# High seasonal overlap in habitat suitability in a non-migratory High Arctic ungulate

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## ARTICLE INFO

## ABSTRACT

Understanding drivers of space use and habitat selection is essential for management and conservation, especially under rapid environmental change. Here, we develop summer and winter habitat suitability models for the endemic wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*). The High Arctic Svalbard tundra is currently subject to the fastest temperature increases on Earth, and reindeer spatial responses to associated environmental change are strongly restricted due to landscape barriers (including 60% glacial coverage) and lack of sea ice as movement corridors. We used an extensive dataset of GPS-collared adult females (2009–2018; N = 268 individual-years) to model seasonal habitat selection as a function of remotely sensed environmental variables , and subsequently built habitat suitability models using an ensemble modelling framework. As expected, we found that reindeer preferred productive habitats, described by the normalized difference vegetation index (NDVI) and plant biomass (derived from a vegetation map), in both seasons. This was further supported by selection for bird cliff areas, rich in forage, improving habitat suitability especially in winter. Contrary to our expectations, the terrain variables had similar, impact on habitat suitability in the two seasons, except for use of higher elevations in winter, likely related to improved forage access due to less snow. Suitable habitat patches covered only a small proportion of the landscape and were highly clustered in both seasons. About 13.0% of the total land area was suitable in both seasons, while summer-only and winter-only areas contributed a marginal addition of around 4.7% and 1.5%, respectively. This suggests, that unlike many continental and migratory *Rangifer* populations, even small geographic areas may encompass sufficient suitable habitat. These first archipelago-wide habitat suitability models provide seasonal baseline maps relevant for the management and conservation of Svalbard reindeer, particularly under rapid environmental alterations from climate change.

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## 1. Introduction

Within a species overall distribution range, typically a limited area is preferred and consistently occupied (Franklin, 1995; Guisan and Zimmermann, 2000). Such variation in space use is generally anticipated to reflect the suitability of the habitat for the species under study and may change across seasons and life-cycle stages (Rivrud et al., 2019; Karcher et al., 2021). In large herbivores, suitable habitats are typically characterised by high forage quantity and quality (Senft et al., 1987). However, the suitability of an area may be modulated by predation risk, competition and human perturbations (e.g., Bukombe et al., 2018, Beumer et al., 2019, Rivrud et al., 2019, Jenkins et al., 2020). Quantifying what is suitable habitat for a species by modelling its habitat preference is fundamental to the understanding of ecological niche requirements and for anticipating how species may be affected by environmental changes and disturbances, including e.g., climate change, habitat loss and habitat fragmentation. Even coarse-scale vegetation and terrain data, commonly used in habitat suitability studies, can be useful to identify which characteristics of the landscape that are the most important in determining space use and habitat distributions of a variety of herbivores (e.g., Jensen et al., 2008, Speed et al., 2009, Matthews and Spooner, 2014, Beumer et al., 2019, Jenkins et al., 2020, Oeser et al., 2020), and to provide background for mechanistic studies (e.g., L'Herault et al., 2013, Chen et al., 2021). Estimates of habitat suitability across the landscape is fundamental knowledge needed for effective conservation, management and monitoring of species (e.g., Thuiller et al., 2018, Jenkins et al., 2020).

Human perturbations are currently affecting the distributions and abundances of Arctic reindeer and caribou populations (e.g., Vors and Boyce, 2009, Mallory and Boyce, 2018, Kvie et al., 2019, Gundersen et al., 2020, Linnell et al., 2020). In contrast, High Arctic caribou and reindeer inhabiting remote areas, are often less affected by humans and more restricted by mountains, fjords and glaciers that form landscape barriers (Tyler and Øritsland, 1989; Jenkins et al., 2016; Mallory and Boyce, 2019). The caribou and reindeer in some of these areas, such as in the High Arctic archipelagos in Svalbard and Canada, are therefore more sedentary (Tyler and Øritsland, 1989; Pond et al., 2016) than their Low Arctic conspecifics, which typically perform long-distance seasonal migrations (Joly et al., 2019). High Arctic reindeer are also challenged by reductions in sea-ice cover and consequent loss of important migration corridors. The loss of such corridors affects the use of seasonal ranges and may cause loss of genetic diversity and population connectivity (Jenkins et al., 2016; Jenkins et al., 2018; Mallory and Boyce, 2019; Kaluskar et al., 2020; Peeters et al., 2020). Detailed knowledge on seasonal habitat use from predictive habitat suitability models may help conservation and management of High Arctic ungulates (Kliskey et al., 1999; Leblond et al., 2014; Jenkins et al., 2020; Kaluskar et al., 2020).

The wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is a subspecies endemic to the High Arctic Svalbard archipelago where climate is changing at the most rapid pace on Earth (Isaksen et al., 2022). Like most High Arctic ungulates, the Svalbard reindeer have no opportunities escaping the effects of warming through migration (Jenkins et al., 2016; Mallory and Boyce, 2018). The reindeer in Svalbard are non-migratory and generally have small seasonal and annual home ranges of only a few square kilometres (Tyler and Øritsland, 1989). Their movements are naturally limited by physical barriers, such as open fjords, alpine mountains, and tide water glaciers. Despite these hinders, Svalbard reindeer have now more or less recovered its distribution and abundance from severe overharvest until a century ago (Le Moullec et al., 2019). Currently, reindeer are distributed across non-glaciated land areas of the archipelago, with an abundance of ∼ 22,000 individuals (estimate for 2013–16) and densities of up to 10 reindeer/km$^2$ in the central inland valleys. Svalbard reindeer are strictly bottom up regulated by a combination of autumn and winter conditions (Albon et al., 2017; Loe et al., 2021) in interaction with density dependence (Hansen et al., 2019a). There is no competition with other large herbivores or insect harassments (Halvorsen and Bye, 1999). This reindeer sub-species typically appears in small groups or even solitary. There is sexual segregation, yet on very small spatial scales (Loe et al., 2006). Predation on Svalbard reindeer is of minor importance (but see Prestrud, 1992, Derocher et al., 2000, Stempniewicz et al., 2021). There are no roads outside settlements and human presence as well as harvest off-take is low (Peeters et al., 2022). The Svalbard reindeer is therefore unique in that many partly confounded factors affecting habitat suitability of other *Rangifer* populations can be considered negligible.

The arctic environment implies strong seasonality in food availability. In the snow free summer months the reindeer graze on a variety of plants in e.g., lowland moss tundra, wetlands, meadows and lower foothills where the vegetation consists of grasses, sedges, forbs, dwarf willow and mosses (Staaland, 1986; Bjørkvoll et al., 2009), and select quantity over quality of forage plants (van der Wal et al., 2000). In the winter, reindeer are often confined to exposed wind-blown ridges, where they graze on sparse vegetation of dwarf willow and graminoids; otherwise, they dig craters in the snow to access the vegetation underneath. They select sites for cratering with no basal ice and attempt to find patches with shallow snow depth and high plant biomass (Hansen et al., 2010a; Beumer et al., 2017). Although mostly stationary, severe winters with 'ice-locked pastures', make reindeer to move between local valleys (Loe et al., 2016), across the sea-ice (Hansen et al., 2010b; Stien et al., 2010), to the seashore (Hansen et al., 2019b) or to higher elevations (Pedersen et al., 2021b) in search for more favourable foraging areas. Factors shaping the seasonal distribution and habitat selection of Svalbard reindeer have mostly been studied at very local scales (see Table 1 and references therein), apart from a spatial density modelling study conducted across the archipelago (Le Moullec et al., 2019). In the latter study, vegetation productivity successfully predicted Svalbard reindeer summer density across the archipelago. Yet, detailed investigation and quantification of suitable habitats considering a wide range of environmental characteristics and across seasons is not fully studied.

The goal of the current management policy for the Svalbard reindeer is to have no impact of human activities on population genetics, demography, and dynamics (Governor of Svalbard, 2009). However, climate is changing rapidly (Hanssen-Bauer et al., 2019; Isaksen et al., 2022) and tourism has increased around the Svalbard archipelago in accordance with the Norwegian national strategy moving away from coal mining industry and towards tourism and research as pillars of the Svalbard society (Ministry of Justice and Public Security, 2015), which may overall increase the area extent of various human activities. In this situation, better knowledge of what is the most suitable habitat for Svalbard reindeer and where they are located under current environmental conditions will

improve the opportunities for knowledge-based conservation and management decisions and provide a baseline for evaluation of future changes. We therefore developed seasonal habitat suitability models for Svalbard reindeer, to assess the extent of suitable habitats across the entire Svalbard archipelago. Our objectives were to 1) identify environmental predictors determining summer and winter habitat selection 2) map the suitable habitats and 3) quantify the seasonal overlap in habitat suitability. We used an extensive dataset of GPS-tracked Svalbard reindeer females (2009–2018; N = 268 female years) together with remotely sensed data on terrain and vegetation characteristics to model reindeer summer and winter habitat suitability at a spatial resolution, assumed to correspond to the scale of a foraging area (30 × 30 m pixel cells). We expected forage quantity to be the most important determinant of habitat suitability, and that terrain characteristics would be more important in winter than in summer, as they shape snow conditions and thereby modify forage accessibility.

## 2. Methods

### 2.1. Study system

The High Arctic Svalbard archipelago (74–81°N, 10–35°E; 62,700 km$^2$), comprises 60% glaciers, 25% barren and sparsely vegetated areas and 15% continuously vegetated areas (Johansen et al., 2012) (Fig. 1). The archipelago encompasses more than 500 islands
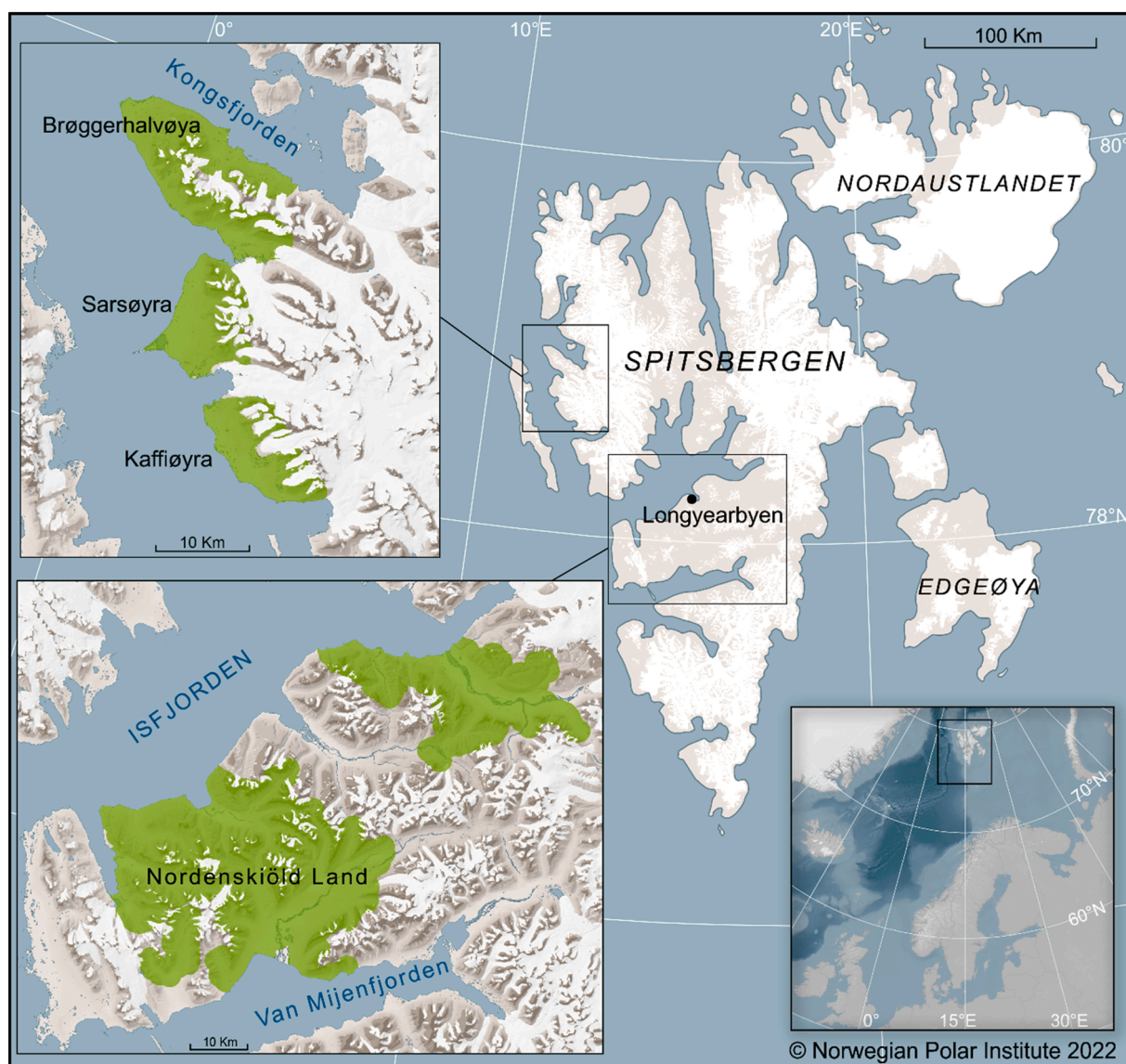


**Fig. 1.** Map showing the Svalbard archipelago (*right panel*) and the local study areas (*left panels*) where female Svalbard reindeer were equipped with GPS collars (smaller squares on the map) during 2009–2018. The study area (i.e., available area for reindeer) is defined by a polygon obtained from all GPS positions with a 2 km radius buffer in the summer months of July–August and winter months of December–March.

with the largest being Spitsbergen, Edgeøya, Barentsøya and Nordaustlandet. Deeply indenting fjords and mountains (up 1700 m above sea level) characterize the coastal areas in the north and west of Spitsbergen. The landscapes contain habitats spanning from productive graminoid tundra to polar desert. The vegetation is short-statured and dominated by mosses, graminoids, dwarf willow *Salix polaris* and herbs (Elvebakk, 1994; Johansen et al., 2012). Svalbard has a relatively mild climate, shifting from typically oceanic in the west to colder and drier climate conditions in northern and eastern parts of the archipelago (Førland et al., 2012).

The data for this study was collected in Central Spitsbergen (78° N, 15–16° E; middle Arctic tundra zone) and on the west coast of Spitsbergen (78° N, 11 – 12° E; High Arctic tundra zone) (Fig. 1). The Central Spitsbergen study area consisted mainly of large glacial valleys in Nordenskiöld Land that are interconnected by smaller valleys with high elevation passes, where reindeer can move between valleys. The west Spitsbergen study area consisted of three peninsulas (Brøggerhalvøya, Sarsøyra and Kaffiøyra) that are dominated by steep alpine mountains with flat coastal plains in the lowlands. Large tidewater glaciers and fjords separate the areas from each other and limit reindeer movements between the three study populations. These two types of landscapes typify many areas of the Svalbard archipelago and represents variation in reindeer habitats.

The study populations differ in terms of population dynamics (Hansen et al., 2019c) and the amount of human traffic is generally low. The population in Nordenskiöld Land has increased steadily over the last three decades (Lee et al., 2015; see also www.mosj.no). In this population, there is limited hunting (on average about 7% annually; Peeters et al., 2022) and human traffic. The reindeer populations along the coast were eradicated by over-harvesting, but reindeer were reintroduced in 1978 to Brøggerhalvøya (Aanes et al., 2000). This sub-population grew quickly, and some individuals moved out of the peninsula and established on Sarsøyra (1994) and Kaffiøyra (1996) after a severe winter of 1993/94. At present the three sub-populations display varying abundance trends (Hansen et al., 2019c). Movements between the peninsulas are restricted due to landscape barriers and lack of sea-ice. Thus, most reindeer are stationary within a peninsula year-round (Pedersen et al., 2018). The populations on these peninsulas are not hunted and human traffic is almost absent.

### 2.2. Reindeer data

#### 2.2.1. Field protocol

Adult female Svalbard reindeer from the two study populations were captured during winter (February to April 2009–2017; 9–48 individuals per year; Appendix A) using a handheld net between a pair of snowmobiles (Omsjoe et al., 2009). After capture, the reindeer were manually restrained and fitted with a GPS-collar from either Vectronic Aerospace (Berlin, Germany; N = 50 individual female reindeer; positions from 2 h intervals stored in the transmitter [ 'store-on-board']) or Tellus Followit (Lindesberg, Sweden; N = 98 individual reindeer; positions from 8 h intervals sent by satellite-link). The median location error was approximately 12 m for both transmitter types (Godvik et al., 2009). Both collar types weighed approximately 850–1000 g (~1–2% of the female's winter body mass). GPS data from the 'store-on board' transmitters were downloaded from the collars during recapture events in February and/or April. All animals were handled according to protocols approved by the Governor of Svalbard, the Norwegian National Research Ethics Committee, and the Norwegian Food Safety Authority.

#### 2.2.2. Pre-processing of the GPS data

We compiled positional data for both study regions between 2009 and 2018 from 268 individual female years and followed the default screening recommendations in the protocols of Bjørneraas et al. (2010). That is, we removed outliers that generated unrealistic travel speeds, distances, and angles between successive locations, e.g., consecutive locations with a mean distance more than 10 km apart and movement rates exceeding 1.5 km/h with sharp turning angles (166–194 degrees). After this procedure, we removed a few additional likely GPS errors (e.g., positions located in the sea when ice free) and subsampled the bihourly GPS dataset to 8-h intervals to homogenize sampling frequency across all collars and to reduce the degree of autocorrelation. Thereafter, we excluded female years with more than 10% of the positions lacking for the study periods (N = 4 and N = 20 female years in winter and summer respectively). From this dataset we first extracted GPS positions for July and August, which is the core snow-free summer season (Loe et al., 2006), and excludes both the calving season (June; Veiberg et al., 2017) and the rut (September/October; Tyler et al., 1987). This dataset contained in total 268 animal years from 123 different female reindeer, corresponding to 48 749 GPS locations. Second, we extracted GPS positions for December to March, which is the core winter season (Hansen et al., 2013). From this dataset we also removed 13 females (i.e., resulting in 19 female years) that undertook longer migrations outside the area anticipated to be the core winter home range. This final dataset contained in total 222 animal-years from 114 different female reindeer, corresponding to 87 485 GPS locations.

### 2.3. Environmental predictors of habitat suitability modelling

We initially selected 9 environmental variables describing vegetation, terrain, and snow characteristics (i.e., all fixed in time and the latter indirectly through terrain variables) relevant to reindeer summer and winter habitat selection (Table 1, Appendix B and C). We first homogenized the spatial resolution among the different environmental raster layers by re-sampling each layer to a pixel cell size of 30 × 30 m as defined by the vegetation raster layer (Johansen et al., 2012). Thereafter, we created raster layers of each

environmental variable at the smallest spatial scale that allowed for neighbourhood calculations. This was done using a moving average approach, assigning each $30 \times 30$ m pixel a new value based on values in its immediate neighbourhood (both summer and winter models; $3 \times 3$ pixels [$90 \times 90$ m]). We calculated the new pixel values as a mean across the moving average window for continuous variables, and as proportions for the categorical variables. We used ArcMap (ESRI 2011) and the packages *raster* and *rgdal* in R 3.3.2 (R Core Development Team 2017) for handling the spatial data.

## 2.4. Data analyses

We developed summer and winter habitat suitability models for adult female reindeer, based on the use-availability approach (Johnson et al., 2006) and design type II (Calenge, 2011). To do so, we went through four analytical steps. First, we selected environmental variables by exploring the differences between environmental characteristics of the GPS locations used by reindeer in summer and winter by implementing the 'Environmental Niche Factor Analysis' (ENFA) (Hirzel et al., 2002), and checked for collinearity in variables by applying the variance inflation factor (Cengic et al., 2020). Second, we modelled habitat suitability

**Table 1**
Overview of available digital vegetation and terrain characteristics assumed relevant for Svalbard reindeer summer and winter habitat suitability. Vegetation variables are based on the digital map of Johansen et al. (2012) spatial resolution $30 \times 30$ m and the NDVI map based on Karlsen et al. (2014) with spatial resolution $240 \times 240$ (mean maximum NDVI [2009–2018]), and terrain variables are based on a digital terrain model (DEM; spatial resolution $20 \times 20$ m, estimated uncertainty is 5–10 m; Norwegian Polar Institute 2010). We resampled initially all data layers to $30 \times 30$ m and calculated environmental layers as averages across years or from individual satellite image scenes.

| | Predictor | Spatial resolution | Unit of measure | Map source | Reindeer habitat relevance |
|---|---|---|---|---|---|
| **Vegetation variables** | Moss tundra | $30 \times 30$ | Proportion (0–1) | Johansen et al. (2012) | **Summer & Winter**: Often characterised by high quantities of palatable vascular food plants and a preferred reindeer habitat (Staaland, 1986; Henriksen et al., 2003; Hansen et al., 2009a; Hansen et al., 2009b). |
| | Heath tundra | $30 \times 30$ | Proportion (0–1) | Johansen et al. (2012) | **Summer & Winter**: Often characterised by high quantities of palatable vascular food plants and a preferred reindeer habitat (Staaland, 1986; Henriksen et al., 2003; Hansen et al., 2009a; Hansen et al., 2009b). |
| | Plant biomass | $30 \times 30$ | Proportion (0–1) | Reclassified map from Johansen [ et al. (2012)] (see Appendix B) | **Summer & Winter**: Reindeer prefer habitats with high plant biomass, and their density increases with biomass (Staaland, 1986; Henriksen et al., 2003; Hansen et al., 2009a; Hansen et al., 2009b; Le Moullec et al., 2019). |
| | NDVI | $240 \times 240$ | 0–1000 | Karlsen et al. (2014) | **Summer & Winter**: Habitat preference and reindeer densityt increase with increasing values of maximum NDVI (Hansen et al., 2009a; Hansen et al., 2009b; Le Moullec et al., 2019), because NDVI reflects plant productivity and biomass (Pettorelli et al., 2005). |
| | Distance to bird cliff areas | $30 \times 30$ | Log (distance) (m) | Sea-bird database NPI, Strøm et al. (unpublished) | **Summer & Winter**: Areas near bird cliffs, fertilized by sea birds, are the most productive habitats in Svalbard (Zwolicki et al., 2013) and observed to be preferred by reindeer (Henriksen et al., 2003). |
| **Terrain variables** | Elevation | $20 \times 20$ | Masl. | DEM, NPI | **Winter**: All else being equal, habitat suitability should increase with elevation because of less snow and basal ground ice accumulation (Hansen et al., 2009b; Pedersen et al., 2021a). **Summer:** All else being equal, habitat suitability should increase at low elevations because of increased amount of forage, in flat lowlands (Hansen et al., 2009a). |
| | Slope | $20 \times 20$ | 0–90 degrees | DEM, NPI | **Winter**: All else being equal, habitat suitability should increase with slope steepness because of less snow and ice accumulation (Hansen et al., 2009b; Peeters et al., 2019). **Summer:** All else being equal, habitat suitability should increase with decreasing slope steepness because of increased amount of forage in flat lowlands (Hansen et al., 2009a). |
| | Terrain shape index ('curvature') | $20 \times 20$ | -1–1 | DEM, NPI | **Summer & Winter**: Increased terrain curvature index values indicate higher amounts of ridges and mounds in the landscape, which might increase terrain heterogeneity and the access to a diversity of habitats, phenological stages and snow conditions (McNab, 1989; Pedersen et al., 2021b). |
| | Terrain ruggedness index | $60 \times 60$ | 0–1 | DEM, NPI, Sappington et al. (2007) | **Summer & Winter**: High terrain ruggedness allows for diverse food resources and variation in phenology, as well as in snow cover and basal ground ice in winter. Reindeer thus tend to prefer rugged terrain in winter (Hansen et al., 2009a; Hansen et al., 2009b; Pedersen et al., 2021b). |

(probability of occurrence) of reindeer in each raster pixel in the study area and, based on model validation from Boyce Index (Hirzel et al., 2006), compiled ensemble models from *biomod2* (Thuiller et al., 2016). Third, we extrapolated results, based on the ensemble habitat suitability models, to the archipelago wide scale, and fourth, we assessed the spatial overlap between the predicted summer and winter habitats and spatial clustering of those habitats. These steps are detailed in the next paragraphs.

For both the summer and winter habitat suitability models, we used the GPS positions of reindeer as used sites and all pixels within a defined study area as available sites (i.e., all pixels within the delineation). We defined the available area for the females by creating a circular buffer of 2 km radius around each of the GPS position obtained during both seasons. This radius was assumed to be within the daily movement distances of a reindeer (Tyler and Øritsland, 1989; Loe et al., 2016). These buffers were subsequently combined to one large polygon defining the available area for both summer and winter modelling. When the buffers did not entirely overlap, we manually filled the remaining small areas to create one large polygon (0.1% of area, see Fig. 1). From this polygon we removed land area covered by glaciers and defined the remaining raster layer as the area available for reindeer. Loe et al. (2006) and Garfelt-Paulsen et al. (2021) described limited spatial habitat segregation during the summer among females of different reproductive status, as well as during winter, thus we pooled data regardless of female reproductive status.

### 2.4.1. Step 1. Selection of environmental predictors for habitat suitability modelling

To assess which variables to include in the habitat suitability modelling of reindeer, we explored habitat selection by applying the environmental niche factor analysis for presence only data (ENFA; Hirzel et al., 2002). ENFA is a multivariate method that investigates potential differences in environmental variables between used and available sites (see Appendix D for further details on the methods). We ran the ENFA separately for the summer and the winter season and included initially the predictor variables related to vegetation and terrain characteristics as described in Table 1. Note that the variable measuring the closeness to bird-cliff was calculated as the inverse of the log-transformed distance, as we expected its effect to be relevant only at proximity of bird-cliffs. Other variables were transformed using the Box-Cox transformation according to recommendations of Hirzel et al. (2002) (Appendix D). The variables 'proportion heath' and 'proportion of moss tundra' had bimodal distributions, which is not adequate for ENFA analysis (see recommendations by Hirzel et al., 2002) and was therefore not assessed in this way. The analyses were done using the *adehabitatHS* package for R (Calenge, 2006). Centring and scaling of the variables were done using the function *dudi.pca* from the R-package *ade4* (Dray and Dufour, 2007). We report ENFA histograms, duality diagrams, and marginalization and specialization coefficients in Appendix D. We inspected the correlations among the relevant environmental variables (Table 1) along the first factorial axis of the ENFA (i.e., correlations between variables with the highest marginality score along 1st axis) and only kept variables with positive scores $\geq 0.20$ and negative scores $\leq -0.20$ as described by Hirzel et al. (2002) for further modelling (Appendix D). Thereafter, we followed the protocols by Cengic et al. (2020) and calculated the variance inflation factor (VIF), which is a measure of multicollinearity, for all variables, including those not analysed by ENFA. We applied the *vifstep* function in R package *usdm* and excluded a variable if its VIF value was above 10. These two steps resulted in including all variables according to Table 1 for both summer and winter habitat modelling. See Appendix E for additional Pearson's correlations coefficients across all variables.

### 2.4.2. Step 2. Single model validation and ensemble development

When predicting habitat selection of species, it is recommended to use several types of statistical models to obtain best predictive ability because different modelling techniques can lead to variable predictions and biases (Araujo and New, 2007; Thuiller et al., 2009). We therefore used the modelling platform *biomod2* (Thuiller et al., 2016; reviewed in Hao et al., 2019), implemented in R for modelling of seasonal habitat selection. *Biomod2* enables concurrent modelling with a set of modelling types and combines inference from the separate models to build an ensemble model. In our analyses we included the default models: generalised boosted models (GBM), generalised linear models (GLM), generalised additive models (GAM), classification tree analysis (CTA), artificial neural networks (ANN), random forests (RF) and the flexible discriminant analysis (FDA). As presence data, we used the GPS locations of reindeer across all study years and regions. Pseudo-absence data were created from the raster layer of available pixel cells according to Johnson et al. (2006). The number of pseudo-absence points was 10 times the presence points, following the recommendations of Barbet-Massin et al. (2012). To evaluate the predictive ability of the candidate models (i.e., transferability sensu; Randin et al., 2006), we validated the models internally by dividing the model development dataset into a calibration (70% of the data) and validation (30%) sub-dataset, and repeated this procedure ten times, in addition to one full run for each model (100% of dataset), totalling 77 model runs. For the summer habitat suitability models, we also evaluated the candidate model transferability using an independent dataset. This dataset consisted of female positional data (N = 239) from 26 field surveys distributed across the entire archipelago in the summers of 2013–2015 (Le Moullec et al., 2019).

We used Boyce index for evaluation of each model run's predictive ability (Hirzel et al., 2006), as recommended by Guisan et al. (2017) (Appendix F). This index, implemented in the R *ecospat* package (Broennimann et al., 2018), takes values between $-1$ and $+1$ where values close to one indicate good to perfect predictions. Values around zero indicates predictions no different than those obtained randomly (Hirzel et al., 2006; Guisan et al., 2017). To construct the ensemble models, we included only models with Boyce index $> 0.9$. For the summer habitat suitability models, we based this on the external validation. For the winter habitat suitability models, we based this on the internal validation (mean of 10 model runs), as no independent winter dataset was available for external

validation. To construct the ensemble models, the full models (100% of dataset) were used as input and assembled using a weighted average method based on TSS scores (Marmion et al., 2009). Standard built-in *biomod2* validation statistics (ROC and TSS) were also calculated as supportive measures for model validation of the ensemble habitat suitability projections (Appendix G).

### 2.4.3. Step 3. Variable importance and ensemble projections

To assess the relative importance of the different predictor variables for reindeer habitat selection, we used the variable importance procedure of *biomod2* as described by Thuiller et al. (2009) and Thuiller et al. (2016). This procedure shuffles the observations of a single variable across the models included in the ensemble, makes model predictions based on this shuffled dataset and computes a simple correlation between the reference predictions and the one based on the shuffled data. The higher the value, the more influence the variable has on the model (i.e., zero assumes no influence). The estimated effects of the predictor variables on habitat suitability were described by a response curve. For building such response curves, n-1 variables are set to their median value and only the one of interest vary across its range. The variations observed and the curve obtained shows the sensibility of model predictions to that specific variable (see Thuiller et al., 2016). We projected the ensemble models across the Svalbard archipelago with a resolution of 30 × 30 m, for both seasons, using the function *ensemble_forecasting()* implemented in the *biomod2* package.

### 2.4.4. Step 4: Calculation of spatial statistics to assess seasonal habitat overlap

First, we calculated total area of suitable and less suitable habitat (km$^2$) in each season, as described by Beumer et al. (2019), using thresholds for habitat suitability values of > 0.50 and < 0.50, respectively (i.e., areas with more or less than 50% probability of being used by reindeer; see also Appendix H for frequency distributions of habitat suitability values). These areas were compared to; 1) the total land area in Svalbard based on maps obtained from Johansen et al. (2012), excluding glaciers, rivers, lakes, and shadow areas (i. e., areas not possible to classify from satellite image), and 2) the total vegetated area in Svalbard, excluding above mentioned classes, and areas characterised as polar desert and gravel areas. Second, we assessed spatial overlap of summer and winter habitat suitability by the Pearson's correlation coefficient between pixel-wise habitat suitability values from the seasonal habitat suitability maps (Appendix H ), and an overlay of the seasonal habitat suitability map (percentage overlap of suitable pixel cells using thresholds for habitat suitability values of > 0.50). Finally, we assessed spatial clustering of suitable habitats, by calculating the nearest-neighbour index (NNI) for all suitable pixels with thresholds > 0.5 as described by Clark and Evans (1954). This index, implemented in the R-package *spatialEco* (Jeffrey et al., 2022) quantifies the mapped habitat suitability pattern in three types, i.e., regularly dispersed, randomly dispersed or clustered. Index values less than 1 indicate clustering of suitable habitats, while index values greater than 1 indicates dispersion. Since we deal with GPS positions in UTM coordinate system, the unit of the clustering index is meter.

## 3. Results

### 3.1. Predictive performance of the habitat suitability models

For summer habitat suitability, the GLM, GAM, GBM and ANN models had a Boyce index above 0.9 in the external validation and were included in the summer ensemble model. For winter habitat suitability, all models had Boyce index values above 0.9 in the internal evaluation and were included in the winter ensemble model (Table 2). The ensemble models for summer and winter habitat suitability had relatively high predictive performance according to Boyce index, 0.972 and 0.856, respectively (Table 2; Appendix G).

**Table 2**

Model evaluation statistics for female Svalbard reindeer summer and winter habitat suitability models. Model validation is based on Boyce index (Hirzel et al., 2006), where values close to one indicate high predictive ability. Single models included in ensemble projections (Boyce index > 0.9, external validation for summer models and internal validation for winter models) are indicated in bold. For the internal validation, Boyce index is presented as mean (SD = standard deviation) across ten runs of the model fitted with 70% and validated with 30% of the dataset. External validation statistic was calculated once, based on all validation data, and therefore only the index value is presented. Only summer habitat suitability models were evaluated with an independent dataset. See appendix G for other supporting validation statistics of the ensemble projections.

| | Summer | | Winter | |
|---|---|---|---|---|
| *Model type[*]/validation* | *Internal* | *External* | *Internal* | *External* |
| GLM | - | **0.942** | **0.980 (0.006)** | - |
| GAM | 0.995 (0.004) | **0.960** | **0.993 (0.005)** | - |
| ANN | 0.958 (0.027) | **0.968** | **0.973 (0.018)** | - |
| CTA | 0.962 (0.030) | 0.603 | **0.983 (0.017)** | - |
| GBM | 0.982 (0.011) | **0.978** | **0.976 (0.011)** | - |
| RF | 0.942 (0.013) | 0.380 | **0.950 (0.009)** | - |
| FDA | 0.958 (0.027) | 0.899 | **0.998 (0.002)** | - |
| Ensemble projection | - | 0.972 | 0.856 | - |

[*] Model shorts are given in the methods section.

### 3.2. Environmental predictors of habitat suitability

In both seasonal habitat suitability models, NDVI and plant biomass had the highest variable importance value (Fig. 2), implying that habitat selection of Svalbard reindeer was driven by vegetation productivity more than terrain features, despite the latter was expected to impact snow distribution in winter. NDVI and biomass had similar, positive, but non-linear effects on habitat suitability. In summer, biomass values ranging between 90 and 636 g/m$^2$ predicted habitat suitability values >0.5, while in winter values were slightly higher (141–636 g/m$^2$) for the same suitability threshold. NDVI values, ranging between 170 and 750, predicted habitat suitability values above 0.5 for both summer and winter habitats (Fig. 3). Interestingly, the productive bird cliff areas were important for habitat suitability of the reindeer, and had a non-linear, positive effect, but more so in winter than in summer (Figs. 2 and 3). The remaining two variables describing vegetation productivity (proportion of heath and moss tundra vegetation) had low variable importance and apparently did not capture habitat selection as expected.
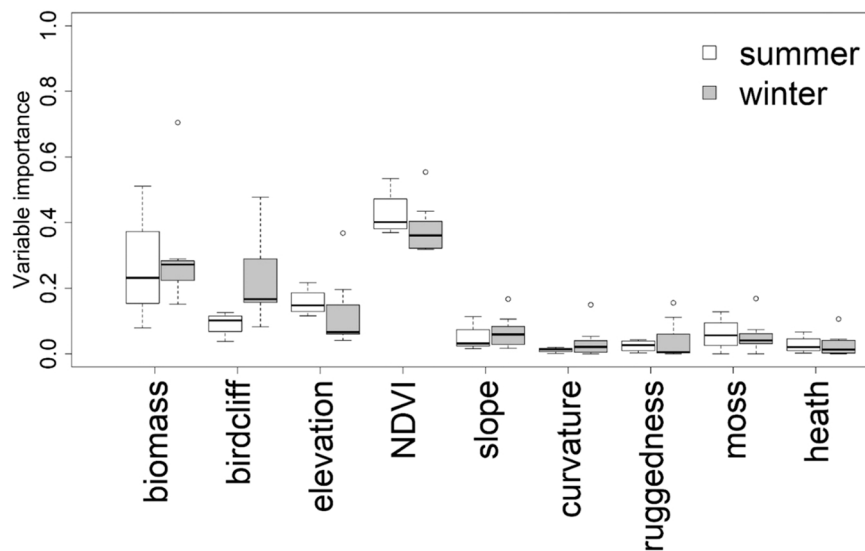


**Fig. 2.** Variable importance (VI), i.e., relative importance of each environmental predictor variable for the selected ensemble models of summer (white) and winter (grey) habitat suitability of female Svalbard reindeer (see methods section for details on VI calculations and Thuiller et al., 2016).
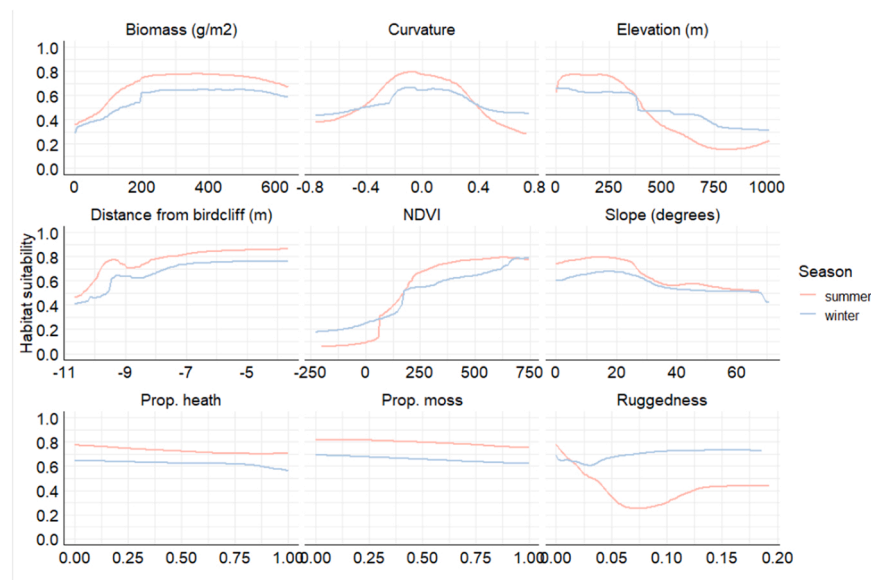


**Fig. 3.** Response curves of the environmental variables included in the ensemble projections for predicting female Svalbard reindeer summer (red) and winter (blue) habitat suitability. For building such response curves, n-1 variables were set to their median value and only the one of interest is varying across its whole range of values. The variations observed and the curve obtained shows the sensitivity of the ensemble model to that specific variable (see Thuiller et al., 2016).

Elevation was the only terrain variable of some importance in the ensemble models. In summer, habitat suitability was high between 0 and 250 m, and decreased at higher elevations (Figs. 2 and 3). Elevation was less important in winter, as signified by the lower variable importance (Fig. 2), but habitat suitability remained around 0.5 till about 600 m (Fig. 3). The remaining terrain variables, curvature, slope, and ruggedness had low variable importance during both seasons (Fig. 2). Curvature and slope had seasonally similar, non-linear effects, with highest habitat suitability in slightly hilly terrain (intermediate values) and in flat areas to gentle sloping mountain sides (e.g., 0–25°). The effect of terrain ruggedness differed between seasons (Fig. 3). The non-linear, negative effect of ruggedness on summer habitat suitability indicates reindeer's use of flat, lowland areas (i.e., low values of the ruggedness index indicate flat terrain), whereas winter habitat suitability was generally high across the entire landscape ruggedness interval. Across the archipelago, habitat suitability in both seasons was highest in productive habitat types. While flat lowlands were important during both seasons, higher elevations such as mountain foothills and plateaus were relatively more suitable in winter (Fig. 4, Appendix I).

### 3.3. Predicted habitat suitability on Svalbard scale

Predicted suitable summer habitat for reindeer, as defined by setting a threshold for habitat suitability $>0.5$, was only a small fraction (17.6%) of the total Svalbard land area, excluding glaciers. This amount of suitable habitat represents 15.5% of the vegetated land areas (Table 3A, Fig. 4). Predicted suitable winter habitat for reindeer covered even a slightly smaller percentage (14.4%), representing 12.6% of the vegetated area (Table 3A, Fig. 4). Areas with suitable habitat were clustered throughout the landscape in both seasons, as indicated by the NNI index $< 1$. For summer, the expected distance between suitable habitat was 65.9 m, while the observed distance was 30.1 m (NNI-score $= 0.46$, z-score $= -2207.5$). Similarly, the expected distance for winter was 72.8 m, while the observed distance was 30.2 m (NNI-score $= 0.41$, z-score $= -2153.0$). In both seasons NNI was near pixel cell size (30 $\times$ 30 m
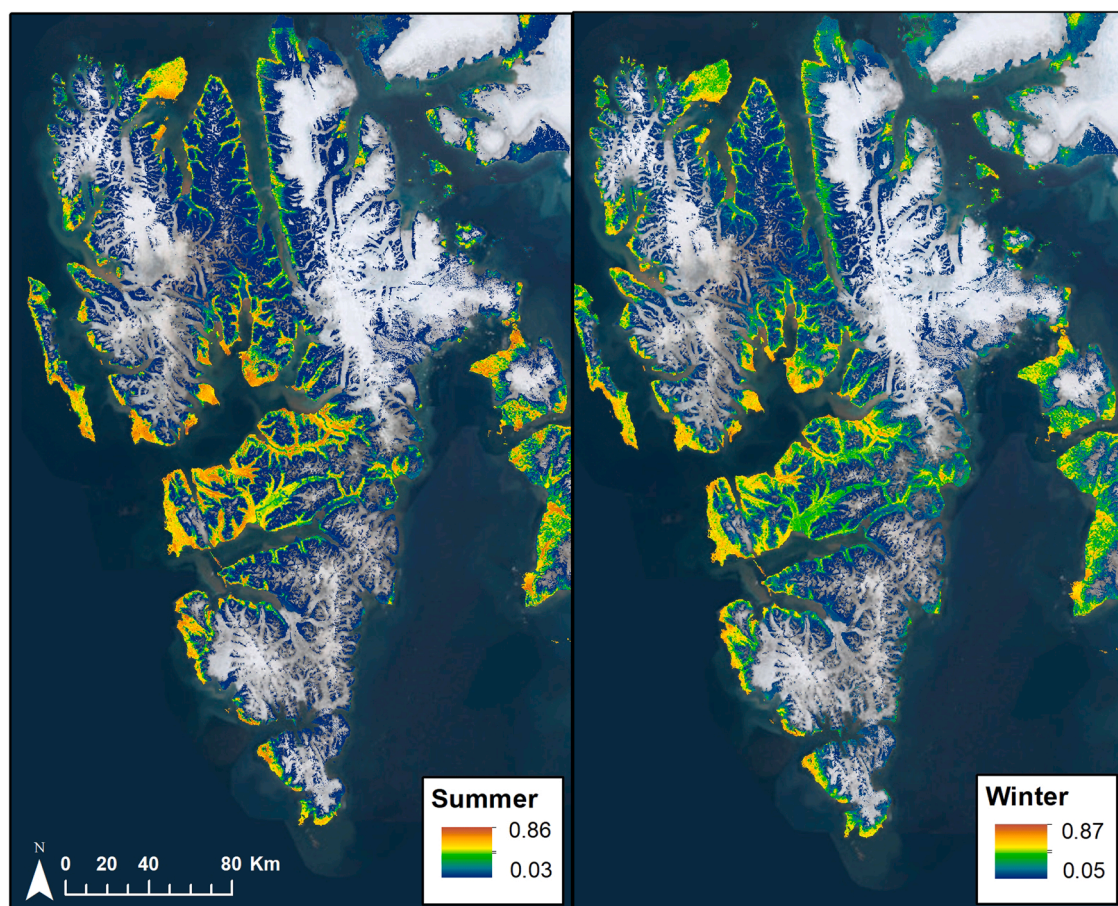


**Fig. 4.** Predicted summer and winter habitat suitability for female Svalbard reindeer in the extrapolated region in Svalbard. The summer habitat suitability map is an ensemble projection based on the four best models (i.e., Boyce index > 0.9) from the external evaluation, and the winter habitat suitability map is an ensemble projection based on all default models (i.e., Boyce index > 0.9; *Biomod2*) from the internal evaluation (see Table 2). The darker red colour, the higher the habitat suitability and the darker blue colour the lower habitat suitability. Note that the spatial extent is determined by the NDVI raster map, which did not cover areas north of 80° degrees and the eastern part of the island of Edgeøya (Karlsen et al., 2014; Karlsen et al., 2018).

**Table 3**

Summary of area statistics (km$^2$) and seasonal habitat overlap and exclusion (% of total area in parentheses) across A) major land cover classes and B) habitat classes according to Table 1 and Appendix B for Svalbard reindeer female summer and winter habitat suitability (HS threshold > 0.5) from the ensemble projections of summer and winter habitat suitability. Areas in square kilometres (% of covered area on land) are derived from habitat classes in Johansen et al. (2012). Non-vegetated landcover indicate all other habitat classes in Johansen et al. (2012), except glaciers, water, and vegetated areas. The total area is calculated based on the extent of the NDVI raster map, which did not cover areas north of 80° degrees and the Eastern part of Edgeøya (Karlsen et al., 2014; Karlsen et al., 2018).

**A)**

| | Area in km$^2$ (% of total area) | | | |
|---|---|---|---|---|
| | Non-vegetated land cover | Glacier/water | Vegetated land cover | Total |
| Suitable summer and suitable winter habitat (>0.5) | 2620.6 (1.1) | 565.5 (0.2) | 26,576.7 (11.5) | 29,762.8 (12.9) |
| Suitable summer habitat (>0.5) and unsuitable winter habitat (<0.5) | 1126.5 (0.5) | 318.0 (0.1) | 9308.6 (4.0) | 10,753.1 (4.7) |
| Suitable winter habitat (>0.5) and unsuitable summer habitat (<0.5) | 700.9 (0.3) | 194.8 (0.1) | 2594.1 (1.1) | 3489.8 (1.5) |
| Unsuitable winter and unsuitable summer habitat (<0.5) | 53,027.9 (23.0) | 31,856.0 (13.8) | 101,964.4 (44.2) | 186,848.2 (80.9) |
| **Total** | 57,476 (24.9) | 32,934.2 (14.3) | 140,443.8 (60.9) | 230,854.0 (100.0) |

**B)**

| | Area in km$^2$ (% of total area) | | | | | |
|---|---|---|---|---|---|---|
| | Barren | Heath | Moss tundra | Unspecified (shadow) | Water | Total |
| Suitable summer and suitable winter habitat (>0.5) | 4920.3 (2.1) | 9640.8 (4.2) | 14,554.3 (6.3) | 296.1 (0.1) | 351.3 (0.2) | 29,762.8 (12.9) |
| Suitable summer habitat (>0.5) and unsuitable winter habitat (<0.5) | 2791.1 (1.2) | 2093.9 (0.9) | 5476.2 (2.3) | 275.1 (0.1) | 116.8 (0.1) | 10,753.1 (4.7) |
| Suitable winter habitat (>0.5) and unsuitable summer habitat (<0.5) | 1275.4 (0.6) | 694.1 (0.3) | 1163.8 (0.5) | 211.1 (0.9) | 145.3 (0.1) | 3489.8 (1.5) |
| Unsuitable winter and unsuitable summer habitat (<0.5) | 111,343.2 (48.2) | 13,596.1 (5.6) | 31,119.7 (13.5) | 25,242.2 (11.0) | 5547.0 (2.4) | 186,848.2 (80.9) |
| **Total** | 120,330.0 (52.1) | 26,024.9 (11.3) | 52,314.1 (22.7) | 26,024.5 (11.3) | 6160.5 (2.7) | 230,854.0 (100.0) |
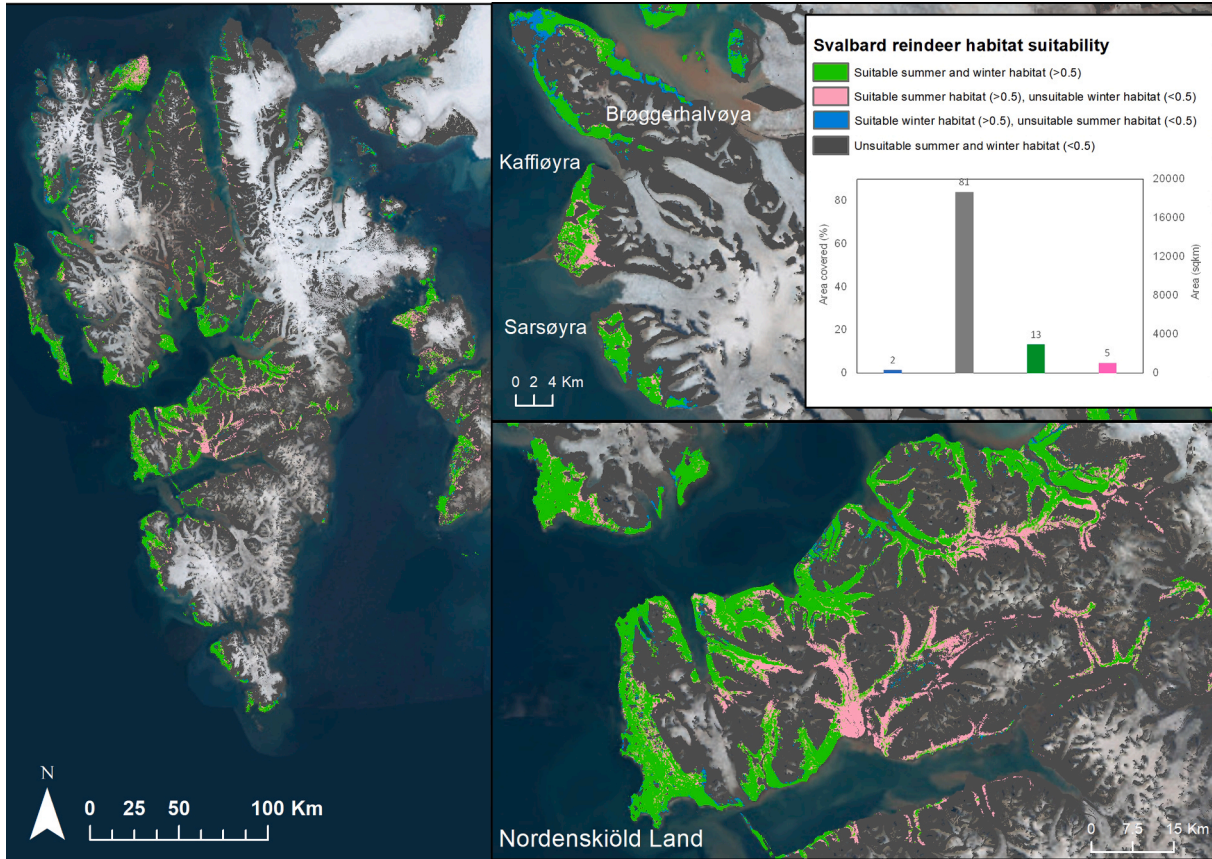
**Fig. 5.** Predicted summer and winter habitat suitability classified into suitable (>0.5) and unsuitable (<0.5) habitat and seasonal overlap for female Svalbard reindeer. *Left panel:* Overview map of suitable and unsuitable habitats for Svalbard reindeer at the spatial extent described in Fig. 4. *Top right panel*: The study area on the west coast of Spitsbergen (Brøggerhalvøya, Sarsøyra and Kaffiøyra). *Bottom right panel*: The study area in Central Spitsbergen (Nordenskiöld Land).

resolution), in practice meaning that suitable habitat pixels nearly always have other suitable pixels as immediate neighbours.

The high Pearson's correlation coefficients $(r = 0.95)$ for pixel-wise comparisons of all pixels with any summer and winter habitat suitability values, indicates substantial overlap in areas. However, areas (pixels-) with low habitat suitability likely drive this correlation (Appendix H). Only a small part of the vegetated land area (11.5%) was suitable habitat in both summer and winter (habitat suitability index > 0.5) (Table 3A), and most of this was in moss tundra and heath habitats (Table 3B). The overlapping areas of high habitat suitability were largely in the valley bottoms, lower foothills, and coastal plains (Fig. 5.). Notably, an even smaller proportion of the vegetated areas was exclusively summer and winter habitat, 4.0% and 1.1%, respectively (Table 3).

## 4. Discussion

This assessment of seasonal habitat suitability of the geographically, genetically isolated High Arctic reindeer across its range, shows that both summer and winter habitat suitability were largely driven by vegetation productivity. Our results suggest bird-cliff areas, which are Arctic 'hot-spots' for biodiversity with rich vegetation, to improve habitat suitability for reindeer, particularly in winter. Contrary to our expectations, the terrain variables had limited impact on habitat selection of the reindeer, despite their linkage through snow to forage accessibility in winter. Overall, only about 13% of the total land area of the Svalbard archipelago had suitable habitats for reindeer. However, the suitable areas were clustered in low land areas and encompassed both winter and summer habitats, suggesting protection of even small geographic areas to conserve year-round reindeer habitats.

We found expectedly that productive habitats were important for reindeer habitat selection, which confirms previous, more local local-scale studies on habitat selection, as well as an archipelago-wide spatial assessment of reindeer density distributions (Hansen et al., 2009a; Hansen et al., 2009b; Le Moullec et al., 2019; Jenkins et al., 2020). We tested several proxies of vegetation productivity, such as the NDVI index, plant biomass and proportion of moss and heath tundra habitat, derived from Johansen et al. (2012), and distance to bird cliffs. These proxies differed in their contributions to the models, from near to none for the habitat types (heath and moss tundra), to NDVI being the most important variable (Fig. 2). This implies that the readily available NDVI index of vegetation productivity (Pettorelli et al., 2005; Karlsen et al., 2014; Vickers et al., 2016), reflects well the amount of forage across the landscape for the reindeer in both seasons, despite shortcomings, such as it cannot distinguish between plants of different palatability (Myers-Smith et al., 2020). Surprisingly, amount and possibly quality of forage was not captured by the predictors 'proportions of heath' and 'proportion of moss tundra' habitat, which we expected would impact winter and summer habitat suitability, respectively. Subsequently, contrasting other studies, who have identified a positive association between high quality vegetation types and grazing time in summer (Skarin et al., 2008, 2010) and selection for patchy snow-free habitats, typically on top of wind-blown ridges, in winter (Romtveit et al., 2021). Also, our re-classified map from Johansen et al. (2012), had substantial areas in e.g., north-facing mountain slopes not classified due to shadows, which significantly may have reduced the accuracy of the land surface classifications and thereby the modelled relationships (Leidman et al., 2021). Interestingly, the only clear seasonal difference among the vegetation variables was the positive influence and the higher importance of distance to bird cliffs on reindeer winter habitat suitability. The bird cliff areas in Svalbard, although relatively small in size, are Arctic 'hot-spots' for biodiversity because of the heavy fertilization from sea birds, resulting in lush, rich moss tundra dominated vegetation (Odasz, 1994; Zwolicki et al., 2013), which improved habitat suitability, particularly in winter. Our findings on archipelago wide scale underline the importance of these Arctic oases and supports an earlier description of bird cliffs areas being an important habitat in home ranges of coastal reindeer (Henriksen et al., 2003). To improve understanding of the role of different characteristics of vegetation on herbivore habitat use and selection, it will be crucial to acquire vegetation data beyond the proxies used here. Particularly, we highlight the need for data that is non-static, conveys information on vegetation quality and quantity, both within and between seasons, and has at spatial resolution that matches that of GPS data of reindeer (i.e., accuracy of ± 12 m). The new Sentinel-2 sensors with a spatial resolution of 10 × 10 m may be better suited to the highly mosaiced vegetation in Svalbard and thereby gives promising possibilities for development of dynamical predictors in time and space for future habitat suitability studies.

Unexpectedly, we found terrain variables to have limited, similar impact on habitat suitability in both seasons, except for the variable 'elevation', that kept habitat suitability values at higher levels for elevations (mountains and plateaus) up till < 1000 m above sea level in winter, as compared to summer. This fact likely relates to snow distribution, accumulation and snow pack properties (Rixen et al., 2022), which in turn are key factors shaping forage access of reindeer in winter (Hansen et al., 2009b; Beumer et al., 2017; Loe et al., 2021; Pedersen et al., 2021a; Pedersen et al., 2021b). For instance, ridges and high-elevation plateaus tend to be wind-blown and therefore have less snow and thereby offer better access to forage. However, terrain variables are indirect proxies of snow properties, and provide no information of within and between year variation and temporal trends in e.g., snow cover extent, depth, or density and basal ice, which ultimately determine forage access for herbivores (Pedersen et al., 2021a). Improving knowledge of how snow pack properties shape winter habitat use likely requires fine-scaled snow models and/or measurements of variables appropriate to describe forage access on spatial and temporal scales within and between years (Reinking et al., 2022).

Suitable habitats were clustered within the overall small proportion of seasonal reindeer habitats (13%; Table 3), which reflects the naturally fragmented, highly heterogeneous landscapes in Svalbard (Tyler and Øritsland, 1989; Johansen et al., 2012). The area of highly suitable habitats (i.e., here chosen to > 0.5 based on Beumer et al., 2019), and the connectivity between them will influence future population sizes. The increasing fragmentation of reindeer habitat, due to loss of sea-ice as dispersal corridors (Peeters et al., 2020), will likely reduce the overall 'effective' area of suitable habitats. Retreating glaciers can, however, open new land and increase connectivity. Over the past century, areas covered by glaciers have shrunk by 10.4% (Geyman et al., 2022), potentially offering more habitat for reindeer. However, establishment of vegetation takes time in High Arctic soils with low nutrient availability (Hodkinson et al., 2003), and newly opened glacier foreland may serve more the purpose for movements between areas than actual grazing

pastures.

Regime shifts in the cryosphere (Peeters et al., 2019) and forecasted increases in temperature and precipitation (Bauer-Hanssen et al., 2019), will have wide implications for the terrestrial plant-based food web in Svalbard, in which the reindeer is a key herbivore. The longer snow-free season (Loe et al., 2021) and the increased plant productivity during warm summers (van der Wal and Stien, 2014), likely result in more available food for herbivores. However, the rate of plant productivity increase is decelerating according to what is expected from summer temperature increase alone (Vickers et al., 2016). This indicates an increasing importance of other drivers impacting vegetation production, including possibly grazing effects of the reindeer themselves and of geese (Eischeid et al., 2021), negative effects of increased frequency of winter rain events (Peeters et al., 2019), which may damage plants encapsulated in ice (Milner et al., 2016; Bjerke et al., 2017). Nevertheless, the expected effects from ice-encasement differ between plant communities, drastically affecting evergreen shrubs, which often are unpalatable to reindeer, but possibly enhancing production of communities dominated by deciduous shrubs, which are heavily used by reindeer (Le Moullec et al., unpublished preprint). Both direct and indirect climate effects can potentially alter plant community composition, productivity and spatial configuration (van der Wal and Stien, 2014; Ravolainen et al., 2020) and lead to different scenarios for future habitat suitability for reindeer. The net outcome of these environmental changes combined on habitat suitability remains unknown.

We provide the first analysis of summer and winter habitat suitability for the High Arctic Svalbard reindeer as a baseline for understanding seasonal patterns in habitat selection. The seasonal habitat suitability maps provide a foundation for assessing future changes in habitat suitability and given continued and improved monitoring of the reindeer and vegetation, carrying capacity of the tundra for this key herbivore. Such knowledge is particularly relevant in this High Arctic environment, with rapidly increasing summer temperatures and extended snow-free seasons (Isaksen et al., 2022; Rantanen et al., 2022). These maps are also highly applicable as an environmental predictor layer in future efforts to redo the spatial estimation of reindeer densities across the archipelago under different future conditions (Le Moullec et al., 2019). They may also guide conservation and management processes that attempt to protect habitats and regulate human area use. The high seasonal overlap in habitat suitability and clustering of suitable habitats, suggest that even protection of small geographic areas encompass both summer and winter habitats of reindeer. The maps highlight variation in female habitat suitability on a large spatial scale, but likely miss the nuances necessary to predict the more fine-scaled distribution of reindeer locally, for instance differences in the coastal and inland areas as a result of varying availabilities, as pointed out in Loe et al. (2012). The habitat suitability maps are static with respect to time, smoothing annual variability, and as such they are less robust compared to dynamic SDMs. The limitations inherent in the static vegetation and terrain predictors, hindered in our case dynamic predictions. We therefore emphasize to acquire relevant dynamic environmental data that allow forage availability to be modelled at annual and seasonal resolutions. This is essential for the development of dynamic models linking individual reindeer fitness components to seasonal habitat selection and use in this rapidly changing tundra landscape.

## CRediT authorship contribution statement

Åshild Ønvik Pedersen, Virve Ravolainen, Eeva Soininen, Brage B. Hansen and Mathilde Le Moullec conceived the idea. Åshild Ønvik Pedersen, Ingrid M. G. Paulsen, Eeva Soininen and Virve Ravolainen wrote the first version of the manuscript. Ingrid M. G. Paulsen, Eeva Soininen and Isabell Eischeid developed the R-scripts and analysed the data with contribution from Åshild Ønvik Pedersen, Brage B. Hansen, Leif Egil Loe, Audun Stien and Arnaud Tarroux. Brage B. Hansen, Leif Egil Loe, Mathilde Le Moullec, Åshild Ønvik Pedersen, Erik Ropstad and Audun Stien collected the data. Hans Tømmervik re-classified the habitat map. Stein Rune Karlsen supplied NDVI data. All authors commented on the manuscript before submission.

## 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

Data will be made available on request.

## Acknowledgement

# Appendix. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02528.

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