

Modelling local distribution of an Arctic dwarf shrub indicates an important role for remote sensing of snow cover

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Abstract

Despite the intensive research effort directed at predicting the effects of climate change on plants in the Arctic, the impact of environmental change on species' distributions remains difficult to quantify. Predictive habitat distribution models provide a tool to predict the geographical distribution of a species based on the ecological gradients that determine it, and to estimate how the distribution of a species might respond to environmental change. Here, we present a model of the distribution of the dwarf shrub *Dryas octopetala* L. around the fjord Kongsfjorden, Svalbard. The model was built from field observations, an Advanced Space-borne Thermal Emission and Reflection Radiometer (ASTER) image, a GIS database containing environmental data at a spatial resolution of 20 m, and relied on generalized linear models (GLMs). We used a logistic GLM to predict the occurrence of the species and a Gaussian GLM to predict its abundance at the sites where it occurred. Temperature and topographical exposure and inclination of a site appeared to promote both the occurrence and the abundance of *D. octopetala*. The occurrence of the species was additionally negatively influenced by snow and water cover and topographical exposure towards the north, whereas the abundance of the species appeared lower on calciferous substrates. Validation of the model using independent data and the resulting distribution map showed that they successfully recover the distribution of *D. octopetala* in the study area ($\kappa=0.46$, AUC=0.81 for the logistic GLM [$n=200$], $r^2=0.29$ for the Gaussian GLM [$n=36$]). The results further highlight that models predicting the local distribution of plant species in an Arctic environment would greatly benefit from data on the distribution and duration of snow cover. Furthermore, such data are necessary to make quantitative estimates for the impact of changes in temperature and winter precipitation on the distribution of plants in the Arctic.

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1. Introduction

Most climate models predict a pronounced climate change in Arctic regions with summer temperatures over land increasing between 4 and 7.5 °C and winter precipitation by 5–80% by the year 2080 (ACIA, 2004; McCarthy et al., 2001). As the physical environment controls plant establishment and growth in the Arctic, climate change will affect plant life in the Arctic tundra (Billings, 1987; Press et

al., 1998). One observed effect of climate change on vegetation is that the spatial distribution of species changes, with populations either expanding, declining, or migrating (Huntley, 1991; Sturm et al., 2001). Such alterations can have implications for vegetation structure (Huntley, 1991), animal life (Thompson et al., 1998), and biosphere atmosphere interactions (Chapin et al., 2000; Wu & Lynch, 2000). In order to predict how the distribution of Arctic plant species will respond to climate change, it is necessary that we are capable of modelling their present distribution with sufficient accuracy.

Predictive habitat distribution modelling provides a tool to mimic the distribution of species given a set of environ-

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mental conditions (Guisan & Zimmermann, 2000). It uses data on the spatial distribution of environmental factors that are assumed important for the species' ecology (predictor variables, Franklin, 1995; Lenihan, 1993). By relating the observed occurrence of a species at sampling sites to the prevailing environmental conditions at those sites, a model of the realized niche of the species is produced (Westman, 1991). This model is then used to assess which sites in the landscape satisfy the niche requirements and thus qualify as a potential habitat for the species (Brown et al., 1995). The accuracy of a model can be quantified, by comparing the predicted habitat distribution with observed patterns of occurrence and abundance.

The outlined method for creating species distribution models assumes a state of (pseudo-)equilibrium between the sampled populations and their environment and is hence also referred to as equilibrium distribution modelling (Guisan & Theurillat, 2000a). The alternative to equilibrium modelling is mechanistic modelling of species distribution based on physiology and demography. Mechanistic modelling relies on extensive knowledge about the processes underlying a species' response to environmental variability, knowledge which is not yet available for most plant species. Equilibrium models, in contrast, are based on observed correlations between environmental gradients and a species performance, requiring little understanding of the processes causing these correlations.

Environmental gradients which can serve as predictor variables in habitat distribution models can be classified into three types, according to the way they affect an organism's performance (Austin, 1980). Resource gradients, such as soil moisture content, represent variables that are consumed by the organism. Direct gradients, such as temperature and pH, are of a direct physiological importance to the species without being consumed. Indirect gradients, such as topography, snow cover or wind speed have no direct physiological meaning for an organism but can affect it through their correlation with direct and resource gradients (Guisan et al., 1999). The mechanism causing this correlation, and thereby the effect of the indirect gradient on a species' performance, is often complex and poorly understood. Nevertheless, indirect gradients are widely used as predictor variables in predictive habitat distribution models, because the main purpose of these models is predictive accuracy rather than biological explanation. Furthermore, indirect gradients can replace a set of resource and direct gradients in a simple way (Guisan et al., 1999). In that case, using them rather than the gradients, they can replace as predictor variables generates more parsimonious models, which are preferred from a statistical point of view. Most importantly, however, direct and resource gradients are often difficult to measure, especially for larger areas (Austin, 2002). Contrastingly, several indirect ecological gradients can be modeled spatially and accurately, thanks to the recent developments in remote sensing and GIS software.

So far, the integration of remotely sensed data in predictive habitat distribution modelling has been limited. Digital elevation models have been used to derive variables related to topography (e.g., Guisan et al., 1999; Jelaska et al., 2003), while data from individual spectral of satellite sensors and snow cover indices from aerial photography have occasionally served as predictor variables in habitat distribution models (Guisan & Theurillat, 2000b). However, high-quality remote sensing data at different resolutions is becoming increasingly available and make it possible to map different ecological variables at various scales. As the demand for distribution models for plants in environments vulnerable to climate change, such as the Arctic, grows, so does the need to investigate where remote sensing can contribute most to such models. More specifically, models should be developed and it should be assessed which predictor variables need to be mapped more precisely to improve the models. Accordingly, the use of new remote sensing techniques available to map important environmental gradients should be investigated and developed further.

Here, we present the first habitat distribution for a plant species in an Arctic environment. We modelled the distribution of *Dryas octopetala* L., a well-studied Arctic species. Advanced Space-borne Thermal Emission and Reflection Radiometer (ASTER) imagery was used for snow mapping, and a GIS database of environmental variables and different types of generalized linear models (GLMs) predict the occurrence and the abundance of the species. We address the following questions: (1) How well does the model describe the distribution of *D. octopetala* in the study area? (2) Is the realized niche model, which was developed to optimize predictive accuracy, consistent with the results of observational and experimental studies on the ecology of the species? (3) How can remote sensing data be of most use to improve predictive habitat distribution models for Arctic plant species?

2. Data and methods

2.1. *Dryas octopetala* L.

D. octopetala ssp. *octopetala* is a perennial dwarf shrub found in large parts of the Arctic tundra and boreal areas, as well as in Alpine tundra at lower latitudes (Hultén, 1959). The species is among the most studied in the Arctic and a large number of observational and experimental studies provide detailed insights into its ecology (e.g., Cooper & Wookey, 2003; McGraw, 1985; McGraw & Antonovics, 1983; Welker et al., 1993). Vegetation dominated by *D. octopetala* ssp. *octopetala* typically develops on alkaline or circumneutral soils, at sites with low soil moisture and little to no snow cover during winter, in particular at wind-exposed sites and on ridges (Elkington, 1971; Elvebakk, 1994). In warmer and less exposed areas, *D. octopetala* is

outcompeted by *Cassiope tetragona* (L.) D. Don. (Elvebakk, 1994).

Experimental studies on *D. octopetala* have shown that different environmental factors control its sexual reproduction and its clonal vegetative growth (Welker et al., 1997; Wookey et al., 1995). More specifically, a rise in temperature greatly favours all aspects of sexual reproduction in *D. octopetala*, which currently is hardly ever successful in the Arctic (Welker et al., 1997; Wookey et al., 1993). While the effects of increased water availability remain unclear (Welker et al., 1993), increases in nutrient availability in the short term lead to higher leaf nitrogen concentration, biomass, and photosynthetic rate (Baddeley et al., 1994). Overall, temperature, snow cover, and soil characteristics seem to be determining environmental factors for *D. octopetala* and are expected to be significant predictor variables in a potential habitat distribution model for the species.

2.2. Study area

The study area comprises the landmasses around the fjord Kongsfjorden (79° N 12° E) in the north-western part of the Svalbard archipelago (Fig. 1). The study was conducted on the peninsula Brøggerhalvøya, the hill Ossian Sars-fjellet and the island Blomstrandhalvøya.

Ny-Ålesund (78°56' N, 11°53' E), a small permanent settlement at Brøggerhalvøya, has a mean temperature of 4.4 °C during the summer months of July and August, and

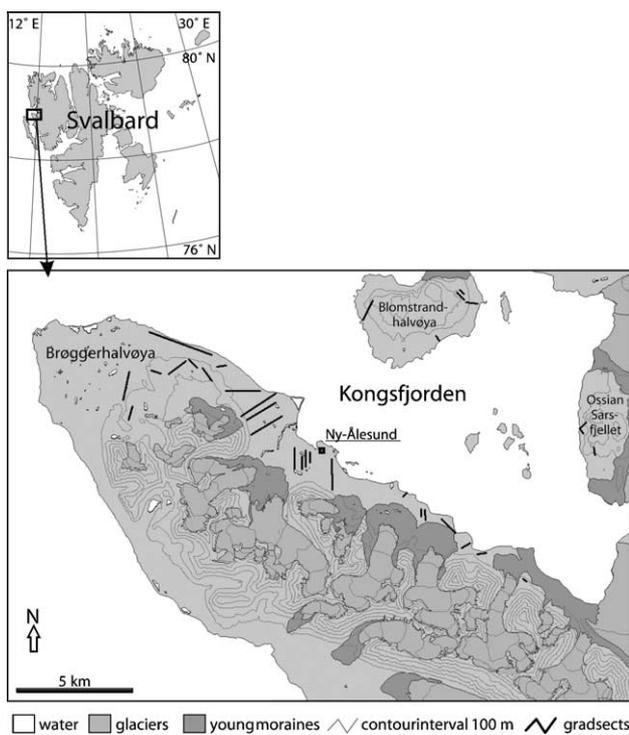


Fig. 1. Svalbard archipelago, the area around the fjord Kongsfjorden and the gradsect sampling design. The gradsects were placed to cover a maximal variation in topography, and vegetation was sampled at 80 m intervals along them (see text for further details).

– 11.7 °C during the winter from October to April (Førland et al., 1997). The mean monthly precipitation values for these periods are 33 and 34 mm, respectively (Førland et al., 1997). On the landmasses surrounding Kongsfjorden, temperature generally increases from west to east (Joly et al., 2003). Snow starts accumulating around mid-September and is redistributed by wind, causing complex spatial variations in snow depth (Winther et al., 2002). The snow cover becomes thinner from the end of May and most of the snow has disappeared by the end of June (Gerland et al., 1999; Lloyd, 1999). The landscape mainly consists of Alpine areas, which are partially covered by ice, marine terraces (especially at Brøggerhalvøya), calcareous ridges and moraines (Brossard et al., 1984). At Brøggerhalvøya, vascular plants are mainly restricted to the coastal platforms that contrast heavily with the steep interior mountains. At Blomstrandhalvøya and Ossian Sars-fjellet, the vegetation extends to more mountainous terrain as well.

2.3. Database development

A GIS database of environmental variables, stored in a raster format at a spatial resolution of 20 m, was created using the IDRISI software (Clark Labs, 2003). This database contained topography, substrate geology, snow and water cover, and air temperature variables.

2.3.1. Topography

A Digital Elevation Model (DEM; spatial resolution 20 m, created from aerial photography at scale 1:15 000), provided by the Norwegian Polar Institute, was used to calculate local elevation, terrain slope, terrain aspect, flow accumulation potential, and topographical position on various scales. Using trigonometric functions of the aspect values on the azimuth scale, two variables with a linear nature were calculated: “southness,” representing a north–south gradient and “eastness,” a west–east gradient (Skidmore, 1989). Areas of flat terrain were assigned a value zero for both variables. Three variables related to topographical position were calculated by subtracting from the elevation of a pixel in the DEM, the average elevation of the window of surrounding pixels (Guisan et al., 1999). Each of these variables used a window with a different diameter, namely, 60, 100 or 300 m. From these continuous variables, additional binary variables were created to distinguish between sites that were exposed in the landscape and sites that were not. To calculate the binary variables, the continuous variables were classified using a threshold of 0.1 m, except for the variable calculated using the 300 m windows where a threshold of 0.5 m was used.

2.3.2. Substrate geology

A geological map in vector format, on a scale 1:100 000 (Hjelle et al., 1999), was converted to a raster format using nearest neighbour resampling. The 23 legend categories present in the study area were reclassified to four general

classes [(1) moraines and alluvial deposits; (2) tertiary substrates and chert; (3) carboniferous dolomites and protozoic marbles; (4) protozoic mica schist) to reduce the number of categories and group the original units according to their significance for vegetation (Elvebakk, 1982).

2.3.3. Snow and water cover

Two binary variables representing water cover and snow cover in the study area were calculated. This was done using a calibrated and atmospherically corrected (Level-2) ASTER image of surface reflectance of the study area, taken on 26 June 2001. Geometrical rectification was performed using georeferenced aerial photographs with a 10-m spatial resolution provided by the Norwegian Polar Institute and a first-order polynomial fitted to 64 control points. The image does not cover the extremity of Brøggerhalvøya, which was therefore excluded from this study.

To produce a map of snow cover, a normalized difference snow index (NDSI, Hall et al., 1995) was applied to the ASTER image. NDSI has previously been calculated as the difference between reflectance in MODIS bands 4 (0.545–0.565 μm) and 6 (1.628–1.652 μm), divided by the sum of bands 4 and 6 (Bitner et al., 2002) or the equivalent bands of the Landsat Thematic Mapper (Vogel, 2002). In the present study, NDSI was calculated from surface reflectance values recorded by bands 1 (0.52–0.60 μm , spatial resolution 15 m) and 4 (1.600–1.700 μm , spatial resolution 30 m) of the ASTER sensor. Misclassification of clouds as snow was improbable since the image had an estimated cloud cover of less than 2% (estimated by the supplier company, Jet Propulsion Laboratory, California Institute of Technology). The calculated NDSI image was resampled by bilinear interpolation to a spatial resolution of 20 m and classified to produce a binary variable distinguishing between snow-covered sites ($\text{NDSI} \geq 0.4$) and snow-free sites ($\text{NDSI} < 0.4$, Dozier, 1989).

Because the ASTER image was taken late in spring when the snow cover was already heavily reduced, an additional binary variable related to water cover was calculated from it. Pixels representing water-covered sites (either liquid or as snow or ice) tend to produce higher reflectance values in ASTER band 1 than in ASTER band 3 (Wessels et al., 2002). Hence, an image of the ratio of reflectance in ASTER band 1 to reflectance in ASTER band 3 (spatial resolution 15 m) was calculated and resampled by bilinear interpolation to the baseline spatial resolution of 20 m. A threshold of 1.2 was then applied on this image to create a binary variable distinguishing between water-free (< 1.2) and water-covered sites (≥ 1.2).

2.3.4. Air temperature

Daily mean temperatures for June, July, and August were modelled using the methods described by Joly et al. (2003) and the DEM of the study area. Temperature data were obtained from 83 loggers (HOBO H8 Pro Temp/external

logger, with external thermocouple sensor, Onset Computing, Bourne, MA), which were placed throughout the study area and recorded for 3 years at 30 min intervals with an accuracy of 0.1 $^{\circ}\text{C}$.

The variables calculated for this study are based on mean daily temperature values for June, July, and August during 2001 and 2002 and June 2003. Some loggers showed mechanical failure during these months, and therefore, the number of records available to create daily temperature maps varied with a minimum of 25. For the maps grouped per month, the root mean square errors using cross-validation were 0.8 $^{\circ}\text{C}$ for June, 0.5 $^{\circ}\text{C}$ for July and 0.5 $^{\circ}\text{C}$ for August and the mean of the errors or bias 0.03, -0.005 and -0.01 $^{\circ}\text{C}$, respectively.

Monthly mean temperatures, monthly minimum temperatures, and monthly maximum temperatures for June, July, and August were used as variables in the present study. In addition, mean temperature was calculated for the period spanning the 3 months. Since the temperature models did not take into account the effect of snow, the temperature variables for June were corrected using the ASTER image. For pixels that were classified as snow covered, mean and maximum June temperatures were set at 0 $^{\circ}\text{C}$ since temperatures in the snow pack are known to be 0 $^{\circ}\text{C}$ or slightly lower from the beginning of snow melt (Gerland et al., 1999).

2.4. Field sampling

Field sampling was carried out during July and August 2003. To measure the cover of *D. octopetala* in the field, a gradsect sampling method (Gillison & Brewer, 1985) was applied. A gradsect is a transect that is purposely oriented so it corresponds to the environmental gradient which is thought to be most influential in the distribution of the focal species in the study area. Based on what is known about the ecology of *D. octopetala*, this gradient was believed to be related to snow cover. At the time of the field work, data on depth and duration of snow cover for the entire study area was unavailable. Therefore, topographical gradients, which are known to partially determine snow cover (Benson & Sturm, 1993; Liston & Sturm, 1998), were used instead to position the gradsects. Using a digitized map (Norsk Polarinstittutt, 1990), 32 gradsects, varying in length from 160 to 2720 m, were placed throughout the study area (Fig. 1). Moraines, on which vegetation is still in a stage of colonisation (Moreau, 2003), and areas higher than 250 m a.s.l. were not sampled.

Along each gradsect, plots measuring 2 m \times 2 m were positioned at 80 m intervals and corresponding to the centres of 20 m \times 20 m pixels in the DEM. The coordinates of the plots were located in the field using a handheld GPS receiver. Once in place, a plot was overlaid with a regular 20 cm \times 20 cm grid and the presence or absence of *D. octopetala* recorded at the 121 intersection points of the grid. Of the 284 plots, 236 were located at

Brøggerhalvøya, 31 at Blomstrandhalvøya, and 17 at Ossian Sars-fjellet and 79% of all plots were located at an altitude under 100 m a.s.l.

2.5. Model development and validation

The establishment of *D. octopetala* at a site depends on successful sexual reproduction, whereas the amount of vegetative cover at sites where it is found depends on vegetative growth. Since reproduction and growth in *D. octopetala* are known to be steered by different environmental factors, we expected the occurrence of the species and its abundance to depend also on different factors (Welker et al., 1997; Wookey et al., 1995). We therefore applied a two-step approach whereby a model for the occurrence and one for the abundance of *D. octopetala* were developed independently (Fig. 2). We used Generalized Linear Models (GLMs) with the environmental variables as predictors and two response variables calculated from the *D. octopetala* cover data: (1) a binary variable reflecting the presence or absence of the species in the plots and (2) a variable reflecting abundance. The abundance variable was calculated as a transformation of percentage cover (abundance = $\text{Arcsine}\sqrt{p}/100$ expressed in radians, with p designating the cover of *D. octopetala* in percent) in order to produce residuals with constant variance when using GLMs with a Gaussian error distribution (Zar, 1996). For all plots sampled in the field, the values of the environmental variables were extracted from the corresponding pixels in the GIS database. The complete data set was then randomly split into a data set for calibrating the GLMs and a data set

for validating the models' performances. The latter represented 30% of the total data set, following the suggestion by Huberty (1994) to use 25–35% of the total data set for model validation only.

Two different types of GLMs were used to predict the occurrence and abundance of *D. octopetala*:

- (1) The presence/absence model was selected among GLMs with a binomial error distribution and a logit link function with the *D. octopetala* presence/absence data as response variable (calibration data set: $n=200$, validation data set: $n=84$). The probability values predicted by this model were classified into predictions of presence and predictions of absence using the probability threshold that minimized $((1-\text{true positive fraction})^2 + (\text{false positive fraction})^2)^{1/2}$ for the calibration data set. The performance of the model was then summarized in a confusion matrix, cross-tabulating the predicted and the observed presence/absence patterns (Fielding & Bell, 1997).
- (2) The abundance model was selected among GLMs with a Gaussian error distribution and an identity link function, which are the GLMs equivalent to ordinary least squares models. These GLMs had the *D. octopetala* abundance data as response variable, but only included the plots where the species was present (calibration data set: $n=83$, validation set: $n=36$).

We calibrated candidate models that were considered biologically plausible and required eight parameter estimates, to avoid over-fitting of the data (as suggested by

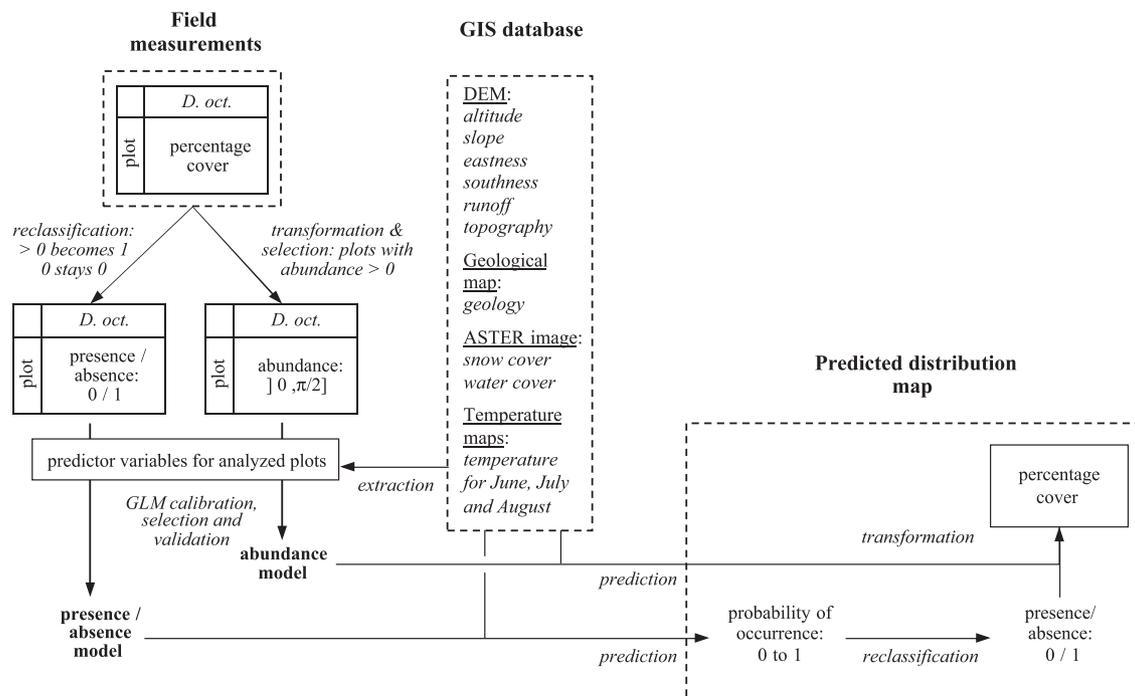


Fig. 2. Flow diagram summarizing the procedures followed to model and predictively map the cover of *D. octopetala* (abbreviated as “*D. oct.*”).

Harrell et al., 1996). Although a quantitative criterion was not set, highly correlated predictor variables, such as the different topographical position variables, were not included simultaneously in the models. Some of the candidate models included second-order polynomials and transformations using the natural logarithm of continuous predictor variables, since non-linear responses to the environmental variables were considered likely. Two-way interaction terms between first-order predictor variables were present in some models. Automated stepwise model simplification, based on minimizing the AIC_C (Hurvich & Tsai, 1989), was used to eliminate non-contributing predictor variables from the candidate models (Venables & Ripley, 2002). The AIC_C is a modified version of Akaike's Information Criterion (AIC, Akaike, 1973) and is preferred over the original AIC when K , the number of parameters estimated in the model, is large relative to the sample size n , i.e., $n/K < \text{about } 40$ (Burnham & Anderson, 2000).

$$AIC_C = AIC + \frac{2K(K+1)}{n-K-1}. \quad (1)$$

Among the resulting models of each type, the GLM with the lowest AIC_C was chosen (Johnson & Omland, 2004). These two models, the presence/absence and the abundance model, were validated and used to predict the distribution of *D. octopetala*.

Three main statistics were used to quantify the predictive performance of the presence/absence model: adjusted d^2 (Guisan et al., 1999), κ (Cohen, 1960), and the area (AUC) under the receiver operating characteristic function (ROC) (Zweig & Campbell, 1993).

The adjusted d^2 is a measure of goodness of fit for models which are fitted using maximum-likelihood estimation. The d^2 quantifies the deviance reduction achieved by a model, just as the r^2 quantifies the variance reduction achieved by a model based on least-squares estimation. The adjusted d^2 is additionally corrected for the sample size n and for K , the number of parameters estimated by the model.

$$\text{adjusted } d^2 = 1 - [(n-1)/(n-K)] \times (1 - d^2). \quad (2)$$

κ is a measure of agreement between observed and predicted values that compensates and corrects for the proportion of agreement that might occur by chance. It is a simple and standardised statistic but depends on the threshold chosen to classify the predicted probability values to presence/absence values (Manel et al., 2001). This is not the case for the AUC, which provides an estimate for the probability that the model correctly ranks a pair consisting of a presence and an absence observation (Deleo, 1993). Finally, the positive predictive power (PPP) and the negative predictive power (NPP) were calculated from the confusion matrix (Fielding & Bell, 1997). The overall predictive performance of the abundance model was evaluated using plots of observed abundance values against predicted abundance values and r^2 .

All statistical analyses were performed using S-Plus 6.1 software (Insightful, 2002) with the library MASS (Venables & Ripley, 2002) enabled and the additional functions developed by Doug Mahoney and Beth Atkinson, for the ROC procedures.

3. Results

3.1. Presence/absence model

The predictor variables in the presence/absence model were related to water cover, temperature, topographical position, aspect, and slope (Table 1). The model predicted a higher probability of *D. octopetala* occurrence at sites with a higher mean temperature in June and exposed towards the south rather than the north. Since a quadratic term was retained for the slope variable, the model fitted a unimodal response curve to this predictor. *D. octopetala* was considered most likely to occur at sites with a topographical slope between 5° and 25° and least likely to occur at sites with a topographical slope steeper than 30° . The occurrence of *D. octopetala* was generally estimated less likely at sites classified as water-covered and more likely to occur at exposed sites.

The model performed well for both the calibration and validation data set (Table 2). The threshold used to classify the predicted probabilities into presence/absence values was set at 0.472, resulting in a κ value of 0.62 using the calibration data set ($n=200$) and 0.46 using the validation data set ($n=84$). For both data sets, the predictions of absence produced by the model were more likely to be correct than the predictions of presence ($NPP > PPP$).

3.2. Abundance model

The predictor variables in the abundance model represented mean August temperature, topographical slope and position, and geology (Table 3). Abundance of *D. octopetala* was predicted to increase with slope and mean August temperature. The effect of topographical exposure on *D. octopetala* abundance is small but clearly positive. Using the geological class termed moraines and alluvial deposits as a reference, an effect of substrate geology

Table 1
Parameter estimates (PE) with their respective standard errors (SE) and the range of the observations used during model calibration ($n=200$) for the predictor variables in the presence/absence model

Variable	PE	SE	Range
Water covered	-0.52	0.24	category
Mean June temperature	0.72	0.29	[0 °C; 4.5 °C]
Topographically exposed (300 m)	1.0	0.2	category
Southness	0.60	0.30	[-1; 1]
Slope	0.36	0.10	[1°; 27°]
Slope ²	-0.012	0.004	

Table 2
Statistical measures of model performance for the presence/absence model

	Adjusted d^2	AUC (SE)	Threshold	κ	PPP	NPP
Calibration ($n=200$)	0.33	0.87 (0.03)	0.472	0.62	0.76	0.82
Validation ($n=84$)		0.81 (0.04)		0.46	0.69	0.77

Adjusted d^2 is given, as are the area under the ROC curve (AUC) with its standard error (SE), Cohen's κ , the positive predictive power (PPP) and the negative predictive power (NPP) for the calibration and the validation data set. The threshold used to classify the predicted probabilities into presence and absence values was determined using the calibration data set.

was only detected for the third class, termed carboniferous dolomites and protozoic marbles, for which a marginally lower abundance was predicted (PE = -0.035, SE = 0.010).

The abundance model explained about half of the variation in the observed abundance of *D. octopetala* ($r^2=0.49$, $n=83$) and one third of the variation in the validation data set ($r^2=0.29$, $n=36$). For the calibration data set, a trend was observed in the relationship of observed abundance values to predicted abundance values: The abundance of *D. octopetala* was generally overestimated by the model for plots where it in fact was low (<10%) and underestimated for plots where it actually was high (>20%) (Fig. 3a). This trend was not as strong in the corresponding plot for the validation data set (Fig. 3b).

4. Discussion

4.1. Predictive accuracy of the model

We compared the distribution map of *D. octopetala* predicted by the model, with a vegetation map covering part of the study area (Fig. 4). This showed that the model gives a good description of the distribution of the species. Elith (2000) considered presence/absence models with an AUC of 0.75 or higher as potentially useful in reserve planning. The AUC of the presented model (0.81) falls well within this range. In a similar study aimed at modelling the distribution of 62 vascular plant species in an Alpine environment, Guisan and Theurillat (2000b) found \hat{e} values ranging from 0.16 to 0.84 for the calibration data set ($n=205$) and from 0 to 0.62 for the validation data set ($n=92$). Compared to these results too, the presence/absence model in our study, with κ values of 0.62 (calibration data set) and 0.47 (validation data set), performs reasonably well. Guisan and Theurillat (2000b) obtained better models for species with clear-cut ecological requirements. In our study area, *D. octopetala* belongs to this group of species and the distribution of other species in the area might thus be more difficult to predict. In the abundance model, a considerable portion of the observed variation remained unaccounted for. This might be caused

by essential ecological gradients not being present in the realized niche model.

4.2. Realized niche model

Nutrient availability, which is known to significantly affect vegetative growth in *D. octopetala*, was not explicitly included as a predictor variable in our study. As an indirect predictor variable, the geological substrate variable, which is based on a geological bedrock map, might not be sufficiently correlated to the nutrient status and other properties of the thin topsoil. This could explain why the abundance model predicts a lower cover of *D. octopetala* on substrates classified as carboniferous dolomites and protozoic marbles, while *D. octopetala* normally thrives on calciferous substrates (Elvebakk, 1982). In this case, the coarse texture of the substrate and consequent lack of soil, rather than its chemical composition and resulting nutrient availability might cause its negative correlation with *D. octopetala* abundance.

The modelled positive effects of summer temperature and exposure towards the south on *D. octopetala* conform to the results of observational and experimental studies on the species (Wada, 1999; Wookey et al., 1995). The same is the case for the preference of *D. octopetala* for exposed sites predicted by both the presence/absence and the abundance model (McGraw, 1985; Rønning, 1965). Only one of the predictor variables derived from the ASTER image was retained in the models. This was the water cover variable, designed to distinguish between dry sites and those covered by snow, ice or liquid water, which was selected in the presence/absence model. The modelled response was expected given the preference of *D. octopetala* for sites with little snow cover during winter (e.g., Elvebakk et al., 1999; Rønning, 1965).

Various indirect environmental gradients, retained as predictor variables, such as topographical position and topographical aspect also account for snow patterns. Strong winds during winter make snow drift extremely common on

Table 3
Parameter estimates (PE) with their respective standard errors (SE) and the range of the observations used during model calibration ($n=83$) for the predictor variables in the abundance model

Variable	PE	SE	Range
Log (mean August temperature+1)	1.0	0.3	[5.0 °C; 6.2 °C]
Log (slope+1)	0.073	0.022	[1°; 27°]
Topographically exposed (100 m)	0.061	0.012	category
Substrate geology:			
Tertiary sandstones and permian chert	0.023	0.026	category
Carboniferous dolomites and protozoic marbles	-0.035	0.010	category
Protozoic mica schist	0.022	0.012	category

The substrate geology variable contained four classes, and therefore, three parameters were estimated in the model using the class termed "moraines and alluvial deposits" as a reference.

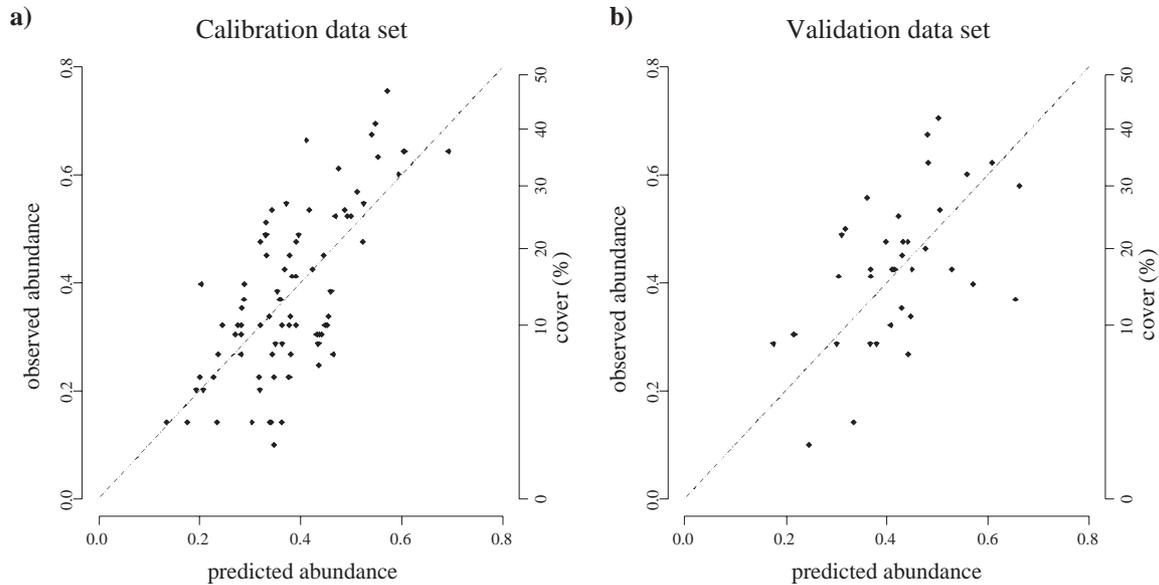


Fig. 3. Observed abundance of *D. octopetala* vs. the abundance as predicted by the abundance model (a) for the calibration data set ($r^2=0.49$, $n=83$) and (b) for the validation data set ($r^2=0.29$, $n=36$). The axes to the right of the plots show the corresponding values of observed abundance, expressed in percentage cover.

Svalbard (Førland et al., 1997). Consequently, exposed sites are expected to have a thinner snow cover of shorter duration (Stow et al., 2004). Sites that are topographically exposed towards the south rather than the north additionally become snow-free earlier because snow melt starts earlier at such sites (Lloyd, 1999). The direct environmental gradient of mean June temperature also partly accounts for snow cover, since sites classified as snow-covered were assigned a value of 0 °C. Furthermore, sites with a higher mean temperature in June can be expected to have been snow-free

earlier, thus creating suitable habitats for *D. octopetala*. Most predictor variables in the presented models therefore affect plant habitat suitability in part through their effect on snow cover.

Snow in the landscape is perhaps the single most important mesoscale variable controlling all biological systems in the Arctic (Walker et al., 1993, 1999). It has a pivotal role controlling direct and resource gradients both during and outside the growing season. The depth of the snow cover affects direct gradients such as winter grazing

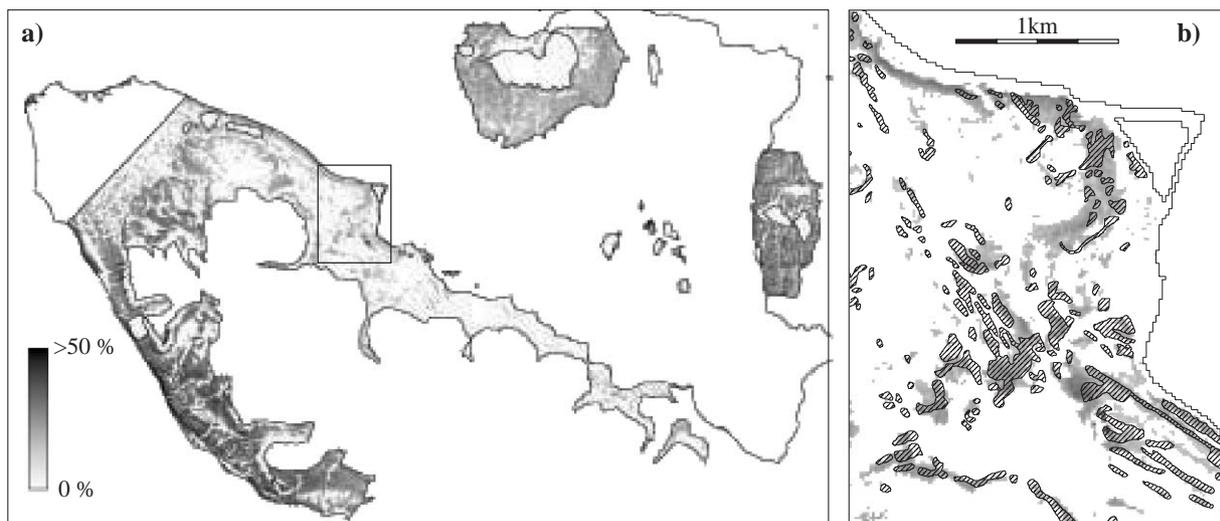


Fig. 4. Predicted percentage cover of *D. octopetala* for (a) the entire study area and (b) the area east of Ny-Ålesund. For the pixels where presence was predicted by the presence/absence model (i.e., predicted probability of occurrence >0.472), the abundance was calculated using the abundance model and back-transformed to a percentage cover scale. For pixels where absence was predicted, the percentage cover was set to 0%. White polygons indicate areas excluded from the study. Diagonally barred polygons indicate areas dominated by *D. octopetala* according to a vegetation map (Brattbakk, 1981).

(Gates et al., 1983), the degree to which plants are protected from abrasion and desiccation by wind (Savile, 1972), the length of the growing season (Bilbrough et al., 2000), and winter temperature (Taras et al., 2002). The spring snow distribution in combination with topography and drainage additionally plays a major role in the availability of water as a resource for plants during the growing season (Liston & Sturm, 1998). This is especially the case in areas such as Svalbard, where more than 75% of the annual precipitation falls as snow or sleet between mid-September and the end of May (Førland et al., 1997). Most of the ecological gradients affected by snow cover are crucial to plant growth in the Arctic but very difficult to map. Hence, in order to create accurate predictive habitat distribution models for Arctic plants, we need to expand our knowledge about the temporal and spatial distribution of snow.

4.3. A need for snow maps

In this study, the only available snow cover data were the variables derived from the single ASTER image taken in late June of 2001, resulting in a useful but relatively crude source of information on patterns of snow distribution and melt. A sequence of remote sensing images, rather than a single picture, could provide more information on these patterns. For modelling on local scales, aerial photography can provide images for snow mapping at a ground resolution of 25 m and less (Blöschl et al., 1991a, 1991b; König & Sturm, 1998). When working on a regional scale, as in our study, high- and moderate-resolution space-borne sensors become a more likely source of data, because they cover large areas thereby reducing the costs to the user. To their disadvantage, however, optical satellite data are heavily affected by clouds and darkness (Slater et al., 1999). In this study, the frequent presence of clouds and fog on the west coast of Spitsbergen, the long polar night, and the rapid snow melt made it impossible to acquire a time series of snow cover images from optical satellite sensors.

An alternative to optical remote sensing of snow is to use Synthetic Aperture Radars (SARs) as they actively use microwaves which penetrate clouds (Hall & Martinec, 1985). Sensors such as SAR and Advanced SAR (ASAR) aboard RADARSAT, the Environment Satellite (ENVISAT), allow for the estimation of snow covered area, and other parameters such as snow water equivalent and snow wetness which have been used to predict water supplies for hydropower stations (e.g., Koskinen et al., 1997) and forecasting floods (e.g., Löw et al., 2002). SAR has excellent properties for detecting wet snow (Nagler & Rott, 2000; Shi & Dozier, 1997), but detection of dry snow is more challenging due to low contrast between bare soil and dry snow (Guneriusen et al., 2001; Rango, 1993). Geometric and radiometric distortion caused by topography may also cause problems, but can be overcome by precise

geocoding and calibration of the data (Malnes & Guneriusen, 2002).

A very promising method for low- and moderate-resolution snow cover mapping is to combine optical and microwave imagery by multitemporal and multi-sensor methods (Tait et al., 2000). Recently, Solberg et al. (2004) have demonstrated the possibility of deriving daily snow cover maps in southern Norway with the use of Moderate Resolution Imaging Spectroradiometer and ASAR data. In the future, the outlined novel snow mapping techniques could be applied to map snow melt in the Arctic across a range of spatial scales, starting ground resolutions as low as 10 m, which is difficult with techniques solely based on optical sensors.

4.4. Incorporating climate change scenarios

A quantitative estimate of the impact of climate change on the distribution of *D. octopetala* in our study area could not be made using the presented models. Previously, equilibrium models for plants have been used to predict species distribution after climate change by manipulating temperature variables in the model prior to predicting habitat suitability (Gottfried et al., 1999; Guisan & Theurillat, 2000a). In the Arctic, however, large-scale alterations in temperature, especially in spring, are likely to affect plant species significantly through their effect on snow cover. If climate warming scenarios are to be incorporated in models of Arctic plant distribution, the impact of temperature variability on the distribution and duration of snow cover will therefore need to be quantified. This could be achieved by integrating physical end-of-winter snow depth models and physical models of temperature-induced differential snowmelt (Marks et al., 1999; Tuteja & Cunnane, 1999) into snow maps. The results would make it possible to simulate the effect of climate change on factors of prime importance for plants in the Arctic landscape. Furthermore, they would allow the incorporation of the impact of winter climate change, both regarding temperature and precipitation, into predictive habitat distribution models. This is essential since winter climate change is likely to be greater than summer climate change in the Arctic (Källen et al., 2001).

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