S. lanata* is also associated with Norwegian alpine regions are but its range is more limited (Elven & Fremstad, 2018). All three of those species were dominant in the study area.

Although *Salix* shrubs reproduce mainly sexually, when a broken *Salix* branch ends up on the ground, vegetative reproduction is possible as well. This kind of reproduction is especially successful along watercourses or disturbed landscapes with few competitors. Together with the property of rapid growth in young stages and early fertility it allows for *Salix* species to colonize an area in an early state of succession, such as cultural landscapes. While there is a lot of outlying land used for livestock grazing in Norway, *Salix* did not have a high abundance there, but since certain areas have remained unbrowsed for some time, *Salix* is recovering in these areas (Elven & Fremstad, 2018).

Design of grazing experiment (2002 - 2015)

The experimental site has a size of approximately 2.7 km^2 and was fenced in in the autumn of 2001, after the grazing season was over. This area was then further divided into nine enclosures enabling for three different sheep density treatments (0, 25 and 80 sheep per km^2) with three replica each (Figure 2). Sheep in the site were of a breed called Norwegian White Sheep. Each enclosure was assigned a treatment by blocked randomization (Steen et al., 2005). In every enclosure, 20 permanent vegetation plots were established, resulting in a total of 180 plots where each measured 50 × 50 cm (Figure 2). The plots were evenly spread across the enclosures with regard to elevation and vegetation type. The corners of every plot were marked by inserting small metal pipes into the ground and an additional larger wooden marker was placed at the plots' northwest corner. The plots' coordinates were registered with a handheld GPS. That facilitated the relocation of the vegetation plots and the identification of their exact orientation at a later point in time (Austrheim et al., 2008b).

Controlled grazing lasted from 2002 to 2015. During this period, several vegetation analyses were conducted at all permanent vegetation plots. Based on those analyses, Speed et al. (2013) sampled *Salix* height and stem diameter in 2010 at every plot where an erect *Salix* species was registered at least once between 2001 and 2009. In the summer of 2016, during the grazing season, all fences were taken down, and since then the study site had a sheep density of 20 to 25 sheep per km^2, which is equivalent to low grazing pressure.

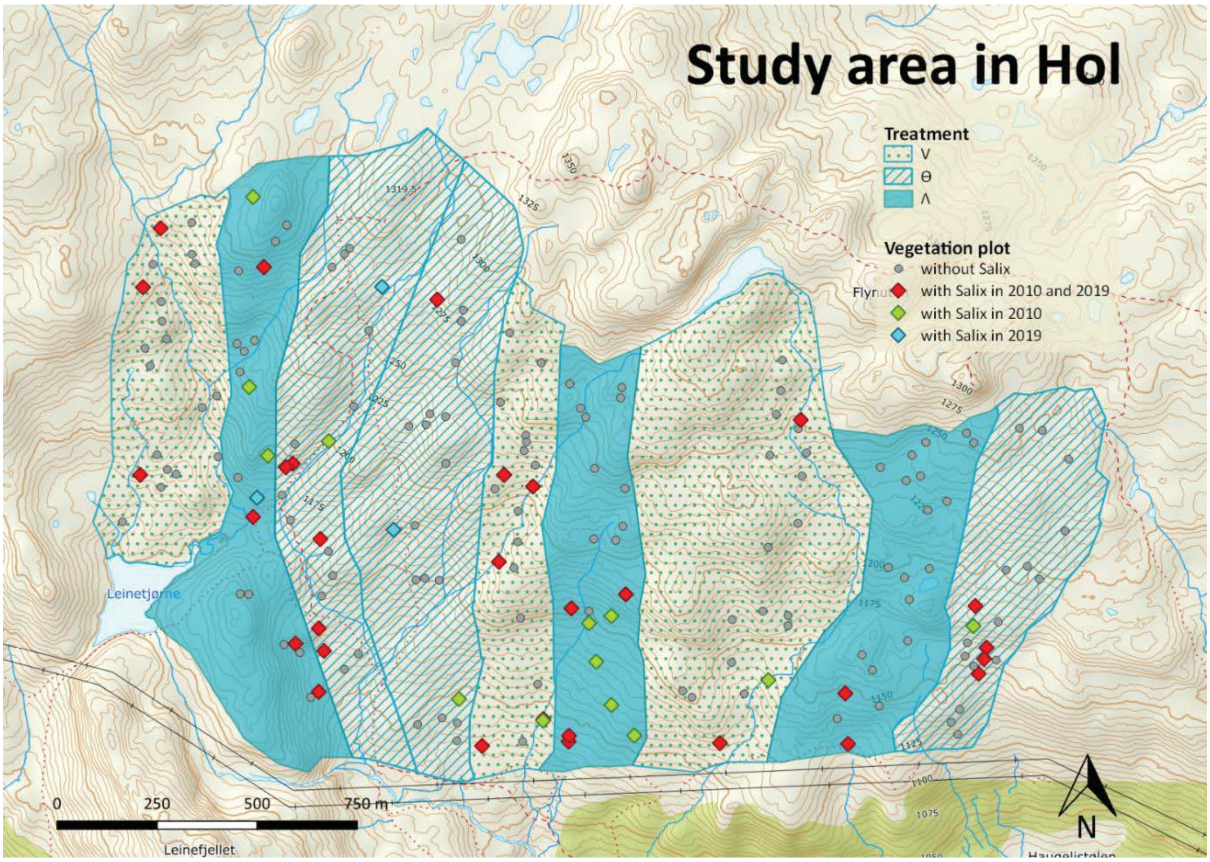

***Figure 2**: Map of study area with sheep density treatments (V - reduction followed by increase, Ө - no change in sheep density, Λ - increase followed by reduction). Vegetation plots where no samples were taken are marked as grey circles. Vegetation plots where samples were taken are marked with diamonds (red – sampled in both 2010 and 2019, green – only sampled 2010, blue – only sampled in 2019). The map was made with QGIS (QGIS Development Team, 2019). In the background is a topographic map of Norway produced by Kartverket.*

Data collection

I used the following definitions during field work:

Shoot: every branch coming out of the ground.

Stem: the main trunk of a shoot which can branch itself but only above ground.

To ensure that the data from the different years could be compared to each other, I followed the sampling method from Speed et al (2013). Our methods differ, however, in the choice of at which plots we conducted the sampling.

Field work in 2019 was conducted between June 27th and July 18th. During that period, I visited each of the 180 vegetation plots (Figure 2). To relocate the plots, I used a handheld GPS receiver. I took measurements at plots that contained at least one *Salix* shoot. For this, I established two transects, each of them 5 meters long while the transects in 2010 were 10 meters long (Figure 3). One transect was running along the plot edge in east-west direction, and the other along the edge in north-south direction. Both transects were thereby bisecting each other and centering at the north-west corner of the plot (Figure 3). I recorded stem diameter and vertical height for every *Salix* shoot intersecting with a transect. I measured the above ground stem diameter as close to the ground as possible with an electronic caliper to the nearest 0.5 millimeter. The shoots' vertical height was measured straight from where the stem diameter was taken to the top of the highest leaf. It was measured with a foldable carpenter's rule to the nearest centimeter.

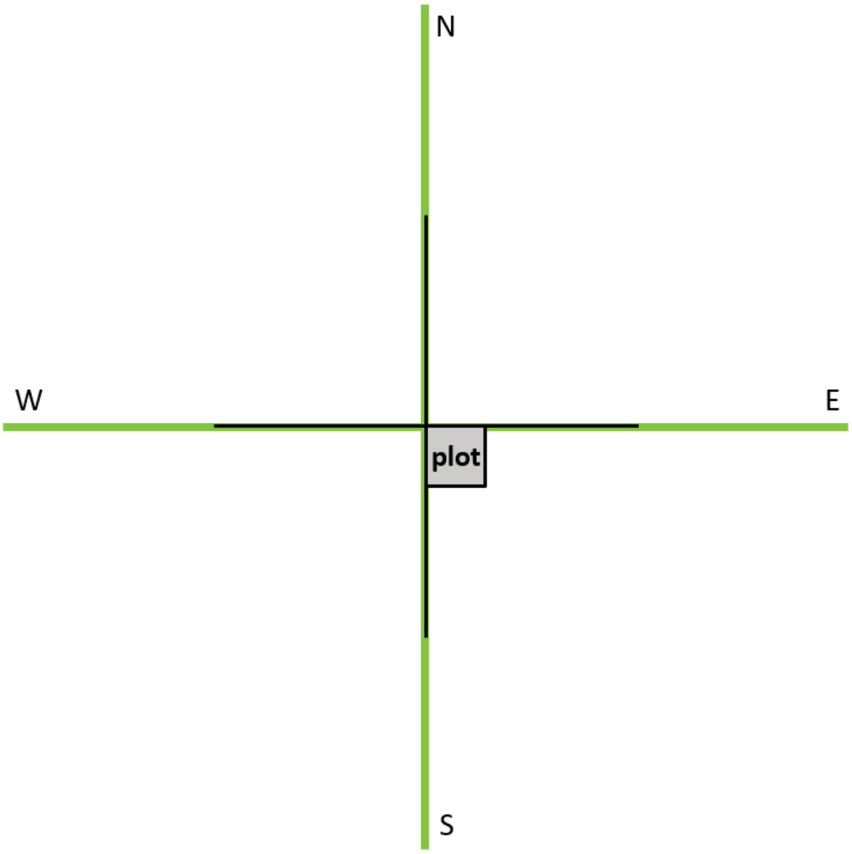

Figure 3*: Transects at a vegetation plot (0,5 x 0,5 m). Green lines show transects in 2010 (10 m), black lines show transects in 2019 (5 m).*

Data processing and analyses

To be able to compare the data from 2019 with the data recorded in 2010, I had to process the data sets before conducting the statistical analyses. During sampling in 2019, when for example a shoot was tall, highly branched or/and close to the north-west corner, it could happen that some shoots were measured more than once because they intersected with more than one transect. If that was the case, I kept the data point which showed the greatest height. Because the transects in 2010 were twice as long as in 2019, I also excluded all data points from 2010 that were further than 2.5 m away from the north-west corner. Since Speed et al. (2013) found no differences in response between the registered *Salix* species, they were analyzed together.

All statistical analyses were performed in RStudio (Rstudio Team, 2020) using the following packages: "lme4" (Bates et a., 2015) and "nlme" (Pinheiro et al., 2020) for the linear mixed effects models, as well as "ggplot2" (Wickham, 2016) to generate figures.All response variables were analyzed at plot level. Thus, I added together the shoots I sampled at each plot which gave me a shoot density per 10 m since each transect was 5 m long. For stem diameter, height and height to stem diameter ratio, I used mean values for every plot.

To investigate if shoot density had changed during the period between 2010 to 2019, I fitted a generalized linear mixed effects model (GLMM). Because shoot density was recorded as count data, I fitted the response as a Poisson distribution. To test if stem diameter, height and height/diameter ratio had changed between 2010 and 2019, I fitted a linear mixed effects model (LMM) for each of those variables. I fitted all the models with year, grazing treatment and elevation as fixed effects, as well as interactions between them. Additionally, because some plots were sampled in both 2010 and 2019, I fitted all the models with plot ID as a random factor effect to avoid pseudoreplication.

To find the model that suited my data best, I conducted model selection as followed:

1) For each variable I ran the whole model with all interactions between the independent variables.

2) If the output did not show any significant interactions for the response variable, I ran the model without interactions between the independent variables.

3) If the output showed any significant interactions, I ran the model two more times: once with the relevant interactions and once without any interactions.

4) For both, the model with relevant interactions and without any interactions, I ran a likelihood ratio test to find out if the interactions would explain the response variable.

5) In the case of a significant likelihood ratio test where the model with interactions were significantly better than the model without interactions, I chose the model with interactions (from step 3). If the likelihood ratio test was not significant, I chose the model without any interaction (from step 3).

To ensure that I detected any significant differences between the years, between the treatments within each year and any significant interactions, I ran the model for each response variable six times. Each time I changed the intercept so that the intercept contained every treatment in 2010 and every treatment in 2019. All tables of the outputs with the different intercept settings can be found in Appendix A.

Results

In 2019, I found 636 shoots of erect *Salix* shrubs in 33 vegetation plots. In 2010, 797 shoots were registered at 43 vegetation plots. Table 1 shows the distribution of those plots across the treatments.

Table 1: *Number of sampled plots (stems) for treatment **V**, **Θ** and **Λ** in 2010 and 2019.*

	V	**Θ**	**Λ**	**total**
2010	12 (268)	14 (229)	17 (300)	43 (797)
2019	10 (208)	12 (228)	11 (200)	33 (636)

Shoot density

According to the GLMM model selection, the best model to analyze shoot density was with interaction between treatment and elevation. There was no significant change in the number of shoots between 2010 and 2019 (Table 2 and Figure 4). Also, elevational differences from 2010 remained in 2019, with the number of shoots increasing with elevation under **V**-treatment, while there was no significant density change depending on elevation under **Θ**- and **Λ**-treatment (Table 2 and Figure 4, see Appendix A for p-values when changing intercept).

Table 2: *Output for generalized linear mixed effects model for Poisson data of* Salix *shoot density. The independent variables are year, grazing treatment and elevation, as well as the interaction between treatment and elevation. **V**-treatment of 2010 is in the intercept.*

Predictors	**Coefficient**	**Std. Error**	**p-value**
Intercept	2.554	0.25	**<0.001**
Year 2019	- 0.046	0.06	0.411
Θ	0.354	0.38	0.357
Λ	0.367	0.32	0.256
Elevation	0.005	0.00	**0.036**
Θ × Elevation	- 0.007	0.00	**0.048**
Λ × Elevation	- 0.008	0.00	**0.016**

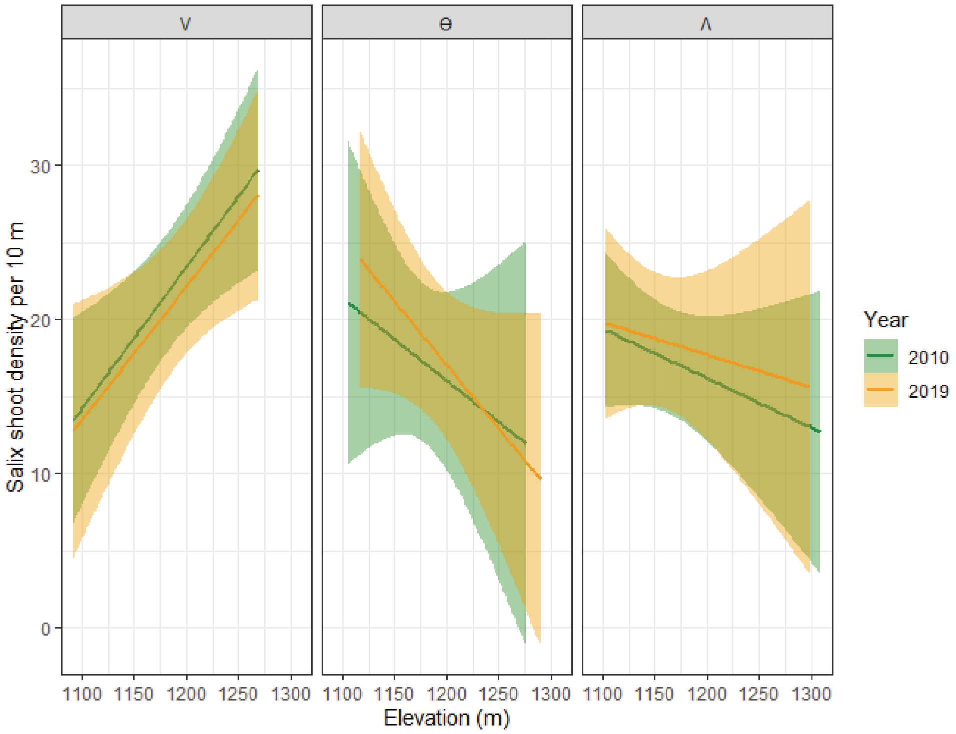

***Figure 4**: For every sheep density treatment, the number of* Salix *shoots per vegetation plot is plotted against elevation and year of sampling. The regression lines are predictions generated by a Poisson generalized linear mixed model. Transparent areas show standard error.*

Height

According to the LMM model selection, the best model to analyze stem height was without any interaction between the independent variables. Regardless of grazing treatment, *Salix* shrubs in 2019 were shorter than in 2010 (Table 3 and Figure 5, see Appendix A for p-values when changing intercept). Stem height in every treatment was decreasing with elevation and the mean stem height was the same for every treatment within the years (Table 3 and Figure 5, see Appendix A for p-values when changing intercept). In treatment **Λ**, however, stems were marginally taller than in treatment **V** (Table 3 and Figure 5).

***Table 3:** Output for linear mixed effects model of* Salix *vertical height. The independent variables are year, grazing treatment and elevation. **V**-treatment of 2010 is in the intercept.*

Predictors	Coefficient	Std. Error	p-value
Intercept	44.21	6.00	**<0.001**
Year 2019	- 7.39	1.96	**0.001**
ϴ	5.39	6.05	0.378
Λ	11.14	5.96	0.069
Elevation	- 0.14	0.04	**0.002**

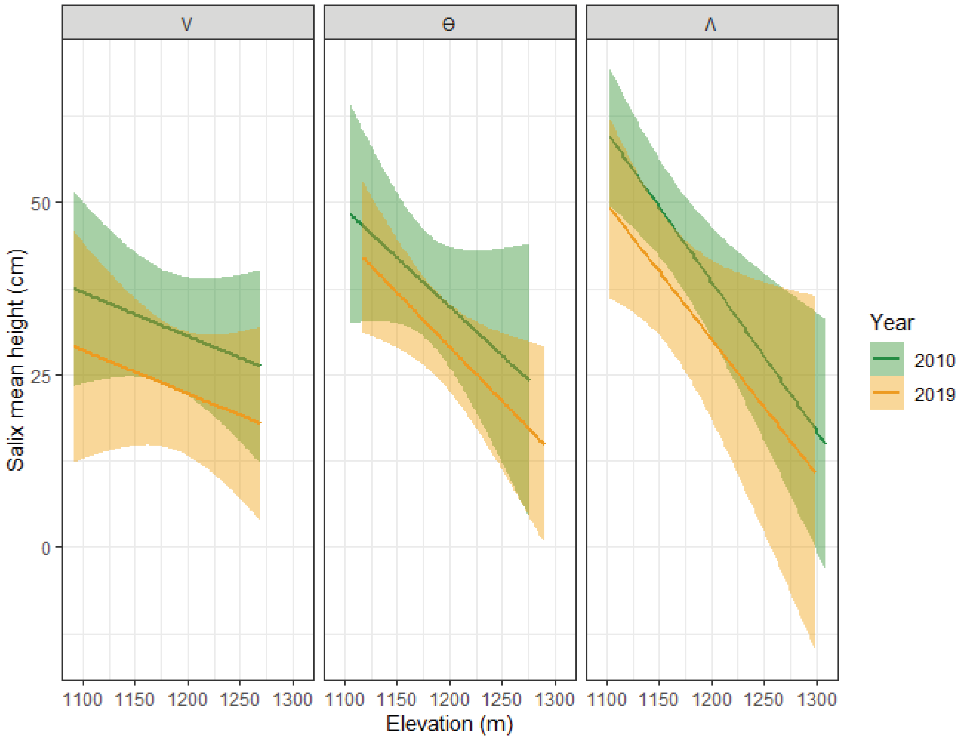

***Figure 5:** For every sheep density treatment, the mean vertical shoot height is plotted against elevation and year of sampling. The regression lines are predictions generated by a linear mixed model. Transparent areas show standard error.*

Stem diameter

A LMM without any interactions between the independent variables turned out to be the best model to analyze stem diameter. Across all treatments, *Salix* shrubs had a larger stem diameter in 2019 (Table 4 and Figure 6, see Appendix A for p-values when changing intercept). For every treatment, both in 2010 and 2019, there was a marginal stem diameter decrease with elevation (Table 4 and Figure 6, see Appendix A for p-values when changing intercept).

Furthermore, there were differences between the treatments in both years. Shrubs in treatment **Λ** had a larger stem diameter than shrubs in treatment **V** (Table 4 and Figure 6, see Appendix A for p-values when changing intercept). In 2019 the mean diameter was 8.4 mm in treatment **V** and 14.1 mm in treatment **Λ**. In 2010 it was 7.2 mm in treatment **V** and 12.4 mm in treatment **Λ**.

Table 4: *Output for linear mixed effects model of* Salix *stem diameter. The independent variables are year, grazing treatment and elevation.* ***V****-treatment of 2010 is in the intercept.*

Predictors	Coefficient	Std. Error	p-value
Intercept	8.85	1.56	**<0.001**
Year 2019	1.63	0.47	**0.002**
ɵ	1.84	1.58	0.251
Λ	4.40	1.56	**0.007**
Elevation	-0.02	0.01	0.064

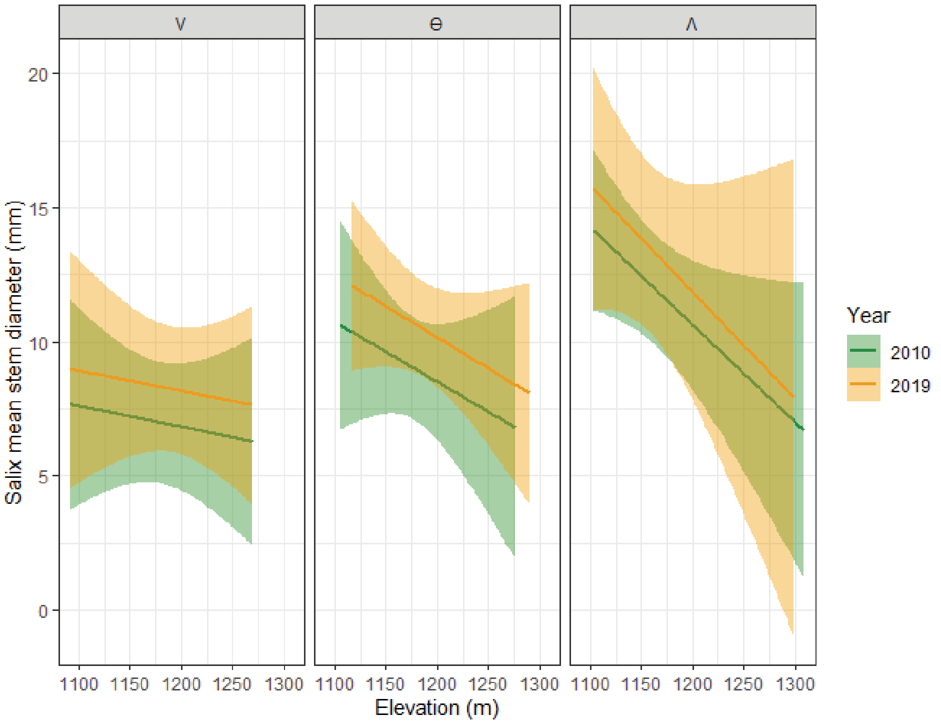

Figure 6: *For every sheep density treatment, mean stem diameter is plotted against elevation and year of sampling. The regression lines are predictions generated by a linear mixed model. Transparent areas show standard error.*

Height to stem diameter ratio

A LMM with interaction between year and treatment turned out to be the best model to analyze height to stem diameter ratio. The height-diameter ratio was significantly lower in every treatment in 2019 compared to 2010 (Table 5 and Figure 7, see Appendix A for p-values when changing intercept). In addition, the differences between the treatments had changed over the years. In 2010, shrubs in treatment **Λ** had a lower height to stem diameter ratio than shrubs in treatment **V**. In 2019, however, the ratio was the same across the treatments (Table 5 and Figure 7, see Appendix A for p-values when changing intercept). That results in greater difference in height-diameter ratio between the years in treatment **V** than in treatment **Λ** (Table 5 and Figure 7). Height to stem diameter ratio was decreasing with elevation in every treatment in both in 2010 and 2019 (Table 5 and Figure 7, see Appendix A for p-values when changing intercept).

Table 5: *Output for linear mixed effects model of* Salix *height to stem diameter ratio. The independent variables are year, grazing treatment and elevation, as well as the interaction between year and treatment.* ***V****-treatment of 2010 is in the intercept.*

Predictors	Coefficient	Std. Error	p-value
Intercept	5.88	0.31	**<0.001**
Year 2019	- 1.94	0.23	**<0.001**
ϴ	-0.42	0.33	0.205
Λ	-1.00	0.32	**0.003**
Elevation	-0.01	0.00	**<0.001**
Year 2019 × **ϴ**	0.20	0.32	0.540
Year 2019 × **Λ**	0.84	0.32	**0.015**

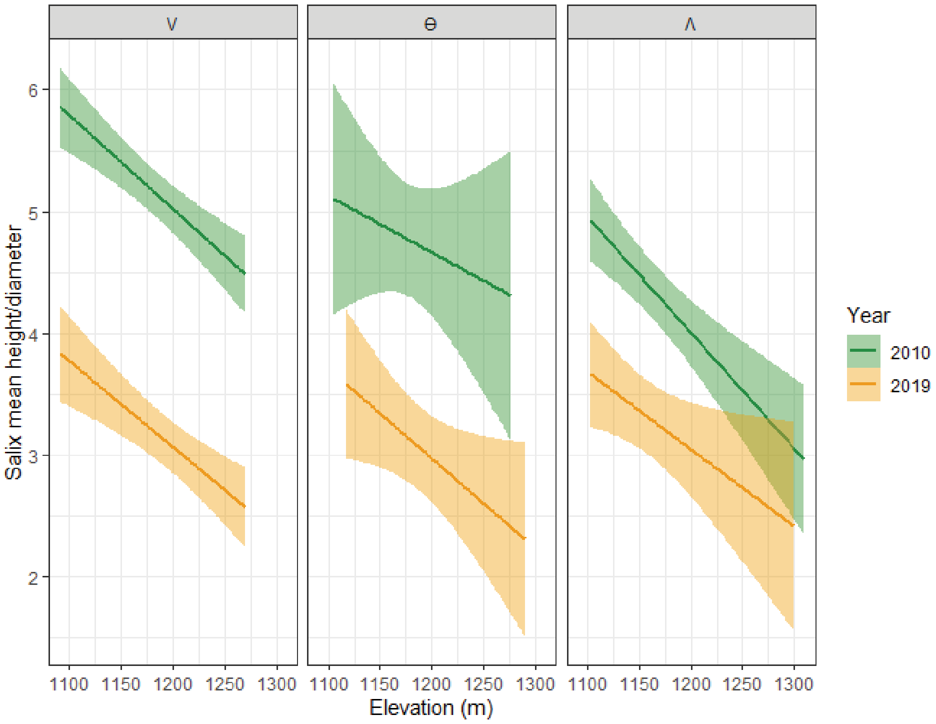

***Figure 7:** For every sheep density treatment, the mean height-diameter ratio is plotted against elevation and year of sampling. The regression lines are predictions generated by a linear mixed model. Transparent areas show standard error.*

Discussion

Browsing by large herbivores affect the growth and reproduction of shrubs and can inhibit their climate-driven expansion. Norwegian mountain regions have a long history of sheep grazing so that the vegetation is adapted to this kind of disturbance. Livestock grazing is regulated by human management. Potential changes in management strategies also influence the vegetation affected by livestock grazing. However, the resilience of alpine vegetation to long-term changes in browsing pressure is not fully understood.

In this study, I investigate how resilient *Salix* shrubs in the treeline ecotone are to a change in browsing pressure. I studied *Salix* shrub resilience by examining shrub density and growth along an elevational gradient three years after the termination of manipulated grazing which lasted for fourteen years. I found that three years with the initial sheep density is not enough for *Salix* shrubs to recover from a long-term change in browsing pressure. Although shrubs quickly adapt their growth pattern to a changing browsing pressure, changes in shoot density might stagnate but do not show regression. Especially a long-term cessation of browsing may lead to the establishment of an alternative state.

Shoot density

Contrary to my expectations, shoot density had not changed from 2010 to 2019 in any of the treatments. In both years, while the number of *Salix* shoots decreased with elevation in treatment **Θ** and **Λ**, it increased in treatment **V**. In 2010, the increase of shoot density with elevation in treatment **V** (exclusion followed by an increase in sheep density) was explained by competition with field-layer vegetation (Speed et al., 2013). Because the area was unbrowsed during fourteen years of manipulated sheep density, field layer vegetation could grow tall at low elevations, inhibiting the establishment of *Salix* shrub recruits. Herb height decreases with elevation (Straume, 2020), reducing the competition for light, which may facilitate the establishment of *Salix* recruits and *Salix* growth, resulting in higher shoot densities. Increased shoot densities along the elevational gradient in treatment **V** in 2019 may suggest that established shoots were not removed by the re-introduction of low sheep density. Another reason could be that three seasons with initial browsing pressure were not enough to reverse the elevational shoot density change. However, because sheep prefer tall herbs in alpine regions (Evju et al., 2009), I expected a reduction of competition at least at low elevations followed by an increase in number of shoots. That this was not the case in 2019 may be explained by the effect browsing can have on shrub reproduction. Christie et al. (2014) observed that ptarmigan and moose browsing inhibited *Salix* shrub reproduction due to bud removal. As a result, the ability to establish shrubs in new areas was weakened. Subsequently, at least on a short time scale, changes in shoot density due to sheep exclusion may not be reversible by reintroduction of low sheep density.

In 2010, there were no differences in shoot density between treatment **ϴ** and **Λ**. As expected, this has not changed in 2019 because treatment **ϴ** represents the initial state which the other treatments develop toward. This suggests that even low densities of sheep had an impact on *Salix* shoot density and could prevent shrub expansion into higher elevation. This has also been observed for mountain birch densities in the same area (Speed et al., 2010). Hence, as long as there are sheep browsing in the area, even in low densities, an increase in the number of sheep may have a limited impact on shoot density. This also suggests that the resilience of *Salix* shrubs to a change in browsing pressure may depend on the initial browsing pressure and whether it is increasing or decreasing.

Height, stem diameter and height to stem diameter ratio

As expected, the height to stem diameter ratio between treatment **V** and **Λ** in 2010 had disappeared in 2019. Shrubs in all treatments had a lower height to stem diameter ratio in 2019. The greatest reduction happened in treatment **V**. The decrease of height to diameter ratio in treatment **ϴ** and **Λ**, however, was against expectations. To find an explanation for this, the single variables, height and stem diameter, have to be considered. There was no treatment-dependent change in neither stem diameter nor height. However, while the shrubs, as expected, had a larger stem diameter in 2019, they were unexpectedly smaller than in 2010.

Height to stem diameter ratio is an index used to describe aboveground allocation patterns in plants. Especially in forestry it is a measure for tree stability and ability to withstand physical impact like windthrow or snow damage. A greater height to stem diameter ratio indicates that more resources are invested to increase height rather than stem diameter. *Salix* shrubs can have creeping growth (Elven & Fremstad, 2018), with stems lying on the ground in extreme cases. That means a low height to stem diameter ratio for shrubs does not necessarily implicate that they use their resources predominantly for stem diameter growth, but rather radial growth of canopy. In Arctic and alpine regions, deciduous shrubs such as *Salix* shrubs have relatively nutritious leaves and litter and a rather short photosynthetic active period (Chapin, et al., 1996). Therefore, they invest usually a large part of their resources to extend their leaf area instead of stem diameter (Chapin, et al., 1996). Those circumstances support that the observed mean stem diameter growth between 2010 and 2019 in all treatments can be attributed to natural growth independent of browsing. Also, trampling by large herbivores facilitates stem diameter growth and at the same time reduces vertical height, thus, strengthening the resistance of shrub stems to physical impact (Xu et al., 2013). Therefore, the previously heavily browsed shrubs in treatment **Λ** could develop thicker stems than the unbrowsed shrubs in treatment **V**. It is conflicting, though, with the former heavily browsed shrubs in treatment **Λ** being taller than the former unbrowsed shrubs **V** (marginally higher according to my analyses, significantly higher especially at low elevation according to Speed et al. (2013)). Speed et al. (2013) argue that shrubs in the unbrowsed areas were smaller due to competition for light with the surrounding fast-growing field vegetation. The slower growing shrubs could not get enough light, which limited their growth. Competition for light does not explain why shrubs in 2019 still are smaller in treatment **V** than in treatment **Λ** because would remove some field vegetation after the fences were removed. They would, however, also browse on Salix shrubs which may inhibit their height growth. It may take more time for the height differences between treatment **V** and treatment **Λ** to disappear.

Furthermore, the reduction of vertical height in treatment **V**, which was unbrowsed for fourteen years before returning to low sheep density, can be an effect of both removal of distal tissue and a shift in growth pattern towards radial growth. Bråthen et al. (2017) argue that, at certain densities, large herbivores can control the height and abundance of shrubs.

By browsing on shrubs within their forage range, herbivores keep shrubs from spreading and growing tall. *Salix* shrubs can compensate for biomass removal, but this compensation has been found to happen due to shoot growth from basal stem parts (Christie et al., 2014). This kind of growth leads to smaller *Salix* shrubs but with complex branching, described as “broomed architecture” (Christie et al., 2014). Stagnated and reduced height growth in combination with a positive stem diameter growth result in a lower height to stem diameter ratio. This has also been found for browsed mountain birch (Speed et al., 2011).

That herbivores can control shrub height and that compensated growth happens from basal stem parts could also be an explanation for the decreased height to diameter ratio treatments **ϴ** and **Λ**. Nevertheless, the reduced shrub height in treatment **ϴ** and **Λ** is unexpected because the shrubs there have constantly been exposed to browsing. The shrub height reduction in treatment **Λ** could be an effect of the heavy browsing pressure being continued for five more years after the first measurements were taken. Then, the following three years with low sheep density were not enough for the shrubs to respond to this change in browsing pressure. Such a delayed response is not unusual. Olofsson (2006) has found that response time depends on the direction in which grazing pressure changes. When grazing pressure was reduced in former heavily grazed areas, as in treatment **Λ**, vegetation responded slower to this change than vegetation that was exposed to a decrease in grazing pressure. This means that shrubs in treatment **V** would respond to changes in grazing pressure earlier than shrubs in treatment **Λ**.

However, the reduction of height to stem diameter ratio in treatment **ϴ,** with unchanged sheep density, cannot be explained by a delayed response. That there was no difference in height to diameter ratio between the treatments indicates that other factors than sheep browsing had an influence on shrubs in the whole study area. Additional browsing by wild herbivores, such as cervids, after fence removal in 2016 can be ruled out because they were able to cross the fences and could browse the whole area during the controlled grazing experiment (Speed et al., 2011). Shrubline ecotone dynamics are complex and there are several factors influencing it. A season with increased snow cover which weighs more down on shrubs, pressing them to the ground and, thus, lowering their height. If, however, average snow depth used to cover the shrubs so that they were not accessible to winter browsing by ptarmigan or cervids, then a reduced snow cover may lead to shrub height reduction because shrubs could exceed snow depth and could be subject to winter browsing.

Conclusion

In this study, I investigated the resilience of alpine *Salix* shrubs along an elevation gradient to a change in browsing pressure. I have shown that three seasons with initial grazing regime are not enough to reverse the changes caused by fourteen years with manipulated sheep grazing. While shrubs seemed to quickly adapt their growth pattern to the reintroduction of low sheep density, the differences in shoot density remained. Because of the different effects of an increase and decrease in sheep density on *Salix* shoot density when the fences were erect, resilience of Salix shrubs to a change in browsing pressure may depend on the initial browsing pressure and whether it increases or decreases. Investigations of field vegetation in the same area also found that certain herbaceous plants still differed in 2019 regarding distribution, height and density between the treatments (Straume, 2020). This could support the assumption of a delayed response because field vegetation is growing faster than shrubs and, therefore, it can be expected that herbaceous plants would show signs of resilience earlier than shrubs. Hence, it would be useful to continue this study to investigate how much time is needed to balance out the differences between the treatments, or whether long-term changes in browsing pressure in alpine regions potentially lead to alternative stable states. The results may be of use for the development of future livestock management strategies in alpine regions.

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Appendix A

Density – Output of GLMM with changed intercept

Intercept with treatment ϴ in 2010

```
                       Estimate Std. Error z value Pr(>|z|)
(Intercept)           2.9074757  0.2888230  10.067   <2e-16 ***
Year2019             -0.0459460  0.0558365  -0.823   0.4106
Treatment1           -0.3538776  0.3840006  -0.922   0.3568
Treatment3            0.0131104  0.3501286   0.037   0.9701
Elevation            -0.0023380  0.0027805  -0.841   0.4004
Treatment1:Elevation  0.0070639  0.0035745   1.976   0.0481 *
Treatment3:Elevation -0.0005484  0.0035653  -0.154   0.8778
```

Intercept with treatment Λ in 2010

```
                       Estimate Std. Error z value Pr(>|z|)
(Intercept)           2.9205575  0.2006756  14.554   <2e-16 ***
Year2019             -0.0459104  0.0558365  -0.822   0.4109
Treatment2           -0.0132955  0.3501124  -0.038   0.9697
Treatment1           -0.3669275  0.3231296  -1.136   0.2561
Elevation            -0.0028857  0.0022234  -1.298   0.1943
Treatment2:Elevation  0.0005484  0.0035651   0.154   0.8778
Treatment1:Elevation  0.0076109  0.0031663   2.404   0.0162 *
```

Intercept with treatment V in 2019

```
                      Estimate Std. Error z value Pr(>|z|)
(Intercept)           2.507612   0.257307   9.746  <2e-16 ***
Year2010              0.045925   0.055837   0.822  0.4108
Treatment3            0.367034   0.323137   1.136  0.2560
Treatment2            0.353685   0.383991   0.921  0.3570
Elevation             0.004726   0.002251   2.099  0.0358 *
Treatment3:Elevation -0.007612   0.003166  -2.404  0.0162 *
Treatment2:Elevation -0.007063   0.003574  -1.976  0.0482 *
```

Intercept with treatment ϴ in 2019

```
                       Estimate Std. Error z value Pr(>|z|)
(Intercept)           2.8612981  0.2913091   9.822   <2e-16 ***
Year2010              0.0459299  0.0558365   0.823   0.4107
Treatment1           -0.3536826  0.3839915  -0.921   0.3570
Treatment3            0.0133443  0.3501211   0.038   0.9696
Elevation            -0.0023366  0.0027804  -0.840   0.4007
Treatment1:Elevation  0.0070626  0.0035744   1.976   0.0482 *
Treatment3:Elevation -0.0005493  0.0035652  -0.154   0.8776
```

Intercept with treatment Λ in 2019

```
                       Estimate Std. Error z value Pr(>|z|)
(Intercept)           2.8746342  0.2027452  14.179   <2e-16 ***
Year2010              0.0459233  0.0558365   0.822   0.4108
Treatment2           -0.0133529  0.3501166  -0.038   0.9696
Treatment1           -0.3670143  0.3231331  -1.136   0.2560
Elevation            -0.0028858  0.0022234  -1.298   0.1943
Treatment2:Elevation  0.0005492  0.0035651   0.154   0.8776
Treatment1:Elevation  0.0076120  0.0031663   2.404   0.0162 *
```

Height – Output of LMM with changed intercept

Intercept with treatment ϴ in 2010

```
               Value Std.Error DF   t-value p-value
(Intercept) 49.60066  5.646165 42  8.784841  0.0000
Year2019    -7.38562  1.963291 29 -3.761856  0.0008
Treatment1  -5.38644  6.048171 42 -0.890589  0.3782
```

```
Treatment3   5.75368  5.553984 42  1.035956  0.3062
Elevation   -0.13808  0.042093 42 -3.280402  0.0021
```

Intercept with treatment Λ in 2010

```
               Value Std.Error DF   t-value p-value
(Intercept)  55.35435  4.914095 42 11.264403  0.0000
Year2019     -7.38562  1.963291 29 -3.761856  0.0008
Treatment2   -5.75368  5.553984 42 -1.035956  0.3062
Treatment1  -11.14012  5.958038 42 -1.869764  0.0685
Elevation    -0.13808  0.042093 42 -3.280402  0.0021
```

Intercept with treatment V in 2019

```
               Value Std.Error DF   t-value p-value
(Intercept) 36.82861  6.077496 42  6.059832  0.0000
Year2010     7.38562  1.963291 29  3.761856  0.0008
Treatment3  11.14012  5.958038 42  1.869764  0.0685
Treatment2   5.38644  6.048171 42  0.890589  0.3782
Elevation   -0.13808  0.042093 42 -3.280402  0.0021
```

Intercept with treatment Θ in 2019

```
               Value Std.Error DF   t-value p-value
(Intercept) 42.21504  5.721037 42  7.378915  0.0000
Year2010     7.38562  1.963291 29  3.761856  0.0008
Treatment1  -5.38644  6.048171 42 -0.890589  0.3782
Treatment3   5.75368  5.553984 42  1.035956  0.3062
Elevation   -0.13808  0.042093 42 -3.280402  0.0021
```

Intercept with treatment Λ in 2019

```
                Value Std.Error DF   t-value p-value
(Intercept)  47.96873  5.066389 42  9.468032  0.0000
Year2010      7.38562  1.963291 29  3.761856  0.0008
Treatment2   -5.75368  5.553984 42 -1.035956  0.3062
Treatment1  -11.14012  5.958038 42 -1.869764  0.0685
Elevation    -0.13808  0.042093 42 -3.280402  0.0021
```

Stem diameter – Output of LMM with changed intercept

Intercept with treatment Θ in 2010

```
                Value Std.Error DF   t-value p-value
(Intercept) 10.691354 1.4728360 42  7.259025  0.0000
Year2019     1.627641 0.4665421 29  3.488733  0.0016
Treatment1  -1.840398 1.5818721 42 -1.163431  0.2512
Treatment3   2.557049 1.4502231 42  1.763210  0.0851
Elevation   -0.020931 0.0109954 42 -1.903650  0.0638
```

Intercept with treatment Λ in 2010

```
                Value Std.Error DF   t-value p-value
(Intercept) 13.248403 1.2821526 42 10.332938  0.0000
Year2019     1.627641 0.4665421 29  3.488733  0.0016
Treatment2  -2.557049 1.4502231 42 -1.763210  0.0851
Treatment1  -4.397447 1.5574277 42 -2.823532  0.0072
Elevation   -0.020931 0.0109954 42 -1.903650  0.0638
```

Intercept with treatment V in 2019

```
                Value Std.Error DF   t-value p-value
(Intercept) 10.478597 1.5827742 42  6.620399  0.0000
Year2010    -1.627641 0.4665421 29 -3.488733  0.0016
Treatment3   4.397447 1.5574277 42  2.823532  0.0072
Treatment2   1.840398 1.5818721 42  1.163431  0.2512
Elevation   -0.020931 0.0109954 42 -1.903650  0.0638
```

Intercept with treatment Θ in 2019

```
                Value Std.Error DF   t-value p-value
(Intercept) 12.318995 1.4892980 42  8.271679  0.0000
Year2010    -1.627641 0.4665421 29 -3.488733  0.0016
Treatment1  -1.840398 1.5818721 42 -1.163431  0.2512
Treatment3   2.557049 1.4502231 42  1.763210  0.0851
```

```
Elevation   -0.020931 0.0109954 42 -1.903650  0.0638
```

Intercept with treatment Λ in 2019

```
                Value Std.Error DF   t-value p-value
(Intercept) 14.876044 1.3156258 42 11.307200  0.0000
Year2010    -1.627641 0.4665421 29 -3.488733  0.0016
Treatment2  -2.557049 1.4502231 42 -1.763210  0.0851
Treatment1  -4.397447 1.5574277 42 -2.823532  0.0072
Elevation   -0.020931 0.0109954 42 -1.903650  0.0638
```

Height to stem diameter ratio – Output of LMM with changed intercept

Intercept with treatment Θ in 2010

```
                        Value Std.Error DF   t-value p-value
(Intercept)          5.457434 0.2890088 42 18.883278  0.0000
Year2019            -1.740224 0.2246950 27 -7.744828  0.0000
Treatment1           0.421102 0.3269745 42  1.287876  0.2048
Treatment3          -0.575230 0.3001149 42 -1.916699  0.0621
Elevation           -0.007914 0.0020659 42 -3.830847  0.0004
Year2019:Treatment1 -0.200789 0.3236292 27 -0.620429  0.5402
Year2019:Treatment3  0.643169 0.3171871 27  2.027727  0.0526
```

Intercept with treatment Λ in 2010

```
                        Value Std.Error DF   t-value p-value
(Intercept)          4.882204 0.2529171 42 19.303572  0.0000
Year2019            -1.097056 0.2236428 27 -4.905392  0.0000
Treatment2           0.575230 0.3001149 42  1.916699  0.0621
Treatment1           0.996332 0.3170880 42  3.142133  0.0031
Elevation           -0.007914 0.0020659 42 -3.830847  0.0004
Year2019:Treatment2 -0.643169 0.3171871 27 -2.027727  0.0526
Year2019:Treatment1 -0.843958 0.3233320 27 -2.610188  0.0146
```

Intercept with treatment V in 2019

```
                        Value Std.Error DF   t-value p-value
(Intercept)          3.937523 0.3232915 42 12.179481  0.0000
Year2010             1.941013 0.2332940 27  8.320032  0.0000
Treatment3          -0.152375 0.3519860 42 -0.432901  0.6673
Treatment2          -0.220314 0.3462158 42 -0.636348  0.5280
Elevation           -0.007914 0.0020659 42 -3.830847  0.0004
Year2010:Treatment3 -0.843958 0.3233320 27 -2.610188  0.0146
Year2010:Treatment2 -0.200789 0.3236292 27 -0.620429  0.5402
```

Intercept with treatment Θ in 2019

```
                        Value Std.Error DF   t-value p-value
(Intercept)          3.717210 0.3043955 42 12.211774  0.0000
Year2010             1.740224 0.2246950 27  7.744828  0.0000
Treatment1           0.220314 0.3462158 42  0.636348  0.5280
Treatment3           0.067939 0.3338308 42  0.203512  0.8397
Elevation           -0.007914 0.0020659 42 -3.830847  0.0004
Year2010:Treatment1  0.200789 0.3236292 27  0.620429  0.5402
Year2010:Treatment3 -0.643169 0.3171871 27 -2.027727  0.0526
```

Intercept with treatment Λ in 2019

```
                        Value Std.Error DF   t-value p-value
(Intercept)          3.785148 0.2774449 42 13.642884  0.0000
Year2010             1.097056 0.2236428 27  4.905392  0.0000
Treatment2          -0.067939 0.3338308 42 -0.203512  0.8397
Treatment1           0.152375 0.3519860 42  0.432901  0.6673
Elevation           -0.007914 0.0020659 42 -3.830847  0.0004
Year2010:Treatment2  0.643169 0.3171871 27  2.027727  0.0526
Year2010:Treatment1  0.843958 0.3233320 27  2.610188  0.0146
```

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