

Effects of cattle and cervids on plants and flower-visiting insects in young spruce plantations

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ARTICLE INFO

Keywords:

Bos taurus
Alces alces
Forest grazing
Boreal forest
Pollinators
Floral resources

ABSTRACT

Livestock summer grazing in mountains and forests in Norway is generally considered beneficial to biodiversity. In this study we investigated if this is the case for cattle in boreal production forest. We collected biodiversity data on field layer vegetation, floral resources and flower-visiting insects in young spruce plantations that were planted 2–10 years ago. We picked young spruce plantations inside and outside well-established cattle grazing areas. On each plantation, we sampled fenced and unfenced plots (20 * 20 m each). This study design allowed us to investigate long-term effects of cattle grazing as well as short-term effects of excluding cervids only and short-term effects of excluding cervids and cattle. Long-term cattle grazing reduced the abundance of woody plants and reduced the abundance of flowers. Excluding cervids for two summers led to reduced height of woody plants (shrubs and heather) and to increased flower abundance. In contrast, excluding cervids and cattle for two summers led to increased height of graminoids, herbs and woody plants, to higher abundance of graminoids, higher flower abundance and higher abundance of flower-visiting insects. In conclusion, cattle affected the studied system in different ways and to a larger extent than native cervids. Our study shows that we must be careful when inferring results from cattle grazing studies on grasslands to forest ecosystems. As this study documents a negative effect of cattle on floral resources and flower-visiting insects, and we currently are facing a global pollination crisis, a careful consideration of the current practice of cattle grazing in boreal forest might be needed.

1. Introduction

In Norway, livestock is grazing in forests during the summer season. With only 3 % of the land area suited for agriculture (SSB, 2023a), Norway can be considered a food-vulnerable country (Farsund and Daugbjerg, 2017) and the goal of Norwegian agricultural policy is increased food security by supporting national food production and preventing overreliance on imports (Farsund and Daugbjerg, 2017). As the agricultural land is used for food and winter fodder production and rarely used for livestock grazing, livestock is sent to the outfields, that is mountains and forests, for summer grazing. This practice has a tradition of thousands of years (Sjögren et al., 2015) and still is of importance for Norwegian agriculture today. In summer 2022, about 1 800 000 sheep

and 260 000 cattle were released to the outfields (SSB, 2023b).

In some parts of the country, increasing carnivore populations make sheep farming challenging (Strand et al., 2019). An often-used argument in the Norwegian large carnivore debate states that carnivores are detrimental to biodiversity, as they make free-ranging livestock disappear from the outfields. This argument builds upon the assumption that livestock is beneficial to biodiversity. Indeed, livestock grazing is a widely used management tool to increase biodiversity in semi-natural habitats (Gaujour et al., 2012; Johansen et al., 2019; Katona and Coetsee, 2019). On the other hand, overgrazing by livestock is known to negatively impact biodiversity in many parts of the world (IPBES, 2018). In this study, we investigated if cattle grazing in boreal production forest is beneficial for biodiversity. We focused on cattle, as the return of large

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carnivores has initiated a shift from sheep husbandry to less depredation-prone cattle husbandry (Aune-Lundberg and Munksterhjelm, 2021; Strand et al., 2019; Zimmermann et al., 2003). We focussed on boreal production forest, as this is the habitat type in which large carnivores and cattle co-occur. Indeed, it is possible to achieve acceptable weight gains for cattle in this grazing system when using breeds suitable for these extensive areas and stocking at moderate densities (Tofastrud et al., 2020).

Boreal production forest is shaped by current clear-cutting practices and dominated by patches of even-aged stands of either Norway Spruce (*Picea abies*) or Scots Pine (*Pinus sylvestris*) (Kuuluvainen et al., 2012; Aasetre and Bele, 2009). A review of all taxa of boreal forest found that production forest was much less species-rich than old-grown forest (Savilaakso et al., 2021). Indeed, 48 % of the species on the Norwegian Red List of Species are found in forest mostly associated with old-growth forest which normally is not allowed to develop beyond the timeframe of a production forest (< 100 years) (The Norwegian Biodiversity Information Centre, 2021). Within this species-poor production forest landscape, the young stands are the most diverse in terms of open habitat species, especially vascular plants (Savilaakso et al., 2021). In some cases, young stands host a large abundance and species richness of pollinators as well, which can be linked to abundant floral resources (Nielsen and Totland, 2014; Rodríguez and Kouki, 2017; Rubene et al., 2015). Nielsen and Totland (2014) found a higher number of species and links (interactions) between plants and pollinators on clearcuts than in young and old growth forests. However, while the diversity of species and links in individual clearcuts was relatively high, the beta-diversity of species and links across old growth forest stands was much higher. This suggests that clearcuts are rather similar in species and link richness, while individual old growth stands have more unique plant and pollinator communities. Clearcuts and young spruce plantations are relatively species-rich stands for vascular plants and pollinators in this otherwise species-poor forest landscape. We should note that most studies on the link between livestock grazing and the abundance and diversity of flowers and pollinators were conducted in grassland ecosystems (Franzén and Nilsson, 2008; Gaujour et al., 2012; Johansen et al., 2019) and that there is a lack of similar studies on the effect of livestock grazing in forested ecosystems, such as boreal production forest.

Large herbivores can affect biodiversity through several mechanisms and the main mechanism is the creation and maintenance of sward structural heterogeneity, particularly as result of dietary choice (Rook et al., 2004). By sward we mean the field layer vegetation, where we find graminoids, herbs and shrubs/heather. The dietary choice of large herbivores alters the competitive advantage among plant species both by direct removal of plant material and by altering the light environment. Other mechanisms are trampling which creates regeneration niches for gap-colonising species, nutrient cycling, and seed dispersal (Rook et al., 2004). A study on sheep roaming in Norwegian mountains for example reported that sheep reduced flowering frequency of the herb community (Lanta et al., 2014). The exception were small herb species, which increased flowering at sites with sheep, probably due to reduced competition with larger plants (Lanta et al., 2014). Herbivore-induced changes in the composition of floral resources indirectly shape pollinator communities (Guy et al., 2021; Lasway et al., 2022; Lázaro et al., 2016; Potts et al., 2003).

An important factor determining the direction and magnitude of herbivore effects on biodiversity are herbivore intensity, which can be manipulated through herbivore density and type (Austrheim et al., 2008; Scimone et al., 2007; Török et al., 2018). Herbivores and vegetation have co-evolved over millions of years and thus show adaptations to each other (Janis, 2008). Evolution has resulted in two feeding behaviours: grazing, defined as foraging on graminoids, i.e., true grasses (Poaceae), sedges (Cyperaceae) and rushes (Juncaceae), and browsing, defined as foraging on herbs and woody plants (Clauss et al., 2008; Janis, 2008). Boreal production forest is a typical browser's habitat, and

home to cervids such as moose (*Alces alces*), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). While red deer as an intermediate feeder is adapted to utilize the entire spectre of forage plants, moose and roe deer are typical browsers (Austrheim et al., 2011). The densities of cervids in Norway have increased drastically between 1949 and 2015 (Speed et al., 2019) and today's moose densities in southeastern Norway are among the highest worldwide (Jensen et al., 2020), with an average of 1–2 moose/km² (Lavsund et al., 2003). Historically, aurochs (*Bos primigenius*), European bison (*Bison bonasus*) and European forest bison (*Bison schoetensacki*) have been part of the mammalian community in Europe (Massilani et al., 2016; Rosengren and Magnell, 2024). The aurochs was a grazer, which probably lived in open habitats and marshlands (Rosengren and Magnell, 2024), and not in the boreal forest. The European bison used the same habitat as cervids, which includes boreal forest, but it was an intermediate feeder, not a grazer (Rosengren and Magnell, 2024). Little is known on the diet of the forest bison. However, it went extinct circa 700 000 years ago (Massilani et al., 2016), which is long before boreal forest established in Norway 7000–8000 years ago, following the last Ice Age (Aasetre and Bele, 2009). In conclusion, boreal forest in Norway has evolved without native grazers and thus, we can expect cattle, which are typical grazers (Spedener et al., 2024a, 2024b) to affect boreal forest differently and to a larger degree than native cervids.

Another important factor is time. Herbivores have immediate effects on sward structure, while changes in plant species composition only occur after a longer time period (Skarpe and Hester, 2008). To better understand the effects of cattle on biodiversity in boreal production forest, we must keep in mind that forestry is the main driver in shaping these forests. Mature stands are harvested by clear-cutting, resulting in open habitat patches, which are replanted and grow back into canopy closed forest after about 15 years (Kuuluvainen et al., 2012; Aasetre and Bele, 2009). We know that cattle roaming in boreal production forest select for young spruce stands with open canopy cover for foraging, as these are more grass-rich than forest stands with closed canopy (Spedener et al., 2019; Tofastrud et al., 2019). Therefore, we focussed on young plantations for this study. We cannot expect cattle to have long-term effects on the forest landscape, as those plantations are meant to grow into pure spruce stands and to be harvested for timber in the end. However, we were interested in knowing to what degree cattle alter the biodiversity on these plantations before they grow into closed canopy forest. Do cattle create temporal biodiversity hotspots? Or are they detrimental to biodiversity found in boreal production forest, which already is low compared to old-grown forest (Savilaakso et al., 2021)?

Whereas the effects of livestock on various parts of various forested ecosystems have been studied previously (Adams, 1975), this is the first study to investigate the effects of cattle on biodiversity in boreal production forest. More precisely, we investigated the effects of cattle and cervids on the field layer vegetation and flower-visiting insects in young spruce plantations inside and outside cattle grazing areas. These areas had been grazed by cattle for many years. On each plantation, we established fenced and unfenced plots during the cattle grazing seasons in 2021 and 2022. This resulted in four ungulate treatments (Fig. 1). We did not include any treatment with cattle only in this study, as cattle never occur without cervids in boreal production forest in Norway. We examined differences between ungulate treatments at three levels: The plants in the field-layer vegetation, the floral resources in the field-layer vegetation and the flower-visiting insects.

As cattle had been summer grazing inside the cattle grazing area for many years, we expected them to have long-term effects on the field layer vegetation. Even though the spruce plantations we focussed on in this study were not older than 2–10 years, restricting the time span in which long-term changes could develop, we expected cattle to increase the abundance of graminoids (as grazers are known to stimulate grass growth), to increase the abundance and species richness of herbs (as grazers are known to alter sward structure in favour for light demanding herbs), to increase the abundance of floral resources (as a consequence

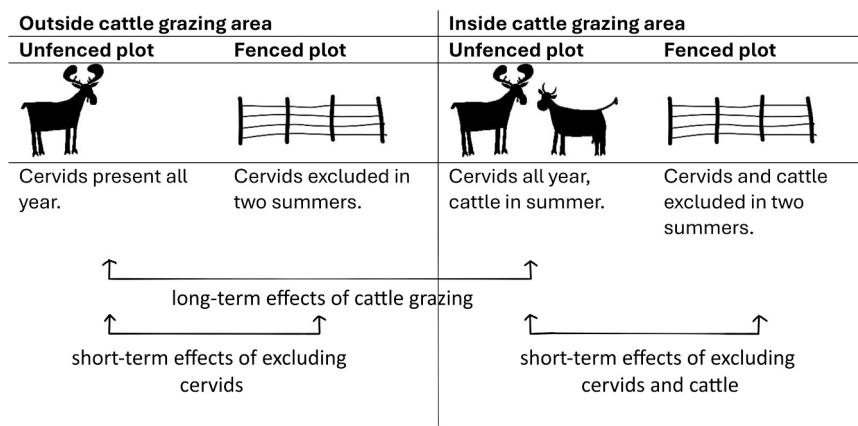


Fig. 1. Schematic figure of the four ungulate treatments used in this study. Please note: Cattle have been summer grazing inside the cattle grazing areas for many years before we collected data in 2021 and 2022. The cattle grazing areas were delimited by virtual fencing technology. Hence cattle were kept within these areas, whereas cervids could leave and enter freely. We fenced plots during summers 2021 and 2022 only. Cervids were present on all plots during winter.

of increased herb abundance) and increase the abundance of flower-visiting insects (as consequence of increased flower abundance). We expected these long-term effects to translate into differences between unfenced plots inside compared to outside the cattle grazing areas (Fig. 1).

Furthermore, we expected that fencing out ungulates outside the cattle grazing area (cervids only) had different effects than fencing out ungulates inside the cattle grazing area (cervids and cattle). We expected that fencing out cervids only would lead to increased height and abundance of woody plants in the field layer vegetation, that is shrubs and heather (due to ceased cervid browsing), leading to lower abundance and species richness of floral resources (due to interspecific competition) and hence to lower abundance and species richness of flower-visiting insects (due to reduced floral resources). We assumed these short-term effects of fencing out cervids to translate to differences between fenced compared to unfenced plots outside the cattle grazing areas (Fig. 1). We expected that fencing out cervids and cattle would lead to increased height and abundance of woody plants (due to ceased cervid

browsing) and graminoids (due to ceased cattle grazing), both leading to lower abundance and species richness of floral resources (due to interspecific competition) and hence to lower abundance and species richness of flower-visiting insects (due to reduced floral resources). We assumed that these short-term effects of fencing out cervids and cattle translate to differences between fenced compared to unfenced plots inside the cattle grazing areas (Fig. 1).

2. Methods

2.1. Data collection

2.1.1. Study area and sampling plots

We collected data in two study areas, Deset and Steinvik, in South-Eastern Norway (Fig. 2), where cattle summer grazing in boreal production forest is practiced. Forest as well as cattle owners were interested in collaborating with us and allowed us to conduct a study on their forest and cattle. Both areas are east facing slopes between 250 and

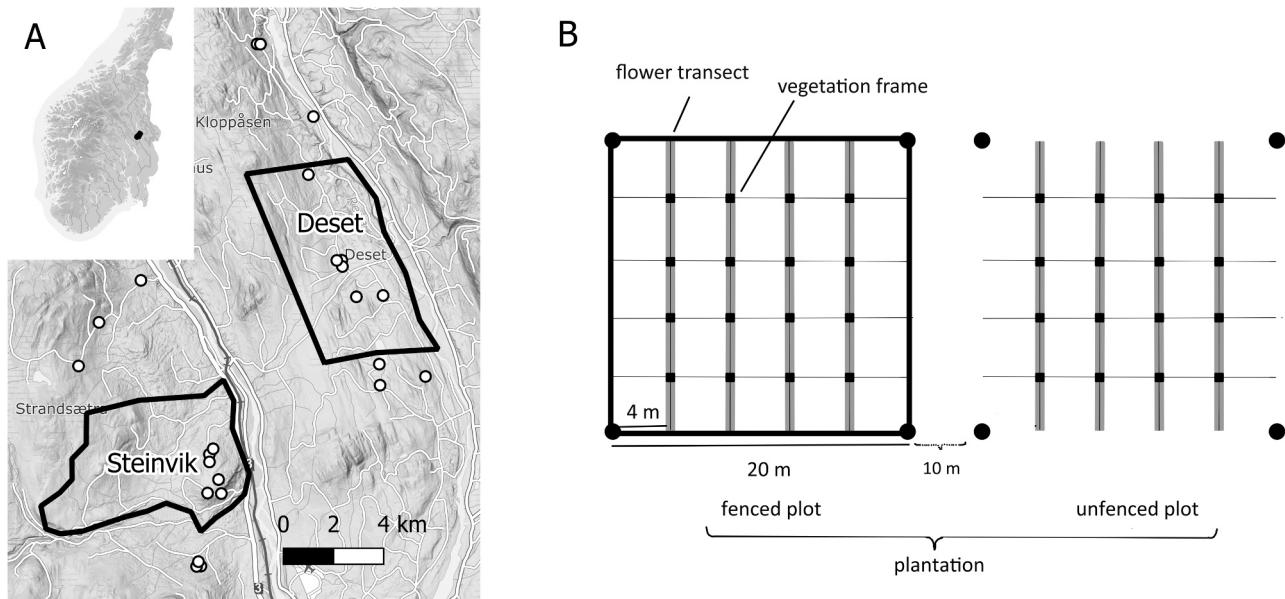


Fig. 2. (A) For each of the two grazing areas (Steinvik and Deset, in black), we selected 12 young spruce plantations (white dots): 6 within the cattle grazing area, three north of it and three south of it. (B) On each of the 24 plantations, we installed a fenced and an unfenced plot of 20×20 m each, at about 10 m from each other. The fences were up during summer and excluded ungulates from the plot. Every 4 m, we counted flowers along 0.5 m wide transects (in grey). Every 4×4 m, we sampled the field layer vegetation in 0.5×0.5 -m frames (in black). On the entire plot, flower-visiting insects were sampled.

600 m.a.s.l. covered with boreal production forest dominated by spruce (*Picea abies*) and pine (*Pinus sylvestris*). The dominating forestry practices are based on age-class structured stands and clear-cutting (even-aged forestry).

The core of both study areas are cattle grazing areas, which are about 35 km² large and delimited by virtual fencing technology (Nofence AS). When approaching the virtual fence, the animals get an audio warning from their collar and if they do not respect this warning, they are given a mild electric pulse. The absence of physical fences allows wildlife to freely enter and leave the grazing area. A study on another brand of virtual fence technology reported that the system successfully prevented the animals from crossing the virtual fence line (Umstatter et al., 2015). The same study found no changes in general activity or lying behaviour (Umstatter et al., 2015), a finding indicating that the cattle were not exposed to stress. This is in accordance with a study looking into cortisol in manure from cattle enclosed with Nofence virtual fencing, which has concluded that there was no evidence of Nofence causing stress in cattle (Sonne et al., 2022). Beef cattle of the breed Hereford, Limousin and Charolais were grazing in the area from the end of May to the end of September both years. Salt stones were provided in the grazing area and the farmers checked weekly on their animals, sometimes feeding pellets from buckets to keep the animals tame and used to human contact. No water was provided, as cattle find streams and ponds in the grazing area. The number of cows released was 68 in 2021 (47, i.e., 1.3 cows/km² in Steinvik and 21, i.e., 0.6 cows/km² in Deset) and 83 in 2022 (60, i.e., 1.7 cows/km² in Steinvik and 23, i.e., 0.7 cows/km² in Deset) and most

cows had a calf with them. The stocking density corresponds to about 30 % of the grazing capacity for this area (Rekdal, 2006). Based on camera trap data (Spedener et al., unpublished), we know that the most common ungulates in our study area are cattle, followed by moose, while red deer and roe deer were far less common.

In each study area, we chose six young spruce plantations within and six outside of the cattle grazing areas (Fig. 2), 24 plantations in total. By young spruce plantation we mean a spruce forest stand that has been harvested by clear-cutting and that has been replanted with spruce saplings 2–10 years ago. We chose plantations in bilberry spruce forest (as described by Fremstad 1997), with spruce trees below 2 m in height, because this forest type is common in South-Eastern Norway and has shown to be preferred by free-ranging cattle (Tofastrud et al., 2019). The distance between neighbouring plantations varied between 150 m and 6.6 km. In each of the 24 plantations, we established two plots of 20×20 m, one of them fenced to exclude all ungulates during summer and one of them only marked with corner poles, available to ungulates during summer (Fig. 2). This resulted in four ungulate treatments (Fig. 1). The fences were up during the grazing seasons in 2021 and 2022. This way cervids could use the plots freely during the rest of the year. The plots were placed in the middle of the stands, to avoid stand edge effects, and about 10 m apart to minimise heterogeneity in vegetation and abiotic conditions. Having pairs of plots (fenced, unfenced) on each plantation allowed us to control for possible differences among plantations, such as size, age, sun exposure and soil properties. Pictures of the plantations are given in Fig. 3 and Suppl. Mat. S1.

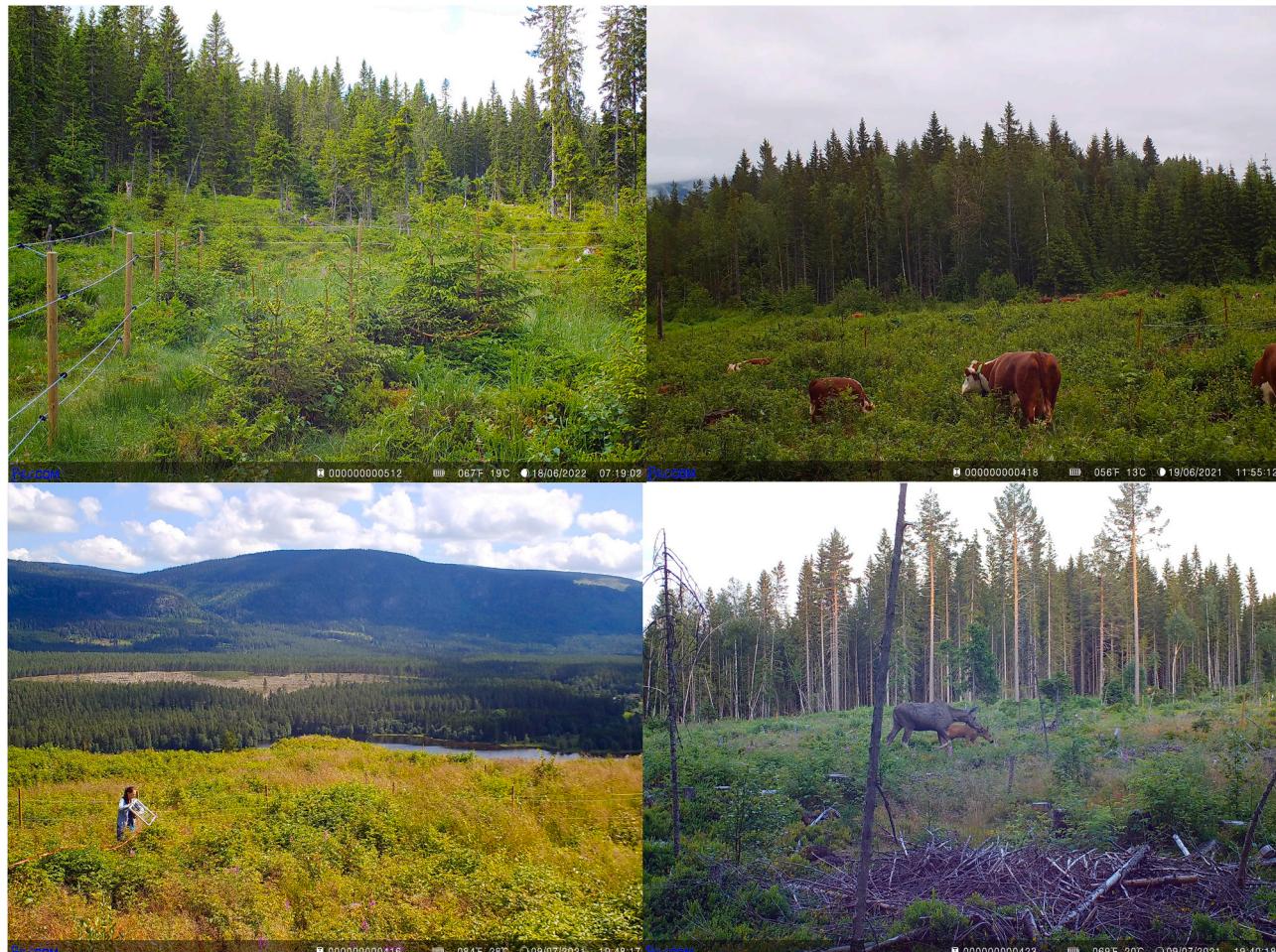


Fig. 3. Pictures of four of the 24 plantations the data was collected on. On the top left picture, you can see the fence that was used to exclude ungulates from the plot. On the top right picture, you can see cows with their calves. On the bottom left picture, you can see a fieldworker sampling the field layer vegetation. On the bottom right picture, you can see a moose cow with her calf. Pictures of the remaining 20 plantations can be found in the [supplementary material \(S1\)](#).

2.1.2. Field layer vegetation

On each of the 48 plots we registered the field layer vegetation in the middle of the peak flowering season in July 2021 and 2022 using the point-intercept method (Speed et al., 2014). We placed vegetation frames (0.5×0.5 m) following a 4×4 -metre grid (Fig. 2). In each frame, we put a thin, long needle vertically into the field layer vegetation following a 0.1×0.1 -m grid and identified all graminoids, herbs and woody plants touching the needle to species level. Plant species identification was based on Lid and Lid (2005) and Mossberg and Stenberg (2012). Sward height (Suppl. Mat. S2), that is the height of the field layer vegetation, was measured in centimetres for each frame using the sward stick method (Stewart et al., 2001). For each frame, plant group was defined as the main plant group with most hits (graminoids, herbs and woody plants). This way, sward height, which was measured for each frame, could be linked to plant group. Plant abundance (Suppl. Mat. S2) was derived on plot level as the sum of the number of hits in all 16 frames, per plant group per round. Plant species richness (Suppl. Mat. S2) was derived on plot level as the sum of species per plant group per round. However, species richness is a challenging variable to work with, as it cannot be measured nor directly estimated by observation (Magurran and McGill, 2010). Indeed, a biological community usually has many species with relatively small abundances. When a random sample of individuals is selected and each individual is classified according to species identity, some rare species may not be discovered. As we have collected abundance data in the field, the Chao1 index is an adequate index to be used to address this challenge (Chao and Shen, 2003; Magurran and McGill, 2010). It is a robust estimator of minimum richness build on a rigorous body of statistical theory (Chao and Shen, 2003; Magurran and McGill, 2010). Therefore, we adjusted species richness using Chao1 in the vegan package (Oksanen et al., 2022) in R (R Core Team, 2022), R Studio (RStudio Team, 2022). Graphs showing the adjusted species richness in relation to the observed species richness can be found in Suppl. Mat. S3A.

2.1.3. Floral resources

To estimate floral resource availability to flower-visiting insects we counted the number of flowers per plant species in each of the 48 plots, following 4 transects 0.5 m wide and 20 m long (Fig. 2). As graminoids are wind-pollinated, they were excluded from the protocol. The plots in Deset were monitored in 2021 and the plots in Steinvik in 2022. For plant species with numerous small flowers, inflorescences (*Filipendula ulmaria*, *Galium palustre*, *Anthriscus sylvestris*, *Alchemilla spec.*) or stems with flowers (*Calluna vulgaris*, *Maianthemum bifolium*, *Veronica officinalis*, *Veronica serpyllifolia*) were counted. Flowers were counted five times in each plot during the peak flowering season, between mid-June and mid-August. Flower abundance (Suppl. Mat. S2) was derived as the sum of flowers per plant group per plot per round. Flower species richness (Suppl. Mat. S2) was derived as the sum of species carrying flowers per plant group per plot per round. As we did for the species richness of plants, we adjusted species richness using Chao1 in the vegan package (Oksanen et al., 2022) in R (R Core Team, 2022), R Studio (RStudio Team, 2022). Graphs showing the adjusted species richness in relation to the observed species richness can be found in Suppl. Mat. S3B. As there were few species of woody plants and little variation in species richness, we excluded woody plants from the flower species richness analyses.

2.1.4. Flower-visiting insects

We caught insects observed on flowers five times in each of the 48 plots during the peak flowering season, between mid-June and mid-August and used the number of flower-visiting insects as a proxy for pollinators. The plots in Deset were sampled in 2021 and the plots in Steinvik in 2022. To minimize the effects of weather and time of day (morning, mid-day, afternoon), both plots on a given plantation were sampled on the same day and time of day. Moreover, we made sure to visit each plantation at different times of the day throughout the summer. Dates and time of day for each plot visit are given in Suppl. Mat. S4.

Two observers moved freely in the plot for 30 minutes, catching flower-visiting insects with mesh nets. The insects were classified as “bumblebee”, “honey bee”, “solitary bee”, “butterfly”, “hoverfly”, “other fly” or “other insect”. They were put into glass vials and preserved in 70 % ethanol. We identify bumblebees and hoverflies to species level, as they are the most important pollinator groups in the boreal forest (Nielsen and Totland, 2014). In the lab, they were dried, pinned, and identified to species level using a microscope. The species identification was based on Løken (1973), (1985) and Ødegaard et al. (2015) for bumblebees and Andersson (1988), Bartsch, Binkiewcs, et al. (2009), Bartsch, Binkiewics, et al. (2009), Hippa et al. (2001), Haarto and Ståhls (2014), Prokhorov et al. (2020), and Vujić et al. (2013) for hoverflies. Insect abundance (Suppl. Mat. S2) was derived as the sum of individuals caught per insect group per plot per round. Due to low numbers of butterflies, honeybees, solitary bees and “other insects” (less than one individual caught per plot per round), we excluded insect abundance of these groups from the analysis. Species richness of bumblebees and hoverflies (Suppl. Mat. S2) was derived as the sum of species caught per insect group per plot per round. As we did for the species richness of plants, we adjusted species richness using Chao1 in the vegan package (Oksanen et al., 2022). Graphs showing the adjusted species richness in relation to the observed species richness can be found in Suppl. Mat. S3C.

2.2. Data analyses

All analyses were done in R version 4.3.1 (R Core Team, 2022), using the R Studio (RStudio Team, 2022) interface. We investigated the effects of cattle and cervids on the plant and pollinator community using generalized linear mixed models (GLMMs) (Bolker et al., 2009), using the package glmmTMB (Brooks et al., 2017). We modelled sward height, plant abundance, adjusted plant species richness, flower abundance, adjusted flower species richness, insect abundance and adjusted insect species richness as responses to grazing area (0 = outside, 1 = inside) and plot fencing (0 = unfenced plot, 1 = fenced plot), in addition to plant group (for plants and flowers) or insect group (for insects). To account for spatial autocorrelation, we included plantation as random factor. To account for temporal autocorrelation, we included year (for plants) or sampling round (for flowers and insects) as random factors. As each plantation was visited several times, we nested year (for plants) and round (for flowers and insects) within plantation. As sward height was measured on frame level and averaging this variable per plot would have led to a high information loss (sward height varied a lot between the 16 frames of a given plot), we kept to the frame level during the analyses for this variable. All other response variables were modelled at plot level.

Based on the models' diagnostic plots (DHARMA package, (Hartig, 2022)), we determined the best family and link-function for each response variable. More specifically, we inspected simulated quantile residuals against the predicted values to assess the goodness of fit and rule out overdispersion. For sward height and plant abundance, we used GLMMs of the Gamma family with a log link function. For plant species richness and flower richness, we used a GLMM of the Poisson family with a log link function. For insect abundance and species richness of insects, we used GLMMs of the negative binomial family with a log link function. Due to large difference in the distribution of abundance between insect groups (hoverflies had a much higher proportion of zeros than bumblebees and other flies), leading to a bad model fit, we fitted separate models (GLMMs of the negative binomial family with a log link function) for abundance for each insect group. For flower abundance, we used a zero-inflated GLMM of the negative binomial family with a log link function.

For each response variable, we created i) a full model with all explanatory variables and their two-way interactions, ii) a model with all explanatory variables without interactions and iii) a null model. To avoid overfitting, we confirmed that we had at least 10 observations per

parameter fit by the model. We compared the goodness of fit with the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson (2002)) using the “model.sel” function within the MuMin library (Barton, 2022). Among the best models within delta AICc < 2, we picked the most parsimonious one. Model predictions were generated with the package ggeffects (Lüdecke, 2018) and plotted using ggplot2 (Wickham, 2016). For the categorical variables cattle grazing area and plot fencing and their interactions, we estimated the contrasts between levels using the package modelbased (Makowski et al., 2020). We defined long-term effects of cattle grazing as difference between unfenced plots inside compared to outside the cattle grazing areas (Fig. 1). We defined short-term effects of fencing out cervids as difference between fenced compared to unfenced plots outside the cattle grazing areas (Fig. 1). We defined short-term effects of fencing out cervids and cattle as difference between fenced compared to unfenced plots inside the cattle grazing areas (Fig. 1).

3. Results

3.1. Field layer vegetation, floral resources and flower-visiting insects

The most abundant plant groups across all plots and monitoring rounds were graminoids and woody plants (Suppl. Mat. S5), with the most abundant species being the woody plants *Rubus idaeus* (59.3 ± 55.0 hits per plot per round, mean \pm standard deviation), *Vaccinium myrtillus* (47.8 ± 63.2) and *Vaccinium vitis-idaea* (21.5 ± 32.0) and the graminoids *Avenella flexuosa* (49.2 ± 48.6), *Calamagrostis spec.* (25.5 ± 45.2), *Agrostis capillaris* (23.2 ± 39.5) and *Deschampsia cespitosa* (19.9 ± 32.0). Herbs were the tallest and the most species rich group of plants and carried most of the flowers (Suppl. Mat. S5). Flowers were most abundant on the herbs *Melampyrum pratense* (214.3 ± 418.7 flowers per plot per round), *Melampyrum sylvaticum* (63.6 ± 137.5) and *Epilobium angustifolium* (41.5 ± 102.3) and the woody plants *Rubus idaeus* ($59.4 \pm$

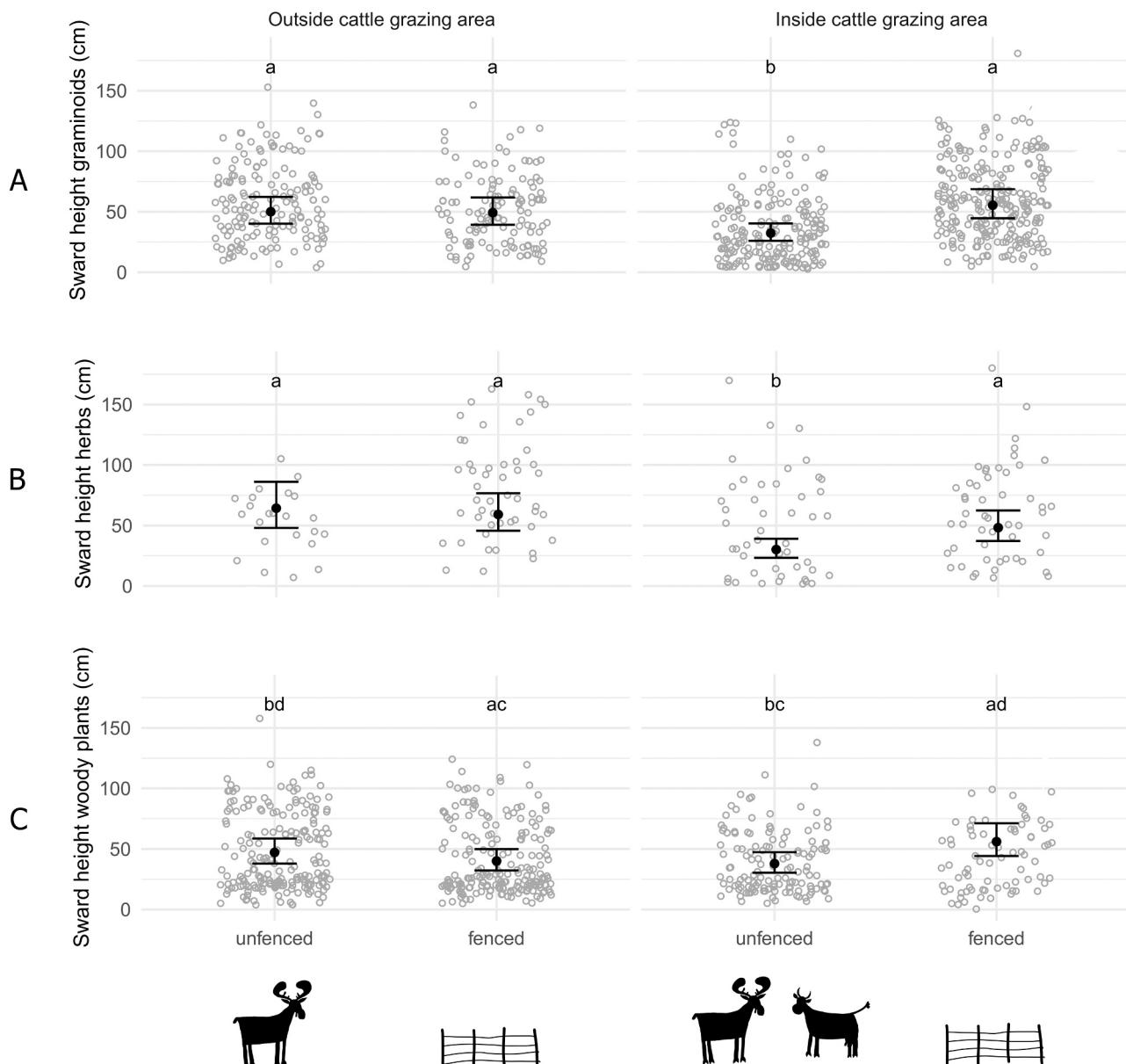


Fig. 4. Model predictions (means and 95 % confidence intervals, in black) for the best model used to explain the variation in sward height of (A) graminoids, (B) herbs and (C) woody plants in relation to grazing area and plot fencing. In grey the observed data, which the models are fitted on. The uncertainty in the random effects is not accounted for in the confidence intervals. Significant contrasts between groups in a given line are marked with small letters. For groups with the same letter, the ratio between the means is not significantly different from 1, with a significance level of < 0.05 .

188.7) and *Vaccinium vitis-idaea* (58.9 ± 282.5). Only three woody plant species (*Calluna vulgaris*, *Rubus idaeus* and *Vaccinium vitis-idaea*) were flowering, resulting in a low adjusted flower species richness with little variation among plots (Suppl. Mat. S5). The most common flower-visiting insects were bumblebees, hoverflies and other flies (Suppl. Mat. S5). The by far most abundant bumblebee species was *Bombus pratorum* (5.1 ± 4.9 individuals per plots per round)), followed by *Bombus cingulatus* (1.4 ± 2.3) and *Bombus jonellus* (1.3 ± 2.0). The most abundant hoverfly species were *Episyrphus balteatus* (0.4 ± 1.0), *Sphaerophoria scripta* (0.29 ± 0.6) and *Volucella bombylans* (0.2 ± 0.5). Hoverflies were less abundant and more species rich than bumblebees.

3.2. Effects of ungulate treatments on field layer vegetation, floral resources and flower-visiting insects

3.2.1. Field layer vegetation

The variation in sward height was best explained by plant group

(graminoids/herbs/woody plants), cattle grazing area (inside/outside), plot fencing (fenced/unfenced) and the two-way interactions between these variables (Suppl. Mat. S6, Suppl. Mat. S7). We found short-term effects of fencing out cattle and cervids on sward height: Fencing out cervids and cattle led to increased sward height of graminoids, herbs and woody plants (that is shrubs and heather) (Fig. 4, Suppl. Mat. S9). Fencing out cervids only lead to lower sward height of woody plants (Fig. 4, Suppl. Mat. S9).

The variation in abundance of plants in the field layer vegetation was best explained by plant group (graminoids/herbs/woody plants), cattle grazing area (inside/outside), plot fencing (fenced/unfenced) and the two-way interactions between these variables (Suppl. Mat. S6, Suppl. Mat. S7). Cattle grazing had a negative long-term effect on the abundance of woody plants (Fig. 5, Suppl. Mat. S9) and fencing out cattle and cervids over two summers led to increased abundance of graminoids (Fig. 5, Suppl. Mat. S9).

The variation in species richness of plants in the field layer

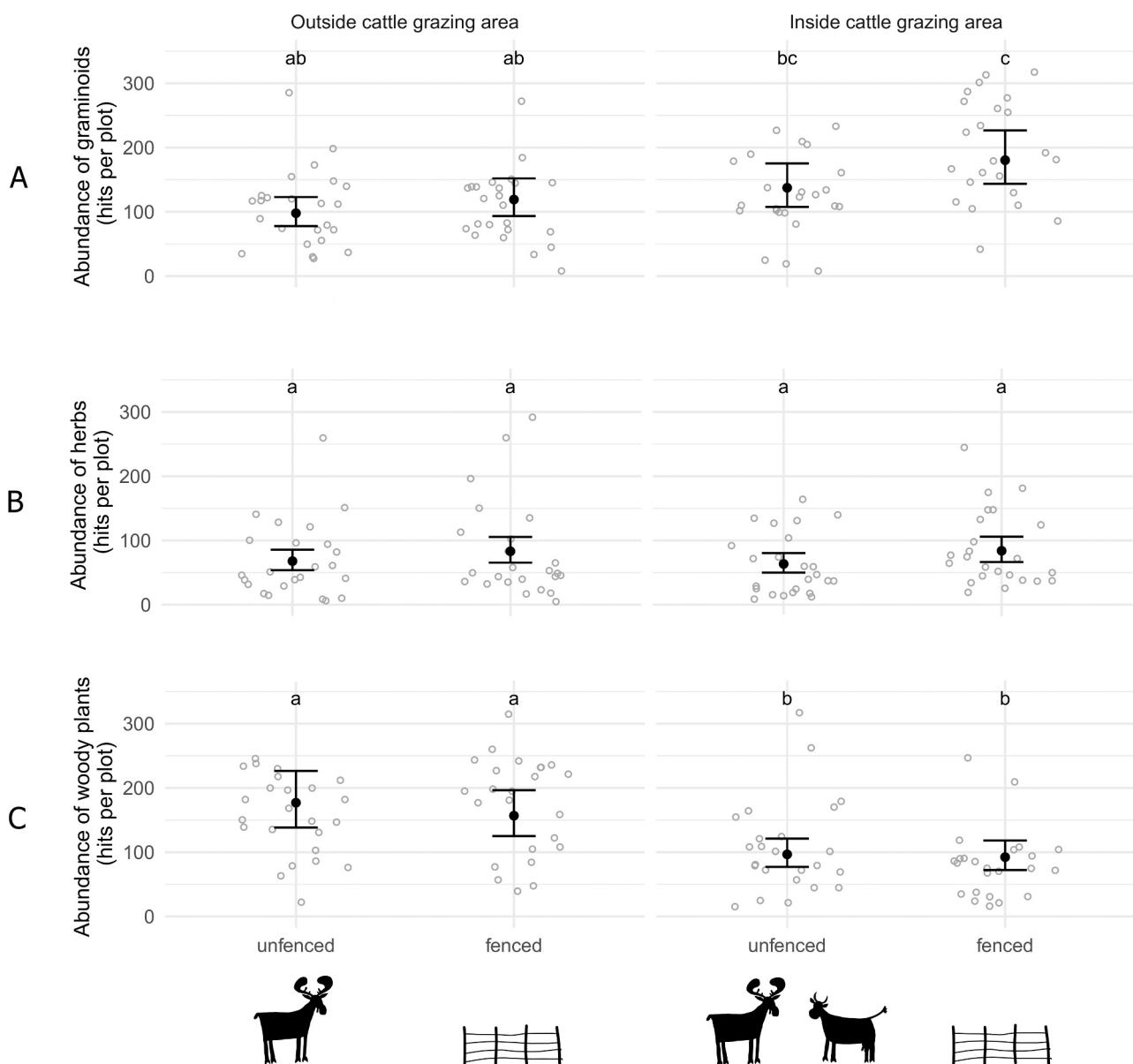


Fig. 5. Model predictions (means and 95 % confidence intervals, in black) for the best model used to explain the variation in abundance of (A) graminoids, (B), herbs and (C) woody plants in relation to grazing area and plot fencing. In grey the observed data, which the models are fitted on. The uncertainty in the random effects is not accounted for in the confidence intervals. Significant contrasts between groups in a given row are marked with small letters. For groups with the same letter, the ratio between the means is not significantly different from 1, with a significance level of < 0.05 .

vegetation was best explained by plant group (graminoids/herbs/woody plants), cattle grazing area (inside/outside), plot fencing (fenced/unfenced) and the two-way interactions between these variables (Suppl. Mat. S9, Suppl. Mat. S7). We found neither long-term effect of cattle grazing, nor short-term effects of fencing out ungulates on plant species richness (Suppl. Mat. S8, Suppl. Mat. S9).

3.2.2. Floral resources

The variation in abundance of flowers carried by plants in the field layer vegetation was best explained by plant group (herbs/woody plants), cattle grazing area (inside/outside) and plot fencing (fenced/unfenced) (Suppl. Mat. S6, Suppl. Mat. S7). Long-term cattle grazing reduced the abundance of flowers on herbs and woody plants (Fig. 6, Suppl. Mat. S9). Furthermore, excluding cervids only, as well as excluding cervids and cattle led to increased flower abundance on herbs and woody plants (Fig. 6, Suppl. Mat. S9).

The variation in species richness of plants in the field layer vegetation carrying flowers was best explained by cattle grazing area (inside/outside), plot fencing (fenced/unfenced) and the two-way interaction between these variables (Suppl. Mat. S6, Suppl. Mat. S7). We did not find any long-term effects of cattle grazing on flower species richness (Fig. 7, Suppl. Mat. S9). Excluding cervids only did not affect flower species richness neither (Fig. 7, Suppl. Mat. S9). Excluding cervids and cattle, on the other hand, led to increased flower species richness in herbs (Fig. 7, Suppl. Mat. S9).

3.2.3. Flower-visiting insects

The variation in abundance of bumblebees was best explained by cattle grazing area (inside/outside), plot fencing (fenced/unfenced) and the two-way interaction between these variables (Suppl. Mat. S6, Suppl.

Mat. S7). The variation in abundance of hoverflies could not be explained by the variables included in this study (Suppl. Mat. S6). The variation in abundance of other flies was best explained by grazing area (inside/outside), plot fencing (fenced/unfenced) and the two-way interaction between these variables (Suppl. Mat. S6, Suppl. Mat. S7). We found no long-term effects of cattle grazing on the abundance of flower-visiting insects (Fig. 8, Suppl. Mat. S9). While excluding cervids only did not alter the abundance of flower-visiting insects, the abundance of bumble bees and flies other than hoverflies increased after excluding cervids and cattle (Fig. 8, Suppl. Mat. S9).

The species richness of flower-visiting insects was best explained by insect group (bumblebees-hoverflies), cattle grazing area (inside/outside) and plot fencing (fenced/unfenced) (Suppl. Mat. S6, Suppl. Mat. S7). Whereas the species richness was significantly higher for bumblebees than for hoverflies, no difference was found between ungulate treatments (Suppl. Mat. S7, Suppl. Mat. S9).

4. Discussion

4.1. Long-term effects of cattle grazing

As cattle had been summer grazing inside the cattle grazing area for many years, we expected them to have long-term effects on the field layer vegetation. Even though the spruce plantations we focussed on in this study were not older than 2–10 years, restricting the time span in which long-term changes can develop, we expected cattle to increase the abundance of graminoids (as grazers are known to stimulate grass growth), to increase the abundance and species richness of herbs (as grazers are known to alter sward structure in favour for light demanding herbs), to increase the abundance of floral resources (as a consequence

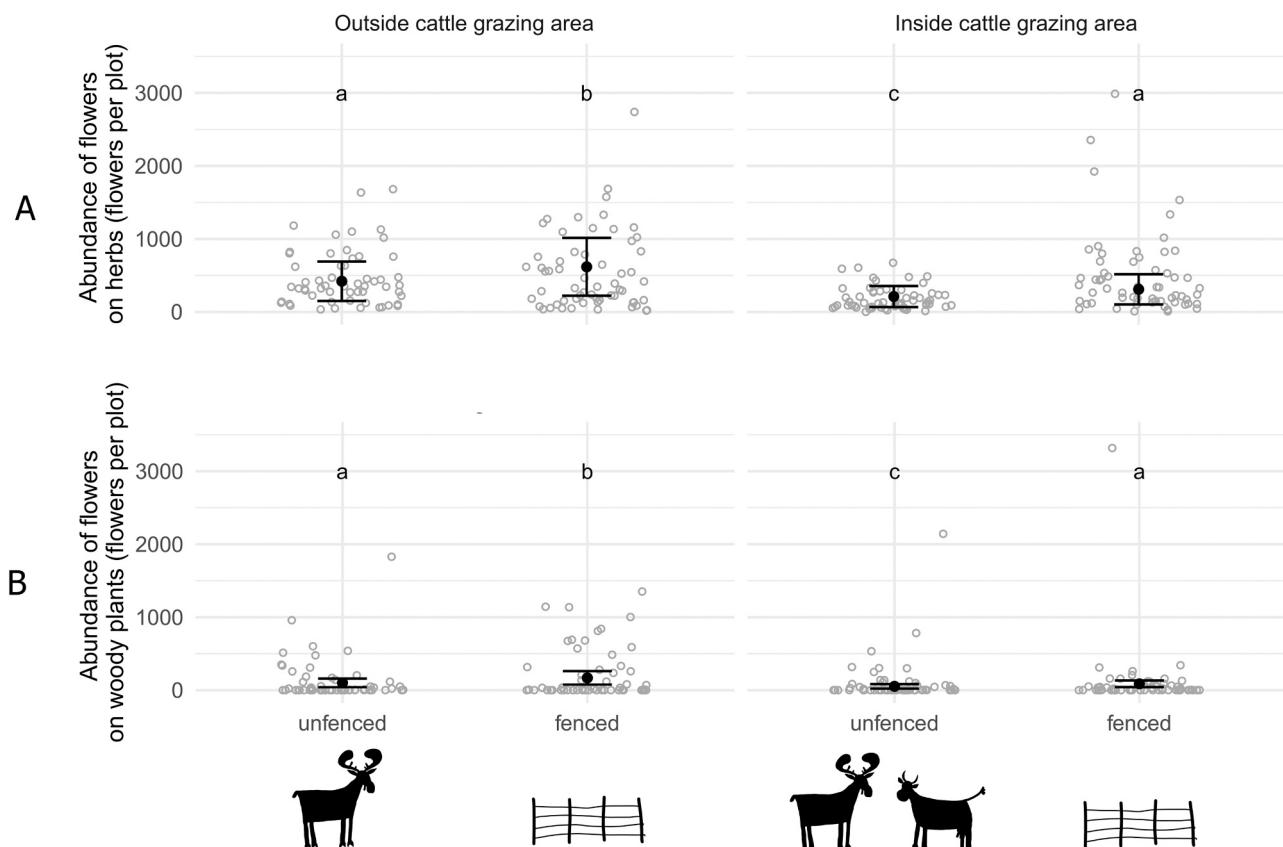


Fig. 6. Model predictions (means and 95 % confidence intervals, in black) for the best model used to explain the variation in abundance of flowers on (A) herbs and (B) woody plants in relation to grazing area and plot fencing. In grey the observed data, which the models are fitted on. The uncertainty in the random effects is not accounted for in the confidence intervals. Significant contrasts between groups in a given row are marked with small letters. For groups with the same letter, the ratio between the means is not significantly different from 1, with a significance level of < 0.05 .

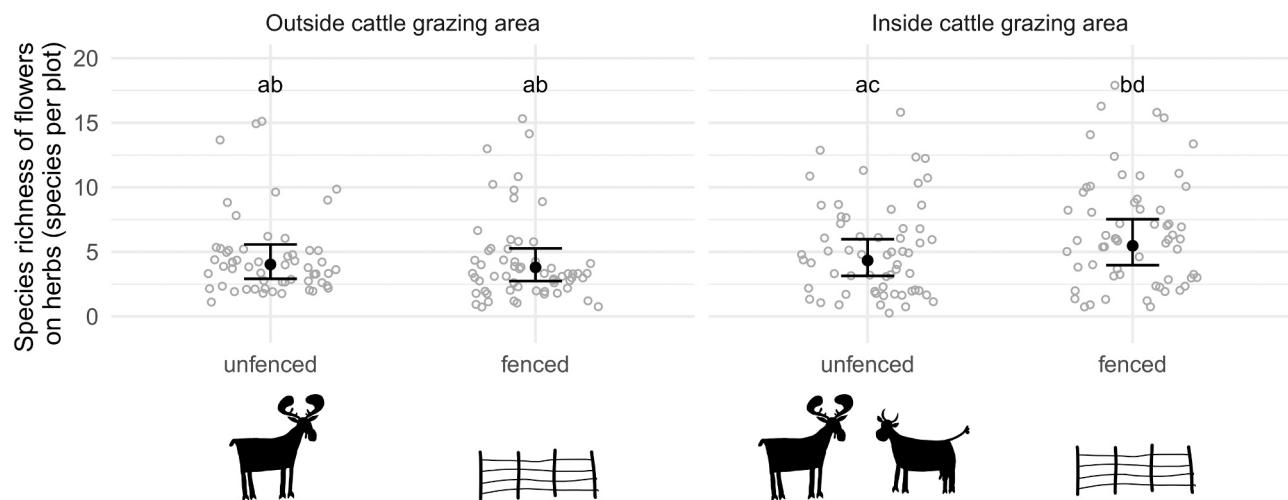


Fig. 7. Model predictions (means and 95 % confidence intervals, in black) for the best model used to explain the variation in species richness of flowers on herbs in relation to grazing area and plot fencing. In grey the observed data, which the models are fitted on. The uncertainty in the random effects is not accounted for in the confidence intervals. Significant contrasts between groups are marked with small letters. For groups with the same letter, the ratio between the means is not significantly different from 1, with a significance level of < 0.05 .

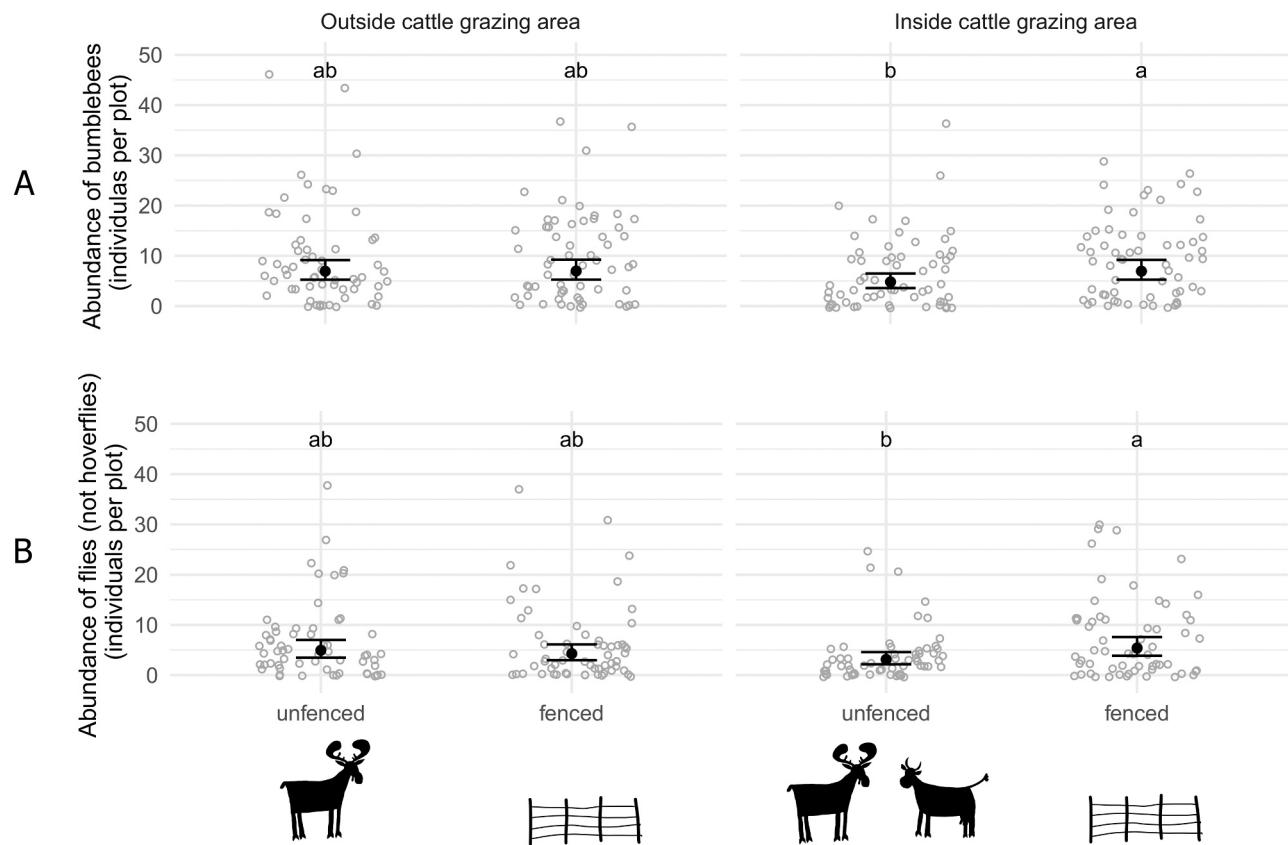


Fig. 8. Model predictions (means and 95 % confidence intervals, in black) for the best model used to explain the variation in abundance of (A) bumblebees and (B) flies other than hoverflies in relation to grazing area and plot fencing. For the hoverflies, the null model performed best, indicating that their abundance was not affected by ungulate treatment. For butterflies, honeybees, solitary bees and other insects, no models were fitted due to small sample sizes. In grey the observed data, which the models are fitted on. The uncertainty in the random effects is not accounted for in the confidence intervals. Significant contrasts between groups in a given row are marked with small letters. For groups with the same letter, the ratio between the means is not significantly different from 1, with a significance level of < 0.05 .

of increased herb abundance) and increase the abundance of flower-visiting insects (as consequence of increased flower abundance). Instead, we found that cattle grazing reduced the abundance of woody plants, reduced the abundance of flowers and had no long-term effects

on flower-visiting insects.

We were surprised to find that the abundance of woody plants (which we expected to be determined by browsers, which were present both inside and outside the cattle grazing areas) was lower inside the

cattle grazing area, whereas there was no difference in the abundance of graminoids (which we expected to be determined by grazers). Intense cattle grazing might have prevented woody plants to establish from seed on young spruce plantations. Even though cattle do not select for woody plants in their diet (Spedener et al., 2024a), they might grab tiny woody plants together with grass when foraging. Another explanation could be higher overall densities of ungulates within the cattle grazing areas, leading to a tipping point behavior of the field layer vegetation. When it comes to the observed pattern for graminoids, we should keep in mind that we do not know the differences between inside and outside the cattle grazing area before the cattle grazing areas were established.

Even though long-term cattle grazing reduced the abundance of flowers, we found no long-term effects on flower-visiting insects. The reduction in floral resources could have been too weak to influence flower-visiting insects. Moreover, insects are mobile, and we did not consider their home range sizes. Some species might have been able to travel between inside and outside the cattle grazing area and diluted the strength of the study design.

4.2. Short-term effects of fencing out cervids and cattle

As expected, we saw different effects of fencing out cervids only compared to fencing out cervids and cattle. Excluding cervids led to reduced sward height of woody plants (shrubs and heather) and to increased flower abundance. In contrast, excluding cervids and cattle led to increased sward height of graminoids, herbs and woody plants, to higher abundance of graminoids, higher flower abundance and higher abundance of flower-visiting insects. However, neither the effects of fencing out cervids only, nor of fencing out cervids and cattle were in line with our expectations.

We expected fencing out cervids only to lead to increased height and abundance of woody plants (shrubs and heather), due to ceased browsing. Instead, we found a decrease in sward height for this plant group, which we have difficulties to explain. The observed increased flower abundance can be explained by lower interspecific competition between woody plants and herbs. Interestingly, excluding cervids did not lead to any changes in abundance or species richness of flower-visiting insects.

A reason for the absence of strong effects of fencing out cervids only could be low cervid densities in the study area, despite moose densities in the region being estimated to 1–2 moose/km² (Lavssund et al., 2003) and thereby among the highest in the world (Jensen et al., 2020). Moose population sizes are regulated by hunting (Lavssund et al., 2003) and match the limited forage resources during winter. Therefore, we can assume that these populations are unable to deplete the abundant forage resources available in summer. Cattle, to the contrary, are fed during winter and kept at much higher population sizes. However, we do not have exact moose density estimates for our study area. We can expect moose densities below the reported 1–2 moose/km², as moose are known to migrate to higher altitudes during summer (Andersen, 1991) and as they might avoid areas used by cattle (Herfindal et al., 2017).

We expected fencing out cervids and cattle to lead to increased height of woody plants and graminoids, due to ceased browsing and grazing. Indeed, excluding cervids and cattle led to increased sward height of graminoids, woody plants and, in addition, herbs. Foraging on herbs is typically considered as browsing (Clauss et al., 2008; Janis, 2008). However, cattle, which are typical grazers, as well are known to include some proportion of herbs in their diet (Spedener et al., 2024a). Hence it is hard to tell if the herbs were shortened by either cervids or cattle. The fact that excluding cervids alone did not lead to reduced sward height of herbs indicates that cattle were the ones reducing herb height. We expected to see a similar pattern for sward height and plant abundance. However, plant abundance was affected only by excluding cervids and cattle, and this was only the case for graminoids, which increased in abundance. This increase was in accordance with our expectations. Still, the fact that grazing leads to biomass removal in the

field layer vegetation during the grazing season and at the same time might trigger field layer vegetation regrowth complicates the interpretation of our results. Proper measurements of biomass removal would have been highly useful in this context. However, biomass removal is a challenging variable to measure, in our case requiring multiple measurements throughout the season and artificial biomass removal to assess plant regrowth ('t Mannetje, 2000). Unfortunately, we did not collect data of such quality in this study.

In a next step, we expected the changes in the field layer vegetation to lead to reduced abundance and species richness of floral resources, due to interspecific competition. Surprisingly, fencing out ungulates (cervids only as well as cervids and cattle) led to increased flower abundance instead. In addition, fencing out cervids and cattle led to increased species richness of flowers. Apparently, a different mechanism than interspecific competition between plants played in here. Our first suggestion is that cervids and cattle selected for flowers when foraging. Flowers are probably nutritious and tasty. In addition, the high proportion of tall herbs, such as fireweed and meadowsweet, might have contributed to the observed pattern. Cattle and cervids might have removed more flowers by shortening these tall herbs, than they enhanced flowering in small herbs by opening the sward canopy. Furthermore, it is common that herbivory causes plants to allocate resources to compensatory vegetative growth at the expense of sexual reproduction (Skarpe and Hester, 2008), which in our case would translate to more regrowth and fewer flowers on the unfenced plots. The fact that fencing out cervids and cattle led to increased flower species richness, whereas fencing out cervids alone did not, could be explained by cattle foraging to a higher degree on herbs and flowers than cervids. This would be in accordance with the findings on sward height of herbs discussed earlier and with the findings on insect abundance.

Indeed, fencing out cervids and cattle affected flower-visiting insects, which experienced an increase in abundance. This finding is in line with another study documenting a reduction of flower-visiting insects due to cattle grazing (Guy et al., 2021). We are confident in assuming that the negative effects of cervids and cattle on flower-visiting insects can be directly linked to the reduction in floral resources, as this link has been observed in other studies too (Lasway et al., 2022; Lázaro et al., 2016). Other possible mechanisms might be trampling and general disturbance that alter the habitat of flower-visiting insects. Indeed, grazing has been found to affect pollinators' survival rate by killing them or destroying their nests through animal trampling (Sjödin, 2007). Considering that cattle are herd animals, roaming in groups of 10–20 animals, while moose, red deer and roe deer during summer live alone or in small groups of 2–3 animals, this mechanism can be considered a plausible explanation for our results as well.

4.3. Implications for cattle grazing management in boreal production forest

This study is the first one to investigate cattle's effects on plant and flower-visiting insects in the boreal forest. In addition, we tried to disentangle the effects of cattle and cervids. Linking plantation-specific cattle and cervid densities to the effect of fencing would be highly interesting to this aim. Indeed, we initially intended to derive cattle and cervid densities based on GPS-data (cattle) and camera trap data (cattle and cervids). Unfortunately, our density data was of poor quality, e.g. the visibility for the camera traps varied considerably between plantations. Furthermore, we were not able to manipulate ungulate densities. This resulted in highly screwed data, with few plantations that were heavily used by cattle. In our eyes, the results of this study are much more robust when analysing the data using ungulate treatments only. These treatments catch a lot of variation, both variation of cattle and cervid densities, as well as variation in plantation characteristics, and provide sound statistical results.

Cattle affected plants and flower-visiting insects in different ways than cervids did, and to a larger extent. While cattle are known to

positively affect biodiversity in semi-natural grasslands in Europe, they did not provide such effects in young spruce plantations in the boreal forest, at least not at the observed cattle stocking rates of 0.6–1.7 cows/km². We must keep in mind that this is the overall stocking density of the grazing areas. As cattle select for spruce plantations (Tofastrud et al., 2019), the densities can be assumed to be higher on those. Spruce plantations are very different from semi-natural grasslands, especially when it comes to their life span. Whereas an important characteristic of grasslands is their continuity (Kuhn et al., 2021), the grassland-like appearance of spruce plantations is short-lived. Grass and herbs establish after the clearcut of mature forest and disappear once the canopy closes again after about 15 years (Tofastrud et al., 2019). In addition, cattle are typical grazers, whereas boreal forest is a typical browser's habitat, that has evolved without native grazers. This study documents a negative effect of the current practice of cattle grazing in boreal forest on floral resources and flower-visiting insects. Flower-visiting insects can be used as proxy for pollinators (Willmer, 2011). As honeybees were absent in our study, flower-visiting insects in our study can be used as proxy for wild pollinators. Since we are currently facing a global pollination crisis (Rhodes, 2018) and the conservation of wild pollinators is of high interest (Stout and Dicks, 2022), a careful consideration of the current practice of cattle grazing in spruce plantations might be needed. There are many good reasons to release cattle for summer grazing into boreal forests in Norway, such as an efficient use of scarce and scattered forage resources and reduced depredation risk to large predators compared to sheep. However, the often-used argument (in Norway) of livestock grazing in the outfields having positive effects on biodiversity is not supported by this study, at least not for cattle grazing in boreal production forest, and should be used with caution.

Funding statement

This study is part of the CarniForeGraze project which is funded by the Norwegian Research Council (project number 302674).

CRediT authorship contribution statement

Barbara Zimmermann: Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Gunnar Austrheim:** Writing – review & editing, Validation, Supervision, Methodology. **Anders Nielsen:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Marie Vestergaard Henriksen:** Writing – review & editing, Validation, Supervision, Methodology. **Karen Marie Mathisen:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Veronika Schubert:** Writing – review & editing, Visualization, Methodology, Investigation, Data curation. **Juliette Helbert:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Jenny Valaker:** Writing – review & editing, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Mélanie Spedener:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data and R script used in the study are available at Mendeley Data, <https://doi.org/doi: 10.17632/k5dm2x57hw.1> (Spedener et al., 2024).

Acknowledgements

We would like to thank the cattle and forest owners for their goodwill and cooperation in the implementation of this study, May Britt Trydal, Sari Dötterer, Laura Niccolai, Pierre Lissillour, Tom Graillot, Lisa Smit, Félix Gilbert, Saskia Wulff, Giulia Cenzi, Felix Fisel, Toby Rumble, Franka Bernhardi and Casper Thomassen for carrying out fieldwork, Stian Bønner for hoverfly species identification, Olivier Devineau for statistical advice and 4 anonymous reviewers for their thorough and constructive comments on the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122258.

References

- 't Mannetje, L., 2000. Measuring biomass of grassland vegetation. Field and laboratory. *Methodod. Grassl. Anim. Prod. Res.* 151–177. <https://doi.org/10.1079/9780851993515.0151>.
- Aaseter, J., Bele, B., 2009. History of forestry in a central Norwegian boreal forest landscape: Examples from Nordli, Nord-Trøndelag. *Nor. Geogr. Tidsskr. Nor. J. Geogr.* 63 (4), 233–245.
- Adams, S.N., 1975. Sheep and cattle grazing in forests: a review. *J. Appl. Ecol.* 152, 143.
- Andersen, R., 1991. Habitat deterioration and the migratory behaviour of moose (*Alces alces* L.) in Norway. *J. Appl. Ecol.* 28 (1), 102–108. <https://doi.org/10.2307/2404117>.
- Andersson, H., 1988. De svenska Xylotini-arterna (Diptera, Syrphidae). *Ent. Tidskr.* 109, 129–137.
- Aune-Lundberg, L., Munsterhjelm, N., 2021. Beitedyras geografi..
- Austrheim, G., Mysterud, A., Pedersen, B., Halvorsen, R., Hassel, K., Evju, M., 2008. Large scale experimental effects of three levels of sheep densities on an alpine ecosystem. *Oikos* 117 (6), 837–846.
- 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? *Wildl. Biol.* 17 (3), 286–298.
- Barton, K. (2022). MuMin: Multi-Model Inference (1.46.0) [Programvare]. (<https://CRAN.R-project.org/package=MuMin>).
- Bartsch, H., Binkiewics, E., Rådén, A., Nasibov, E., 2009. *Tvåvingar: Blomflugor: Syrphinae. Diptera: Syrphidae: Syrphinae. Nationalnyckeln Till Sveriges Flora Och Fauna. SLU.*
- Bartsch, H., Binkiewics, E., Klintbjer, A., Rådén, A., Nasibov, E., 2009. *Tvåvingar: Blomflugor: Eristalinae & Microdontinae. Diptera: Syrphidae: Eristalinae & Microdontinae. Nationalnyckeln till Sveriges flora och fauna. SLU.*
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24 (3), 127–135.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skauge, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J. 9* (2), 378–400. <https://doi.org/10.32614/RJ-2017-066>.
- Burnham, K.P., Anderson, D.R., 2002. Avoiding pitfalls when using information-theoretic methods. *J. Wildl. Manag.* 66 (3), 912–918. <https://doi.org/10.2307/3803155>.
- Chao, A., Shen, T.-J., 2003. Nonparametric estimation of Shannon's index of diversity when there are unseen species in sample. *Environ. Ecol. Stat.* 10 (4), 429–443. <https://doi.org/10.1023/A:1026096204727>.
- Clauss, M., Kaiser, T., Hummel, J., 2008. The morphophysiological adaptations of browsing and grazing mammals. *The Ecology of Browsing and Grazing*. Springer, pp. s. 47–88.
- Farsund, A.A., Daugbjerg, C., 2017. Debating food security policy in two different ideological settings: a comparison of Australia and Norway. *Scand. Political Stud.* 40 (4), 347–366. <https://doi.org/10.1111/1467-9477.12091>.
- Franzen, M., Nilsson, S.G., 2008. How can we preserve and restore species richness of pollinating insects on agricultural land? *Ecography* 31 (6), 698–708.
- Fremstad, E., 1997. NINA•NIKU Stiftelsen for naturforskning og kulturminneforskning. Veg. i Nor. (<http://hdl.handle.net/11250/2837231>).
- Gaujour, E., Amiaud, B., Mignolet, C., Plantureux, S., 2012. Factors and processes affecting plant biodiversity in permanent grasslands. A review. *Agron. Sustain. Dev.* 32 (1), 133–160. <https://doi.org/10.1007/s13593-011-0015-3>.
- Guy, T.J., Hutchinson, M.C., Baldock, K.C.R., Kayser, E., Baiser, B., Staniczenko, P.P.A., Goheen, J.R., Pringle, R.M., Palmer, T.M., 2021. Large herbivores transform plant-pollinator networks in an African savanna. *Curr. Biol.* 31 (13), 2964–2971.e5. <https://doi.org/10.1016/j.cub.2021.04.051>.
- Haarto, A., Ståhls, G., 2014. When mtDNA COI is misleading: Congruent signal of ITS2 molecular marker and morphology for North European *Melanostoma Schiner*, 1860 (Diptera, Syrphidae). *ZooKeys* (431), 93.
- Hartig, F. (2022). DHARMA: Residual Diagnostics for Hierarchical (Multi_Level / Mixed) Regression Models (version 0.4.5) [Programvare]. (<https://CRAN.R-project.org/package=DHARMA>).

- Herfindal, I., Lande, U.S., Solberg, E.J., Rolandsen, C.M., Roer, O., Wam, H.K., 2017. Weather affects temporal niche partitioning between moose and livestock. *Wildl. Biol.* 2017 (4) <https://doi.org/10.2981/wlb.00275>.
- Hippa, H., Nielsen, T.R., & Steenis, J. van. (2001). The West Palaearctic species of the genus *Eristalis* Latreille (Diptera, Syrphidae). *Norwegian Journal of Entomology*, 48, 289–289.
- IPBES. 2018. The IPBES assessment report on land degradation and restoration. Zenodo. <https://doi.org/10.5281/zenodo.3237393>.
- Janis, C., 2008. An Evolutionary History of Browsing and Grazing Ungulates. In: Gordon, I.I.J., Prins (Eds.), *The Ecology of Browsing and Grazing*. Springer Berlin Heidelberg, pp. 21–45. https://doi.org/10.1007/978-3-540-72422-3_2.
- Jensen, W.F., Rea, R.V., Penner, C.E., Smith, J.R., Bragina, E.V., Razenkova, E., Balciuscas, L., Bao, H., Bystiansky, S., Csányi, S., Chovanova, Z., Done, G., Hackländer, K., Heurich, M., Jiang, G., Kazarez, A., Pusenius, J., Solberg, E.J., Veeroja, R., Widemo, F., 2020. A review of circumpolar moose populations with emphasis on eurasian moose distributions and densities. *Alces: A J. Devoted Biol. Manag. Moose* 56, 63–78.
- Johansen, L., Taigourdeau, S., Hovstad, K.A., Wehn, S., 2019. Ceased grazing management changes the ecosystem services of semi-natural grasslands. *Ecosyst. People* 15 (1), 192–203.
- Katona, K., Coetsee, C., 2019. Impacts of browsing and grazing ungulates on faunal biodiversity. *I The Ecology of Browsing and Grazing II*. Springer, pp. s. 277–300.
- Kuhn, T., Domokos, P., Kiss, R., Ruprecht, E., 2021. Grassland management and land use history shape species composition and diversity in Transylvanian semi-natural grasslands. *Appl. Veg. Sci.* 24 (2), e12585 <https://doi.org/10.1111/avsc.12585>.
- Kuuluvainen, T., Tahvonen, O., Aakala, T., 2012. Even-aged and uneven-aged forest management in boreal Fennoscandia: A review. *Ambio* 41 (7), 720–737.
- Lanta, V., Austrheim, G., Evju, M., Klimešová, J., Mysterud, A., 2014. Linking sheep density and grazing frequency to persistence of herb species in an alpine environment. *Ecol. Res.* 29 (3), 411–420. <https://doi.org/10.1007/s11284-014-1132-7>.
- Lasway, J.V., Steffan-Dewenter, I., Njovu, H.K., Kinabo, Neema R., Eardley, C., Pauly, A., Peters, M.K., 2022. Positive effects of low grazing intensity on East African bee assemblages mediated by increases in floral resources. *Biol. Conserv.* 267, 109490 <https://doi.org/10.1016/j.biocon.2022.109490>.
- Lavssund, S., Nygrén, T., Solberg, E.J., 2003. Status of moose populations and challenges to moose management in fennoscandia. *Alces: A J. Devoted Biol. Manag. Moose* 39, 109–130.
- Lázaro, A., Tscheulin, T., Devalez, J., Nakas, G., Petanidou, T., 2016. Effects of grazing intensity on pollinator abundance and diversity, and on pollination services. *Ecol. Entomol.* 41 (4), 400–412. <https://doi.org/10.1111/een.12310>.
- Lid, J., & Lid, D.T. (2005). *Norsk flora* (7. utg.).
- Løken, A., 1973. Studies on Scandinavian bumblebees (Hymenoptera, Apidae). *Nor. Entomol. Tidsskr.* 20, 1–218.
- Løken, A. (1985). *Humler. Tabell til norske arter* (Bd. 9). Norsk entomologisk forening. (http://www.entomologi.no/journals/pdf/Norske_Insekttabeller_09.pdf).
- Lüdecke, D., 2018. ggeffects: tidy data frames of marginal effects from regression models. J. Open Source Softw. 3, 772. <https://doi.org/10.21105/joss.00772>.
- Magurran, A.E., & McGill, B.J. (2010). *Biological diversity: Frontiers in measurement and assessment*. OUP Oxford.
- Makowski, D., Ben-Shachar, M.S., Patil, I., & Lüdecke, D. (2020). *Estimation of Model-Based Predictions, Contrasts and Means*. CRAN. (https://github.com/easystats/mod_elbased).
- Massilani, D., Guimaraes, S., Brugal, J.-P., Bennett, E.A., Tokarska, M., Arbogast, R.-M., Baryshnikov, G., Boeskorov, G., Castel, J.-C., Davydov, S., Madelaine, S., Putelat, O., Spasskaya, N.N., Uerpmann, H.-P., Grange, T., Geigl, E.-M., 2016. Past climate changes, population dynamics and the origin of Bison in Europe. *BMC Biol.* 14 (1), 93. <https://doi.org/10.1186/s12915-016-0317-7>.
- Mossberg, B., & Stenberg, L. (2012). *Gylldendals store nordiske flora* (Rev. og utvidet utg.). Gylldental. (https://urn.nb.no/URN:NBN:no_nb_digibok_201030248841).
- Nielson, A., Totland, Ø., 2014. Structural properties of mutualistic networks withstand habitat degradation while species functional roles might change. *Oikos* 123 (3), 323–333.
- Ødegaard, F., Staverløkk, A., Gjershaug, J.O., Bengtson, R., Mjelde, A., 2015. Humler i Norge: Kjennetegn, utbredelse og levesett. Norsk institutt for naturforskning. (https://urn.nb.no/URN:NBN:no_nb_digibok_2018020848055).
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., Solymos, P., Stevens, M.M.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H.B.A., FitzJohn, R., ... Weedon, J. (2022). vegan: Community Ecology Package (R package version 2.6-2) [Programvare]. (<https://CRAN.R-project.org/package=vegan>).
- Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., Willmer, P., 2003. Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* 84 (10), 2628–2642. <https://doi.org/10.1890/02-0136>.
- Prokhorov, A.V., Popov, G.V., Shparyk, V.Y., Vasilyeva, Y.S., 2020. New records of hoverflies (Diptera, syrphidae) from Ukraine. *V. Zodiversity* 54 (3), 237–258.
- R Core Team, 2022. R: A Language and Environment for Statistical Computing [Programvare]. R. Found. Stat. Comput. (<https://www.R-project.org/>).
- Rekdal, Y., 2006. Størfebeite i utmark for eiendommene Løsset, Deset og Rød. *ÅAmot kommune. Oppdragsrapp. fra Skog Og. Landsk.*
- Rhodes, C.J., 2018. Pollinator decline – an ecological calamity in the making? *Sci. Prog.* 101 (2), 121–160. <https://doi.org/10.3184/003685018X15202512854527>.
- Rodríguez, A., Kouki, J., 2017. Disturbance-mediated heterogeneity drives pollinator diversity in boreal managed forest ecosystems. *Ecol. Appl.* 27 (2), 589–602. <https://doi.org/10.1002/eaap.1468>.
- Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G., Mills, J., 2004. Matching type of livestock to desired biodiversity outcomes in pastures – a review. *Biol. Conserv.* 119 (2), 137–150. <https://doi.org/10.1016/j.biocon.2003.11.010>.
- Rosengren, E., Magnell, O., 2024. Ungulate niche partitioning and behavioural plasticity of aurochs in Early Holocene southern Scandinavia revealed by stable isotope analysis of bone collagen. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 648, 112257 <https://doi.org/10.1016/j.palaeo.2024.112257>.
- RStudio Team. (2022). *RStudio: Integrated Development Environment for R* [Programvare]. RStudio, PBC. (<http://www.rstudio.com/>).
- Rubene, D., Schroeder, M., Ranius, T., 2015. Diversity patterns of wild bees and wasps in managed boreal forests: effects of spatial structure, local habitat and surrounding landscape. *Biol. Conserv.* 184, 201–208.
- Savilaakso, S., Johansson, A., Häkkilä, M., Uusitalo, A., Sandgren, T., Mönkkönen, M., Puttonen, P., 2021. What are the effects of even-aged and uneven-aged forest management on boreal forest biodiversity in Fennoscandia and European Russia? A systematic review. *Environ. Evid.* 10 (1), 1. <https://doi.org/10.1186/s13750-020-00215-7>.
- Scimone, M., Rook, A.J., Garel, J.P., Sahin, N., 2007. Effects of livestock breed and grazing intensity on grazing systems: 3. Effects on diversity of vegetation. *Grass Forage Sci.* 62 (2), 172–184. <https://doi.org/10.1111/j.1365-2494.2007.00579.x>.
- Sjödin, N.E., 2007. Pollinator behavioural responses to grazing intensity. *Biodivers. Conserv.* 16 (7), 2103–2121. <https://doi.org/10.1007/s10531-006-9103-0>.
- Sjögren, K.G., Austrheim, G., Stene, K., Hjelle Loe, K., Rosvold, J., & Tretvik, A.M. (2015). Fjellets kulturlandskapshistorie. I *Fjellets kulturlandskap: Arealbruk og landskap gjennom flere tusen år* (s. 159–179) (https://www.ntnu.no/documents/10476/1264108740/Fjellets+kulturlandskap.5korr.pdf/d_03c841e-9b8a-4529-9d87-4506978b0cfd).
- Skarpe, C., & Hester, A.J. (2008). Plant Traits, Browsing and Gazing Herbivores, and Vegetation Dynamics. I I. J. Gordon & H. H. T. Prins (Eds.), *The Ecology of Browsing and Grazing* (Bd. 195, s. 217–261). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-72422-3_9.
- Sonne, C., Alstrup, A.K.O., Pertoldi, C., Frikke, J., Linder, A.C., Styrihave, B., 2022. Cortisol in manure from cattle enclosed with no fence virtual fencing. *Animals* 12 (21), 3017.
- Spedener, M., Tofastrud, M., Austrheim, G., Zimmermann, B., 2024a. A Grazer in a Brower's Habitat: resource selection of foraging cattle in productive boreal forest. *Rangel. Ecol. Manag.* 93, 15–23. <https://doi.org/10.1016/j.rama.2023.12.004>.
- Spedener, M., Tofastrud, M., Devineau, O., Zimmermann, B., 2019. Microhabitat selection of free-ranging beef cattle in south-boreal forest. *Appl. Anim. Behav. Sci.* 213, 33–39.
- Spedener, M., Zimmermann, B., Mathisen, K.M., Tofastrud, M., Nielsen, A., & Henriksen, M.V. (2024b). *Data and R code used to study the effects of cattle and cervids on plants and pollinators on young spruce plantations in boreal forest* (Versjon 1) [dataset]. Mendeley Data. <https://doi.org/doi.org/10.17632/k5dm2x57hw1.1>.
- Speed, J.D.M., Austrheim, G., Hester, A.J., Meisingset, E.L., 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. *Oikos* 123 (10), 1270–1280. <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 rewetting rates in space and time. *PLOS ONE* 14 (5), e0217166. <https://doi.org/10.1371/journal.pone.0217166>.
- SSB. (2023a). *Arealbruk og arealressurser*. SSB. (<https://www.ssb.no/natur-og-miljo/a-real/statistikk/arealbruk-og-arealressurser>).
- SSB. (2023b). *12660: Livestock grazing on outfield pastures (M)* 1995 - 2022. Statbank Norway . SSB. (<https://www.ssb.no/en/statbank/table/12660>).
- Stewart, K.E.J., Bourn, N.A.D., Thomas, J.A., 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. *J. Appl. Ecol.* 38 (5), 1148–1154.
- Stout, J.C., Dicks, L.V., 2022. From science to society: Implementing effective strategies to improve wild pollinator health. *Philos. Trans. R. Soc. B: Biol. Sci.* 377 (1853), 20210165 <https://doi.org/10.1098/rstb.2021.0165>.
- Strand, G.-H., Hansen, I., de Boon, A., Sandström, C., 2019. Carnivore management zones and their impact on sheep farming in Norway. *Environ. Manag.* 64 (5), 537–552. <https://doi.org/10.1007/s00267-019-01212-4>.
- The Norwegian Biodiversity Information Centre, 2021. Results from the 2021 Red List for Species. (https://www.biodiversity.no/Pages/135386/Results_from_the_2021_Red#224178).
- Tofastrud, M., Devineau, O., Zimmermann, B., 2019. Habitat selection of free-ranging cattle in productive coniferous forests of south-eastern Norway. *For. Ecol. Manag.* 437, 1–9. <https://doi.org/10.1016/j.foreco.2019.01.014>.
- Tofastrud, M., Hesse, A., Rekdal, Y., Zimmermann, B., 2020. Weight gain of free-ranging beef cattle grazing in the boreal forest of south-eastern Norway. *Livest. Sci.* 233, 103955 <https://doi.org/10.1016/j.livsci.2020.103955>.
- Török, P., Penksza, K., Tóth, E., Kelemen, A., Sonkoly, J., Tóthmérész, B., 2018. Vegetation type and grazing intensity jointly shape grazing effects on grassland biodiversity. *Ecol. Evol.* 8 (20), 10326–10335. <https://doi.org/10.1002/ece3.4508>.
- Umstatter, C., Morgan-Davies, J., Waterhouse, T., 2015. Cattle responses to a type of virtual fence. *Rangel. Ecol. Manag.* 68 (1), 100–107.
- Vujić, A., Ståhls, G., Acánski, J., Bartsch, H., Bygberg, R., Stefanović, A., 2013. Systematics of Pipizini and taxonomy of European Pipiza Fallén: Molecular and morphological evidence (Diptera, Syrphidae). *Zool. Scr.* 42 (3), 288–305.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag. (<https://ggplot2.tidyverse.org>).
Willmer, P. (2011). *Pollination and floral ecology*. Princeton University Press.

Zimmermann, B., Wabakken, P., Dötterer, M., 2003. Brown bear-livestock conflicts in a bear conservation zone in Norway: are cattle a good alternative to sheep? Ursus 72–83.