

Where do trophic interactions happen?

A spatial assessment of shared habitat between the three Svalbard herbivores:
Svalbard reindeer, Svalbard rock ptarmigan, and pink-footed geese



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Front page photos: NPI/Cornelia Jaspers (overview), Tore Nordstrad (reindeer), Isabell Eischeid (ptarmigan), Jesper Madsen (pink-footed goose)



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Contents

1. Preface and acknowledgments	3
2. Summary.....	4
3. Introduction.....	5
4. Methods	7
4.1. Existing data layers and habitat models.....	7
4.1.1. Goose grubbing model	7
4.1.2. Ptarmigan habitat model.....	7
4.1.3. Vegetation map	7
4.1.4. Digital Elevation Model	8
4.2. Methods for data layers developed in this project	8
4.3. Field data collection herbivore abundance and vegetation.....	9
4.4. Habitat overlay analysis methods	11
5. Results and discussion.....	12
5.1. Reindeer summer habitat use and habitat suitability.....	12
5.2. Data distribution and species-wise habitat characteristics.....	14
5.3. Habitat overlays.....	16
5.3.1. Habitat overlays: Spatial distribution of herbivores.....	16
5.3.2. Habitat overlays: Vegetation Classes	19
5.3.3. Habitat overlays: Elevation.....	20
5.3.4. Field based assessment of herbivores and habitat overlap	21
6. Conclusions.....	24
7. References.....	25
Appendix.....	26
Goose grubbing modelled by Speed et al. (2009).	26
Ptarmigan breeding habitat suitability, modelled by Pedersen et al. (2007).	27
Biomass of plants in vegetation classes	28
The original project description	31
Prosjektbeskrivelse: Klimavinnere og tapere på Svalbardtundraen – hvor skjer interaksjonene?.....	31

1. Preface and acknowledgments

The primary aim of this project was to investigate where on Svalbard we find the highest likelihood of interactions between the herbivores pink-footed goose, Svalbard reindeer and Svalbard rock ptarmigan and to characterize these habitats. Second, the project aimed for identifying “hot spot” areas of ecosystem interactions between the harvested herbivore species and their food sources. The knowledge gained informs area management and guides establishment of a suite of sites for large-scale monitoring of plant-herbivore-climate interactions in Svalbard. This project did, according to the aims, collate and investigate available data layers for all the three herbivores and the vegetation they rely on as food source. We produced new knowledge about reindeer summer habitat suitability, and describe areas where the overlap amongst the three herbivores is likely highest, and where they can, based on spatially shared habitat, interact with each other.

The project was carried out in accordance with the project plan (see Appendix), with field work in 2015 and 2016 and analysis and modelling in 2016 and 2017. We focused on summer habitat models as it is in the summer season all the three herbivores can co-occur. We have used multiple data sources, including previous habitat models and location data acquired in previous SMF projects (e.g. SMF 13/60, SMF 14/115, SMF 12/115 and SMF 13/49).

The project was led by the Norwegian Polar Institute and conducted in collaboration with Norwegian Institute for nature research, University of Aarhus, the Norwegian University of Science and Technology, and Norwegian University of Life Sciences. Synergies with other field work for example at NPI including logistics and transport facilities, and collaborations with colleagues within COAT-Climate-ecological Observatory of Arctic Tundra and in the Herbivory network broadened the data base for the field data.

We’d like to thank Eeva Soininen from UiT-The Arctic University of Norway, Arnaud Tarraux at Norwegian Institute for Nature Research, Hans Tømmervik at Norwegian Institute for Nature Research, Petr Maćek and Tomas Hajek at University of South Bohemia Ingunn Tombre at Norwegian Institute for Nature Research, Leif Egil Loe at Norwegian University of Life Sciences, Audun Stien at Norwegian Institute for Nature Research, James Speed at NTNU University Museum, Norwegian University of Science and Technology, Eva Fuglei at Norwegian Polar Institute, and Jesper Madsen at University of Aarhus for advice, data collection or analysis support. The data are available from NPI and COAT (primary contacts Virve Ravolainen, Åshild Ønvik Pedersen). Results will be published in international scientific journals, planned publications are: *Distribution of herbivores in high Arctic landscape and their spatial habitat overlap* and *The greener the better: Predicting habitat suitability in a high-Arctic predator-free large herbivore*.

The work was financed by Svalbard Environmental Protection Fund and also received some funding from the Fram Centre to the COAT-Climate-ecological Observatory of Arctic Tundra.

2. Summary

The most important results This project determined habitat overlap and hence potential interactions among the herbivores – Pink-footed goose, Svalbard reindeer, and Svalbard rock ptarmigan - in the Svalbard archipelago. To do so we used published habitat models for geese and ptarmigan and developed a predictive habitat suitability model for reindeer using GPS- and positional data from female reindeer in coastal and inland regions. The results showed that only a small fraction of the land area on Svalbard is suitable for all the three herbivores. The highest overlaps in the landscape are characterised by moss tundra in the lowlands and by *Dryas octopetala* vegetation in the slopes. The nearly continuously vegetated lowlands of Nordenskiöld Land and especially moss tundra and sea bird moss tundra are highly suitable for geese and reindeer, while reindeer and ptarmigan share the higher elevation ridges and different types of less productive heath vegetation including *Dryas octopetala*, *Cassiope tetragona* and *Saxifraga oppositifolia* vegetation. The overlap of ptarmigan breeding and goose grubbing habitats are almost absent, which means that the potential for interactions in early summer season is limited. The areas highly suitable for all three herbivores can be looked upon as potential “hot spot” for herbivore interactions. Interestingly, the overlap analysis and the habitat assessment based on feces counts from the field corresponded well with the modelled habitat suitability for all species. This underlines the importance of certain vegetation types present in the landscape for herbivore interactions.

Environmental benefits The new knowledge gained in the project, the habitat suitability map for reindeer and the overlap map of habitat suitability for all the three herbivores can be used to locate the most important parts of the landscape for the herbivore community. This knowledge is relevant for future area management, and has already been utilized in the knowledge summary of the central Spitsbergen.

Recommended actions There are no direct recommended actions based on project results, but the results are expected to be relevant for future area management.

Environmental management implications We have shown that habitat suitability for all the three herbivores is spatially restricted and largely confined to the most productive vegetation types in summer, as well as the ridges and upslope *Dryas octopetala* vegetation that is likely more important in the winter. The results provide new knowledge about area use and “hot-spots” (i.e. bird-cliff moss tundra and lowland moss tundra communities) for endemic (ptarmigan and reindeer) and migrating herbivores, which underlines the importance of minimizing disturbance of these shared herbivore habitats.

Follow up We are incorporating the results from the project to the study design of the ecosystem monitoring within the COAT – *Climate-ecological monitoring of Arctic Tundra on Svalbard*. COAT aims to document and understand climate-driven changes in the structure and function of the tundra ecosystem. The vegetation types we identified will be targeted in the monitoring, along with relevant climatic gradients. Our results suggest the need for ecosystem-based monitoring to cover multiple landscapes to capture several types of overlap areas and their inherent characteristics. We recommend development of a pink-footed goose habitat model, to capture summer habitat suitability of this numerous and expanding species that has a great potential for forage resource competition with reindeer. We also recommend the development of regional habitat suitability models for reindeer winter space use since the winter season determines the carrying capacity of reindeer.

3. Introduction

Plants, herbivores and predators make up the terrestrial food chain on Svalbard, with several species and functional groups at each level. Climate change is influencing species and species groups at all levels, and we can expect species and groups of species to respond differently to the changing climate. Based on known responses of plants we can expect grasses and sedges, as well as some shrubs, to tackle warmer summer temperatures better than cryptogams (mosses and lichens) [1]. Likewise, pink-footed geese have in the last decades had vigorous population growth and can be expected to maintain high abundance on Svalbard where they migrate to for nesting [2]. For Svalbard reindeer and Svalbard rock ptarmigan the expected response to climate change is complex depending on the net effects of warmer and longer summer seasons. The changing winter conditions with ground-ice formation under mild spells are considered as one of the potentially most influential phenomena [3]. In a simplified terminology, species and species groups may become “winners” or “losers” under the influence of climate change (Figure 1).

One of the current research challenges is to predict how climate change will affect these plants and animals because they are all directly and indirectly linked to each other in the food chain or through shared habitat or predators, and can be directly or indirectly affected by climate. The goose populations [4] and the reindeer [5] have an impact on Svalbard vegetation but it is not known to what extent this could lead to competition for food and habitat between these herbivores. While demonstrating food or habitat competition is a large research task, a starting point for understanding potentially existing competition is knowledge about shared habitat and food resources, which this project addresses.

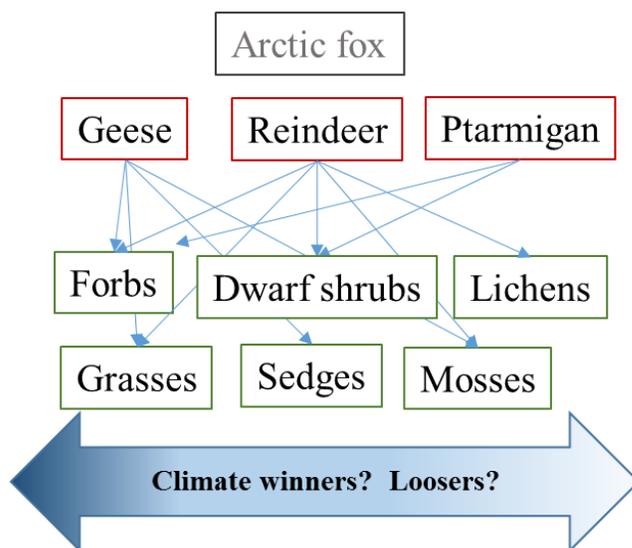


Figure 1. A simplified illustration of the terrestrial food web on Svalbard, with species or species groups that may differ in whether they benefit or suffer from climate change. A knowledge gap that limits our understanding of the interactions between the species, and what this project addressed, is to know where the species spatially overlap and what characterises their eventually shared habitat.

Ecosystem interactions is a timely framework for studying and monitoring effects of climate change. The lack of information on how climate change effects *ecosystem interactions* is the drive behind recent efforts to expand nature monitoring on Svalbard through programmes such as Climate Observatory for

Arctic Tundra - COAT. The goal of COAT is to understand interactions between tundra species and in particular how they are influenced by climate change [3]. The focal species (geese, reindeer, fox, ptarmigan and vegetation) have been chosen because of their high management relevance and the possibility to actively change their population sizes. Moreover, they contribute highly to Svalbard's ecosystem services (outdoor recreation and recreational hunting) and respond to a changing climate. For herbivores, some of the main questions in COAT are "What are the climate effects on and consequences of: 1) food access at the time of the year critical for population size development and 2) access to high quality forage?". International assessments have pointed out the very same critical questions for the Arctic in general [6] and monitoring that addresses these themes is on high demand [7].

Successful monitoring of the Svalbard tundra ecosystem is dependent on already existing time series (reindeer, foxes, and ptarmigan) and the establishment of new, complimentary, time series to achieve a robust spatial and temporal cover. For example, we need to establish integrated vegetation and herbivore monitoring that covers a range of climatic, vegetation and animal density gradients. The need for coordinated, spatially replicated vegetation monitoring has been called upon in the terrestrial MOSJ project (Environmental monitoring of Svalbard and Jan Mayen) evaluations [8] and is in line with the requests from international bodies like the CBMP (The Circumpolar Biodiversity Monitoring Programme)[7]. An important requirement to advance research on the terrestrial ecosystem and to build up an ecosystem-based monitoring system for the terrestrial food web on Svalbard is knowledge on where on Svalbard we can expect habitat overlap between herbivores to such an extent that they are likely to interact.

4. Methods

This project combined information from existing spatial data layers, which have not been previously combined and analysed together (vegetation map, terrain model, habitat models for ptarmigan and geese), with a new habitat model for reindeer developed in this project and new field data for food plants and grazing pressure.

Previously published habitat models for goose and ptarmigan were an important source of information to identify herbivore habitat overlap on Svalbard. They have been created through diverse types of fieldwork; field counts, GPS collars, and landscape assessments. The aim of the predictive habitat model is to predict suitable habitat by extrapolating findings from some areas to a larger area, such as the whole of Svalbard via the use of digital maps. Moreover, an existing, satellite-based vegetation map and a terrain model were used. Below are brief summaries on how these digital layers were created.

4.1. Existing data layers and habitat models

4.1.1. Goose grubbing model

Grubbing by pink-footed geese using local field surveys in Sassendalen (2006), Colesdalen and Bohemansflya (2007) and measuring maximum intensity grubbing (from 0-100%) in 35 cm x 35 cm and 5 m x 5 m plots spaced at 30 meter distance along transects was found to occur more likely in wet habitats. For example, there is a 1000 times higher likelihood of presence in wet habitat compared to barren ground. Especially, fen habitat was an important predictor for grubbing to take place. Fen habitat is most likely selected for due to a greater abundance of species such as *Bistorta vivipara*, *Eriophorum spp.* and *Dupontia fisherii*, that have nutritious below ground parts the geese eat in the summer. More information about the methodology and results can be found in Speed et al. [4].

4.1.2. Ptarmigan habitat model

We used a published habitat suitability model for breeding Svalbard rock ptarmigan [9] that re-evaluated the relationship between territorial Svalbard rock ptarmigan male presence and ecological relevant variables related to vegetation, terrain and snowmelt. The model builds on 11 years (2000-2010) of presence/absence data of territorial males, a multi-scale statistical generalized linear modelling framework (GLMs) and recent advances in digital satellite based vegetation mapping. The final habitat model contained four significant predictors related to vegetation, terrain (altitude and slope) and a heat load index, as a proxy for snowmelt. Increasing amount of one particular habitat type, 'established dense *Dryas* heath' influenced habitat suitability positively at a small scale, while gentle sloping landscapes of intermediate steepness (10-25°) and altitude in the upper south-west facing part of the mountain slopes characterized occurrence at the landscape scale. For further information, see Pedersen et al. [9].

4.1.3. Vegetation map

The vegetation map of Svalbard is based on processing Landsat TM/ETM+ images [10]. Automatic images classification from the original vegetation map were for the purpose of this project summarized to fewer vegetation/ground cover classes.

The vegetation classes of the original vegetation map by Johansen and colleagues [10] were validated through field based measurements in 2015 by V. Ravolainen. The field work at 13 locations in Isfjorden-Forlandsundet-Kongsfjorden region, covering total of 52 km of 2 meter wide transects revealed that most classes were correct about 50% of the time (Ravolainen et al unpublished data). Therefore, in this project, a simplified classification that included 3 main vegetation classes: *barren*, *Dryas heath* and *moss tundra* was used. *Barren* terrain is comprised of terrain with no vegetation as well as sparsely vegetated areas such as polar desert (for example barren ground with occasional occurrence of *Potentilla pulchella*). The vegetation class *dryas heath* includes areas that are dominated by *Dryas octopetala*, *Salix polaris* or *Cassiope tetragona*. *Moss tundra* is comprised of mesic and moist habitats, dominated by mosses, *Salix polaris* and graminoids.

4.1.4. Digital Elevation Model

The digital elevation model (DEM) was obtained from the Norwegian Polar Institute. The DEM was constructed from aerial photographs (1:50 000) and has an uncertainty of approximately 5-10 meters. The DEM is a mosaic of older and newer regional DEMs, therefore the data spans from before 1990 to the latest updating in 2014. (Norwegian Polar Institute (2014). Terrengmodell Svalbard, S0 Terrengmodell, <https://doi.org/10.21334/npolar.2014.dce53a47>)

4.2. Methods for data layers developed in this project

Summer reindeer habitat model

We developed a habitat suitability model for reindeer by using all existing GPS location data from female reindeer on Brøgger, Kaffiøyra and Nordenskiöld land during 2009-2015 (SMF 13/60 and 14/115). First, we selected environmental variables describing vegetation and terrain characteristics relevant to reindeer summer habitat use [11] and describe the characteristics of area used by reindeer. Summer was defined as the snow free months from July to August. Depending on collar type, the GPS where transmitting positional data every two hours or eight hours, which resulted in a total of 119 animal years available to predict summer habitat suitability. Second, we used the results to predict summer habitat suitability across the entire Svalbard using the *biomod2* package implemented in R [12]. *Biomod2* enables concurrent modeling with a set of modeling types and combines inference from the separate models to an ensemble forecast, and we applied this procedure at both foraging-patch and home-range scales. We used spatial data from GPS reindeer on Sarsøyra (SMF 14/115) and positional data from a study that surveyed reindeer across the entire archipelago (Le Moullec, Pedersen et al., in prep). The final habitat suitability map for the forage patch scale (used in this project) has a pixel size of 90 × 90 meters and was originally created in the projection WGS 1984 UTM 33N. The habitat suitability model for reindeer is expected to be published late autumn 2018.

4.3. Field data collection herbivore abundance and vegetation

Feces counts were used as an index of herbivore presence and abundance, and biomass estimates to support the mainly remotely sensed vegetation data were collected from multiple field sites in 2015 and 2016. Field localities are shown in Figure 2.

Field work was coordinated with NPI field work by V. Ravolainen. While the 2015 survey had the purpose to describe general habitat characteristics, the 2016 survey focused on *Dryas octopetala* vegetation, moss tundra and sea bird fertilized moss tundra vegetation. The primary means of transportation in the field was by foot. Between the localities transport was in small boats (rubber boats, Polarcircle, sail boat), and in 2016 also onboard R/V Lance. Localities in Gipshuksletta, Mathiesondalen, Ebbadalen, Pyramiden, and Nidedalen were sampled by Peter Maćek and Tomas Hajek (University of South Bohemia). All other localities were sampled by Virve Ravolainen, Åshild Ønvik Pedersen and their field teams.

Feces counts were done in small plots that were organized in 30 m long transects (2015) or in a systematic grid (2016), using a common unit of feces presence/m². The biomass of plant species and groups, as well as vegetation type was collected using the non-destructive point frequency method. Plots of 0.5 x 0.5 m size, organized in short 12 m transects (2015) or in a systematic grid orientated in the cardinal directions (2016) were used. Sampling locations for feces and vegetation, in both 2015 and 2016, were chosen in a stratified random design, where selection of sampling locations was done in a hierarchical manner. First, valleys or peninsulas were selected in order to cover geographical gradients in the Isfjorden area and along the west coast of Spitsbergen. Then within each valley or peninsula, random locations were selected before field work. In 2015, entirely random GPS points were created before field work, while in 2016 the vegetation map of Johansen et al [10] was used to pre-select points where we could expect to find either *Dryas* heath or moss tundra vegetation. The NPI sea bird colony database was used to locate bird cliffs in 2016 prior to field work. Field measurements were then spread areas as far as possible in each location, amongst the *a priori* created GPS points, given logistic constraints such as landing sites and terrain.

Field permits were obtained for field work in the national parks and the Ossian Sars nature reserve, and all sampling was non-destructive and done in accordance with the Svalbard Environmental Protection Act.



Figure 2. Field localities for the 2015 and 2016 surveys. In 2015 a general assessment of habitats was made, while in 2016 the focus was on describing herbivore occurrence in *Dryas* heath, moss tundra and sea bird influenced moss tundra.

4.4. Habitat overlay analysis methods

4.4.1. Data preparation

All data preparation was conducted in R 3.3.2. and presented with ArcGIS 10.5.1 (Esri). The original spatial resolution for the vegetation map, DEM, goose, reindeer and ptarmigan models were not the same. The vegetation map and goose grubbing model have a resolution of 30x30 meter, the DEM a 20x20 meter resolution and the reindeer summer habitat model one of 90x90 meter. The ptarmigan habitat predictive model resulted in a Svalbard wide map with 100 meter resolution. Therefore, the DEM, reindeer and goose model maps were interpolated (bilinear) in R to fit the size of the ptarmigan model (100x100m). The vegetation map was resampled to 100 meter cell sizes using via a nearest neighbour method assigning each cell the vegetation class of the closest original pixel. The original models for geese and ptarmigan were recording percentages of suitability (0-100) and data was scaled down to be consistent with the reindeer study to a scale from 0 to 1. The spatial suitability maps, vegetation class and elevation maps were stacked on top of each other (rasterstack R) and converted into a table (where each row is one pixel with information for each layer in columns) for further data analysis.

4.4.2. Habitat overlay

The habitat models score habitat suitability (or likelihood for species to occur) on a relative scale from 0 to 1. For the purpose of mapping, suitable habitat all values below 0.2 were excluded as “not suitable”. This is an arbitrary cut-off driven by the data structure. A large proportion of the habitat suitability values were lying below the 0.2 cut off (see Figure 4) and the probability of finding suitable habitat for a given species is very low. The Svalbard herbivore habitat suitability map (Figure 6) therefore represents areas where all three species have a habitat suitability value of 0.2 and above.

We also compared pairwise habitat overlap between the herbivores (Figure 7). Here we chose a higher threshold of 0.5, as this value can be interpreted as “higher than 50 % chance of finding suitable habitat”. For each pixel we calculated if two or more species scored a habitat suitability values above 0.5. The resulting map shows areas that are suitable for pair-wise combinations of the herbivores. Additionally, habitat overlays were also compared to the vegetation and elevation classes, giving completely new insights in what kind of landscape shared habitat may occur.

We used ecological niche analysis to look at spatial overlap (Figures 8, and 11). Ecological niche is defined as the environmental conditions that a species or several species lives in. It often uses food resources or spatial living ranges. The analysis we used for looking at spatial overlap makes a prediction, assuming that finding that a type of habitat in a location is suitable for a herbivore will lead to a similar distribution of the species across landscapes at other locations. We calculated spatial niche overlap following the simplified approach from Warren et al. [13] to calculate overall niche overlap between species pairs by multiplying the scaled values from 0 to 1 with one another. This results in niche overlap values between 0 (no overlap) and one (full overlap). For the modelled species distributions the unit for

overlay assessment was each pixel (100x100m) and for the field based measurements we treated each plot (0.5x0.5m) as its own unit.

5. Results and discussion

5.1. Reindeer summer habitat use and habitat suitability

At the *foraging site scale*, the utilized habitat in the available habitat-space differed from the mean available resources. This indicate that the resources (niche) was narrower than the distribution of the available resources in our study landscape, meaning that reindeer select certain areas of the available landscape. Female reindeer used preferentially habitat with higher plant biomass values, higher NDVI (an index for plant biomass/production) and higher proportion of moss tundra. On the contrary, terrain characterized by high altitude and sloping areas and high proportion of barren ground was avoided. Used and available habitat did not differ with respect to the proportion of heath habitat (dominated by *Dryas octopetala/Cassiope tetragona*). The internal validation of the model (i.e. validating the model based on subsets from the data), scored relatively, but models validated on positional data across Svalbard and GPS data (Sarsøyra 2016) indicated lower predictive ability. Such validation results indicate that use and interpretation of the habitat model should be done conservatively until more positional data from other regions of Svalbard is available for validation of the predictive ability of the model. However, for the purpose of this project that focus on large, scale regional patterns, the habitat suitability model for reindeer is evaluated to be feasible for habitat overlay analyses (see validation statistics in Pedersen et al., unpublished) (Figure 3).

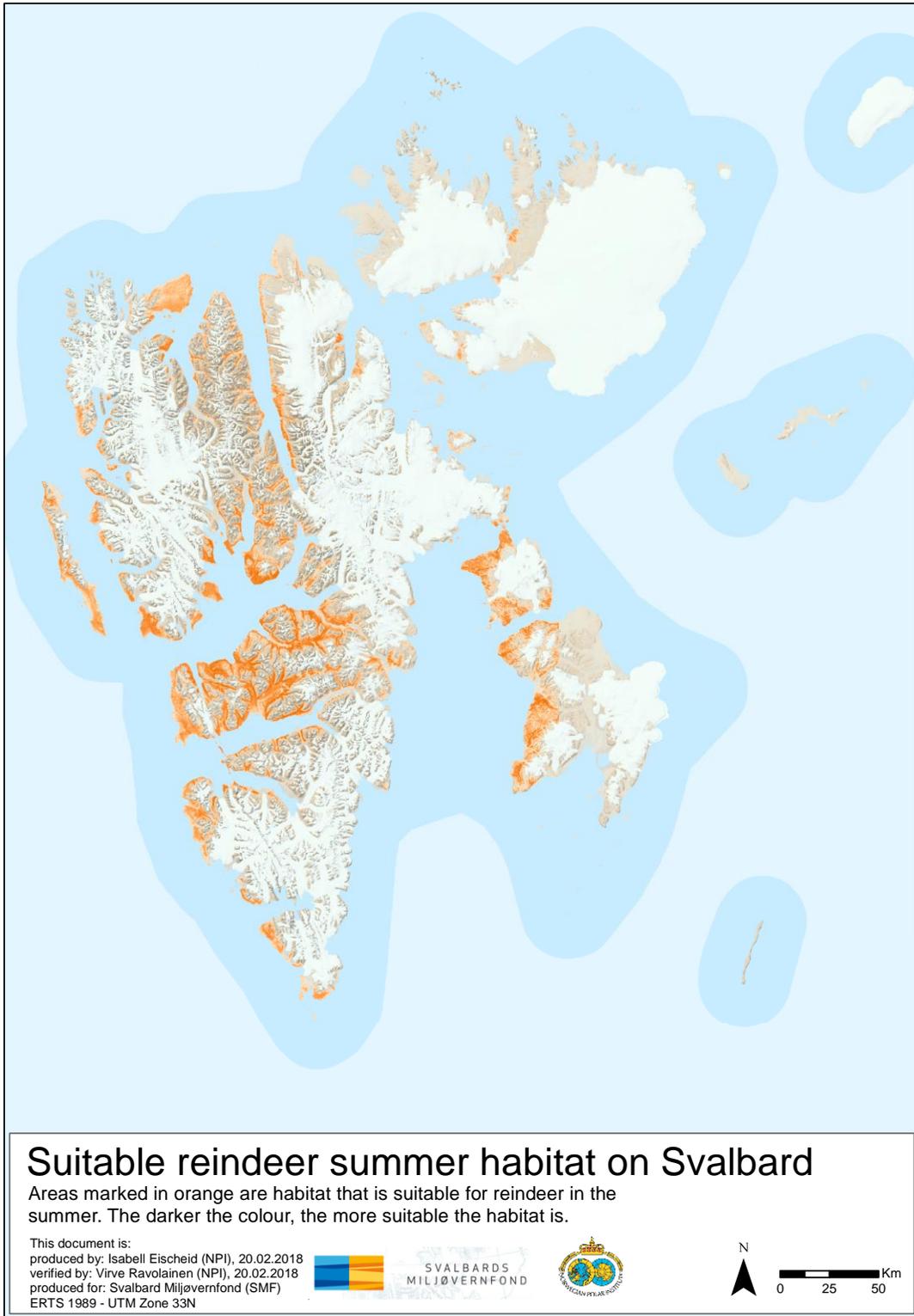


Figure 3. Predicted summer habitat suitability for female Svalbard reindeer in the extrapolation region based on the ensemble forecasts from *biomod2* at feeding site scale (Pedersen et al. unpublished).

5.2. Data distribution and species-wise habitat characteristics

The majority of the area where herbivore habitat suitability was modelled had very low suitability for all three species (Figure 4). This is probably mainly due to the large percentage (60%) of glacial land cover. The very low frequency of highly suitable habitat also suggests that the areas suitable for the herbivores are of limited extent and of critical importance.

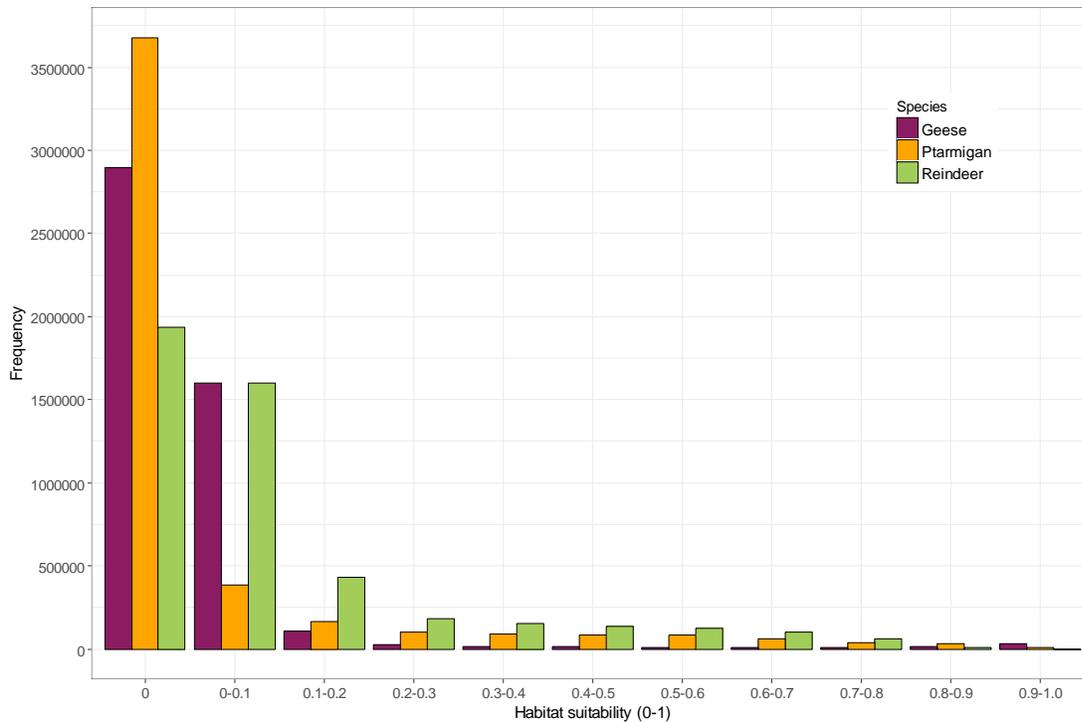


Figure 4. Frequency of habitat suitability values (for 100x100 meter cell size) for geese, reindeer and ptarmigan based on the habitat models by Pedersen et al. (2017), Speed et al. (2009) and the Svalbard reindeer model developed in this project.

Suitable habitat for pink-footed geese decreases with elevation, and ptarmigan habitat suitability is highest in the 50m-100m range (see Appendix and Figure 5). Reindeer, in summer time, have their optimal, modelled elevation approximately between 50m – 150m above sea level. Their suitable habitat decreases with elevation and is rarely found above 450 meters altitude in summer (Figure 3, Figure 5, Pedersen et al. unpublished). For geese the highest habitat suitability values (Figure 5, Appendix, and Speed et al. 2009) are in the parts of the landscape that on the satellite-based vegetation map (Johansen et al. 2012) classify as different types of wetlands and moss tundra vegetation. The least suitable habitat for all three species is in areas identified as barren using the satellite based vegetation map.

Overall, there is relatively little suitable geese grubbing habitat compared to the quantity of suitable habitat for reindeer and ptarmigan (see Figure 5 and geese grubbing and ptarmigan map in the appendix). The reindeer summer habitat model (Figure 3 and 5) shows that Svalbard reindeer can be found in most valleys and coastal sites across the archipelago as long they are not covered by ice, too high in elevation or completely barren. Ptarmigan are mostly confined to a mid-elevation belt avoiding the valley bottoms and high altitudes (Figure 5).

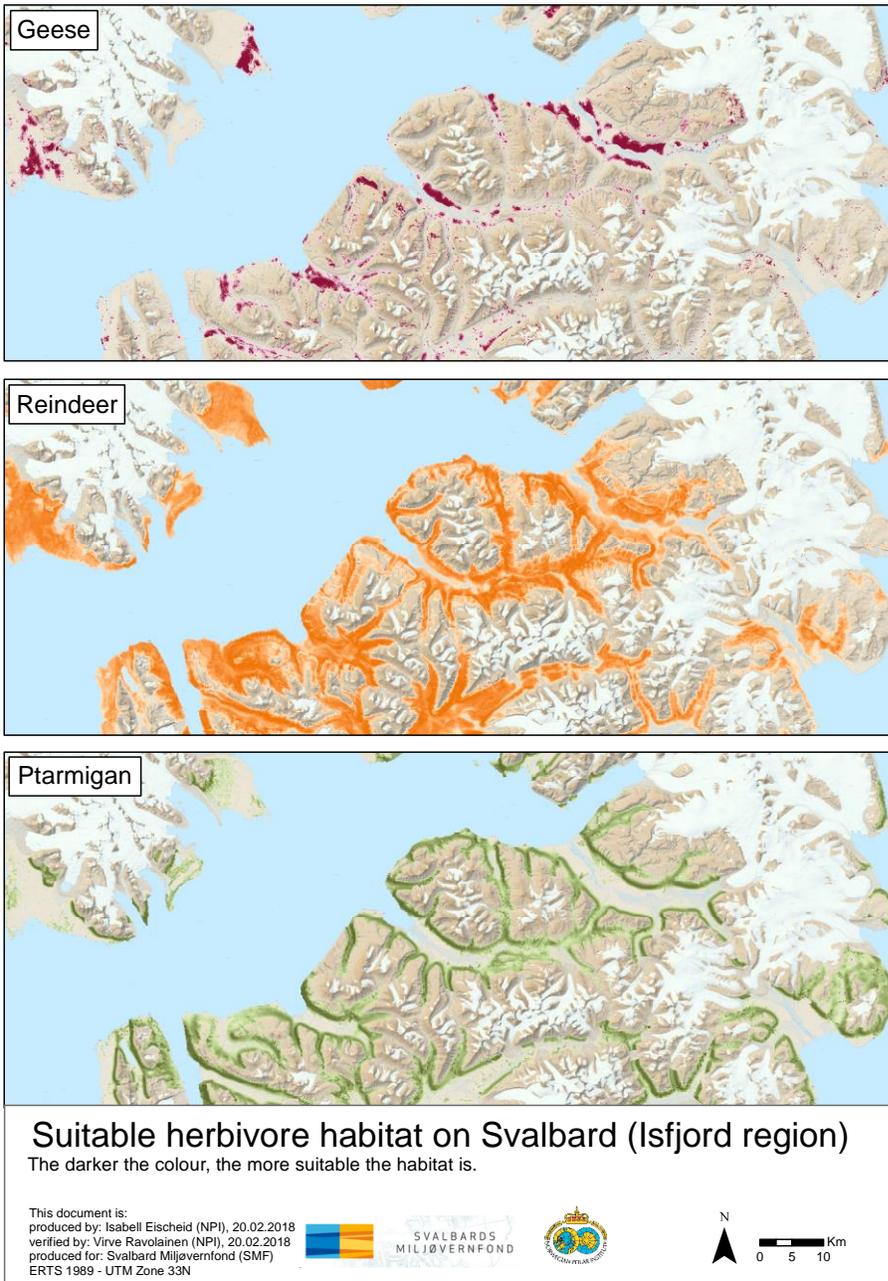


Figure 5. Suitable habitat for reindeer, ptarmigan and geese in Isfjorden region (geese and ptarmigan: [4, 9], reindeer, Pedersen et al. unpublished).

5.3. Habitat overlays

5.3.1. Habitat overlays: Spatial distribution of herbivores

Suitable predicted habitat for geese (Speed et al. 2009), reindeer (Pedersen et al. unpublished) and ptarmigan (Pedersen et al. 2007) displayed on top of each other show that most of the habitat suitable for all the herbivores lies within the lowlands and notably on Nordenskiöld Land, Bohemansflya and Daudmannsøyra (Figure 6). Note that ptarmigan habitat suitability was not predicted for Edgeøya due to the short growing season (see Pedersen et al. 2017 for details). The cut-off value of habitat suitability of 0.2 is arbitrarily chosen, but lower values than 0.2 are expected to be of very little value for herbivores. Hence the 0.2 cut-off for displaying suitable habitat is a conservative choice.

Looking at the combinations of herbivores two and two at the time in more detail we see distinct patterns in the big valleys of Nordenskiöld Land (Figure 7). Here a cut-off value of 0.5, which can be interpreted as 50% or higher likelihood of suitable habitat for two species combined, was used. Reindeer and geese share suitable habitat in the valley bottoms, while reindeer and ptarmigan share the mid-elevation ridges. The modelled ptarmigan breeding territories and pink-footed goose grubbing habitat overlay almost never overlap. This may have been subject to change since geese grubbing has been documented to expand in the landscapes since the making of the grubbing map [14, 15] (see also Figure 10), or simply be due to that these two herbivores use very different sections of the landscape. In cases where highly suitable geese and ptarmigan habitat overlap, the habitat is also suitable for reindeer.

Outside of the big valley systems, the distribution of overlapping suitable habitat is less structured (not shown). However, the general patterns are the same; reindeer and ptarmigan share the mid-elevation ridges and geese habitat is often too far in the lowlands to share suitable habitat with ptarmigan. An exception are some areas on Brøgger peninsula, where suitable goose grubbing habitat extends further into the ridges which they would share the habitat with ptarmigan (Figure 7).

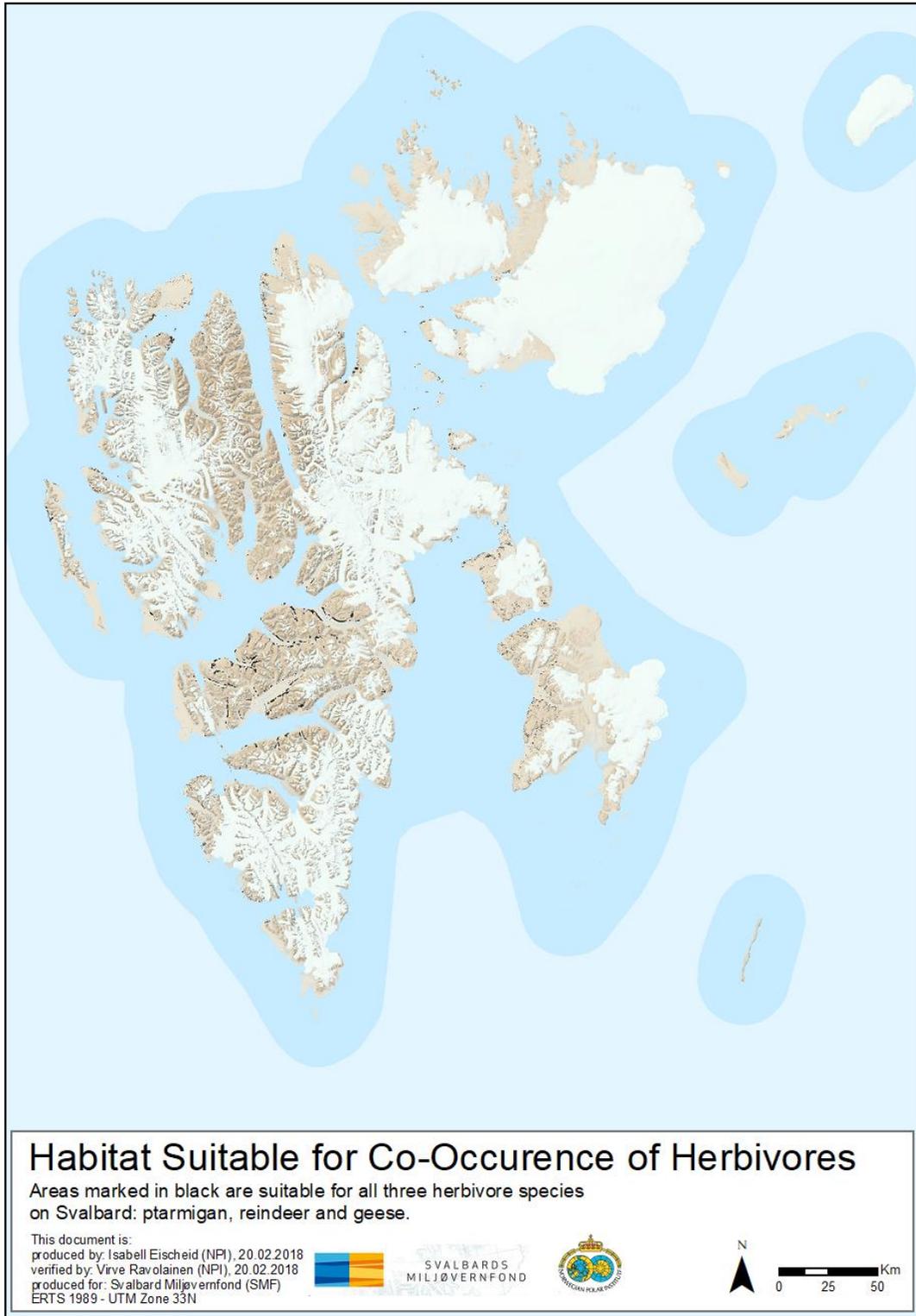


Figure 6. Predicted habitat suitability map for geese (Speed et al. 2009), reindeer (this project) and ptarmigan (Pedersen et al. 2017) on Svalbard based on habitat overlay analysis. Habitat suitability values, arbitrarily chosen above 0.2 are shown for geese, reindeer and ptarmigan, respectively. Suitable habitat is displayed on top of each other, without notion of which combinations of the species the areas are suitable for.



Figure 7. Areas where suitable habitat for the herbivores overlap to illustrate potential hot spots for herbivore interactions. Areas that had a suitability ranking of 0.5 or higher for two species or more are colored.

5.3.2. Habitat overlays: Vegetation Classes

When suitable habitat for the herbivores was organized according to broad, combined categories of the satellite-based vegetation map (Johansen et al. 2012), reindeer and ptarmigan have the highest average shared suitable habitat overlays across all vegetation classes (Figure 8). The overlay between these two species is highest for heath habitats, followed by moss tundra and lowest overlays between ptarmigan and reindeer are found in the barren vegetation classes. For all species combinations, overlays are lowest in the barren. Geese share most of their suitable habitat with reindeer and ptarmigan in the moss tundra habitats. Average habitat suitability overlay values between geese and reindeer are more than twice as high for moss tundra compared to heath habitats and close to zero for the barren vegetation class.

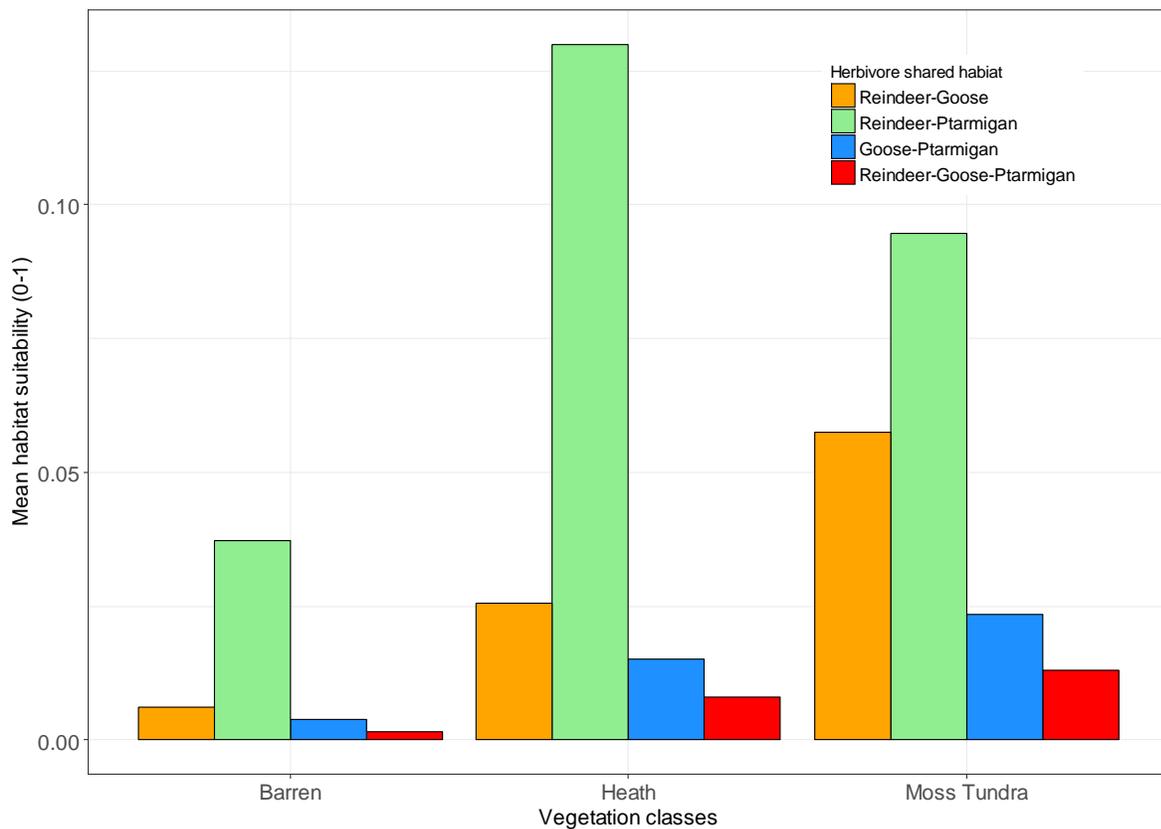


Figure 8. Mean habitat suitability values for paired species and three species overlays for different vegetation classes recombined from Johansen et al (2012). Moss tundra as presented here is a very broad class, including bird cliff vegetation, meadows and wetlands. The heath includes *Dryas octopetala*, *Cassiope tetragona* and *Saxifraga oppositifolia* vegetation classes from the map. Barren includes all the sparse categories.

5.3.3. Habitat overlays: Elevation

The highest habitat overlay values for all three species are in the elevation class of 50-100m (Figure 9). All three species find suitable habitat together up to an elevation of 350 meter. Overall, highest overlays are found for ptarmigan and reindeer, especially between 50-200m elevations but also below and above. Goose – reindeer habitat overlays are highest in the low elevations and decrease gradually with elevation. Goose - ptarmigan overlays are generally lowest. Highest mean overlay between these two species found to be at 50-150m elevations and slightly less below and above this range.

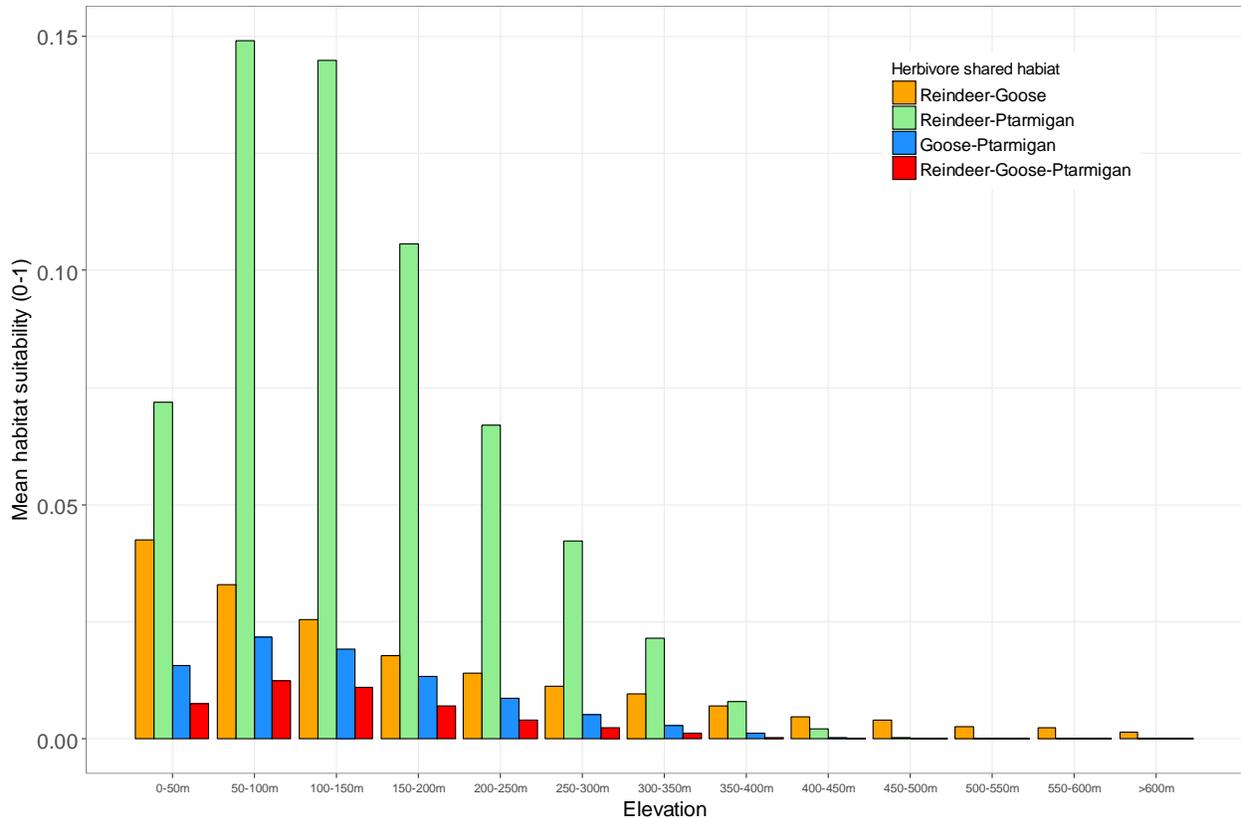


Figure 9. Mean habitat suitability values and of paired species and three species overlays at different elevations.

5.3.4. Field based assessment of herbivores and habitat overlap

Our field based measurements of herbivore co-occurrence suggest that the modelled results on the importance of moss tundra are correct (Figures 10 and 11). As could be expected from the grubbing map that shows modelled spring activity in early season after snow melt, we found the highest proportion of grubbed area in moss tundra: a third of all the randomly selected plots was grubbed (Figure 10a). More goose feces were found in moss tundra and in sea bird moss tundra than in the *Dryas* vegetation (Figure 10 b). Largest amount of winter reindeer feces were found in *Dryas* heath and in sea bird moss tundra (Figure 10 c), while in the summer reindeer feces amount was clearly highest in the sea bird moss tundra (Figure 10 d). There is evidence from Hornsund that sea bird fertilized moss tundra is important for herbivores [16], and our results suggest this is not just a local phenomenon on Svalbard.

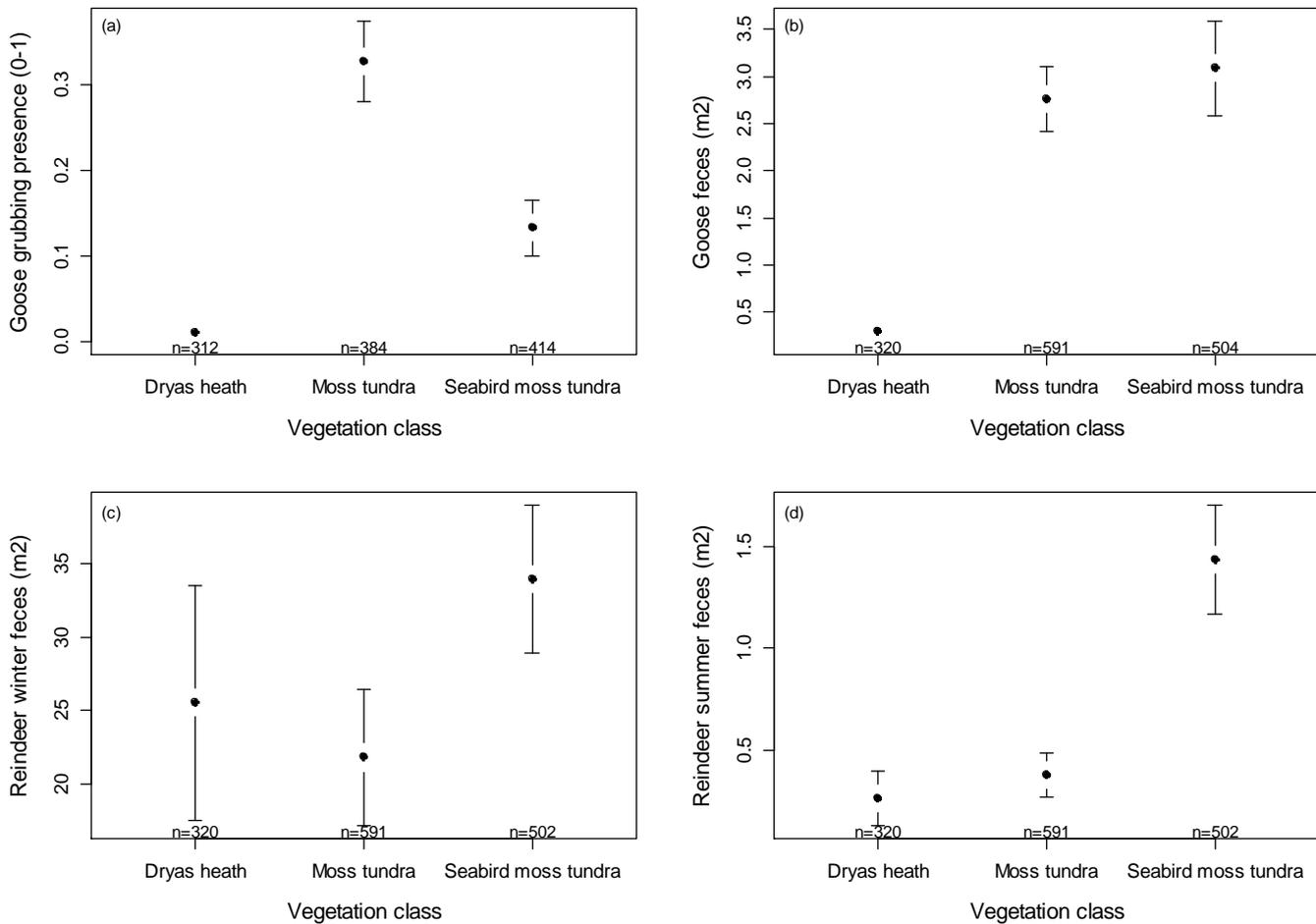


Figure 10. Goose grubbing signs (presence), goose feces, reindeer summer and winter feces (number of feces) counted during a field survey in 2016 (locations in Figure 3), in vegetation classes *Dryas* heath, moss tundra and sea bird fertilized moss tundra below bird colonies.

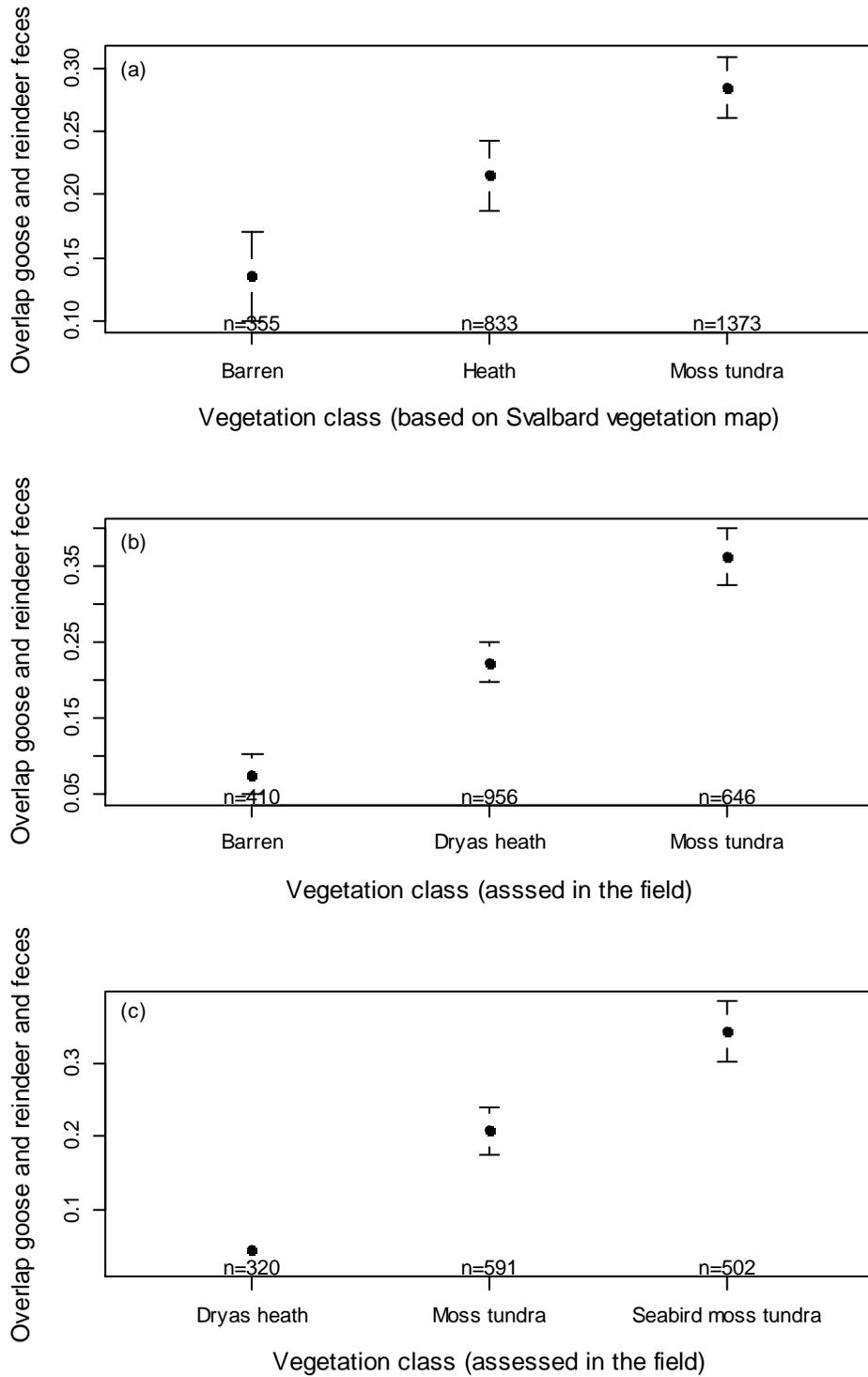


Figure 11. Spatial overlap of reindeer and geese in different vegetation types. Vegetation types were detected from the satellite based vegetation map (a) or given in the field (b), and combined into broad categories to facilitate analysis and comparisons. During the 2015 field survey, vegetation types were recorded along randomly selected, 200 m long transects (a and b) and in 2016 sea bird influenced and *Dryas* vegetation types were targeted to compare towards moss tundra (c). Localities are given in Figure 3.

We used feces counts of reindeer and geese in combination with the vegetation map to assess habitat overlap between these two herbivores. The results show the same pattern as in the modelled analysis (see Figure 8 goose-reindeer and Figure 11). The results of vegetation map (Figure 11 a) replaced with field based vegetation classification (Figure 11 b) were almost identical. A more detailed look within the moss tundra habitat (Figure 11c) reveals that especially areas fertilized by sea birds have the highest spatial overlay of geese and reindeer.

The data were obtained from multiple locations along the coast (Figure 2), and a total of approximately 3000 m² was recorded. Too little data was obtained for ptarmigan to allow for analysis of overlap of ptarmigan with the other herbivores, even with the high number of plots recorded, suggesting feces counts are not a successful field method for recording ptarmigan abundance.

The predicted habitat model for reindeer suggested moss tundra is important for reindeer, but could not distinguish the sea bird influenced moss tundra. The satellite based data in habitat modelling has a resolution of 90x90 m. The fertile slopes under sea bird colonies are too small to be detected in the habitat model, while they could be targeted with the field data. This highlights the importance of combining field and remote sensing methods for a best possible understanding of ecological patterns. We could only record feces accumulated over many years. The moss tundra would have the highest decomposition and turnover rates. Hence our observations of the importance of the sea bird moss tundra for reindeer can be seen as conservative, as accumulated feces would decompose slower in the *Dryas* heath.

The field measurements of herbivore co-occurrence strengthen the modelled results and allow more detail to importance of moss tundra with and without sea bird influence. The field results underline the importance of the productive, lush vegetation (relative to the barrens and heath) for the herbivores, even if it especially along the coast can occur in very restricted areas (see Figure 2 for sampling locations).

6. Conclusions

This project has developed a new habitat model for reindeer, predicting summer habitat suitability. We have for the first time investigated spatial overlap in habitat suitability for the whole vertebrate herbivore community on Svalbard, finding that only a small fraction of the vegetated landscape holds habitat suitable for all the herbivores. Especially the different moss tundra types, and particularly the sea bird fertilized moss tundra hold highly suitable habitat for all the herbivores, and are, according to our field data, the areas where the spatial overlap between the herbivores is highest. The productive, lush patches of vegetation, which can be small in area, are hence of importance for both goose, reindeer and ptarmigan on Svalbard. The project aimed at producing new knowledge on herbivore habitat suitability, and did so by collating the majority of available information on habitat characteristics and herbivore habitat use.

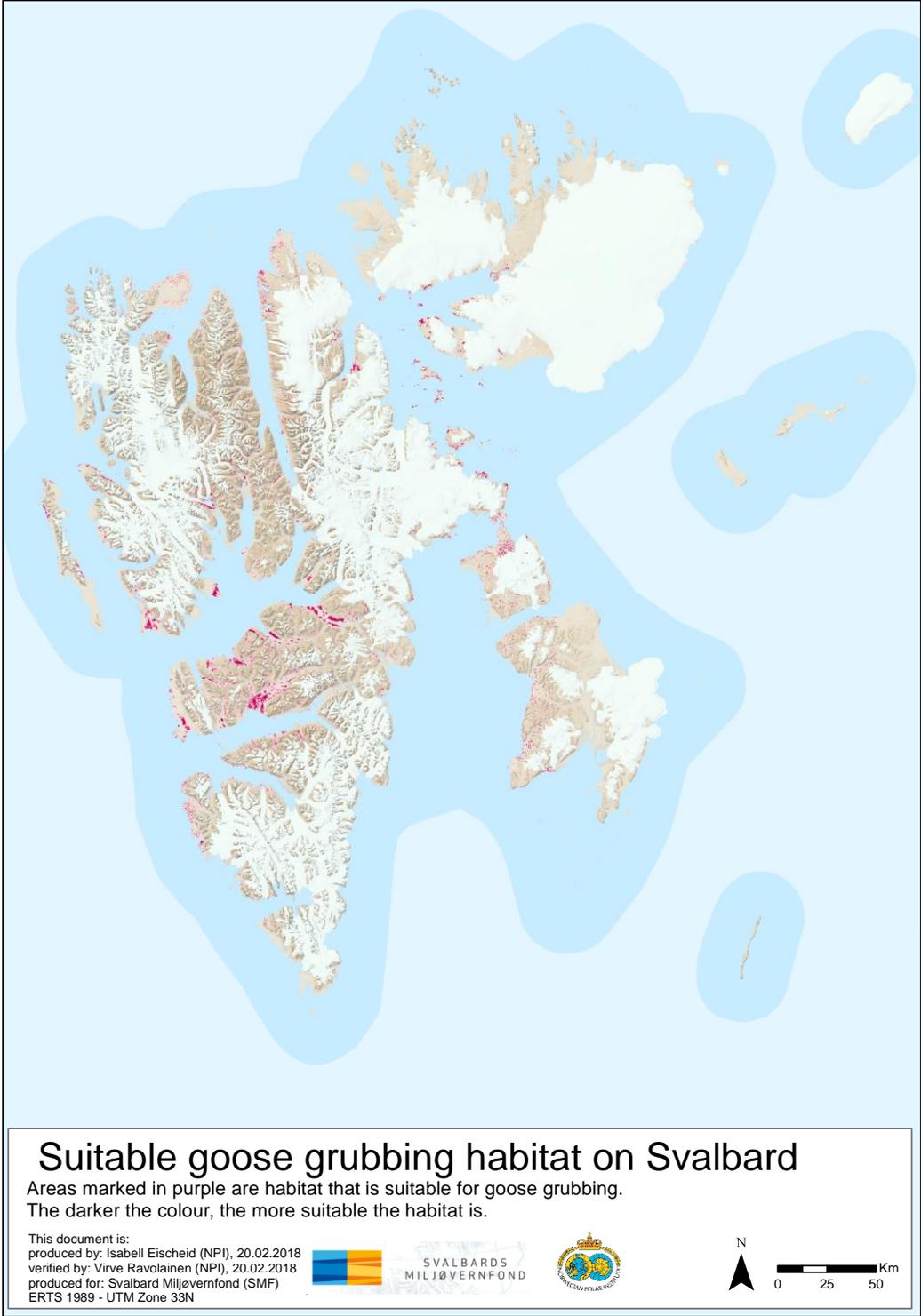
Climate change induced changes in the terrestrial food web, which was the overarching theme for the project, might, based on our results, manifest in the types of habitats here identified to be of importance for all the herbivores. The knowledge gained can inform area and environmental management (see e.g. [17]). The results guide establishment of large-scale monitoring of plant-herbivore-climate interactions in Svalbard within the program COAT-Climate-ecological Observatory for Arctic Tundra.

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Appendix

Goose grubbing modelled by Speed et al. (2009).



Ptarmigan breeding habitat suitability, modelled by Pedersen et al. (2007).



Biomass of plants in vegetation classes

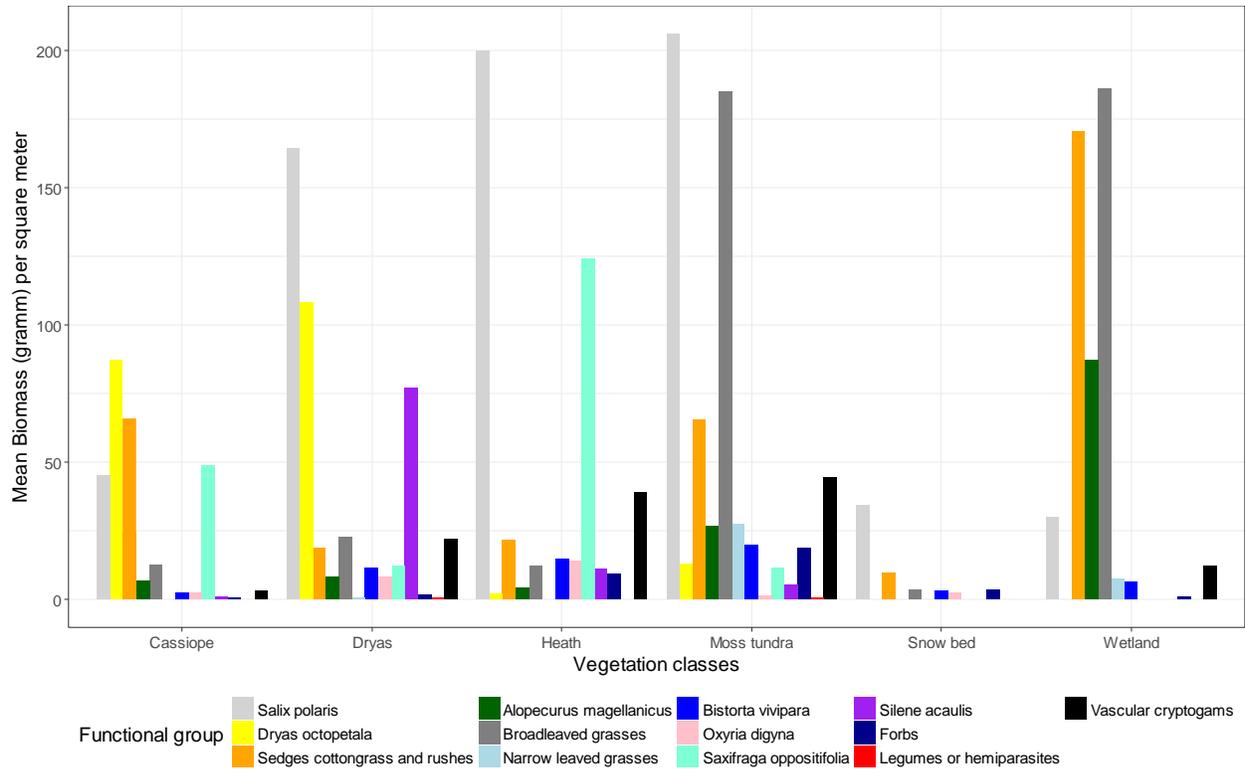


Figure 1. Mean biomass of plant species and functional groups in different vegetation types. Biomass values were obtained in the field by using point frequency method and converting the field values to biomass estimates following the conversion factors in Ravolainen et al. [18]. The moss tundra vegetation type is characterized by high values for broad-leaved grasses (all grasses that have leaves with a clear blade, as opposed to species with needle-like, inrolled leaves, except for the common species *Alopecurus magellanicus* that is shown separately). The amount of forbs species (*Bistorta vivipara*) and forbs as a group is also high in moss tundra.

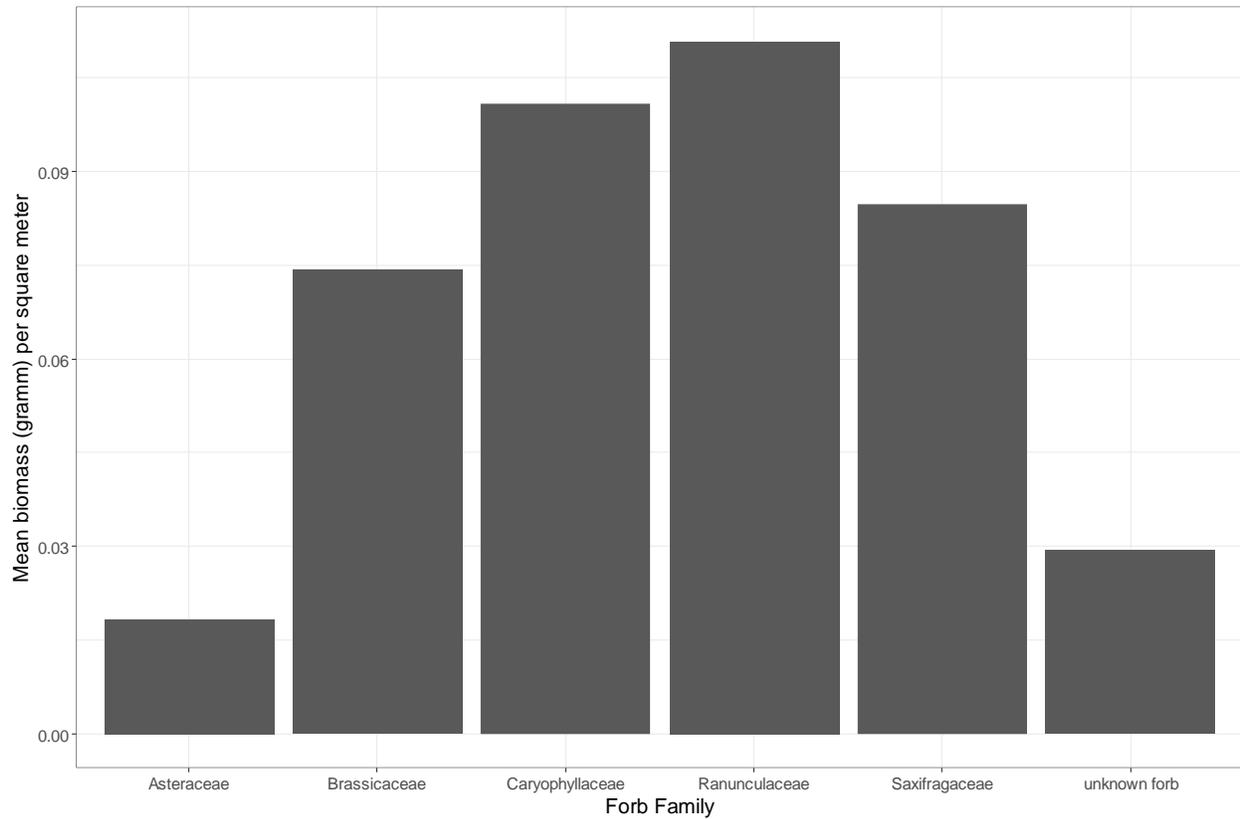


Figure 2. Distribution of plant families within the forb category. Included in each of the families:
 Brassicaceae: *Braya purpurascens*, *Braya sp.*, *Cardamine pratensis*, *Cardamine sp.*, *Drab asp.* Asteraceae: *Petasites frigidus*, Caryophyllaceae: *Caryophyllaceae sp.*, *Cerastium sp.*, *Cerastium alpinum*, *Cerastium arcticum*, *Minuartia sp.*, *Sagina nivalis*, *Sagina sp.*, *Silene sp.*, *Stellaria sp.*, Ranunculaceae: *Ranunculus sp.*, *Ranunculus hyperborea*, *Ranunculus nivalis*, *Ranunculus pygmaeus*, *Ranunculus sulphurous*, Saxifragaceae: *Saxifraga sp.*, *Saxifraga cernua*, *Saxifraga cespitosa*, *Saxifraga hieracifolia*, *Saxifraga hirculis*, *Saxifraga nivalis*

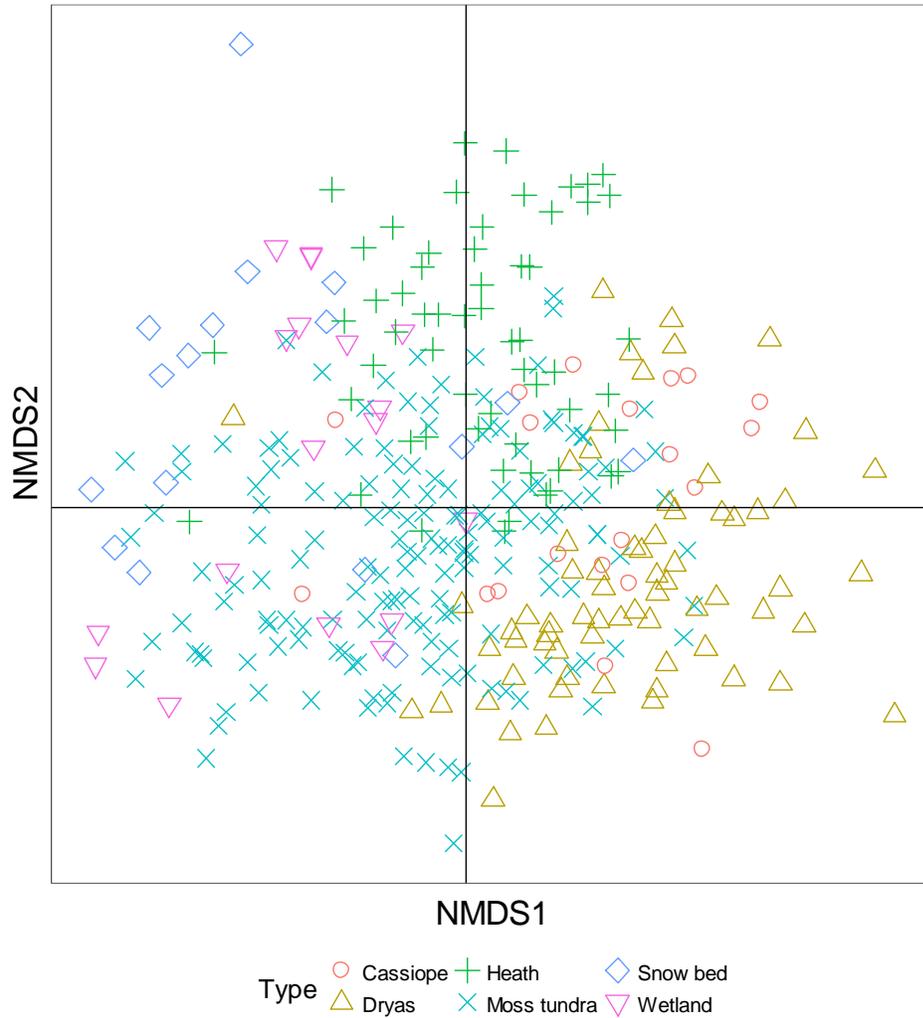


Figure 3. Distribution of field data in vegetation types.

Vegetation types with graminoid and forb dominance (wetland and moss tundra) group together when using plant abundances to structure the data. The *Dryas* vegetation is quite separated from the other types. The figure contains data at a functional group level, excluding plots with only three functional groups or less because there would be too little data per species to perform a species level analysis. The forb category was split into families for this analysis.

The original project description

Prosjektbeskrivelse: Klimavinnere og tapere på Svalbardtundraen – hvor skjer interaksjonene?

BAKGRUNN: Næringskjeden i landøkosystemet på Svalbard har tre hovednivåer: planter, plantespisende dyr og rovdyr. På alle disse nivåene er det noen «klimavinnere» og «klimatapere»^{1,2}. Det er likevel utfordrende å forutsi hva klimaendringene betyr for disse artene fordi klimaeffekter ofte er indirekte og involverer samhandlinger (interaksjoner) mellom artene. For eksempel, milde vintre i overvintringsområdene og tidligere vårer på Svalbard har forårsaket en formidabel bestandsoppgang for kortnebbgås³. Det er imidlertid uvisst om effektene gress har på plantene fører til økt matkonkurranse mellom beitedyrene og i hvilke deler av landskapet habitatbruken er sammenfallende for artene. Vi vet heller ikke hvilken effekt beitedyrene, som enkeltvis påvirker plantene direkte men ulikt, samlet sett har på mengden gode matplanter i vegetasjonen. Likeså er det åpne spørsmål om bestandsnedgang for rev, rein, rype og østmarkmus, forårsaket av regnværperioder om vinteren⁴, kompenseres for av varmere somre i det lange løp, og om økt vekst av gress og urter på bekostning av moser og lav gir mer produktive beiter på tundraen⁵. Utfordringene knyttet til slike direkte og indirekte klimaeffekter på landøkosystemet gjenspeiles i det at *økosysteminteraksjoner* er et av hovedområdene i kunnskapsmatrisen med stort behov for økt kunnskap¹. Behovet for å skaffe en bedre forståelse over *klimaeffekter på økosysteminteraksjoner* ligger også til grunn for en omfattende utvidelse av den nåværende overvåkingen av naturmiljøet på Svalbard. I vitenskapsplanen til «Klimaøkologisk Observatorium for Arktisk Tundra»⁶ (KOAT) er det beskrevet problemstillinger som omhandler samhandlinger mellom artene og nivåene i næringskjeden. Fokusartene i planen (gås, rev, rein, rype) er valgt ut fordi de har stor relevans for forvaltningen (høstbare arter), økosystemtjenester (friluftsliv og rekreasjonsjakt) og responderer på klimaendringene¹. For beitedyrene omfatter problemstillingene bl.a. konkurranse om beiteplanter gjennom endret 1) mattilgang i sesonger som er kritiske for bestandsutvikling (fenologisk «mismatch» mellom mattilgang og kritisk behov for næring) og 2) tilgang på beiteplanter av god nok næringskvalitet. Vellykket overvåking er avhengig av opprettholdelse av de lange tidsserier (rein, rype, rev) og av etablering av nye for å komplementere eksisterende romlig og tidsmessig oppløsning og dekning⁷. For eksempel trengs vegetasjonsovervåking i områder der bestandsmål på beitedyr finnes, og på en romlig skala som dekker variasjon både i vegetasjon, klima og beitedyr tetthet^{7,8} for å komplementere eksisterende vegetasjonsregistreringer (jfr. SMF 14/38) som enten dekker store skala men har lite informasjon om matplanter (fjernmåling) eller der detaljenivået er høyt men dekningen for lokal til å muliggjøre tolking i forhold til beitedyr. Behovet for koordinert og romlig replikert vegetasjonsovervåking ble nylig påpekt i en evaluering av den terrestre delen av «Miljøovervåking Svalbard og Jan Mayen (MOSJ)»⁷, og er i tråd med den internasjonale overvåkingsplanen «Circumpolar Biodiversity Monitoring (CBMP)»⁹. To enkle men *sentrale forutsetninger* for å bygge et slikt komplett overvåkingssystem for økosysteminteraksjoner er: 1) *Kunnskap om hvor i Svalbards landskap vi kan forvente at beitedyrenes habitatbruk overlapper i så stor grad at samspillet mellom dem påvirkes eller endres* og 2). *kunnskap om hvordan beiteplanter varierer i disse habitatene*. Det omsøkte prosjektet vil fremskaffe denne kunnskapen. Vi vil bidra til å bygge opp et storskala koordinert overvåkingsdesign som i fremtiden kan gi svar på hvordan dyrene og plantene og samspillet mellom dem takler og tilpasser seg klimaendringene.

¹ jfr. «Miljøforvaltningens kunnskapsbehov på Svalbard»: B1, I3a

MÅL: Hovedmålet med prosjektet er å undersøke hvor i Svalbards landskap det er størst sannsynlighet for samspill mellom både klimavinnere og tapere fra to nivå (planter og beitedyr) i næringsnettet (Fig.1). Ved å se på sammenfallende habitatbruk mellom beitedyrene og hvilke viktige habitattyper og beiteplanter disse områdene rommer, vil vi identifisere «hot spots» for økosysteminteraksjoner mellom høstbare arter (gås, rein og rype) og viktige matplanter (urter, gress, polarvier, moser og lav) på Svalbard. Et utvalg av disse områdene vil danne grunnlag for etablering av en framtidig storskala overvåking av 'plante-beitedyr-klima' interaksjoner på Svalbard.

METODE: I prosjektet vil vi kombinere informasjon fra eksisterende digitale landskapsdata (vegetasjonskart, terrengmodell), publiserte habitatmodeller (rype og kortnebbgås), og nyutviklede habitatmodeller for rein med nye felldata om romlig fordeling av matplanter og beitetrykk. Mer spesifikt vil vi:

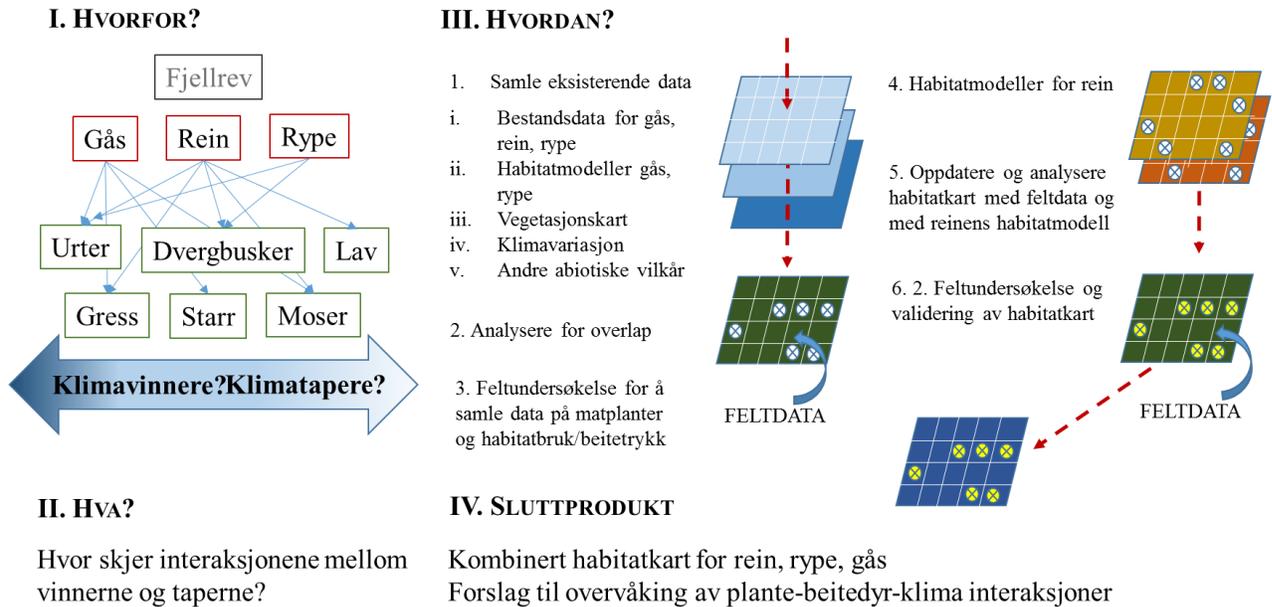
Sammenstille eksisterende datasett (bestandsstørrelser av beitedyr, romlige observasjonsdata for beitedyr, klima) og digitale landskapsdata (vegetasjon, topografi) (Fig. 1 punkt 1 og 2) med heldekkende habitatmodeller for svalbardrype (hekkeutbredelse^{10,11}; SMF 09/74), kortnebbgås (hekkeutbredelse¹² og beitegrad¹³; SMF 12/118) og svalbardrein (se nedenfor og ¹⁴).

Feltvalidere habitatmodeller og samle inn data om matplantenes romlige fordeling i ulike habitattyper med ulik grad av beitetrykk (Fig. 1 punkt 3). Antatte klimavinnere (gress, urter, polarvier, gås og rein [?]) og tapere (lav, mose og rype [?]) er i fokus for datainnsamlingen.

Utvikle sesongmessige habitatmodeller for svalbardreins potensielle leveområder basert på innsamlede GPS-data fra Nordenskiöld Land (SMF 12/115 og 13/49) og Brøggerhalvøya/Kaffiøyra (SMF 13/60 og 14/114), bestands- og observasjonsdata og digitale landskapsdata (Fig. 1 punkt 4).

Analysere habitatbruk og grad av overlappende habitatbruk for beitedyrene og identifisere hvor plantene kan forventes å bli mest påvirket av en eller flere av beitedyrene (Fig. 1 punkt 5).

Feltvalidere sluttproduktet (Fig. 1 punkt 6).



Figur 1. Skjematisert fremstilling av prosjektplan. **Hvorfor og hva:** Mulige klimaresponser og kjente interaksjoner mellom beitedyr og planter er skissert. **Hvordan Stegene 1-3:** Vi vil kombinere eksisterende informasjon om beitedyrenes habitatbruk (gås og rype¹⁰⁻¹²) med et heldekkende vegetasjonskart¹⁵. Sammenstilling av dette med abiotiske forhold (temperatur, nedbør osv.¹⁶) danner grunnlag for et første utvalg av feltlokaliteter. I dette steget vil vi koordinere prosjektet vårt med pågående pilot for vegetasjonsovervåking der sammenfatting pågår i regi av NP (SMF 14/38). Vi vil feltvalidere det utvalget av lokaliteter som peker seg ut for overlappende habitatbruk mellom gås, rein og rype⁷ i habitater som har ulike vilkår for plantevekst. I den første feltsesongen (2015) vil vi registrere biomasse av beite- og klimasensitive plantearter og tilstedeværelse av beitedyrene (møkk, tråkk, tegn etter «grubbing»). Det at data om vegetasjon og beitedyr samles på samme sted og med samme feltdesign sikrer at dataene kan kombineres i senere analyser og overvåking⁸. **Hvordan Stegene 4-6:** Vi vil bruke bestandsdata for rein og data fra GPS-merkede simler fra jaktområdene og Brøggerhalvøya/Kaffiøyra og utdype og forklare hvilke miljøfaktorer i landskapet (vegetasjon, planteproduktivitet/plantebiomasse og topografi) som bestemmer og begrenser arealbruken til reinen i disse områdene. Feltdataene vil bidra inn i habitatmodellarbeidet for rein ved å gi detaljert informasjon om romlig fordeling av viktige matplanter i ulike habitattyper som alene ikke kan oppnås gjennom digitale vegetasjonskart. Deretter vil vi utvikle sesongmessige habitatmodeller som beskriver leveområdenes egnethet og ekstrapolere habitatmodellene til hele øygruppa for å kartlegge potensielle leveområder og derved mulig utbredelse av svalbardreinen på Svalbard. Analyser følger standard metoder for habitatmodellering som prosjektdeltakerne har god erfaring med^{10,11,14,17,18}. Vi vil gjennom analyse kombinere de romlige habitatmodellene (gås, rein og rype på Svalbardskala) med datalagene om vegetasjon og klima for å identifisere habitattyper der habitatbruken til de ulike beitedyrene overlapper i stor eller liten grad. Vi vil feltvalidere et utvalg av lokaliteter basert på det utviklede kombinerte habitatkartet i den andre feltsesongen (2016; se metoder over). Statistiske habitatmodeller og habitatkart kan relativt enkelt lages for romlig utbredelse av en art av gangen, men det mangler analytiske metoder for å beregne sannsynligheten for at en interaksjon faktisk skjer mellom artene basert på slik type data¹⁹. Prosjektets resultater og produkter gir derfor ikke absolutte «svar» på hvor dyrene og plantene vil ha sterke interaksjoner, men synliggjør sammenfallende habitatbruk og identifiserer viktige habitattyper der beitedyrenes habitatbruk overlapper i så stor grad at samspillet mellom dem kan påvirkes eller endres.

PRODUKTER: Vi vil produsere ny vital kunnskap og et kart som sammenstiller og synliggjør habitatbruken til de viktigste beitedyrene i tundraøkosystemet på Svalbard. Som en del av denne prosessen vil vi utarbeide et nytt habitatkart for reinsdyr som viser egnethet og derved potensiell utbredelse av rein på Svalbard. Alle produkter leveres som digitale filer og nettbaserte kartutsnitt. Det sammensatte habitatkartet vil vise: A) «Hot spots» for økosysteminteraksjoner på Svalbard, B) habitatoverlapp for og konkurransepotensiale mellom forvaltede dyrearter (jf. høstede arter) og C) områder/habitater hvor vi

kan forvente at beitedyrenes habitatbruk overlapper i så stor grad at samspillet mellom dem påvirkes eller endres. Resultatene fra prosjektet bidrar direkte til etablering av et romlig dekkende, replikert oppsett av vegetasjonsovervåking som omfatter både planter og beitedyr i ulike habitat- og klimagradianter^{6,7}. En slik overvåking er avgjørende for å tette kunnskapshull om hvordan beitedyrene og plantene på tundraen samhandler, takler og tilpasser seg klimaendringene (se også ²⁰). Sluttproduktene (kunnskap og kart) kan brukes til å utvikle felles forvaltningstiltak (for eksempel verneplaner, forvaltningsplaner for enkeltarter, samfunn eller verneområder, kanalisering av ferdsel), å utpeke områder der vegetasjonen kan være utsatt for beitetrykk fra flere av dyrene og vegetasjonsendringer, og ikke minst et utvalg av områdene vil danne grunnlag for etablering av en storskala overvåking av 'plante-beitedyr-klima' interaksjoner på Svalbard.

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