Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

Hallvard Hafsås

Long term effects of red deer browsing and an extreme winter drought event on bilberry in boreal forests

Gunnar Austrheim

NTNU
Norwegian University of
Science and Technology

Hallvard Hafsås

Long term effects of red deer browsing and an extreme winter drought event on bilberry in boreal forests

Master's thesis in Biology
Supervisor: Gunnar Austrheim
Co-supervisor: Unni Støbet Lande, Erling Meisingset, James D. M. Speed
December 2022

Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

NTNU

Norwegian University of
Science and Technology

Abstract

Changes in climate, human land use and wild game management have altered the levels and nature of disturbances in Norwegian boreal forests. Bilberry is a keystone species in boreal ecosystems and is known to be affected by browsing by the rapidly increasing red deer populations of western Norway. In this study I have examined the long-term effects of a browsing exclosure experiment on bilberry biomass, mean shoot length and shoot density at 9 sites in Tingvoll municipality, Norway. During the experiment, a severe winter drought affected the study area, killing around 63% of above-ground bilberry biomass, giving a unique opportunity to investigate the regrowth combined with the effects of red deer browsing on bilberry in the years following this disturbance. I found that the browsing exclosure treatment resulted in significantly higher growth rates in bilberry biomass and mean shoot lengths, but it had no effect on shoot density. Forest type influenced the relative effect size of the exclosure treatment and was found to be an important predictor of bilberry recovery from a severe winter drought.

In coniferous forests (n=6), bilberry responded to the winter drought with a vigorous compensatory growth of new shoots, quickly replacing and even surpassing the pre-drought shoot density. The shoot density reached a peak 4 years after the drought, after which it dropped back down presumably due to self-thinning, as the biomass and mean shoot lengths continued to increase. This was the case in both browsed and unbrowsed plots, but unbrowsed plots ended up with significantly higher biomass and mean shoot lengths than the browsed plots. This indicates that bilberry in open pine forests has sufficient surplus energy, to reassign a significant amount of energy to temporary accelerated growth to compensate for damage caused by disturbances, even under the high red deer density of present day Tingvoll.

In deciduous forests (n=3), the growth rates in bilberry biomass, mean shoot lengths and shoot density were the same before and after the winter drought indicating a lower ability to quickly recover from such disturbances. Though the growth rates in browsed deciduous plots were positive, recovery was so slow that frequent droughts could possibly lead to extirpation of bilberry. This indicates that the resource allocation strategy of bilberry in deciduous forests might be more constrained, leaving no significant room to reassign resources to temporary accelerated growth to compensate for damage caused by disturbances, at least under the high red deer density of present day Tingvoll.

Overall, bilberry resilience is high. To cause lasting decreases in bilberry abundance it must be subjected to multiple stressors such as shade, competition, and high browsing pressure, in addition to destructive disturbances such as severe winter droughts. Browsing at the current day red deer density of Tingvoll municipality likely improves bilberry resilience in coniferous forest by preventing the establishment of highly competitive common heather and deciduous trees, but lowers bilberry resilience in deciduous forest by reducing growth rates to a critically low rate where its susceptibility to major disturbances is increased. I recommend no substantial changes to the red deer population of Tingvoll on account of bilberry, as the current density mediates stability and resilience in the main habitiat of bilberry.

Sammendrag

Forandringer i klima, arealbruk og viltforvaltning har ført til endringer i nivå og type av forstyrrelser i norske boreale skoger. Blåbær er en nøkkelart i boreale økosystem og det er kjent at den blir påvirket av beiting fra de raskt økende hjortebestandene på vestlandet. I denne studien har jeg undersøkt langtidseffektene etter en eksperimentell utgjerding av hjort på blåbærplantas biomasse, skuddlengde, og skuddtetthet på 9 steder i Tingvoll kommune, Møre og Romsdal. Underveis i forsøksperioden var det en alvorlig tørkeepisode om vinteren som drepte omtrent 63% av den delen av biomassen til blåbær som er over bakken. Dette har gitt en unik mulighet til å undersøke gjenveksten etter denne forstyrrelsen og hvordan den blir påvirket av hjortebeiting. Jeg fant at utgjerding av hjort førte til signifikant høyere vekstrater i biomasse og skuddlengde hos blåbær, men skuddtetthet var upåvirket. Skogtypen påvirket både hvor stor effekt utgjerdinga hadde, og hvordan blåbær hentet seg inn igjen etter alvorlig vintertørke.

I barskog (n=6) reagerte blåbær på vintertørken med kraftig kompenserende tilvekst av nye skudd, som etter kort tid førte skuddtettheten tilbake til samme nivå som før tørken og senere til enda høyere nivå. Skuddtettheten nådde en topp 4 år etter tørken. Etter denne toppen sank skuddtettheten, trolig på grunn av en selvtynningseffekt, mens biomassen og skuddlengden fortsatte å vokse. Dette skjedde i både beita og ubeita felt, men de ubeita feltene endte opp med signifikant høyere biomasse og skuddlengde enn de beita feltene. Dette tyder på at blåbær i forholdsvis åpen furuskog har tilstrekkelig energioverskudd til å midlertidig omfordele ressurser til økt vekst for å kompensere for skader påført av forstyrrelser som alvorlig tørke. Dette gjelder selv under den høye hjortetettheten i dagens Tingvoll kommune.

I løvskog var vekstratene til blåbær i form av biomasse og skuddlengde like store før og etter vintertørken. Dette tyder på en redusert evne til å hente seg raskt inn igjen etter slike forstyrrelser. Selv om vekstratene i beita løvskog var positive, gikk gjenveksten så sent at hyppige alvorlige tørkeepisoder kan føre til stedvis lokal utryddelse av blåbær. Dette tyder på at strategiene som blåbær i løvskog har for ressursfordeling kan ha større begrensninger enn i barskog. Dette kan føre til en manglende evne til å omfordele ressurser til midlertidig økt vekst for å kompensere for skader forårsaket av forstyrrelser som alvorlig vintertørke, i alle fall under dagens høye hjortetetthet i Tingvoll.

Jevnt over viser blåbær en høy grad av robusthet. For at blåbær skal oppleve varig nedgang må den utsettes for flere stressmoment som skygge, konkurranse og høyt beitetrykk, i tillegg til ødeleggende forstyrrelser som alvorlig vintertørke. Beiting fra dagens tette hjortebestand i Tingvoll forsterker trolig robustheten til blåbær i barskog ved å hindre konkurransedyktige arter som røsslyng og løvtrær i å etablere seg, men senker robustheten til blåbær i løvskog ved å redusere vekstraten til et kritisk lavt nivå der sårbarheten for alvorlige forstyrrelser øker. Jeg anbefaler ingen markant endring i hjortebestanden i Tingvoll for blåbærplantas skyld, ettersom dagens tetthet av hjort vedlikeholder stabiliteten og robustheten til hovedhabitatet til blåbær.

Preface

The datasets used in this thesis have been provided by NIBIO, Tingvoll, and has been collected by their researchers as well as various students involved in the SUSTHERB project. No one mentioned, no one forgotten.

Acknowledgments

I would like to thank my supervisors Gunnar Austrheim and Erling Meisingset for their patience and support during difficult times, and their prompt and insightful feedback and guidance during "easy" times throughout this thesis work. Thanks to James Speed for his useful inputs and suggestions, especially on the data analyses. Thanks to Unni Støbet Lande and Hanne Iren Dalen who braved the mosquitoes, gnats, and ticks of Tingvoll, patiently counting bilberry leaves with me. Finally, I'd like to thank my family and friends for their support and encouragement.

Contents

Figures

Tables

1 Introduction

Changes in climate and human land use patterns worldwide impact biodiversity of various taxa in most habitats. In a warming world, the areas where various species have their temperature optimum shifts upwards and northwards. To survive and persist species need to adapt or migrate (Graae et al., 2018). Humans play a significant role in many ecosystems, through agriculture, forestry, land use, animal husbandry and through active management of many wildlife species.

Many ungulate populations in the northern hemisphere have increased in density and range occupation in recent decades (McShea et al., 1997; Putman et al., 2011). The majority of these ungulate species are now widespread in many countries and often with high population densities (Apollonio et al., 2010). In Norway, changes in agricultural practice and wildlife management practices since about 1970 has caused a major shift in the large herbivore communities of Norwegian forests away from livestock in favour of wild cervids (Austrheim et al., 2011; Speed et al., 2019). The forest cervid species of Norway, red deer (*Cervus elaphus*), moose (*Alces alces*), and roe deer (*Capreolus capreolus*), have all increased dramatically in density during the last decades because of the changes in wildlife management (Meisingset, 2015) and have contemporarily benefitted from higher access to food resources due to less livestock and favourable forestry practices like clear-cutting (Andersen et al., 2010; Austrheim et al., 2011; Speed et al., 2019).

Herbivores affect vegetation in myriad ways (Côté et al., 2004; Kolstad et al., 2019; Kolstad et al., 2018; Speed, Austrheim, et al., 2014), with cascading effects onto other trophic levels such as birds (Allombert, Gaston, et al., 2005) and invertebrates (Allombert, Stockton, et al., 2005; Melis et al., 2006). However, various herbivore species have dissimilar effects on vegetation due to different grazing, browsing, and habitat preferences (Austrheim et al., 2011; Garcia et al., 2012). Overall, cervids browse more and graze less than the most common livestock species (Austrheim et al., 2011; Côté et al., 2004). In western Norway, red deer is the dominant forest cervid species. Red deer is an intermediate feeder, mainly grazing and browsing in the field layer (Albon & Langvatn, 1992) and can mediate plant heterogeneity in boreal forests (Lilleeng et al., 2016).

Bilberry *(Vaccinium myrtillus)* is a dominant species in the field layer of many of Norway's boreal forests. It is a keystone species, providing shelter and food for many animal species, including cervids like red deer *(Albon & Langvatn, 1992; Faber & Lavsund, 1999; Gebert & Verheyden-Tixier, 2001; Mysterud, 2000; Spitzer et al., 2020)*. While bilberry performance in boreal forests is affected by red deer browsing at present densities (Côté et al., 2004; Hegland et al., 2010; Hegland et al., 2005; Lilleeng, 2018; Parlane et al., 2006; Welch et al., 1994), the species has adaptations that gives it some measure of tolerance for herbivory, such as compensatory vegetative growth with increased branching (Emanuelsson, 1984; Tolvanen et al., 1992) and growth of compensatory leaves (Bjerke et al., 2018). Indeed, while most dwarf shrubs have the highest relative abundance under no or low browsing intensity (Hegland & Rydgren, 2016), bilberry has been shown in some circumstances to have a higher relative abundance under intermediate browsing intensity than under no or low browsing intensity (Hegland & Rydgren, 2016; Kolstad et al., 2018).

Herbivory is not the only challenge that plants in the boreal forest face. All boreal plant species need adaptations for surviving winter, as living plant tissue can be damaged by frost. Adaptations can include chemical and morphological defence mechanisms against the cold (the evergreen way), defending most of the plant but felling the leaves (the deciduous way), surviving in the root system but growing new above-ground parts every year (the perennial way), or living only one season and overwintering as seeds (the annual way). Plants of short stature can also have an advantage when covered with snow, as winter conditions are less harsh under snow cover (Kreyling et al., 2012). The strategy that bilberry relies on depends to a large degree on having sufficient snow cover to protect it from frost and winter drought (Kreyling et al., 2012; Tahkokorpi et al., 2007), but it is also a deciduous dwarf shrub, felling its leaves each autumn, while the evergreen stems and the rhizome goes dormant. This contrasts with other common dwarf shrubs like lingonberry *(Vaccinium vitis-idaea)* and common heather *(Calluna vulgaris)*, which are evergreen.

Coastal Norway is expected to get less reliable snow cover as climate change progresses, as well as more frequent periods of warm, wet, or dry weather during winter (IPCC, 2001, 2007; Räisänen & Eklund, 2012). As winter temperatures in these coastal regions often is around zero degrees, periods with thawing and freezing are frequent. Such variation is stressful for species like bilberry especially when combined with little snow cover (Tahkokorpi et al., 2007). Even though the climate in general is increasingly warmer and wetter, more frequent and longer periods with dry weather are also expected. Such winter drought events can lead to increased mortality and reduced fitness in many plants (Bjerke et al., 2017; Meisingset et al., 2015; Tahkokorpi et al., 2007), though surviving will often lead to increased resistance to such events in the future (Jump & Peñuelas, 2005; Walter et al., 2013).

Given the rapid changes in both the herbivore populations and the climate over the last several decades, an understanding of how possible interactions of climate and herbivory may affect keystone species like bilberry is a pressing matter. Previous studies have shown that cervid herbivory can mediate a change in the rate and direction of succession after disturbances (Côté et al., 2004; Kolstad et al., 2018), with long-lasting effects (Nuttle et al., 2014), or lead to alternate stable states where a species will do fine or be extirpated based on initial abundance (Augustine et al., 1998). Red deer browsing has been found to impact bilberry by causing smaller individual ramet sizes and reducing total bilberry biomass (Hegland et al., 2005), despite efforts by bilberry to compensate with vegetative growth (Emanuelsson, 1984; Tolvanen et al., 1992). However, bilberry responses to browsing has been shown to be highly context-dependent, with reactions differing due to resource availability (Hegland et al., 2010), forest type (Speed, Austrheim, et al., 2014), and browsing intensity (Hegland & Rydgren, 2016; Hegland et al., 2005). Depending also on the responses of other species to herbivory and the other species' ability to compete with bilberry, bilberry can thus both increase (or decrease less) or decrease (or increase less) in relative abundance due to browsing. In several species, larger individual plants have been found to be selected for browsing (Côté et al., 2004), impacting the morphology of the vegetation by lowering and homogenizing plant heights.

Browsing lawn is a concept describing a system where woody plants form a dense and productive but short cover, kept stable by continued browsing hindering height growth (Cromsigt & Kuijper, 2011). In the strictest definition, a browsing lawn should be shaped by intense browsing leading to increased resource availability (facilitated by dung deposition etc.), system productivity and share of palatable species. Though examples of true browsing lawns in the strictest sense seem to be rare, at least in Norway, systems with superficial similarity to browsing lawns have been found for rowan (*Sorbus aucuparia*) browsed by red deer (Speed, Meisingset, et al., 2014), as well as rowan and bilberry browsed by moose (Kolstad et al., 2018). In both these examples the investigated plants within the exclosures responded by growing larger individuals and more biomass, but a lower density of individual shoots compared with their browsed control.

One possible explanation for the large variance in plant responses to herbivory could be different resource allocation strategies, which might depend on the biotic and abiotic factors the plant is subjected to. According to the compensation continuum hypothesis (Maschinski & Whitham, 1989), plants have a decreased ability to compensate after herbivory if they experience higher competition or lower resource availability. Since bilberry has its optimum in relatively nutrient poor soils, but is heavily affected by light availability (Eckerter et al., 2019; Eldegard et al., 2019; Hester et al., 1991), one would expect the resource availability for bilberry in the context of the compensation continuum hypothesis to be decided more by light availability than soil nutrient availability.

According to the theory of growth-differentiation balance, plants have a trade-off between allocating resources to growth or defence (Herms & Mattson, 1992). In a highly productive habitat, bilberry would face stronger competition from other plant species, and might have to allocate more resources to growth, leaving less resources to be allocated freely to defence, reproduction, or compensation. Bilberry has indeed been shown to be more palatable to both invertebrates and rodents when growing in more productive habitats (Pedersen et al., 2011; Schrijvers-Gonlag et al., 2020), and in more shaded habitats (Schrijvers-Gonlag et al., 2020). Bilberry also seem to tolerate higher stand density in pine forest than in deciduous forest (Eldegard et al., 2019), and has been shown to have a poorer tolerance to red deer browsing in deciduous forests than in pine forests (Speed, Austrheim, et al., 2014).

While warm winters have been shown to impact bilberry negatively (Ogren, 1996; Wipf et al., 2009), the relationship is likely complex, as other studies have found no impact of warmer winters on bilberry performance (Boulanger-Lapointe et al., 2017). Even when it is severely affected, bilberry has been shown to often survive and start growing new shoots to compensate for lost tissue (Tolvanen, 1997). Even after fires, which are rare disturbances that remove large amounts of above-ground biomass, bilberry has been shown to compensate well by growing new shoots, but require several years to fully recover biomass and coverage (Marozas et al., 2007; Skre et al., 1998). Geometrid moth outbreaks and higher densities of rodents that eat bilberry shoots has also been linked to reduced bilberry performance (Boulanger-Lapointe et al., 2017). When a severe winter drought is accompanied by outbreaks of defoliating geometrid moths, bilberry suffers high mortality (Bjerke et al., 2017). Though geometrid moth outbreaks in Norway is a phenomenon mainly linked to mountain birch (*Betula pubescens* ssp. *Tortuosa)* forest, the results of Bjerke et al. (2017) and Boulanger-Lapointe et al. (2017) do establish that a combination of climate events and herbivory can have profound effects on bilberry. However, none of these examples of effective bilberry compensation after high impact disturbances are from highly productive habitats. Presumably, the same possible limitations regarding resource allocation strategies that bilberry might face in the context of the small-scale disturbance of browsing, might also apply in the case of severe disturbances such as droughts, fires, and geometrid moth outbreaks.

This study addresses the long-term effects of red deer browsing combined with a severe winter drought event on the performance and morphology of bilberry in a Norwegian boreal forest ecosystem. The study has involved the experimental exclusion of red deer browsing from several forest locations in a part of western Norway from 2008 to 2021, comprising both deciduous and coniferous forest. During the experiment, in the winter of 2013-2014, a severe winter drought hit the west coast of Norway, including the study area (Bjerke et al., 2017; Meisingset et al., 2015).

I examined the effects of red deer exclusion on the biomass, shoot length, and shoot density of bilberry. The effects were examined three times before and five times after a severe drought and in both coniferous and deciduous forest locations. I predict bilberry biomass and shoot length to increase over time in the unbrowsed exclosures, while shoot density decreases. I predict the exclosure treatment to have a stronger effect in deciduous forests than in coniferous forests. I expect the severe winter drought has caused an immediate sharp drop in bilberry biomass, shoot length, and shoot density, followed by increased growth rates in all three due to compensatory growth. Furthermore, I predict that this compensatory growth response will be weaker in browsed control plots than in the unbrowsed exclosures, and weaker in deciduous forest locations than in coniferous forest locations.

2 Material and methods

2.1 Study area

All field data was collected in Tingvoll municipality in Møre & Romsdal county in central Norway, approximately at 62.9 ̊N, 8.2 ̊E (Figure 1). The municipality is mostly within the middle boreal vegetation zone (Moen, 1998). The climate is oceanic (Moen, 1998), with a mean annual precipitation of 1160 mm per year during the 1961-1990 climate normal (Førland, 1993). The mean annual temperature for the same period was 5.6 °C, while the mean was -0.6 for the winter months (January-March) and 13.1 for the summer months (June-August) (Aune, 1993). In the new 1991-2020 climate normal, mean annual precipitation in Tingvoll was 1243 mm per year (Meteorologisk institutt (MET), 2021a), while the mean annual temperature was 6.8 °C, with a mean of 1.1 °C for the winter months and 13.9 °C for the summer months (Meteorologisk institutt (MET), 2021b). Moving inland, gradually lower temperatures and precipitation, but more snow should be expected (Mysterud et al., 2000). As the average temperature during winter is close to zero, the snow cover is highly variable, both in the amount, duration, and timing.

Tingvoll municipality is a peninsula characterised by rolling forested hills broken up by farmland, wetlands, and settlements. The forests in Tingvoll are dominated by pine on acidic soil, and a mix of boreal and boreonemoral deciduous tree species on more alkaline soils. Livestock mostly does not graze in the woods in this region, and while there are some moose and roe deer in the area, red deer remains the dominant large herbivore species at an estimated metabolic biomass of around 215 kg/km^2 in 2015 (Speed et al., 2019), or an estimated winter population of a total of around 2600 individual red deer in 2021 which equals to around 8,4 deer per km^2 (Omholt & Meisingset, 2022).

In 2008 a project was started in Norway to study moose, red deer, and their food sources, aiming to provide data to enable a sustainable management of cervid populations (SUSTHERB, https://www.ntnu.edu/museum/sustherb), see also Speed, Meisingset, et al. (2014). As a part of this project, an experiment has been conducted in Tingvoll, involving the experimental exclusion of red deer from forest plots, to investigate the effects on the plants in the field layer. The six coniferous locations in the study are all relatively low productivity and mostly dominated by ericoid dwarf shrubs, of which bilberry is the most abundant. The three deciduous locations are varied, but they are all significantly more productive than the coniferous locations. They include abundant forbs and graminoids competing or co-existing with bilberry. The scope of this study is, however, limited to effects on bilberry.
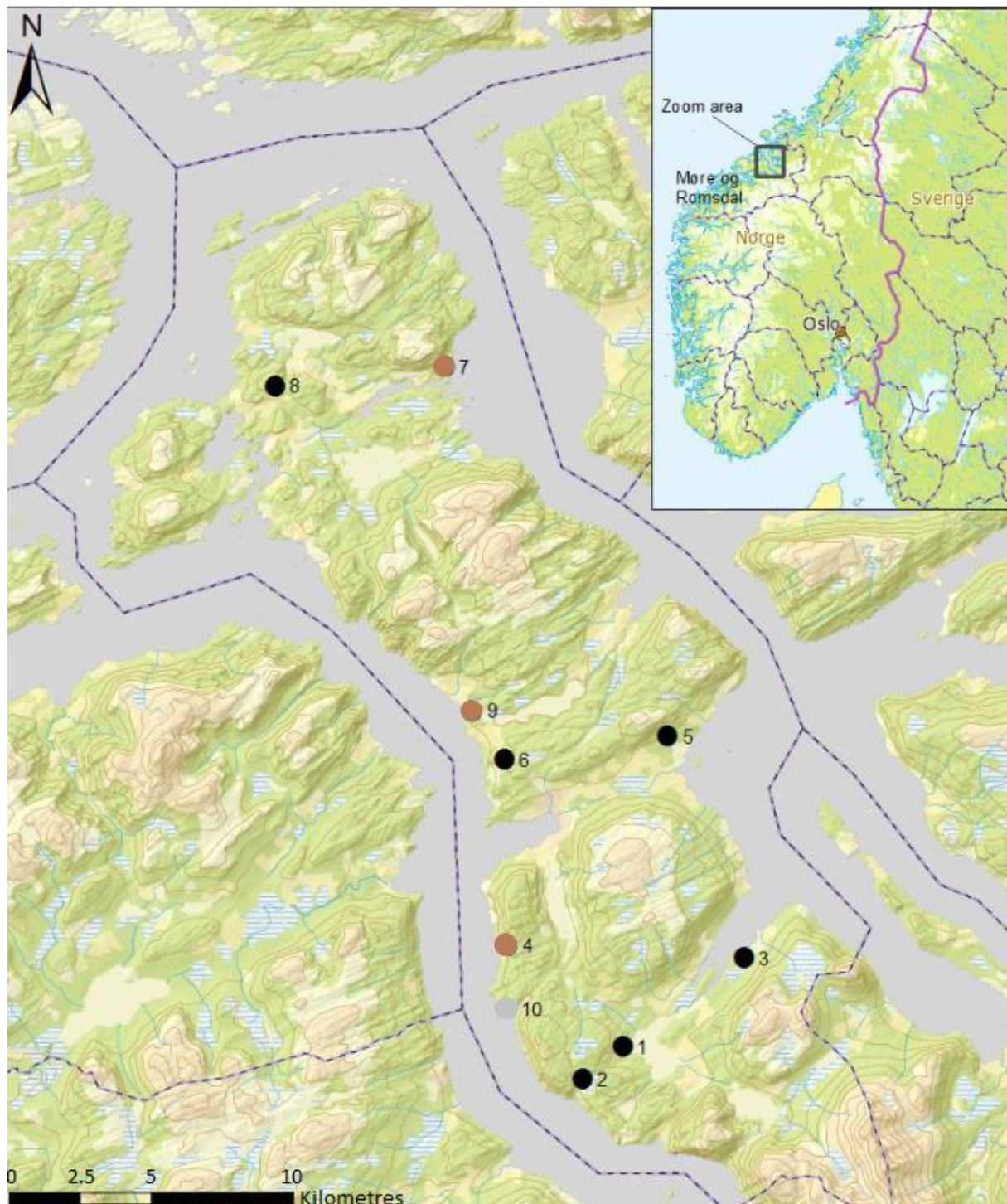
Figure 1: A map of Tingvoll municipality in Møre & Romsdal county with the locations involved in the SUSTHERB-project together with an overview map. The black dots are coniferous forest locations, the brown dots are deciduous forest locations. The location names are 1) Haltbakken, 2) Rottås, 3) Åsprong, 4) Ormset, 5) Holmeid, 6) Bråttvika, 7) Kanestraum, 8) Gjengset and 9) Gyl. Location 10 is no longer part of the project due to an incident where livestock got into the exlosure. Reproduced and altered with permission from (Meisingset, 2015).

2.2 Experimental design

Data was sampled from 18 permanent plots measuring 20 by 20 m. They were blocked so that each of the 9 locations still in the study (Figure 1) had one treatment plot surrounded by a fence and one control plot roughly 20-50 m apart. The treatment fence was three meters tall, consisting of 10 by 10 cm mesh. This fence excluded all red deer and other large herbivores from the treatment plots, but allowed invertebrates, birds, and small mammals access (e.g., small rodents). In each plot, 10 permanent subplots of 0.5 x 0.5 m were randomly distributed, from which data would be collected. The plots were established late in 2008, after the baseline data was collected.
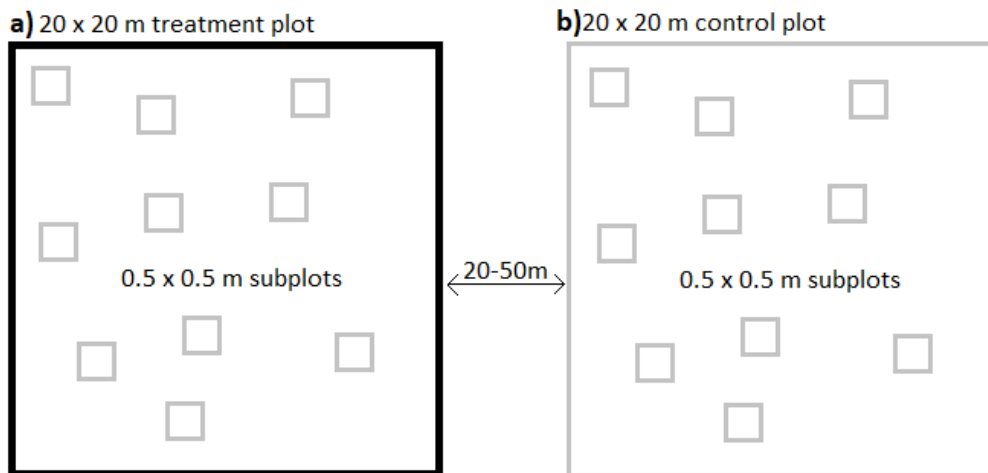
Figure 2: The experimental design had a treatment and control plot at each of the nine locations, with each plot having 10 different randomly distributed permanent subplots from which the data was sampled. Grey outlines signify open plots while the solid black outline around the treatment plot signify the deer excluding fence. The figure is not to scale.

2.3 Bilberry sampling

Data was sampled from the subplots by placing down a 0.5 x 0.5 m frame divided into a grid of 25 cells (Figure 3). The relative biomass of bilberry was then measured by proxy using the point-intercept method (Jonasson, 1988) registering the total number of bilberry hits per subplot across the 16 points defined by the cell grid.
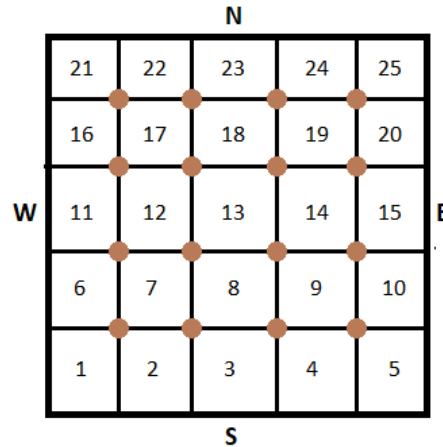
Figure 3: A schematic drawing of the 0.5 x 0.5 m point-intercept frame that was placed over the subplots to aid in the sampling methods. The 25 cells are numbered in the order from which they were sampled. The 16 intercept points at which the point-intercept method was used are marked with a green dot. Not to scale, every cell is 10 x 10 cm.

For each sub-plot the mean shoot length (cm) was estimated by measuring at least 10 shoots, beginning from the south-western-most cell in the 0.5 x 0.5 m frame and moving first eastwards cell by cell, and then opening new rows northward according to need. As soon as 10 shoots had been registered, the remaining shoots in the last cell were also included. In cases where there were fewer than 10 shoots in the whole frame, the frame was moved 1 m to the north and counting continued. This could be repeated by setting the frame 1 m west, 1 m east and 1 m south of the subplot. If the total number of shoots were still below 10, counting fewer than 10 was finally accepted. Data has been sampled over a period of 13 years (2008, 2010, 2012, 2014, 2016, 2018, 2020 and 2021). The mean number of shoots of a single cell was calculated by dividing the number of shoots measured in a subplot by the number of cells over which they were distributed. From this, the shoot density per square meter was estimated by multiplying the mean number of shoots per cell by 100. For each shoot, it was registered whether they had any visible signs of browsing. From this, a ratio of browsed shoots was calculated by dividing the number of measured shoots that had been browsed by the total number of shoots measured in that subplot that year.

2.4 Statistical methods

The data was analysed using R version 4.13 (R Core Team, 2022). LMM (Linear mixed models) was chosen to test the response variables. The lme function of the R package nlme (Pinheiro et al., 2022) was chosen for the modelling, because of its extensive options for modelling correlation structures. Due to the blocked design, all models used subplot nested under plot as a random effect to account for spatial autocorrelation. To check whether we had to account for temporal autocorrelation, all response variable time series were tested by comparing simple models of all responses against an equally simple model including an autoregression-structure and checking whether including the structure would improve the model significantly by reducing the AICc-value. The corARMA(1) function assumes an autoregressive moving average along a continuous variable along an explicit structure. In this case along the variable time, structured by subplots nested under plot. I.e., it assumes that the biomass in a particular subplot in a particular plot will correlate with the biomass of the same subplot in the same plot one year earlier. For every response variable, the tested corARMA(1) structure significantly improved the model, and so was included further in the modelling procedure.

Table 1: An overview of the variables used in the analyses.

Response variables	
Bilberry biomass index	Based on number of hits per subplot. Log-transformed.
Bilberry shoot length	Average length of the shoots in each subplot in centimetres. Log-transformed.
Bilberry shoot density	Average density shoots in each subplot in number per square meter. Square root transformed.
Fixed effects	
Time	Number of years since start of experiment. Continuous.
Treatment	Boolean unbrowsed fenced plots or browsed control plots.
Drought event	Boolean before or after the winter drought event of 2014.
Other	
Forest type	Boolean coniferous or deciduous
Rate of browsed shoots	Ratio of shoots that have fresh or up to several years old visible signs of damage from browsing.

The biomass proxy and the shoot mean lengths were log+1-transformed and the shoots per square meter was square root transformed to approach a normal distribution of error. To enable testing the effects of the winter drought, a variable was created and defined as 0 for all datapoints before 2014 and as 1 for all datapoints from 2014. This variable thus distinguishes whether or not the datapoint is before or after the winter drought of 2014, which dried out much of the bilberry in the region (Meisingset et al., 2015).

To test the long-term effects of the treatment and the winter drought on the response variables, I needed to test the effects of time, treatment and the drought event and all interactions, in separate models for each response variable. All variables involved in the analyses can be found in table 1. To test for the effects of the forest type, the forest type also had to be included in the analysis. Since the deciduous forest locations were visually very different from the coniferous locations (Speed, Austrheim, et al., 2014), and to avoid the potential for hard to interpret four-way interactions, separate models were created for coniferous and deciduous locations instead of including the forest type as yet another explanatory variable.

An initial model was constructed for each of the two forest types and for each of the response variables (Table 1). The initial models included all three explanatory variable (Table 1), as well as all possible interactions between them. The dredge function of the MuMin package in R (Barton, 2022) was used to find the most parsimonious model for each response variable. The model spending the fewest degrees of freedom among the model alternatives with a delta-AICc value of 2 was selected. For every model, but one, the selected model was also the best ranked by AICc. The selected model for bilberry shoot density in coniferous forests was ranked fourth by AICc. The selected model was tested against the best model ranked by AICc. However, neither model was found to be significantly better than the other at $p < 0.05$ using a simple ANOVA test. Tables containing the results from the dredge process can be found in appendix 1.

The final models were validated by the visual evaluation of residual plots (Appendix 2). The r.squaredGLMM function of the MuMin package in R was used to generate pseudo-R-squared values for every final model. Like regular R squared quantifies goodness of fit as a ratio of variation being explained by a simple linear regression, pseudo-R-squared can do the same for mixed effects models. When used with mixed effects models the r.squaredGLMM function returns two values, one for how much of the variation is explained by the fixed effects, and the other for how much of the variation is explained by the entire model.

3 Results

3.1 Browsing ratio

The ratio of browsed shoots per subplot varied from 0 to 1, with an average of 0.24 (SD=0.26) in the browsed control plots over the entire time series (Raw data). After 2014 there was a large temporal variation, with highest browsing ratio in 2016 and 2021. In the unbrowsed plots, the ratio of browsed shoots gradually fell to 0 by 2014 and stayed there (Figure 4).
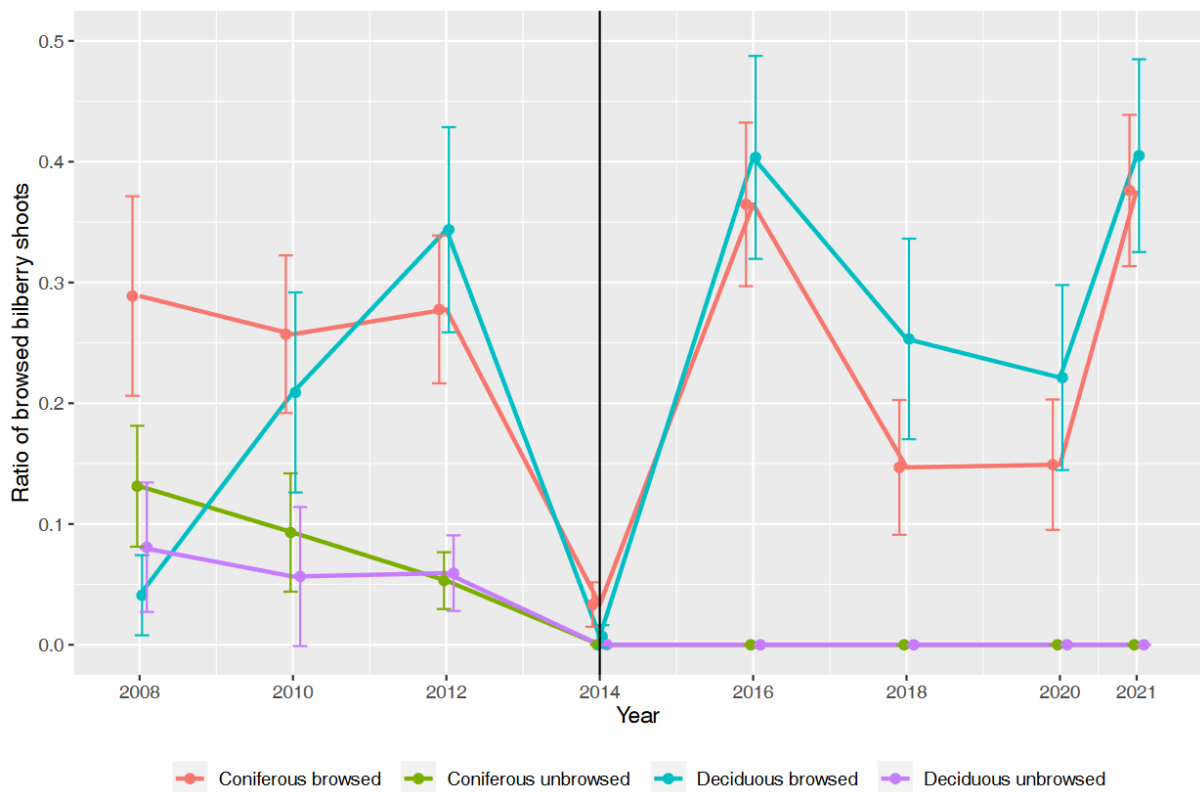
Figure 4: The mean ratio of browsed bilberry shoots over the years 2008-2021 of subplots in all configurations of treatment and forest type. The vertical solid line marks the year of the winter drought. The error bars represent the 95% confidence-interval.

3.2 Biomass

The bilberry biomass index varied from 0 to 109 with a mean of 27 (SD=17) in coniferous forest subplots and from 0 to 39 with a mean of 3 (SD=5) in deciduous forest subplots over the entire time series (Raw data).
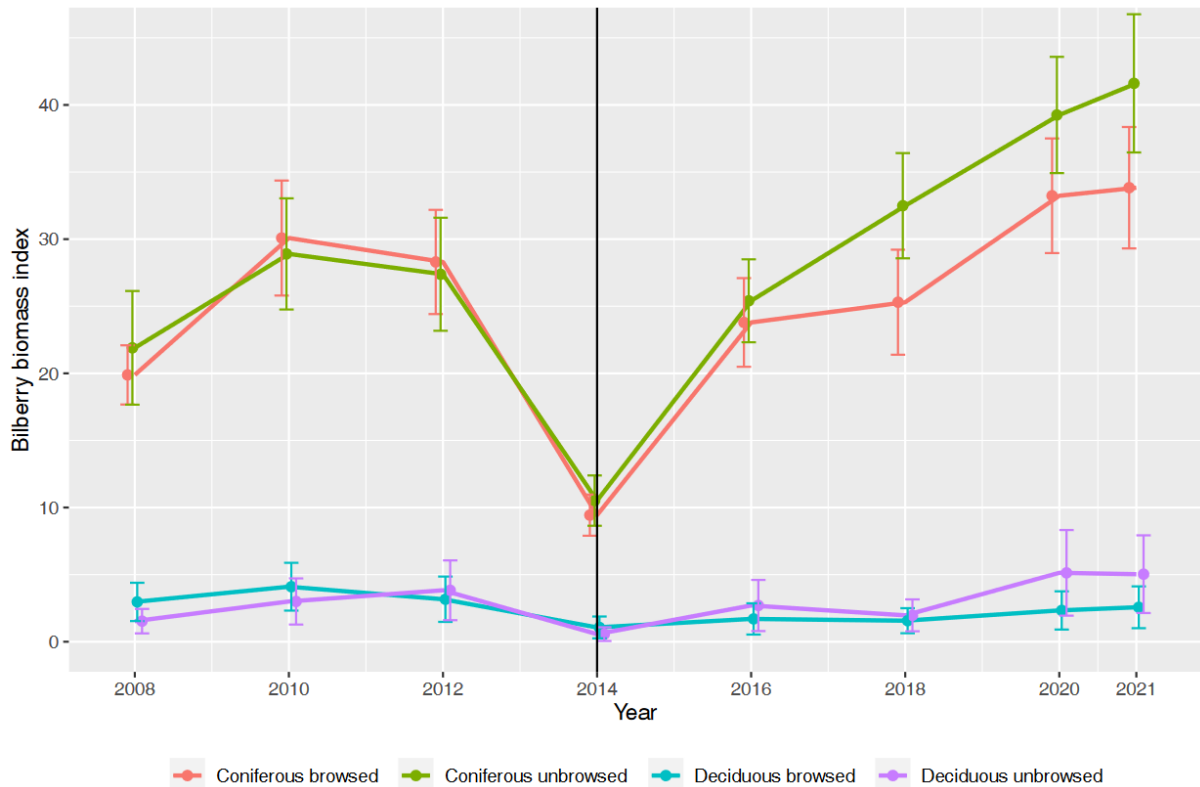
Figure 5: The mean bilberry biomass index over the years 2008-2021 in all configurations of treatment and forest type. The vertical solid line marks the year of the winter drought. Based on raw data, not modelling. The error bars represent the 95% confidence-interval.

For each forest type the final model for bilberry biomass index included all three variables time, treatment, and the drought event, as well as the two-way interaction between treatment and time (Table 2). The model for the coniferous forest type also included the two-way interaction between the drought event and time (Table 2). The explanatory power of the model for the coniferous forest type was 22% for the fixed effects, and 60% for the entire model including correlation structures (Table 2). For the deciduous forest type these values were 48% and 70% respectively (Table 2). The results from the model selection can be found in appendix 1, tables 1 & 4.

In the coniferous forest type before the drought event, bilberry biomass increased by 5.4% per year in the browsed control plots, and by 8.4% per year in the unbrowsed exclosures (Figure 5, Table 2). The browsed control plots and unbrowsed exclosure treatment plots were not significantly different at the onset of the experiment, but the exclosure treatment increased yearly growth in bilberry biomass by 2.8% per year (Figure 5, Table 2). The winter drought caused an immediate reduction of 63% of biomass, which was followed by an increase in the yearly bilberry biomass by 12.1% in the browsed control plots (Figure 5, Table 2). Together with the additive effect of treatment (2.8%), this brought the biomass in the unbrowsed treatment plots to an increase of a total of 15.3% per year (Figure 5, Table 2). No significant multiplicative interaction was detected between the exclosure treatment and the post-drought development.

Table 2: The model outputs and pseudo-R-squared values of the final models for the response variable bilberry biomass in coniferous and deciduous forest locations. All fixed effects and interactions included in the models are listed. The effect size is on a log scale and includes the standard error in parentheses. The code for significance is as follows: ***=P<0.01, grey font = insignificant at P<0.1.

Forest type	Pseudo R squared fixed effects (entire model)	Fixed effects	Effect size (SE)	Significance
Coniferous forest	0.22 (0.60)	(Intercept)	3.030 (0.166)	
		Time	0.053 (0.017)	***
		Treatment	-0.096 (0.232)	
		Drought event	-1.690 (0.100)	***
		Time:Treatment	0.028 (0.009)	***
		Time:Drought event	0.114 (0.019)	***
Deciduous forest	0.48 (0.70)	(Intercept)	0.988 (0.331)	***
		Time	0.037 (0.013)	***
		Treatment	-0.430 (0.468)	
		Drought event	-0.734 (0.098)	***
		Time:Treatment	0.052 (0.014)	***

In the deciduous forest type before the drought event, bilberry biomass increased by 3.8% per year in the browsed control plots and by 9.3% in the unbrowsed exclosures (Figure 5, Table 2). The browsed control plots and unbrowsed exclosure treatment plots were not significantly different at the onset of the experiment, but the exclosure treatment increased yearly growth in bilberry biomass by 5.3% per year (Figure 5, Table 2). The winter drought caused an immediate reduction of 52% of biomass but caused no significant alteration of the yearly growth rate in bilberry biomass (Figure 5, Table 2). No significant interaction was detected between the exclosure treatment and the post-drought development.

3.3 Shoot length

The mean bilberry shoot length varied from 4.4 cm to 46.5 cm with a mean of 17.0 cm (SD=5.9) in coniferous forest subplots and from 4 cm to 28.4 cm with a mean of 11.8 cm (SD=4.2) in deciduous forest subplots over the entire time series (Raw data).
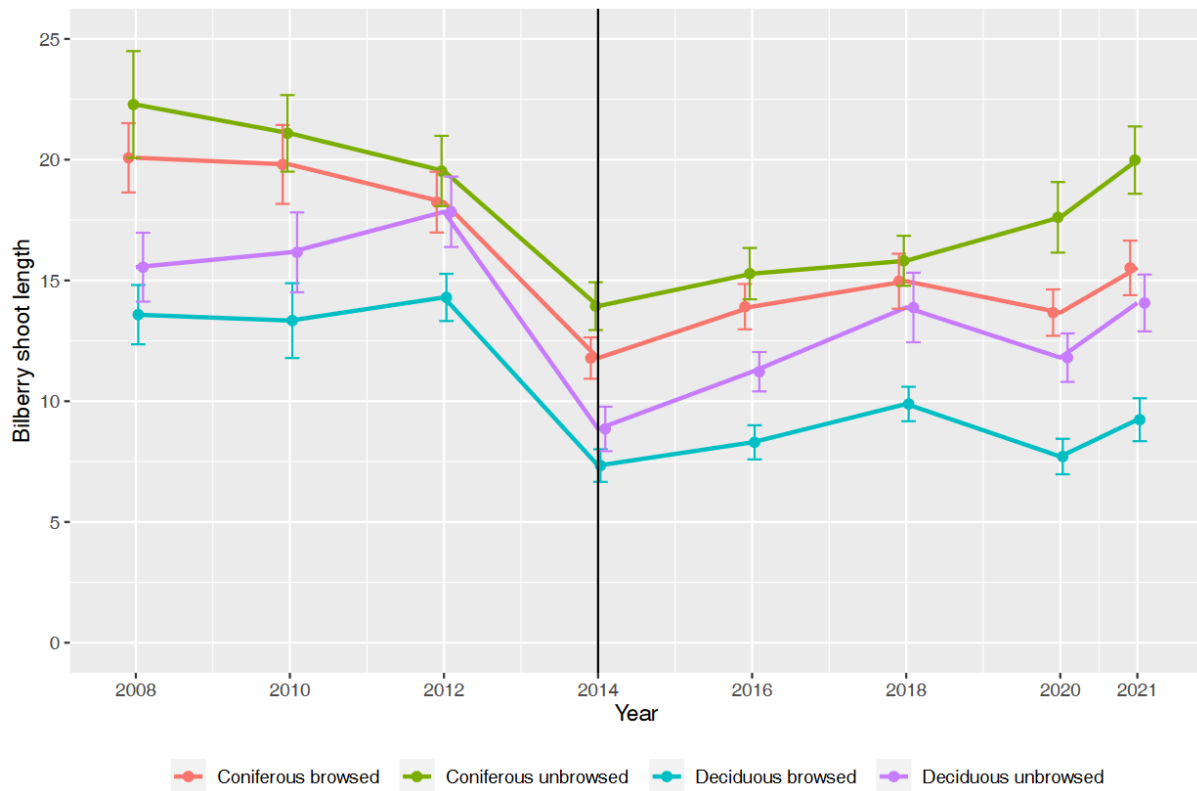
Figure 6: The mean bilberry shoot length (cm) over the years 2008-2021 in all configurations of treatment and forest type. The vertical solid line marks the year of the winter drought. Based on raw data, not modelling. The error bars represent the 95% confidence-interval.

For each forest type the final model for mean bilberry shoot length included all three variables time, treatment, and drought event, as well as the two-way interaction between treatment and time (Table 3). The model for the coniferous forest type also included the two-way interaction between the drought event and time (Table 3). The explanatory power of the model for the coniferous forest type was 24% for the fixed effects, and 61% for the entire model including correlation structures (Table 3). For the deciduous forest type these values were 46% and 68% respectively (Table 3). The results from the model selection can be found in appendix 1, tables 2 & 5.

In the coniferous forest type before the drought event, the mean bilberry shoot lengths decreased by 2.5% per year in the browsed control plots, but only by 1.2% per year in the unbrowsed exclosures (Figure 6, Table 3). The browsed control plots and unbrowsed exclosure treatment plots were not significantly different at the onset of the experiment, but the treatment increased mean bilberry shoot lengths by 1.3% per year (Figure 6, Table 3). The winter drought caused an immediate reduction of 28.1% of mean shoot length, which was followed by an increase in the yearly mean bilberry shoot lengths by 3.1% in the browsed control plots (Figure 6, Table 3). Together with the additive effect of treatment (1.3%), this brought the mean shoot length in the unbrowsed treatment plots to an increase of a total of 4.5% per year (Figure 6, Table 3). No significant multiplicative interaction was detected between the exclosure treatment and the post-drought development.

Table 3: The model outputs and pseudo-R-squared values of the final models for the response variable bilberry shoot length (cm) in coniferous and deciduous forest locations. All fixed effects and interactions included in the models are listed. The effect size is on a log scale and includes the standard error in parentheses. The code for significance is as follows: ***=P<0.01, grey font = insignificant at P<0.1.

Forest type	Pseudo R squared fixed effects (entire model)	Fixed effects	Effect size (SE)	Significance
Coniferous forest	0.24 (0.61)	(Intercept)	3.028 (0.077)	***
		Time	-0.025 (0.007)	***
		Treatment	0.029 (0.107)	
		Drought event	-0.666 (0.042)	***
		Time:Treatment	0.013 (0.004)	***
		Time:Drought event	0.056 (0.008)	***
Deciduous forest	0.46 (0.68)	(Intercept)	2.625 (0.079)	***
		Time	0.025 (0.005)	***
		Treatment	0.067 (0.114)	
		Drought event	-0.646 (0.038)	***
		Time:Treatment	0.021 (0.005)	***

In the deciduous forest type before the drought event, the mean bilberry shoot length increased by 2.5% per year in the browsed control plots, and by 4.7% per year in the unbrowsed control (Figure 6, Table 3). The browsed control plots and unbrowsed exclosure treatment plots were not significantly different at the onset of the experiment, but the treatment increased yearly growth in mean bilberry shoot lengths by 2.1% per year (Figure 6, Table 3). The winter drought caused an immediate reduction of 47.5% in mean shoot lengths but caused no significant alteration of the yearly growth rate in mean bilberry shoot lengths compared with pre-drought growth rates (Figure 6, Table 3).

3.4 Shoot density

The mean bilberry shoot density varied from $0/m^2$ to $1400/m^2$ with a mean of $341/m^2$ (SD=222) in coniferous forest subplots and from $0/m^2$ to $550/m^2$ with a mean of $92/m^2$ (SD=99) in deciduous forest subplots over the entire time series (Raw data).
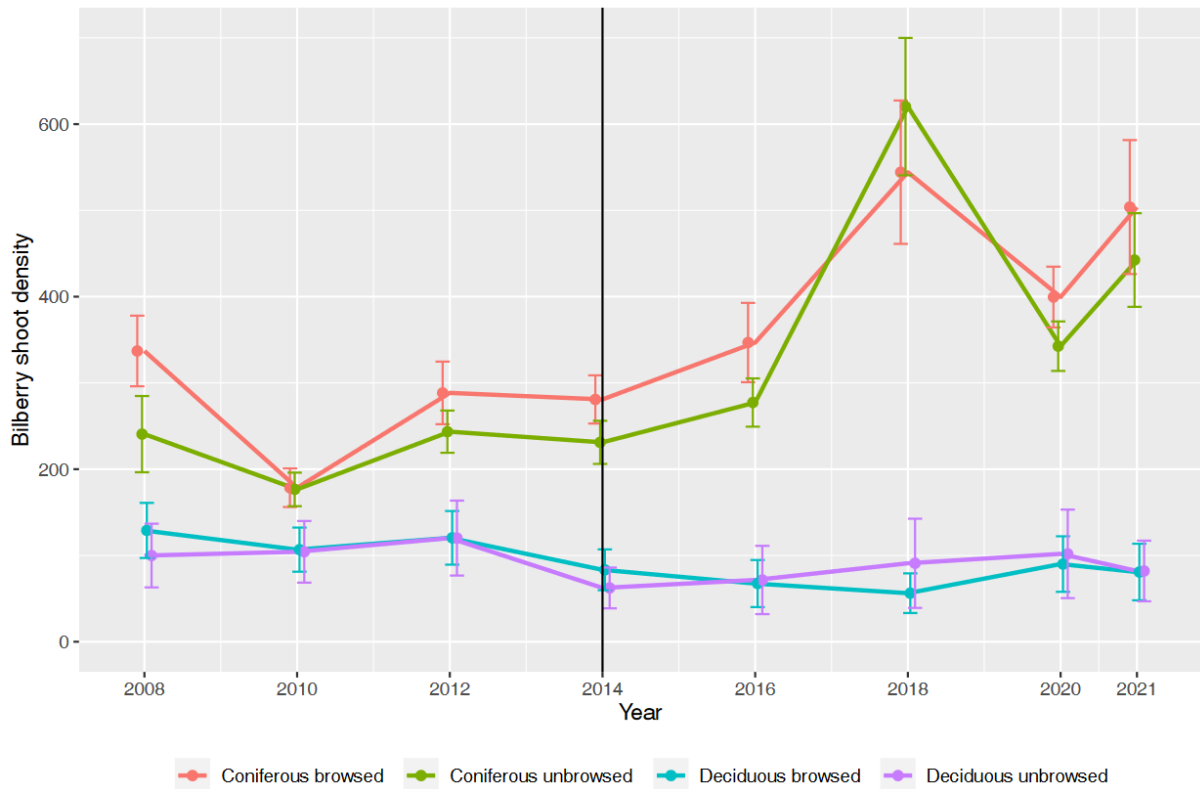
Figure 7: The mean bilberry shoot density over the years 2008-2021 per square metre in all configurations of treatment and forest type. The vertical solid line marks the year of the winter drought. Based on raw data, not modelling. The error bars represent the 95% confidence-interval.

For each forest type the final model for bilberry shoot density included the variable drought event (Table 4). The model for the coniferous forest type also included the variable time and the two-way interaction between the drought event and time (Table 4). The explanatory power of the model for the coniferous forest type was 20% for the fixed effects, and 37% for the entire model including correlation structures (Table 4). For the deciduous forest type these values were 3% and 51% respectively (Table 4). The results from the model selection can be found in appendix 1, tables 3 & 6.

In the coniferous forest type before the drought event, the mean bilberry shoot density was 221 shoots/m^2 in and did not change significantly over time (Figure 7, Table 4). The browsed control plots and unbrowsed exclosure treatment plots were not significantly different at the onset of the experiment, and the treatment had no significant effect on the change in bilberry shoot density over time (Figure 7, Table 4). After the drought event, the bilberry shoot density started increasing by an average of 9.7% per year until the end of of the time series (Figure 7, Table 4). No significant interaction was detected between the exclosure treatment and the post-drought development.

Table 4: The model outputs and pseudo-R-squared values of the final models for the response variable bilberry shoot density in coniferous and deciduous forest locations. All fixed effects and interactions included in the models are listed. The effect size is on a square root scale and includes the standard error in parentheses. The code for significance is as follows: ***=P<0.01, grey font=insignificant at P<0.1.

Forest type	Pseudo R squared fixed effects (entire model)	Fixed effects	Effect size (SE)	Significance
Coniferous forest	0.20 (0.37)	(Intercept)	14.874 (0.624)	***
		Time	0.009 (0.148)	
		Drought event	-2.917 (0.855)	***
		Time:Drought event	0.730 (0.167)	***
Deciduous forest	0.03 (0.51)	(Intercept)	9.316 (1.370)	***
		Drought event	-2.007 (0.372)	***

In the deciduous forest type before the drought event, the mean bilberry shoot density was 86 shoots/m^2 and did not change significantly over time (Figure 7, Table 4). The browsed control plots and unbrowsed exclosure treatment plots were not significantly different at the onset of the experiment, and the treatment had no significant effect on the change in bilberry shoot density over time (Figure 7, Table 4). After the winter drought, there was an immediate decrease in mean shoot density by 38.4%, but the winter drought had no significant effect on the rate of change in bilberry shoot density over time (Figure 7, Table 4).

4 Discussion

The dynamics of bilberry and other plants can be affected by several factors (Bernes et al., 2018; Bjerke et al., 2017; Hegland & Rydgren, 2016; Jump & Peñuelas, 2005). Browsing may alter plant development in different ways, often by reducing biomass and individual plant sizes. However, the health and growth of many plants can also be greatly affected by climatic conditions, either directly such as by drought, frost, and wind, or indirectly by affecting the extent of herbivory, fungal diseases, and/or insect attacks.

My study has shown that browsing from red deer affected bilberry biomass and shoot length, but not shoot density. Furthermore, my study has shown that the severe winter drought during the winter of 2014 resulted in a dramatic reduction in bilberry biomass, but in the coniferous forest there was a compensatory growth of new shoots to quickly replace dead shoots in numbers, after a few years even reaching a higher shoot density than before the drought. This compensatory growth was reduced, but still effective when bilberry was browsed. In the deciduous forest bilberry did not respond with increased growth rates after the drought, but only failed to recover well when also browsed by red deer. My study highlights that bilberry has a high ability to recover and even increase in biomass after extreme weather conditions. Thus, though browsing may reduce bilberry recovery and regrowth after climatic events like severe winter droughts, bilberry can tolerate it well, especially in coniferous forest. This study has shown that bilberry is a highly resilient species, but that both browsing and climatic factors alone or in interaction may induce large changes in biomass and growth.

4.1 Bilberry dynamics and red deer browsing

For both forest types, both bilberry biomass and mean shoot length increased significantly more in unbrowsed exclosed treatment plots than in the browsed control plots. This agrees with my predictions and concurs with Hegland et al. (2005), and partially with Speed, Austrheim, et al. (2014). The latter found the same results for red deer in deciduous forest, but inconclusive results in coniferous forest over a short-term (4 years). Interestingly, in my models for biomass the time:treatment effect size ±SE in the model for deciduous forest was greater than the time:treatment effect size ±SE in the model for coniferous forest with no overlap. Though the growth rates of bilberry in the browsed deciduous plots of this study were positive, they were also low. This shows that the exclosure treatment had a relatively larger effect on bilberry growth in the higher productivity deciduous forest locations than in the lower productivity coniferous forest locations, which fits my expectations and concurs with Hegland et al. (2010). In a sheep exclosure experiment spanning 60 years in a nutrient poor deciduous forest in England, bilberry ramet size quickly grew, eventually leading to bilberry dominance in the field layer (Vild et al., 2021). Vild et al. (2021) also found that bilberry increased from 2% cover to around 35% cover over 60 years, with about 12% cover in plots where sheep had been excluded for only 30 years. This supports the results of my study, which are that the effects of herbivore exclusion accumulate over time. Furthermore, it shows that such accumulation can continue for long time periods. Conversely, since the full effects have taken time to manifest, it makes sense that short-term studies sometimes have failed to find conclusive results.

While the bilberry shoot density differed between the two forest types, the way shoot density responded to the exclosure treatment was the same. Contrary to my expectations, the treatment had no effect on shoot density. This contrasts with Kolstad et al. (2018), which found bilberry density to increase in open plots browsed by moose. This may be explained by different feeding strategies of red deer and moose when it comes to bilberry or different total browsing pressures due to herbivore density. Interestingly, both cervid species seem to have similar effects on rowan, as Kolstad et al. (2018) and Speed, Meisingset, et al. (2014) found rowan density to be higher but rowan biomass to be lower in open plots browsed by moose and red deer respectively. As browsing pressure increases, negative effects on dwarf-shrubs increases (Hegland & Rydgren, 2016). Bilberry is the most browsing tolerant of the dwarf shrubs, having been shown to have the highest relative abundance under an intermediate browsing pressure (Hegland & Rydgren, 2016). Common heather can otherwise outcompete bilberry in habitats with plenty of light (Hester et al., 1991).

Presumably, given the results of this study, the current day red deer density of Tingvoll results in a browsing pressure in the coniferous forest locations that is high enough to remove competition for bilberry by removing common heather and deciduous tree species but not so high as to favour forbs and graminoids over bilberry. Meanwhile, the current day red deer density of Tingvoll seems to result in a browsing pressure that is tolerated poorly by bilberry in the deciduous forest locations. Whether this is caused by inherent differences in the browsing tolerance of bilberry depending on which habitat it grows in or if the browsing pressure by red deer on bilberry varies between locations cannot be determined with certainty based on my results, as browsing pressure here is only measured by the binary toggle between total exclusion or ambient red deer density.

Though there seems to be no significant difference between the forest types in the ratio of browsed shoots in this study (Figure 4), it has been shown that red deer browsing pressure on bilberry has high spatial variation linked to habitat (Morellet & Guibert, 1999). Thus, it is unclear whether the browsed shoots rate is a good measurement for browsing pressure on bilberry. Hypothetically, if bilberry shoots die younger and are replaced more often in one forest type, then the ratio of browsed shoots could be lower, even at higher browsing pressures. To investigate the causes and mechanisms of why bilberry has poorer browsing tolerance in deciduous forest, it would be useful to have data on space use by red deer. Though camera traps have been placed at the control plots of all locations of this study for the duration of 2021, this data has yet to be analysed. Preliminary data exploration has shown great spatial and temporal variation in red deer activity, however, with all 3 deciduous locations in this study being among the top 4 in total yearly observations (not shown).

4.2 Bilberry dynamics and climate

All three response variables were significantly reduced immediately after the 2014 winter drought in both forest types, as expected. However, the dynamics after the winter drought differed greatly between the forest types. In the coniferous forest type, though most above-ground shoots died, they were quickly replaced by new shoots and there was a substantial increase in the growth rates of biomass and shoot length. This reaction of increased vegetative growth to compensate for frost damage is corroborated by the findings of Tolvanen (1997) and is in line with my predictions. After the drought, the coniferous forest bilberry shoot density peaked after four years (in 2018), after which it decreased. This suggests that 4-5 years after the winter drought, bilberry coverage had recovered fully, and self-thinning of shoots started due to increased intra-specific competition. Interestingly, 5 years has also been found to be the time needed for bilberry to recover after forest fires (Marozas et al., 2007) and severe experimental clipping (Tolvanen et al., 1994) in similar habitats.

I expected the rates of change in all the response variables due to the exclosure treatment to be different before and after the winter drought. In other words, that there would be a time:treatment:drought three-way interaction. My results showed no such effect. However, whether the additive relationship between the time:treatment and the time:drought interactions that I found, or if the three-way interaction would be a better explanation remain uncertain, because the latter spent too many degrees of freedom for my number of independent observations to retain sufficient statistical power. Therefore, while we can conclude that the exclosure treatment has had an effect during the time series of this study, we cannot safely say whether the divergent trajectories between the browsed and unbrowsed plots started at the onset of the experiment or after the winter drought of 2014. However, the study of Vild et al. (2021) shows a gradual accumulation of bilberry biomass and coverage when large herbivores are excluded in the absence of high-impact disturbances, supporting the notion that the divergent trajectories started at the onset of the experiment.

Thus, in habitats where bilberry dominates in the field layer, such as the coniferous boreal forests of this study, it is highly resilient and can recover from a high-impact disturbance such as a winter drought destructive enough to kill virtually all above-ground biomass, through a mechanism of compensatory vegetative growth. Also, red deer browsing even at the current high density deer population in Tingvoll, though it negatively affects bilberry, was not enough to prevent successful recovery.

In the deciduous forest, the shoot density did not recover, while biomass and shoot length continued growing at the same rates as before the drought. Assuming exponential growth at the average growth rates I found, biomass and shoot length should recover after roughly 8 and 15 years respectively in the unbrowsed plots and around 19 and 28 years respectively in the browsed plots. Thus, in deciduous forest, bilberry is still somewhat resilient when large herbivores are excluded, but in browsed deciduous forest, it needs multiple decades to recover from high-impact disturbances such as a severe winter drought. If such droughts were to occur every decade or so, that would likely have major ramifications for bilberry abundance in deciduous forests browsed by red deer. Vegetation types are formed more by climate extremes than climate averages (Beigaitė et al., 2022), and bilberry has been shown to have a poor ability to conserve water (Janke, 1970). Combined with the findings of Økland and Eilertsen (1993), that the forests where bilberry has its optimum almost never experience drought, it makes sense that more frequent droughts would lead to lower abundances of bilberry. Furthermore, there might be a cut-off minimum growth rate to survive a particular disturbance regime. The higher the impact and frequency of disturbances, the higher growth rate is needed to survive. Though the bilberry growth rate is positive in browsed deciduous forest, it may be insufficient for survival in a system of frequent severe droughts.

More frequent extremes such as the winter drought of 2014 is not the only way that climate change might affect bilberry. Higher average temperatures can also affect plant communities directly by favouring or enabling some species over others. One typical example being the colonization of arctic or alpine tundra by trees and shrubs (Kaplan & New, 2006; Paulsen & Körner, 2014). This advance of woody growths has been shown to be hampered by vertebrate herbivory (Christie et al., 2015; Mienna et al., 2022; Post & Pedersen, 2008). However, if herbivory is temporarily discontinued for a number of years, trees may grow into a height refuge, where they are safe from vertebrate herbivores, permanently altering the succession trajectory and allowing the expansion of the treeline (Mienna et al., 2022). Climate warming also seems to favour deciduous tree growth in the boreal forest (Fisichelli et al., 2012; Vuorinen et al., 2020), though, interestingly, both Fisichelli et al. (2012) and Vuorinen et al. (2020) found cervid herbivory to effectively cancel out this effect due to cervids selectively browsing these deciduous species.

A hypothetical total lack of red deer browsing combined with climate warming might lead many of the open pine forests of today to shift into mixed forests functionally emulating the deciduous forest locations in this study. Since bilberry has been shown to compete well in unbrowsed nutrient poor deciduous forest over the long term (Vild et al., 2021), one would expect bilberry to do well in this scenario. However, if red deer were to be reintroduced again later, these new mixed forests would likely not transition back to open pine forest as a great number of deciduous trees would have grown into a height refuge from browsing. Instead, bilberry performance and resilience might decrease, emulating the situation in the deciduous forests of today. Thus, continued red deer browsing can be said to increase bilberry resilience by maintaining a forest type in which it reliably performs well, despite the warming climate which favours succession into a forest type in which bilberry could perform worse, especially if browsed.

4.3 Bilberry resilience and resource allocation strategy

The poorer ability of bilberry to compensate after disturbances in the deciduous forest when browsed agrees with my predictions and the framework of the compensatory continuum hypothesis (Maschinski & Whitham, 1989) can help explain it. Though this hypothesis posits stronger compensation with resource availability, the limiting factor for bilberry does not seem to be soil nutrition, as seen by its optimum being in mesic low-productivity systems (Økland & Eilertsen, 1993). Combined with the frequent adverse reactions of bilberry to high shade (Eckerter et al., 2019; Eldegard et al., 2019; Hester et al., 1991), higher shading from the canopy, especially in deciduous forests (Eldegard et al., 2019), one might deduce that bilberry has a smaller surplus of energy in highly shaded habitats. The increased competitive pressure from other plant species in a more productive habitat, could further constrain the resource allocation strategies of bilberry by making relatively high vegetative growth rates "mandatory" to avoid being outcompeted, leaving little room to change priorities due to disturbances such as browsing or severe winter droughts.

Bilberry growing in high shade and high productivity habitats have been shown to be more palatable (Pedersen et al., 2011; Schrijvers-Gonlag et al., 2020). This can be explained in the framework of the theory of growth-differentiation balance (Herms & Mattson, 1992). Not only compensatory growth responses, but also defences against herbivory might by necessity have been deprioritized in bilberry growing in highly shaded productive habitats in favour of continuously high rates of vegetative growth. This is further corroborated by Pedersen et al. (2011) finding an interaction effect between browsing intensity and habitat productivity on bilberry palatability, with vole preferring to feed on previously unbrowsed bilberry from low productivity habitats, but previously browsed bilberry from high productivity habitats. This indicates that the bilberry in low productivity habitats can reallocate resources to chemical defences as a response to browsing, while bilberry in high productivity habitats cannot.

The effects of light availability on bilberry are likely complex, with studies showing that bilberry maximizes photosynthetic activity already at fairly low light levels (Väisänen et al., 1977), and that bilberry can dominate the forest floor in long-term unbrowsed deciduous forest exlosures (Vild et al., 2021), indicating high shade tolerance, while other studies show that shade hampers bilberry performance (Eckerter et al., 2019; Eldegard et al., 2019; Hester et al., 1991), especially in deciduous forest (Eldegard et al., 2019). Bilberry has been shown to be more palatable both when it grows in shaded habitats, in more fertile habitats, and when browsed, resulting in an increase in insect herbivory (Schrijvers-Gonlag et al., 2020). Bilberry has also been shown to handle defoliation (such as by insect herbivory) poorly compared to experimental clipping of shoots (emulating cervid herbivory) (Tolvanen et al., 1992). In Hegland et al. (2005), it was found that red deer browsing decreased insect herbivore abundances in mature pine forest. Geometrid moth outbreaks such as described in Bjerke et al. (2017) and Boulanger-Lapointe et al. (2017) only happen in forested areas, begin in the canopy of a deciduous tree species (mountain birch), and drop down to attack bilberry only after the canopy is virtually empty of leaves. In 2021, data on insect herbivory on bilberry was collected in my study area. While the data has not yet been analysed, preliminary data exploration suggests there might be a higher intensity of insect herbivory on bilberry in

deciduous forest (Not shown). All these factors suggest the possibility that the poor bilberry performance in browsed deciduous forest might also be mediated by a mechanism of apparent competition between bilberry and deciduous trees. An increased palatability to insect larvae combined with an increased exposure of bilberry to insect larvae that both might occur in habitats with high shade, high productivity, and browsing could lead to an increased rate of defoliation by insects. This could again lead to a higher shoot mortality. Such a mechanism could also explain the conflicting reports on the shade tolerance of bilberry, as shade and "larvae rain" from deciduous trees could conceivably be confounded.

4.4 Future research

Since browsing intensity (Hegland & Rydgren, 2016; Hegland et al., 2005) and timing (Tolvanen et al., 1993) can be such important components in explaining the effect of browsing on the vegetation in general and on bilberry in particular, the experimental setup with browsing intensity as a simple toggle between total exclusion and ambient browsing intensity of unknown and varying intensity and timing might be insufficient to fully explain the effects of red deer browsing on bilberry. Also, while shading and fertility through visual evaluation seem to be highly correlated with the binary forest type definition in the locations of this study, there might still be meaningful variation in these variables within each forest type, that could help explain some of the residual variation in my models. Also, the possible mechanism of an apparent competition between bilberry and deciduous trees mediated by insect herbivory could be tested with data on tree species coverage and insect grazing intensity on bilberry. If continuous variables describing shading, fertility, tree species coverage, insect grazing intensity, and the variance in red deer activity through time and space were available and used as explanatory variables in a model for all locations, regardless of forest type, that might have allowed gaining an even greater insight into the suggested interplay between habitat differences, red deer browsing, and bilberry performance. Also, the drought susceptibility of soil is an important gradient for structuring plant species assemblages in forests and is also a gradient along which bilberry has a clear optimum (Økland & Eilertsen, 1993). Spatial data on this environmental gradient should also be considered when examining bilberry performance in the context of a changing climate with more frequent drought event.

4.5 Concluding remarks

My findings show that at the current red deer density in Tingvoll, Norway, bilberry is highly resilient to both severe winter droughts and red deer browsing in relatively open coniferous forests. Though red deer browsing has direct negative effects on bilberry performance it also shapes and maintains the open coniferous forest in which bilberry dominates, through preventing the recruitment of selected deciduous tree species into higher size classes (Fisichelli et al., 2012; Kolstad et al., 2018; Speed, Meisingset, et al., 2014; Vuorinen et al., 2020). These deciduous tree species might otherwise have been favoured by the warming climate and increased in abundance at the expense of bilberry.

The bilberry of the deciduous forests in Tingvoll showed poorer resilience than the bilberry of the coniferous forests, due to being unable to quickly compensate after a severe winter drought, especially when subjected to red deer browsing at the current day red deer density. At current deer density, bilberry could be extirpated from the most drought-susceptible deciduous forests if severe droughts start to happen more frequently, which is likely, due to climate change.

Since red deer browsing on bilberry shows high spatial variation (Morellet & Guibert, 1999), finetuning red deer browsing effects on any particular bilberry patch by red deer management at the municipality level is likely futile. Effects will likely be at the landscape level, and so this is the level that red deer management must consider.

A hypothetical total lack of cervid browsing together with climate warming might lead many of the open pine forests of today to shift into mixed forests emulating the deciduous forest locations in this study. While this might not do much to hamper bilberry performance and resilience at first, such a shift would not be reversible by simply reintroducing cervids, but a reintroduction of red deer would harm bilberry performance and resilience. Thus, a stable red deer population is better for bilberry performance and resilience than the removal of red deer. This study does not say whether the current red deer density is ideal for bilberry, or if a slightly higher or lower population might be better. This is likely only a minor flaw, as practical wildlife management should consider other metrics more important than min-maxing the performance of bilberry, given the apparent high resilience of bilberry.

Overall, in coniferous forest the indirect positive effects on bilberry by the current high densities of red deer in Tingvoll through reducing potential competition from deciduous trees and common heather in the habitat where it already dominates, likely outweigh the direct negative effects on bilberry from browsing by red deer. An expansion of deciduous trees like rowan due to global warming might otherwise have harmed bilberry performance and resilience by shifting optimal habitats into suboptimal habitats. In deciduous forest red deer browsing harms bilberry resilience by reducing growth rates to a level where bilberry is vulnerable to high drought frequencies.

5 References

Albon, S. D., & Langvatn, R. (1992). Plant Phenology and the Benefits of Migration in a Temperate Ungulate. *Oikos*, *65*(3), 502-513. https://doi.org/10.2307/3545568

Allombert, S., Gaston, A., & Martin, J.-L. (2005). A natural experiment on the impact of overabundant deer on songbird populations. *Biological Conservation*, *126*, 1-13. https://doi.org/10.1016/j.biocon.2005.04.001

Allombert, S., Stockton, S., & Martin, J.-L. (2005). A Natural Experiment on the Impact of Overabundant Deer on Forest Invertebrates. *Conservation Biology*, *19*(6), 1917-1929. https://doi.org/10.1111/j.1523-1739.2005.00280.x

Andersen, R., Lund, E., Solberg, E. J., & Sæther, B.-E. (2010). Ungulates and their management in Norway. In M. Appolonio, R. Andersen, & R. Putman (Eds.), *European ungulates and their management in the 21st century* (pp. 14-36). Cambridge university press.

Apollonio, M., Andersen, R., & Putman, R. (2010). *European ungulates and their management in the 21st century*. Cambridge University Press.

Augustine, D. J., Frelich, L. E., & Jordan, P. A. (1998). Evidence for Two Alternate Stable States in an Ungulate Grazing System. *Ecological Applications*, *8*(4), 1260-1269. https://doi.org/10.2307/2640978

Aune, B. (1993). *Temperaturnormaler, normalperiode 1961-1990* (02/93). https://cms.met.no/site/2/klimaservicesenteret/Klimanormaler/_attachment/10911?_ts=159b2cddfb3

Austrheim, G., Solberg, E. J., & Mysterud, A. (2011). Spatio-temporal variation in large herbivore pressure in Norway during 1949-1999: has decreased grazing by livestock been countered by increased browsing by cervids? *Wildlife Biology*, *17*(3), 286-298, 213. https://doi.org/10.2981/10-038

Barton, K. (2022). *MuMIn: Multi-Model Inference*. In (Version 1.47.1) https://cran.r-project.org/package=MuMIn

Beigaitė, R., Tang, H., Bryn, A., Skarpaas, O., Stordal, F., Bjerke, J. W., & Žliobaitė, I. (2022). Identifying climate thresholds for dominant natural vegetation types at the global scale using machine learning: Average climate versus extremes. *Glob Chang Biol*, *28*(11), 3557-3579. https://doi.org/10.1111/gcb.16110

Bernes, C., Macura, B., Jonsson, B. G., Junninen, K., Müller, J., Sandström, J., Lõhmus, A., & Macdonald, E. (2018). Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates. A systematic review. *Environmental Evidence*, *7*(1), 13. https://doi.org/10.1186/s13750-018-0125-3

Bjerke, J. W., Treharne, R., Vikhamar-Schuler, D., Karlsen, S. R., Ravolainen, V., Bokhorst, S., Phoenix, G. K., Bochenek, Z., & Tømmervik, H. (2017). Understanding the drivers of extensive plant damage in boreal and Arctic ecosystems: Insights from field surveys in the aftermath of damage. *Sci Total Environ*, *599-600*(-), 1965-1976. https://doi.org/10.1016/j.scitotenv.2017.05.050

Bjerke, J. W., Wierzbinski, G., Tømmervik, H., Phoenix, G. K., & Bokhorst, S. (2018). Stress-induced secondary leaves of a boreal deciduous shrub (Vaccinium myrtillus) overwinter then regain activity the following growing season. *Nordic journal of botany*, *36*(10), e01894-n/a. https://doi.org/10.1111/njb.01894

Boulanger-Lapointe, N., Jarvinen, A., Partanen, R., & Herrmann, T. (2017). Climate and herbivore influence on Vaccinium myrtillus over the last 40 years in northwest Lapland, Finland. *Ecosphere*, *8*. https://doi.org/10.1002/ecs2.1654

Christie, K. S., Bryant, J. P., Gough, L., Ravolainen, V. T., Ruess, R. W., & Tape, K. D. (2015). The role of vertebrate herbivores in regulating shrub expansion in the Arctic: A synthesis. *BioScience*, *65*(12), 1123-1133.

Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., & Waller, D. M. (2004). Ecological Impacts of Deer Overabundance. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 113-147. http://www.jstor.org/stable/30034112

Cromsigt, J. P. G. M., & Kuijper, D. P. J. (2011). Revisiting the browsing lawn concept: Evolutionary Interactions or pruning herbivores? *Perspectives in Plant Ecology, Evolution and Systematics*, *13*(3), 207-215. https://doi.org/https://doi.org/10.1016/j.ppees.2011.04.004

Eckerter, T., Buse, J., Förschler, M., & Pufal, G. (2019). Additive positive effects of canopy openness on European bilberry (Vaccinium myrtillus) fruit quantity and quality. *Forest Ecology and Management*, *433*, 122-130. https://doi.org/10.1016/j.foreco.2018.10.059

Eldegard, K., Scholten, J., Stokland, J. N., Granhus, A., & Lie, M. (2019). The influence of stand density on bilberry (Vaccinium myrtillus L.) cover depends on stand age, solar irradiation, and tree species composition. *Forest Ecology and Management*, *432*, 582-590. https://doi.org/10.1016/j.foreco.2018.09.054

Emanuelsson, U. (1984). Ecological effects of grazing and trampling on mountain vegetation in northern Sweden.

Faber, W. E., & Lavsund, S. (1999). Summer foraging on Scots pine Pinus sylvestris by moose Alces alces in Sweden - patterns and mechanisms [https://doi.org/10.2981/wlb.1999.013]. *Wildlife Biology*, *5*(2), 93-106. https://doi.org/https://doi.org/10.2981/wlb.1999.013

Fisichelli, N., Frelich, L. E., & Reich, P. B. (2012). Sapling growth responses to warmer temperatures 'cooled' by browse pressure [https://doi.org/10.1111/j.1365-2486.2012.02785.x]. *Global Change Biology*, *18*(11), 3455-3463. https://doi.org/https://doi.org/10.1111/j.1365-2486.2012.02785.x

Førland, E. J. (1993). *Nedbørnormaler, normalperiode 1961-1990* (39/93). https://cms.met.no/site/2/klimaservicesenteret/Klimanormaler/_attachment/10912?_ts=159b2ce35a5

Garcia, R. R., Fraser, M. D., Celaya, R., Ferreira, L. M. M., Garcia, U., & Osoro, K. (2012). Grazing land management and biodiversity in the AtlanticEuropean heathlands: a review. *Agroforest Syst*, *87*, 19-43. https://doi.org/10.1007/s10457-012-9519-3

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

Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J.-C., Hylander, K., Ehrlén, J., Speed, J. D. M., Klanderud, K., Bråthen, K. A., Milbau, A., Opedal, Ø. H., Alsos, I. G., Ejrnæs, R., Bruun, H. H., Birks, H. J. B., Westergaard, K. B., Birks, H. H., & Lenoir, J. (2018). Stay or go – how topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology, Evolution and Systematics*, *30*, 41-50. https://doi.org/https://doi.org/10.1016/j.ppees.2017.09.008

Hegland, S. J., Jongejans, E., & Rydgren, K. (2010). Investigating the interaction between ungulate grazing and resource effects on Vaccinium myrtillus populations with integral projection models. *Oecologia*, *163*(3), 695-706. https://doi.org/10.1007/s00442-010-1616-2

Hegland, S. J., & Rydgren, K. (2016). Eaten but not always beaten: winners and losers along a red deer herbivory gradient in boreal forest [https://doi.org/10.1111/jvs.12339]. *Journal of Vegetation Science*, *27*(1), 111-122. https://doi.org/https://doi.org/10.1111/jvs.12339

Hegland, S. J., Rydgren, K., & Seldal, T. (2005). The response of Vaccinium myrtillus to variations in grazing intensity in a Scandinavian pine forest on the island of Svanøy. *Canadian Journal of Botany*, *83*(12), 1638-1644. https://doi.org/10.1139/b05-132

Herms, D. A., & Mattson, W. J. (1992). The Dilemma of Plants: To Grow or Defend. *The Quarterly Review of Biology*, *67*(3), 283-335. http://www.jstor.org/stable/2830650

Hester, A. J., Miles, J., & Gimingham, C. H. (1991). Succession from Heather Moorland to Birch Woodland. I. Experimental Alteration of Specific Environmental Conditions in the Field. *Journal of Ecology*, *79*(2), 303-315. https://doi.org/10.2307/2260714

IPCC. (2001). *Climate Change 2001: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press.

IPCC. (2007). *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press.

Janke, R. A. (1970). Transpiration Resistance in Vaccinium myrtillus. *American Journal of Botany*, *57*(9), 1051-1054. https://doi.org/10.2307/2441270

Jonasson, S. (1988). Evaluation of the Point Intercept Method for the Estimation of Plant Biomass. *Oikos*, *52*(1), 101-106. https://doi.org/10.2307/3565988

Jump, A. S., & Peñuelas, J. (2005). Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, *8*(9), 1010-1020. https://doi.org/https://doi.org/10.1111/j.1461-0248.2005.00796.x

Kaplan, J. O., & New, M. (2006). Arctic climate change with a 2 ∘C global warming: Timing, climate patterns and vegetation change. *Climatic Change*, *79*(3), 213-241. https://doi.org/10.1007/s10584-006-9113-7

Kolstad, A., Austrheim, G., Graae, B., Solberg, E. J., Strimbeck, R., & Speed, J. (2019). Moose effects on soil temperatures, tree canopies, and understory vegetation: a path analysis. *Ecosphere*, *10*, e02966. https://doi.org/10.1002/ecs2.2966

Kolstad, A., Austrheim, G., Solberg, E. J., De Vriendt, L., & Speed, J. D. M. (2018). Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species [https://doi.org/10.1002/ecs2.2458]. *Ecosphere*, *9*(10), e02458. https://doi.org/https://doi.org/10.1002/ecs2.2458

Kreyling, J., Haei, M., & Laudon, H. (2012). Absence of snow cover reduces understory plant cover and alters plant community composition in boreal forests. *Oecologia*, *168*(2), 577-587. https://doi.org/10.1007/s00442-011-2092-z

Lilleeng, M. S. (2018). *Ecological impacts of red deer browsing in boreal forest* [PhD, NMBU].

Lilleeng, M. S., Hegland, S. J., Rydgren, K., & Moe, S. R. (2016). Red deer mediate spatial and temporal plant heterogeneity in boreal forests. *Ecological Research*, *31*(6), 777-784. https://doi.org/10.1007/s11284-016-1391-6

Marozas, V., Racinskas, J., & Bartkevicius, E. (2007). Dynamics of ground vegetation after surface fires in hemiboreal Pinus sylvestris forests. *Forest Ecology and Management*, *250*(1), 47-55. https://doi.org/10.1016/j.foreco.2007.03.008

Maschinski, J., & Whitham, T. G. (1989). The Continuum of Plant Responses to Herbivory: The Influence of Plant Association, Nutrient Availability, and Timing. *The American Naturalist*, *134*(1), 1-19. http://www.jstor.org/stable/2462272

McShea, W. J., Underwood, H. B., & Rappole, J. H. (1997). *Science of overabundance*. Smithsonian Institution Press.

Meisingset, E. (2015). *Space use of red deer and its implications for management.* [Dissertation for the degree of PhD, University of Oslo]. Norway.

Meisingset, E., Austrheim, G., Solberg, E. J., Brekkum, Ø., & Lande, U. S. (2015). *Effekter av klimastress på hjortens vinterbeiter. Utvikling av blåbærlyngen etter tørkevinteren 2014* (NIBIO Rapport, Issue. NIBIO.

Melis, C., Buset, A., Aarrestad, P. A., Hanssen, O., Meisingset, E. L., Andersen, R., Moksnes, A., & Røskaft, E. (2006). Impact of Red Deer *Cervus elaphus* Grazing on Bilberry *Vaccinium myrtillus* and Composition of Ground Beetle (Coleoptera, Carabidae) Assemblage. *Biodiversity & Conservation*, *15*(6), 2049-2059. https://doi.org/10.1007/s10531-005-2005-8

Meteorologisk institutt (MET). (2021a). *Nedbørnormaler per måned og år*. https://www.met.no/kss/_/attachment/download/2aa2056c-c637-4373-92d2-cac3989dcd05:c3f2b161e4bf474af587cd4a4e8f3b78a24bc530/StNormaler_mnd_nedbor_1991-2020.txt

Meteorologisk institutt (MET). (2021b). *Temperaturnormaler per måned og år*. https://www.met.no/kss/_/attachment/download/a2d191d6-b9ef-4d78-ac26-9eee4ce28743:969dfb48bad54d95b9dca7685778f05448f42892/StNormaler_mnd_middeltemp_1991-2020.txt

Mienna, I. M., Austrheim, G., Klanderud, K., Bollandsås, O. M., & Speed, J. D. M. (2022). Legacy effects of herbivory on treeline dynamics along an elevational gradient. *Oecologia*, *198*(3), 801-814. https://doi.org/10.1007/s00442-022-05125-8

Moen, A. (1998). *Nasjonalatlas for Norge: Vegetasjon*. Statens Kartverk.

Morellet, N., & Guibert, B. (1999). Spatial heterogeneity of winter forest resources used by deer. *Forest Ecology and Management*, *123*(1), 11-20.

Mysterud, A. (2000). Diet overlap among ruminants in Fennoscandia. *Oecologia, Springer-Verlag*(124), 130-137.

Mysterud, A., Yoccoz, N. G., Stenseth, N. C., & Langvatn, R. (2000). Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *Journal of Animal Ecology*, *69*(6), 959-974. https://doi.org/https://doi.org/10.1111/j.1365-2656.2000.00454.x

Nuttle, T., Ristau, T. E., & Royo, A. A. (2014). Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years [https://doi.org/10.1111/1365-2745.12175]. *Journal of Ecology*, *102*(1), 221-228. https://doi.org/https://doi.org/10.1111/1365-2745.12175

Ogren, E. (1996). Premature Dehardening in Vaccinium myrtillus During a Mild Winter: A Cause for Winter Dieback? *Functional Ecology*, *10*(6), 724-732. https://doi.org/10.2307/2390507

Omholt, S., & Meisingset, E. (2022). Bestandsestimering av hjort ved bruk av

jegerrapporterte data. *NIBIO Rapport*, *8*(118). https://nibio.brage.unit.no/nibio-xmlui/bitstream/handle/11250/3020708/NIBIO_RAPPORT_2022_8_118.pdf?sequence=1

Parlane, S., Summers, R. W., Cowie, N. R., & Gardingen, P. R. (2006). Management proposals for bilberry in Scots pine woodland. *Forest Ecology and Management*, *222*, 272-278. https://doi.org/10.1016/j.foreco.2005.10.032

Paulsen, J., & Körner, C. (2014). A climate-based model to predict potential treeline position around the globe. *Alpine Botany*, *124*(1), 1-12. https://doi.org/10.1007/s00035-014-0124-0

Pedersen, S., Andreassen, H. P., Persson, I.-L., Julkunen-Tiitto, R., Danell, K., & Skarpe, C. (2011). Vole preference of bilberry along gradients of simulated moose density and site productivity. *Integr Zool*, *6*(4), 341-351. https://doi.org/10.1111/j.1749-4877.2011.00260.x

Pinheiro, J., Bates, D., & R Core Team. (2022). *nlme: Linear and Nonlinear Mixed Effects Models*. In https://CRAN.R-project.org/package=nlme

Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences*, *105*(34), 12353-12358.

Putman, R., Apollonio, M., & Andersen, R. (2011). *Ungulate management in Europe: problems and practices*. Cambridge University Press.

R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Räisänen, J., & Eklund, J. (2012). 21st Century changes in snow climate in Northern Europe: a high-resolution view from ENSEMBLES regional climate models. *Climate Dynamics*, *38*(11), 2575-2591. https://doi.org/10.1007/s00382-011-1076-3

Schrijvers-Gonlag, M., Skarpe, C., & Andreassen, H. P. (2020). Influence of light availability and soil productivity on insect herbivory on bilberry (Vaccinium myrtillus L.) leaves following mammalian herbivory. *PLOS ONE*, *15*(3), e0230509.

Skre, O., Wielgolaski, F. E., & Moe, B. (1998). Biomass and Chemical Composition of Common Forest Plants in Response to Fire in Western Norway. *Journal of Vegetation Science*, *9*(4), 501-510. https://doi.org/10.2307/3237265

Speed, J. D. M., Austrheim, G., Hester, A. J., Meisingset, E., Mysterud, A., Tremblay, J.-P., Øien, D.-I., & Solberg, E. J. (2014). General and specific responses of understory vegetation to cervid herbivory across a range of boreal forests [https://doi.org/10.1111/oik.01373]. *Oikos*, *123*(10), 1270-1280. https://doi.org/https://doi.org/10.1111/oik.01373

Speed, J. D. M., Austrheim, G., Kolstad, A. L., & Solberg, E. J. (2019). Long-term changes in northern large-herbivore communities reveal differential rewilding rates in space and time. *PLOS ONE*, *14*(5), e0217166. https://doi.org/10.1371/journal.pone.0217166

Speed, J. D. M., Meisingset, E., Austrheim, G., Hester, A., Mysterud, A., Tremblay, J.-P., & Solberg, E. J. (2014). Low Intensities of Red Deer Browsing Constrain Rowan Growth in Mature Boreal Forests of Western Norway. *Ecoscience*, *20*, 311-318. https://doi.org/10.2980/20-3-3619

Spitzer, R., Coissac, E., Felton, A., Fohringer, C., Juvany, L., Landman, M., Singh, N. J., Taberlet, P., Widemo, F., & P.G.M. Cromsigt, J. (2020). Small shrubs with large importance? Smaller deer may increase the moose-forestry conflict through feeding competition over Vaccinium shrubs in the field layer. *Forest Ecology and Management*, 118768. https://doi.org/https://doi.org/10.1016/j.foreco.2020.118768

Tahkokorpi, M., Taulavuori, K., Laine, K., & Taulavuori, E. (2007). After-effects of drought-related winter stress in previous and current year stems of Vaccinium myrtillus L. *Environmental and Experimental Botany*, *61*(1), 85-93. https://doi.org/https://doi.org/10.1016/j.envexpbot.2007.03.003

Tolvanen, A. (1997). Recovery of the bilberry (Vaccinium Myritillus L.) from artificial spring and summer frost [Article]. *Plant Ecology*, *130*(1), 35-39. https://doi.org/10.1023/A:1009776200866

Tolvanen, A., Laine, K., Pakonen, T., Saari, E., & Havas, P. (1992). Compensatory responses of a deciduous dwarf shrub, the bilberry (Vaccinium myrtillus L.) to simulated herbivory - some comparisons with the evergreen lingonberry (Vaccinium vitis-idaea L.). *13*, 607-615.

Tolvanen, A., Laine, K., Pakonen, T., Saari, E., & Havas, P. (1993). Effect of habitat and time of clipping on the recovery of the bilberry (Vaccinium myrtillus). *Annales Botanici Fennici*, *30*(1), 15-20.

Tolvanen, A., Laine, K., Pakonen, T., Saari, E., & Havas, P. (1994). Responses to harvesting intensity in a clonal dwarf shrub, the bilberry (Vaccinium myrtillus L.). *Vegetatio*, *110*(2), 163-169. https://doi.org/10.1007/BF00033396

Vild, O., Douglas Rotherham, I., & Ohlemuller, R. (2021). Long-term exclosure of sheep-grazing from an ancient wood: Vegetation change after a sixty-year experiment. *Applied vegetation science*, *24*(1), n/a. https://doi.org/10.1111/avsc.12543

Vuorinen, K. E. M., Kolstad, A. L., De Vriendt, L., Austrheim, G., Tremblay, J.-P., Solberg, E. J., & Speed, J. D. M. (2020). Cool as a moose: How can browsing counteract climate warming effects across boreal forest ecosystems? [https://doi.org/10.1002/ecy.3159]. *Ecology*, *101*(11), e03159. https://doi.org/https://doi.org/10.1002/ecy.3159

Väisänen, E., Kellomäki, S., & Hari, P. (1977). Annual growth level of some plant species as a function of light available for photosynthesis.

Walter, J., Jentsch, A., Beierkuhnlein, C., & Kreyling, J. (2013). Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. *Environmental and Experimental Botany*, *94*, 3-8. https://doi.org/https://doi.org/10.1016/j.envexpbot.2012.02.009

Welch, D., Scott, D., Moss, R., & Bayfield, N. G. (1994). *Ecology of blaeberry and its management in British moorlands*. I. o. T. Ecology.

Wipf, S., Stoeckli, V., & Bebi, P. (2009). Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic Change*, *94*(1), 105-121. https://doi.org/10.1007/s10584-009-9546-x

Økland, R. H., & Eilertsen, O. (1993). Vegetation-environment relationships of boreal coniferous forests in the Solhomfjell area, Gjerstad, S Norway. *Sommerfeltia*, *16*(1), 1-259. https://doi.org/doi:10.2478/som-1993-0002

6 Appendices

Appendix 1: Dredge output tables

Appendix 2: Final model diagnostic plots

6.1 Appendix 1

This appendix contains tables with the dredge outputs from the model selection process. The tables show which effects and interactions were included in each model, but not significance, as well as the degrees of freedoms spent, the log likelihood, AICc-value, and the delta-AICc-value from the best ranked model in the dredge process.

6.1.1 Coniferous

6.1.1.1 Biomass

(Intercept)	treatment	drought	time	treatment:drought	treatment:time	drought:time	treatment:drought:time	df	logLik	AICc	delta
3,030	+	-1,689	0,053		+	0,114		10	-790,164	1600,561	0,000
3,006	+	-1,801	0,066	+		0,114		10	-790,963	1602,159	1,598
3,029	+	-1,725	0,056	+	+	0,114		11	-790,019	1602,317	1,757
2,996	+	-1,638	0,073	+	+	0,092	+	12	-789,324	1602,979	2,419
2,981		-1,692	0,067			0,114		8	-795,414	1606,980	6,419
2,938	+	-1,692	0,067			0,114		9	-795,327	1608,844	8,284
2,865	+	-1,252	0,139		+			9	-807,134	1632,459	31,898
2,841	+	-1,362	0,153	+				9	-807,848	1633,887	33,327
2,864	+	-1,288	0,142	+	+			10	-806,990	1634,213	33,653
2,820		-1,253	0,152					7	-811,770	1637,659	37,099
2,777	+	-1,253	0,152					8	-811,683	1639,518	38,957
2,888	+		0,021		+			8	-947,859	1911,870	311,309
2,842			0,035					6	-951,209	1914,507	313,946
2,798	+		0,035					7	-951,119	1916,356	315,795
3,276		-0,330						6	-959,254	1930,597	330,036
3,280	+	-0,415		+				8	-957,491	1931,133	330,573
3,237	+	-0,339						7	-959,147	1932,411	331,851
3,073								5	-970,907	1951,877	351,316
3,029	+							6	-970,817	1953,722	353,161

6.1.1.2 Shoot length

| (Intercept)	treatment	drought	time	treatment:drought	treatment:time	drought:time	treatment:drought:time	df	logLik	AICc	delta
3,028	+	-0,666	-0,025		+	0,056		10	117,321	-214,406	0,000
3,028	+	-0,677	-0,024	+	+	0,056		11	117,403	-212,522	1,884
3,015	+	-0,716	-0,018	+		0,056		10	115,836	-211,435	2,971
3,018	+	-0,649	-0,019	+	+	0,049	+	12	117,812	-211,288	3,118
3,045		-0,670	-0,019			0,057		8	110,542	-204,930	9,476
2,988	+	-0,670	-0,019			0,057		9	111,232	-204,271	10,135
2,951	+	-0,453	0,017	+	+			10	93,640	-167,044	47,361
2,937	+	-0,491	0,023	+				9	92,028	-165,863	48,543
2,965		-0,440	0,023					7	86,723	-159,326	55,080
2,908	+	-0,440	0,023					8	87,379	-158,604	55,802
2,998	+	-0,338		+				8	67,402	-118,650	95,756
3,027		-0,289						6	62,808	-113,526	100,880
2,970	+	-0,290						7	63,495	-112,870	101,536
2,956	+		-0,024		+			8	-19,287	54,729	269,134
2,970			-0,017					6	-24,051	60,191	274,597
2,913	+		-0,017					7	-23,373	60,865	275,271
2,861								5	-46,961	103,985	318,391
2,804	+							6	-46,300	104,690	319,096

6.1.1.3 Shoot density

(Intercept)	treatment	drought	time	treatment:drought	treatment:time	drought:time	treatment:drought:time	df	logLik	AICc	delta
15,946	+	-2,913	-0,066		+	0,730		10	-2850,5	5721,223	0,000
16,413	+	-3,505	-0,338	+	+	1,020	+	12	-2848,7	5721,679	0,456
15,960	+	-2,457	-0,109	+	+	0,731		11	-2850,2	5722,681	1,458
14,874		-2,908	0,008			0,730		8	-2853,4	5723,043	1,820
15,454	+	-2,908	0,008			0,730		9	-2852,7	5723,607	2,383
15,719	+	-3,341	0,008	+		0,730		10	-2851,7	5723,714	2,490
14,810	+		0,485		+			8	-2860,1	5736,380	15,157
13,738			0,558					6	-2863	5738,085	16,862
14,804	+	-0,261	0,509		+			9	-2860	5738,235	17,011
14,320	+		0,558					7	-2862,3	5738,635	17,412
14,818	+	0,197	0,466	+	+			10	-2859,7	5739,701	18,478
13,732		-0,258	0,582					7	-2862,9	5739,935	18,712
14,314	+	-0,258	0,582					8	-2862,2	5740,490	19,266
14,577	+	-0,691	0,583	+				9	-2861,2	5740,657	19,433
14,958		4,110						6	-2897,9	5807,934	86,710
15,548	+	4,110						7	-2897,2	5808,464	87,240
15,803	+	3,689		+				8	-2896,4	5808,884	87,661
17,490								5	-2943,5	5897,067	175,844
18,140	+							6	-2942,7	5897,396	176,173

6.1.2 Deciduous

6.1.2.1 Biomass

(Intercept)	treatment	drought	time	treatment:drought	treatment:time	drought:time	treatment:drought:time	df	logLik	AICc	delta
0,988	+	-0,735	0,037		+			9	-438,01	894,406	0,000
1,040	+	-0,891	0,009		+	0,038		10	-437,15	894,778	0,372
0,988	+	-0,694	0,033	+	+			10	-437,93	896,321	1,914
1,041	+	-0,850	0,006	+	+	0,038		11	-437,07	896,703	2,296
1,056	+	-0,896	-0	+	+	0,050	+	12	-437	898,658	4,252
0,915	+	-0,896	0,063	+				9	-441,28	900,947	6,540
0,968	+	-1,053	0,035	+		0,038		10	-440,44	901,349	6,942
0,773		-0,732	0,063					7	-444,68	903,601	9,194
0,824		-0,891	0,035			0,038		8	-443,89	904,076	9,669
0,820	+	-0,732	0,063					8	-444,65	905,608	11,201
0,871	+	-0,891	0,035			0,038		9	-443,85	906,092	11,685
1,073	+	-0,467		+				8	-455,76	927,823	33,417
0,942		-0,322						6	-458,59	929,353	34,947
0,989	+	-0,322						7	-458,56	931,351	36,944
0,995	+		-0,03		+			8	-464,46	945,227	50,820
0,751								5	-470,31	950,749	56,343
0,778			-0					6	-470,18	952,529	58,122
0,798	+							6	-470,28	952,738	58,332
0,825	+		-0					7	-470,14	954,527	60,120

6.1.2.2 Shoot length

(Intercept)	treatment	drought	time	treatment:drought	treatment:time	drought:time	treatment:drought:time	df	logLik	AICc	delta
2,624	+	-0,646	0,025		+			9	79,546	-140,643	0,000
2,625	+	-0,612	0,022	+	+			10	80,101	-139,653	0,990
2,640	+	-0,689	0,017		+	0,011		10	80,038	-139,526	1,117
2,641	+	-0,655	0,014	+	+	0,011		11	80,597	-138,533	2,110
2,635	+	-0,641	0,016	+	+	0,007	+	12	80,674	-136,564	4,078
2,598	+	-0,697	0,034	+				9	74,931	-131,413	9,229
2,613	+	-0,741	0,025	+		0,011		10	75,432	-130,313	10,329
2,568	+	-0,651	0,034					8	71,573	-126,788	13,854
2,585	+	-0,699	0,025			0,012		9	72,105	-125,761	14,881
2,666		-0,651	0,034					7	69,651	-125,024	15,619
2,683		-0,698	0,026			0,012		8	70,168	-123,978	16,665
2,676	+	-0,459		+				8	47,649	-78,941	61,702
2,651	+	-0,415						7	44,734	-75,190	65,453
2,751		-0,415						6	42,693	-73,177	67,465
2,637	+		-0,036		+			8	-27,909	72,175	212,818
2,580	+		-0,027					7	-32,572	79,423	220,065
2,683			-0,027					6	-34,721	81,649	222,292
2,408	+							6	-56,873	125,954	266,597
2,511								5	-58,983	128,113	268,756

6.1.2.3 Shoot density

| (Intercept)	treatment	drought	time	treatment:drought	treatment:time	drought:time	treatment:drought:time	df	logLik	AICc	delta
9,316		-2,007						6	-1208,24	2428,653	0,000
10,030	+	-2,007						7	-1208,07	2430,369	1,716
9,322		-2,000	-0,002					7	-1208,24	2430,712	2,059
10,083	+	-2,102		+				8	-1208,03	2432,375	3,722
10,036	+	-2,000	-0,002					8	-1208,07	2432,437	3,784
9,242		-1,611	0,055			-0,085		8	-1208,11	2432,534	3,881
10,491	+	-2,002	-0,072		+			9	-1207,08	2432,551	3,898
10,483	+	-1,637	-0,102	+	+			10	-1206,78	2434,039	5,386
9,956	+	-1,610	0,055			-0,085		9	-1207,94	2434,268	5,615
10,411	+	-1,618	-0,016		+	-0,084		10	-1206,96	2434,394	5,741
10,089	+	-2,095	-0,001	+				9	-1208,03	2434,452	5,798
10,403	+	-1,251	-0,046	+	+	-0,084		11	-1206,66	2435,889	7,236
10,008	+	-1,706	0,055	+		-0,085		10	-1207,91	2436,292	7,639
10,492	+	-1,678	-0,108	+	+	0,009	+	12	-1206,51	2437,694	9,041
9,276		-0,169						6	-1217,04	2446,267	17,614
9,989	+	-0,169						7	-1216,87	2447,982	19,329
10,445	+	-0,240		+				8	-1215,92	2448,153	19,500
8,190								5	-1222,04	2454,206	25,553
8,916	+							6	-1221,86	2455,903	27,250

Appendix 2

Here follows the diagnostic plots for the final models for every response variable. The plots are in order: 1) Normal QQ plot, 2) fitted versus residuals plot, 3) density plot and 4) residuals plot.
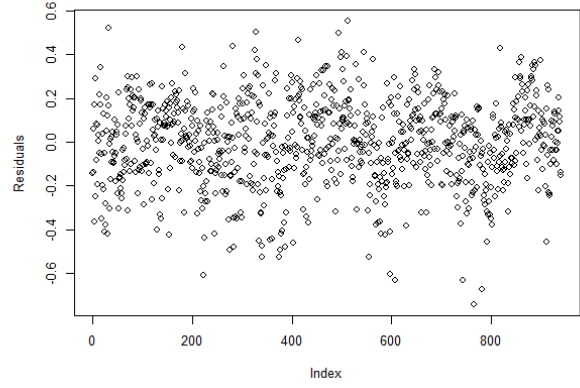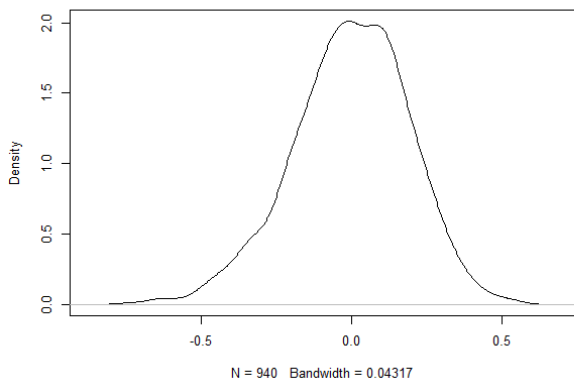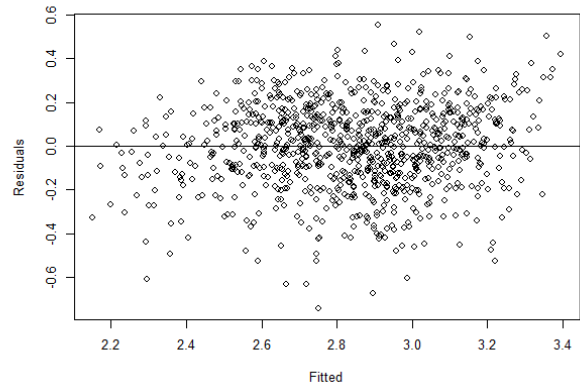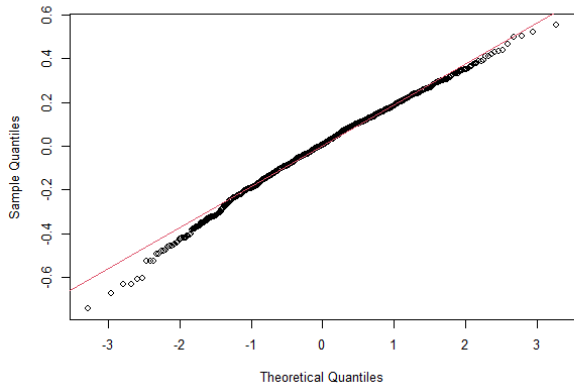
Coniferous bilberry biomass model
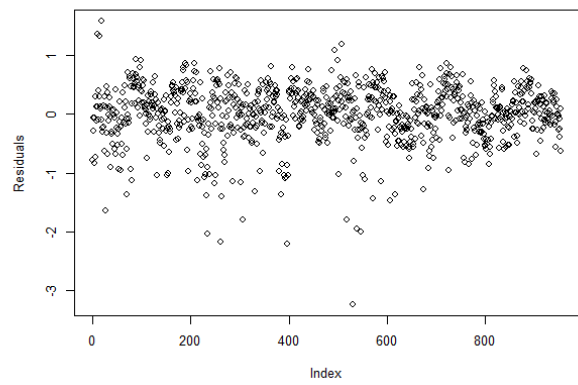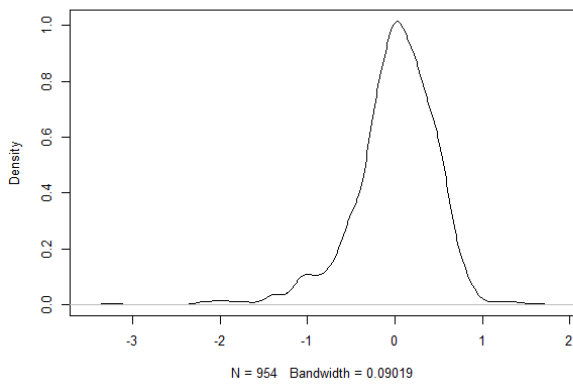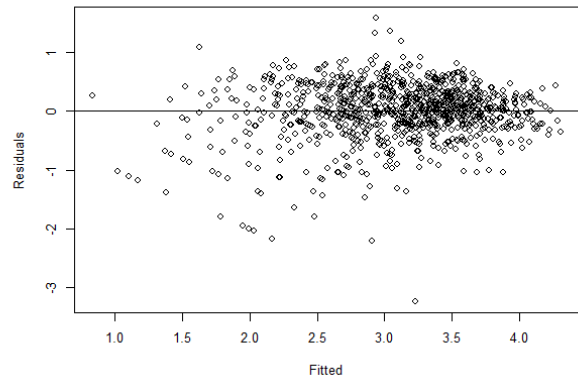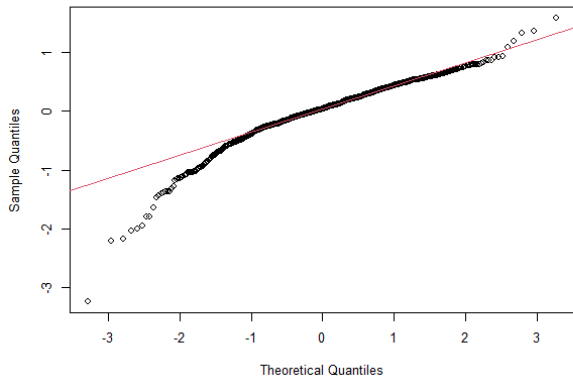
Deciduous bilberry biomass model
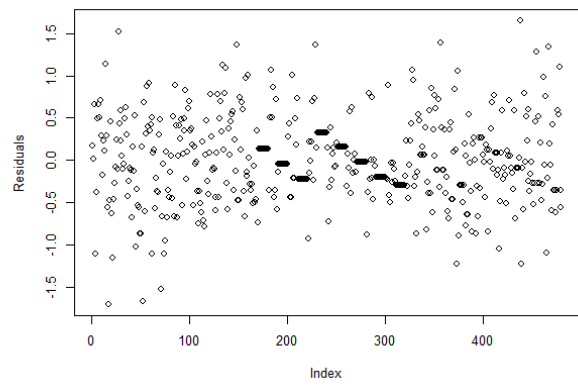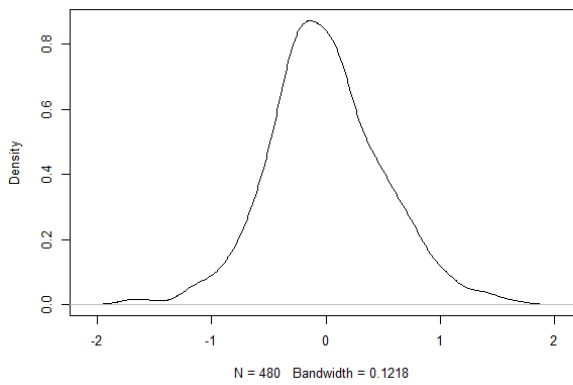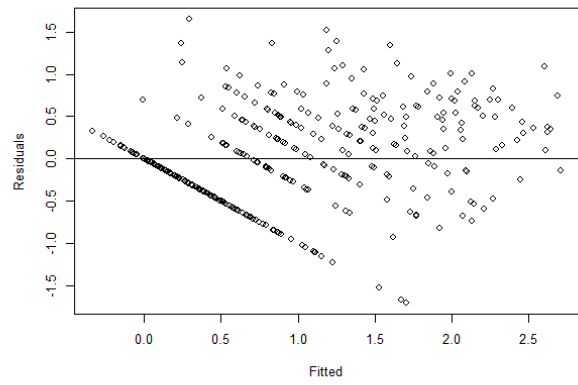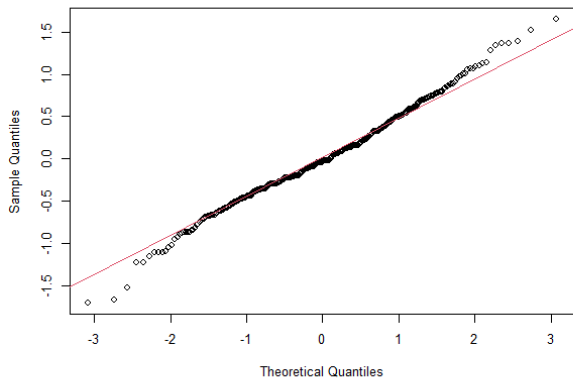
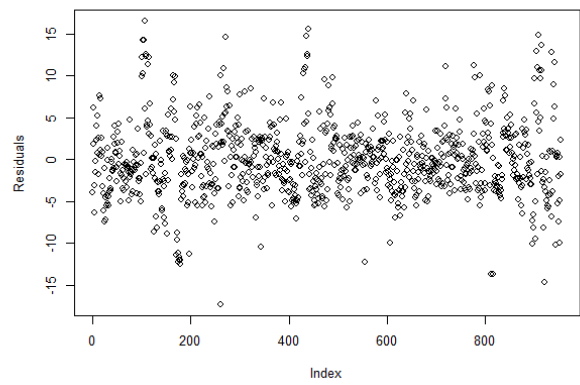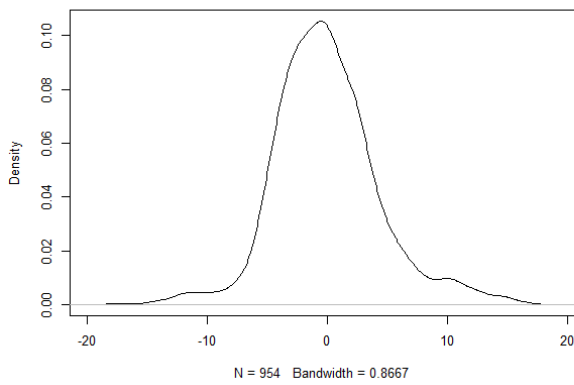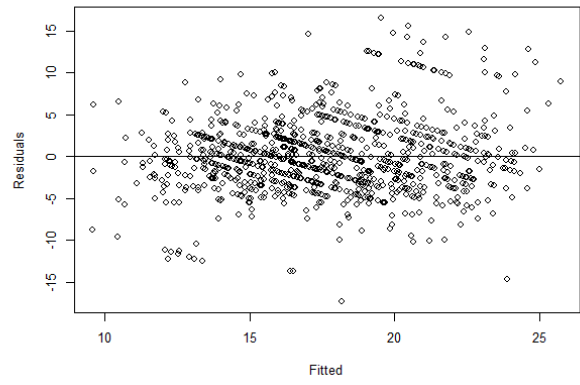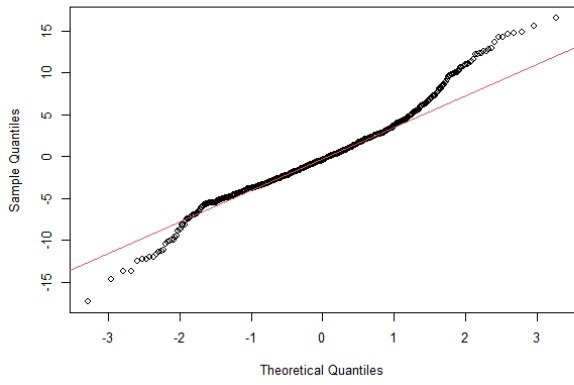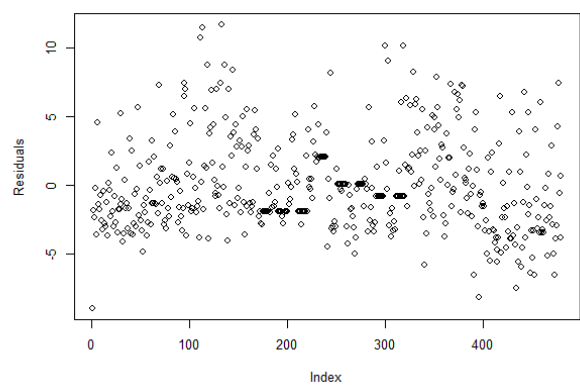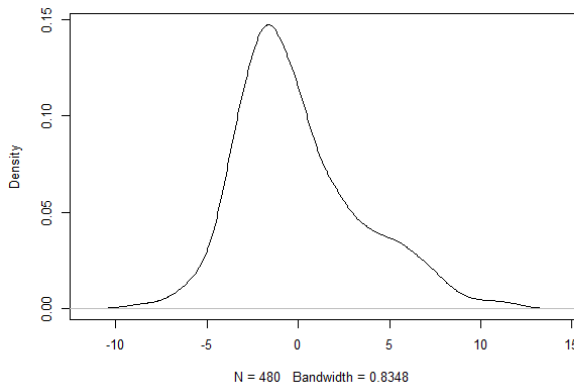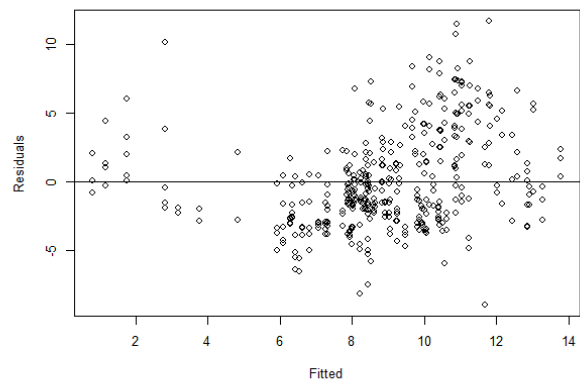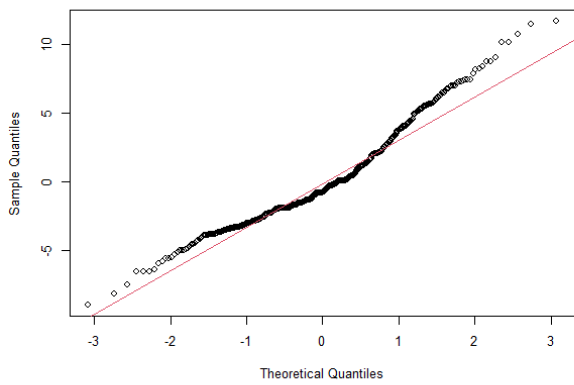**Coniferous bilberry shoot length model**

Deciduous bilberry shoot length model
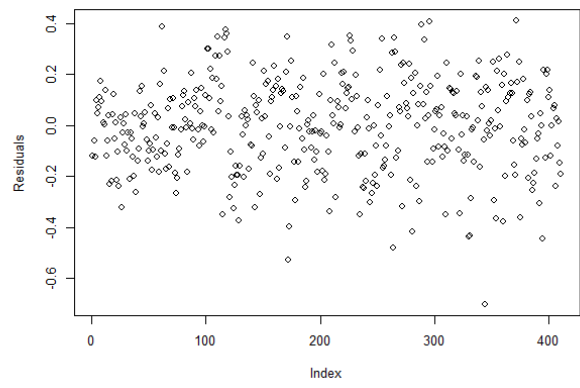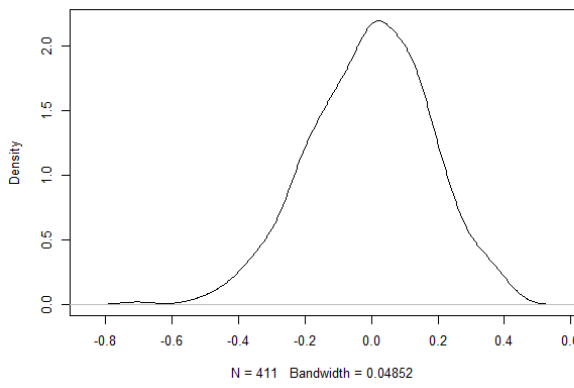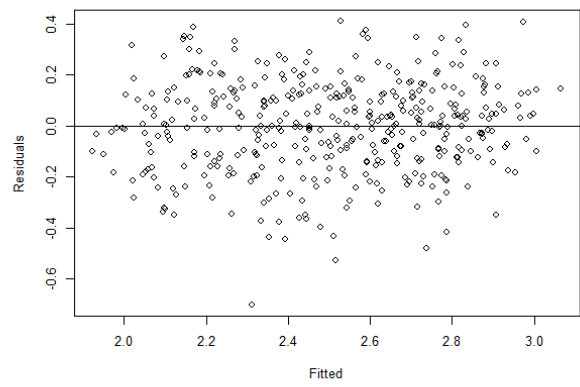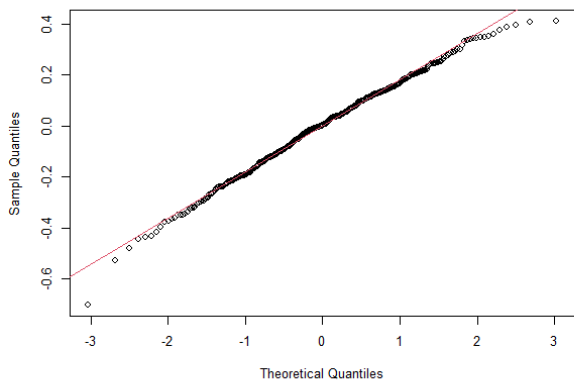
Coniferous bilberry shoot density model

Deciduous bilberry shoot density model