The importance of snow in species distribution models of arctic vegetation

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Snow cover is characteristic of high-latitude and -altitude ecosystems where snowpack properties regulate many ecological patterns and processes. Nevertheless, snow information is only rarely used as a predictor in species distribution models (SDMs). Methodological difficulties have been limiting both the quality and quantity of available snow information in SDMs.

Here, we test whether incorporating remotely sensed snow information in baseline SDMs (using five climate-topography-soil variables) improves the accuracy of species occurrence and community level predictions. We use vegetation data recorded in 1200 study sites spanning a wide range of environmental conditions characteristic of mountain systems at high-latitudes. The data consist of 273 species from three ecologically different and evolutionarily distant taxonomical groups: vascular plants, mosses, and lichens.

The inclusion of the snow persistence variable significantly improved the predictive performance of the distribution and community level predictions. The improvements were constant, irrespective of the evaluation metric used or the taxonomic group in question. Snow was the most influential predictor for 36% of the species and had, on average, the second highest variable importance scores of all the environmental variables considered. Consequently, models incorporating snow data produced markedly more refined distribution maps than simpler models. Snow information should not be neglected in the construction of species distribution models where ecosystems characterized by seasonal snow cover are concerned.

Snow is one of the most important determinants of ecosystem functions in high-latitude and -altitude regions, where snow dominates the landscape for most of the year (Walker et al. 1993, Callaghan et al. 2011b, Bokhorst et al. 2016). Uneven snow accumulation produces a wide spectrum of habitats, therefore enabling the regional co-occurrence of a large range of ecologically and evolutionarily different species (Billings and Bliss 1959, Billings and Mooney 1968, Carlson et al. 2015): chionophilous (snowdependent) species inhabit the snowbeds, and chionophobous (snowavoiding) occupy the other extreme (Gjaerevoll 1956, Odland and Munkejord 2008). Snowpack properties, such as snow cover duration and thickness, have multiple ways of filtering the species able to survive under certain snow conditions (Table 1). Snow not only alters the surface conditions during winter but also during the growing season by limiting its length and, hence, its thermal sum. Many observational and experimental studies have highlighted the regulative role of snow in multiple biological functions and ecological properties: e.g. vegetative biomass and growth (Choler 2015), vascular plant species richness and assemblages (Odland and Munkejord 2008, Carlson et al. 2015), soil microbial activity and composition (Schimel et al. 2004, Zinger et al. 2009), overwintering survival (Rapacz et al. 2014), root dynamics and mortality

(Templer 2012), and photosynthetic capacity (Saarinen et al. 2016).

Local snow conditions also affect hydrology and biogeochemical processes, such as litter decomposition and carbon sequestration (Hobbie and Chapin 1996, Baptist et al. 2010), availability of nitrogen and phosphorus (Edwards et al. 2007), soil moisture (Johansson et al. 2013), and surface water dynamics and chemistry (Brooks et al. 1998). These phenomena act as mechanisms for how snow affects species growth and survival, and, consequently, species distributions. Recent observations have shown that the Arctic has a pronounced warming trend, particularly during the winter months (Kirtman et al. 2013, Bintanja and Andry 2017). Thus, it is inevitable that continuing warming will change the duration of snow cover with substantial effects on high-latitude ecosystem functions (Bintanja and Andry 2017).

At the landscape level, snow accumulation is highly spatially variable over complex terrains of open tundra as wind redistributes the snow and accumulation, sublimation and melting processes differ from one topographic position to another (Anderton et al. 2004, Litaor et al. 2008). Also, vegetation itself influences the snowpack by capturing the drift snow by its canopy (Liston 2004). Still, most of the tundra

Table 1. Ecophysiological impacts and stress factors of early or late snow melt for individual plants or plant communities.

	Early snowmelt	Late snowmelt	Main references
Overwintering survival	• Extreme frost events • Wind abrasion and desiccation	• Relatively warm winter • Snow moulds (fungi infections)	Rapacz et al. 2014
Productivity	• Long growing season • Spring frost damage	• Limited growing season length	Templer 2012, Bjerke et al. 2015
Reproductive success	• Flower damage by spring frost	• Reproduction only in most favourable years → uncertainty	Billings 1987, Bienau et al. 2014
Nutrient availability	• Cold winter limits nutrient cycles • Freeze/thaw cycle releases nutrients from microbes	• Snowpack captures nutrients • Accelerated nutrient cycles during winter	Edwards et al. 2007, Semenchuk et al. 2015
Water availability	• Earlier melt water supply, late summer drought	• Late summer melt water supply	Ayres et al. 2010, Blankinship et al. 2014

vegetation is low-growing and the strong capturing effect of plants may be limited to forests and the tallest willow thickets. However, as demonstrated in multiple studies, the spatial pattern remains relatively similar from year to year even if the overall snow depth and persistence varies interannually (Anderton et al. 2004, Schirmer et al. 2011). The thickness of insulating snowpack varies along mesotopographical gradients from windblown, almost snow-free ridges to snow accumulation areas in sheltered slopes and depressions (Billings and Bliss 1959, Litaor et al. 2008). Consequently, local soil surface temperature is highly decoupled from air temperature during the snow season (Wahren et al. 2005, Wundram et al. 2010). Therefore, the use of air temperature data is relevant for low-growing vegetation only during the snow-free season, which may constitute a small portion of the year in cold climates.

Considering the importance of snow in winter dominated ecosystems, it is surprising how rarely snow information has been incorporated into species distribution models. One obvious reason is the shortage of snow data: there are major methodological and practical difficulties in measuring snow conditions and persistence across large areas at fine spatial resolutions. This limits both the quality and quantity of available snow information in (macro-)ecological studies. Nonetheless, some authors have included snow as a predictor in species distribution models or in species richness or community models (Table 2). However, the snow information has typically been derived from low quantities of remote

Table 2. Summary of studies using snow as a variable in multivariate distribution models.

Author	Location	Snow variable	Input snow data	Resolution (m)	Response variables	SDM methods
Randin et al. 2006	Alps (Switzerland and Austria)	Number of days with snow cover	Geophysical PREVAH – model with DEM and climate station records	25	54 vascular plant species	GLM, GAM
Randin et al. 2009	Alps (Switzerland)	Snow accumulation index	Geophysical SnowTran-3D – model with DEM and wind data	25	91 vascular plant species	GLM
Guisan and Theurillat 2000	Alps (Switzerland)	Two snow cover indices	Four aerial images from two years	Not mentioned	63 vascular plant species	GLM
Guisan et al. 1998	Alps (Switzerland)	A snow cover index	Two aerial images from March and June	Not mentioned	An alpine sedge species Carex curvula ssp. curvula	GLM
Gottfried et al. 1998	Alps (Austria)	Terrain curvature	DEM	1–100	21 vascular plant species, species community types	CCA
Dirnbock et al. 2003	Alps (Austria)	Snow cover duration	11 SPOT satellite images and topographical and geophysical variables	20	85 vascular plant species	GLM
Dirnbock and Dullinger 2004	Alps (Austria)	Snow cover duration	11 SPOT satellite images and topographical and geophysical variables	20	71 vascular plant species	GLM
Beck et al. 2005	Svalbard (Norway)	Binary snow occurrence	One ASTER satellite image taken on 26th June	20	An arctic dwarf shrub Dryas octopetala	GLM
Fischer 1990	Alps (Switzerland)	Snow cover	Landsat MSS images. The method or number of images not specified	50	63 vegetation types	PCM[1]
Carlson et al. 2015	Alps (France)	Snow duration corrected radiation	26 Landsat images, aerial photograph, and topographical variables	15	Vascular plant species richness and functional diversity	LM

[1]Probabilistic contingency model.

sensing data (Guisan and Theurillat 2000, Dirnbock et al. 2003, Beck et al. 2005) or topographical surrogates of snow accumulation patterns (Gottfried et al. 1998), or is based on geophysical snowpack models (Randin et al. 2006). All the studies referred to here have been conducted in European Alps except one: Beck et al. (2005) modelled the distribution of one arctic dwarf shrub species in Svalbard using snow data derived from one satellite image. Additionally, some studies have used winter precipitation as a proxy of amount of snow at global and continental scales to model distributions of species or vegetation types (Pearson et al. 2013). However, it is controversial how well winter precipitation can be related to the actual snow depth or timing of melt, and the sub-grid variation of snow accumulation is large at coarse scale and the spatial differences are further amplified during the snow melt (Karl et al. 1993, Liston 2004). This may limit the ecological relevance and usability of winter precipitation as a snow-variable especially in areas with rough terrains. As far as we know, we are the first to utilize an over 30-year time-series of snow observations to construct a realistic spatio-temporal snow map for modelling the distribution patterns of a large number of species from three ecologically different taxonomical groups.

Vascular plants are one of the most intensively studied taxonomical group and have been used as study organisms in a large amount of SDM studies through different biomes and scales (Elith and Leathwick 2009, Soininen and Luoto 2014). Mosses and lichens, on the other hand, are far less studied components of vegetation, despite their well-known functional importance in cold ecosystems (Cornelissen et al. 2007, Turetsky et al. 2012). Studies that have modelled distributions of lichens and mosses are rare, but even fewer have modelled these species groups in parallel with vascular plant species and compared the distribution patterns and drivers between the taxa (but see le Roux et al. 2013, Mod et al. 2016).

The ecology and evolutionary strategies vary greatly between these species groups and, therefore, it is expected that the groups respond differently to environmental gradients. In general, lichens and mosses are more tolerant of momentary extreme temperatures and short-term drought, though many of the moss species favor constantly moist conditions (Cornelissen et al. 2007, Turetsky et al. 2012). Both lichens and mosses are capable of rapidly recovering their photosynthetic capacity after unfavorable periods, and lichens may photosynthesize even under a thin snow-pack and in very low ambient temperatures (Bjerke et al. 2013). They are better adapted to cold climates than most vascular plants, and they can grow at low temperatures compared to their thermal optima (Furness and Grime 1982, Glime 2007). Moreover, because lichens and mosses are poikilohydric, they are much less well equipped to face long-term drought and warm conditions than vascular plants (Mateo et al. 2016). The longevity and cold tolerance may give mosses and lichens a competitive advantage in harsh conditions. On the other hand, mosses and lichens are very slow- and low-growing, and therefore vulnerable to shading and litter accumulation by taller vascular plants (Cornelissen et al. 2001).

Here, we examine if the incorporation of fine-scale snow information can significantly improve the accuracy of species distribution models for 273 species from the three main taxonomical groups of arctic vegetation: vascular plants, mosses, and lichens. Specifically, we examined 1) if the predictive accuracy of relatively simple SDMs (based on climate-topography-soil variables) is improved by the addition of remotely sensed snow persistence as a predictor, 2) if the snow information upgrades the capability of stacked SDMs to reconstruct the local community composition, and 3) what is the relative importance of snow persistence in SDMs compared to other predictors. To achieve this, we analyzed a large (1200 study sites) plant dataset collected in a relatively compact, but heterogeneous mountain system in northern Norway. The generality of our results is enhanced by comparing responses across three ecologically differing and evolutionarily distant groups of plants that are rarely examined simultaneously.

Material and methods

Research area

The study area is located in Finnmark, northern Norway (70°0'N, 26°14'E). We conducted extensive vegetation sampling around two mountain massifs: Rastigaisa and Geidnogaisa (Fig. 1). Altitude ranges from 120 to 1064 m a.s.l., generating wide climatic differences corresponding to a latitudinal shift of hundreds of kilometers. According to a high resolution gridded climate dataset based on measurements from 942 climate stations in Scandinavia (30 yr climate period: 1981–2010; more information in Aalto et al. 2017), the whole study area faces sub-zero annual average temperatures (–0.3 to –5.7°C) and an annual precipitation rate between 457 and 669 mm. The majority of the area is acidic Precambrian crystalline rock covered by glacial till, but all the mountain massifs are fringed by a thin layer of easily weathering shales (Hyolithus zone) that provide good sub-stratum for more nutrientdemanding vegetation (Ryvarden 1969).

The area is part of the circumpolar arctic vegetation zone with slight oro-arctic and sub-arctic nuances (Virtanen et al. 2016). The forest line lies at about 250–350 m a.s.l. depending on slope aspect. Thus, only the lowest valley bottoms are covered by mountain birch forests *Betula pubescens* ssp. *chzerepanovii*. The main vegetation type in the area is xeric tundra heath, occupied mostly by dwarf shrubs (e.g. *Betula nana* and *Empetrum hermaphroditum*). Towards the moister and more nutrient rich habitats, vegetation gradually transitions into herb-rich meadow. The study area also contains a wide range of more restricted habitats, from different snowbeds and lichen heaths to arctic wetlands and willow thickets. The highest altitudes are composed of open boulder fields with patchy vegetation. The species pool is a mix of true arctic, alpine, and boreal species, and thus, the area is a transition zone between the main biomes of the northern high-latitudes.

Data collection

The vegetation dataset consists of occurrence records for 460 vascular plant, moss, and lichen taxa observed in
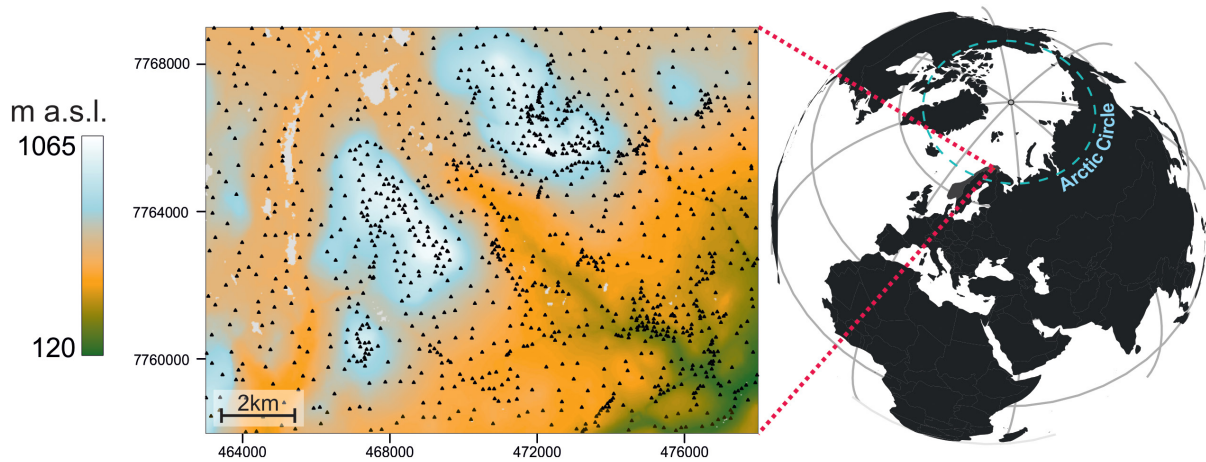
Figure 1. The study area in northern Norway. Rastigaisa is the more northern mountain massif and Geidnogaisa the southern one. The study sites (1200 black triangles) span the whole 165 km² study area. Lakes are represented in gray.

1200 study sites. Each of the study sites is composed of four 1 m × 1 m vegetation plots situated 5 m from the study site center towards each of the four principal compass directions. Most the study sites were positioned in the field in a semi-random manner but, to guarantee the representativeness of the data along the main environmental gradients, a small proportion of the sites were located beforehand using stratified sampling. To reduce spatial autocorrelation in the data, the minimum distance between study sites was 50 m. Vegetation sampling was conducted during the peak growing season for three years (2014–2016). All the species were identified at the species level with a few exceptions that cannot be distinguished reliably at the species level or have unresolved taxonomy (*Alchemilla* spp., *Taraxacum* spp., *Cladonia chlorophaea* section, *Lepraria* spp.). In addition, lichens and mosses inhabiting rock surfaces were excluded from the data, as such species are often hard to distinguish and are not dependent on the resources or physical conditions of the soil, unlike vascular plants. Thus, all the studied species are ground-dwelling and therefore intercomparable. Nomenclature and species identification follows Hämet-Ahti et al. (1998) for vascular plants, Laine et al. (2011), Hallinbäck et al. (2006, 2008), and Hedenäs and Hallinbäck (2014) for mosses, and Stenroos et al. (2011) for lichens.

Landsat data

We downloaded all available clear sky (less than 50% cloud cover) Landsat TM 5, ETM 7 and OLI 8 images covering the whole study area from March to October from 1984 to 2016 (total of 540 scenes) from USGS database (< https:// earthexplorer.usgs.gov/ >). Images were USGS surface reflectance products, which were preprocessed (georeferencing and atmospheric corrections) by USGS (for further information see USGS 2016, 2017). We visually interpreted all the images and selected those that were georeferenced correctly and cloudless over the whole study area. As we are here only interested in snow melt dates, the images from autumn that had new snow fall cover were also excluded from the analysis. We focused only on the end of the snow

season as the onset in autumn is more uniform through the landscape, and the spatial heterogeneity evolve during the winter and spring months (Liston 2004). Additionally, the growing of plants has already ended at the time of the first snow (Garonna et al. 2014), indicating less influence for the tundra plants compared to the timing of the beginning of the growing season. The total number of suitable images was 124.

Snow persistence map

We followed approximately the same procedure as Macander et al. (2015) to construct a snow persistence map from multi-temporal Landsat imagery. We utilized normalized difference snow index (NDSI) to transform the multispectral reflectance information into binary snow maps (Hall et al. 1995, Macander et al. 2015). NDSI is a widely used spectral index in snow-related RS studies and is based on the relative difference in reflectance between green and shortwave infrared (SWIR) spectral bands:

$$NDSI = (Green - SWIR)/(Green + SWIR) \qquad (1)$$

Each pixel in an individual image was interpreted as snow if the NDSI value was over 0.4 (Macander et al. 2015). The water bodies were later masked from the final snow persistence map. The snow persistence map was constructed using generalized linear models (GLM) for binary data. Every pixel had two strings of information that were passed as inputs for pixel-based GLMs: 1) a string of binary scores of snow occurrence (one score from each of the 124 images), and 2) a string of the corresponding day-of-year values (DOY). In the pixel-based GLMs, the binary snow scores were treated as a dependent variable and the DOYs as the predictor. After the model was fitted, it was used to predict the probability of snow occurrence for every possible DOY value from day 1 (January 1st) to day 273 (September 30th). We estimated the average snowmelt date to be the DOY in which the probability breaks the 0.5 probability threshold. All the image processing and statistics were performed in statistical software R (R Core Team) with Raster package (Hijmans 2016).

Exploring the snow variable

To test whether the snow persistence pattern is spatially consistent from year to year, we calculated true skill statistics (TSS; Allouche et al. 2006) for each pair of the individual binary snow images with less than two percentage points difference in snow cover proportion. The images from the extreme ends of the snow proportion range (snow cover < 5% or > 95%) were excluded from the analysis.

Environmental variables

In addition to the snow persistence variable (hereafter, SNOW when concerning the predictor), we selected five other commonly used environmental predictors to represent macro-climate, soil quality, and topographical position: growing degree days (GDD), topographic wetness index (TWI), potential incoming radiation (RAD), soil edaphic conditions (EDAP), and surface deposit quality (SOILQ). GDD sums the daily mean temperature of the days when the mean temperature exceeds the selected temperature threshold, in this case 3°C. GDD is modelled with generalized additive models (GAM) for the study area using climate information from 942 climate stations in Scandinavia (Norway, Finland and Sweden; Aalto et al. 2017). TWI and RAD were derived from a 10 m resolution digital elevation model (DEM) [data portal of Norwegian Mapping Authority (<http://data.kartverket.no/download/>)]. SAGA wetness index (hereafter termed TWI) algorithm was used to estimate soil moisture conditions (Böhner and Selige 2006). The DEM was first preprocessed by filling sinks (Wang and Liu 2006) and then used to calculate the specific catchment area and slope, as required by the TWI algorithm. SAGA wetness index was chosen over the traditional topographic wetness index (Beven and Kirkby 1979) as it mimics water flow patterns more realistically in flat areas by assuming rather homogenous hydrologic conditions in areas with very small elevational differences (Böhner and Selige 2006). The potential annual direct solar radiation was calculated $(MJ/cm^{-2}/yr^{-1})$ by using the equations of McCune and Keon assuming clear sky conditions (McCune and Keon 2002). SOILQ is a six-class classification of surface geology (peat, fluvial sediments, moraine, bolder field, and bare rock) based on field surveys and visual interpretation of aerial and satellite images (resolution 0.5–1.4 m). EDAP is an index determined as the downhill Euclidean distance to the shale belt (the only base-rich rock type in the area) scaled from 1 to 100. Regions located on the shale belt were valued at 100 and contrarily, areas uphill from shale belt or outside the area where the shale belt drains were set as zero. The geological data were downloaded from the bedrock geology database maintained by geological survey of Norway (<http://geo.ngu.no/kart/berggrunn/>).

Species distribution models

Only species with at least 8 presence sites were included in the analyses: 273 species in total (132 vascular plants, 71 mosses, and 70 lichens). The binary distributions of individual species were modelled using four modelling methods (generalized linear model=GLM, generalized additive models=GAM, generalized boosted method=GBM, random forest=RF). The GLMs were fitted without interactions but including quadratic terms. The GAMs were fitted without interaction and the smoothing factor was set as four. The GBMs were fitted using out-of-bag estimates of model improvement and the main parameters were set as follows: n.trees=1000, interaction depth=4, shrinkage=0.001, bag fraction=0.75. The RFs were fitted with 500 trees and a minimum node size of 5. SDMs were implemented with 'biomod2' R package (Thuiller et al. 2009).

To test if the inclusion of the SNOW variable improved the fit of the SDMs, we followed the methodology of Zimmermann et al. (2009) and le Roux et al. (2013), first modelling each species occurrence as a function of climate-topography-soil variables, and a randomly shuffled SNOW variable (differing from the references above).

$$\text{Base model} = GDD + RAD + TWI + SOILQ + EDAP + SNOW_{shuffled} \qquad (2)$$

Next, we incorporated the original SNOW variable in the model

$$\text{Snow model} = GDD + RAD + TWI + SOILQ + EDAP + SNOW_{original} \qquad (3)$$

By randomly permuting SNOW in the base model we ensured that the relationships between SNOW and response variables and other predictors were broken, but that both base and snow models still had a similar model structure and number of parameters.

To test the predictive accuracy of SDMs for individual species, we randomly split the data into calibration data (70% of the data) and evaluation data (30%): the former was used to fit the models and then to predict occurrence values to the latter. This procedure was repeated ten times for each species. During each cross-validation round, area under curve (ROC) and threshold-maximized true skill statistics (TSS) were calculated to evaluate predictive accuracy.

We used non-random ten-fold cross-validation for community assemblage analysis to ensure that each of the sites were predicted once per species to construct the whole community assemblage predictions. First, the data were randomly split into 10 segments. Then, data from nine segments were used to calibrate the models, which were then used to predict the occurrences of the species in the withheld data, with the procedure repeated ten times until each data segment had been withheld once. For each species and for each site, we used the median of projected probabilities of occurrence from four modelling methods. Simply stacking the binary predictions usually overestimates the number of species present at a certain site and thus SESAM framework was established with functions of ecospat library (Broennimann et al. 2016) to construct the final predicted species assemblages (Guisan and Rahbek 2011). The SESAM framework works as follows: in each study site, the projected probabilities of all the species occurrence models were summed up and this number was used as the maximum

species count of the site. The species were ordered by the projected probability values and the first n-number (the n determined in the prior step by summing the probabilities) of species were selected to be present. The species assemblages were produced using both the base and snow models and were compared with the observed species assemblages using Sørensen and Jaccard similarity indices. The goodness of community predictions was also evaluated by comparing the observed species richness and stacked species distribution models (SSDM; constructed with SESAM). We bootstrapped (random selection with replacement) the data 1000 times, and within each permutation two linear models were fitted: we treated the observed species richness as the response variable and SSDM species richness estimates from 1) the base model, or 2) the snow model as the predictor. Intercept, slope, and R^2 were recorded for each permutation (Mod et al. 2015). We used Wilcoxon's paired rank test to test the statistical significance of improvement in predictive accuracy for community and species level predictions between the base and snow models. We also tested whether the inclusion of SNOW into the models improved the predictions for species with different snow persistence optimum. The species specific optimum was calculated as the median SNOW value of the presences of the species.

The range of the optima (134–201) was divided into quartiles and the statistical significance of the AUC and TSS improvements were tested as above for the species falling into the first (early melting), the last (late melting) or into the two quartiles in the middle (intermediate melting).

To examine the response shapes of species-environment relationships and the relative importance of predictor variables in snow models, we utilized data from all 1200 study sites. For each species, the individual importance of all predictors was assessed in biomod2. The randomization procedure uses Pearson correlation between the standard predictions and predictions where a given predictor has been randomly permutated (Breiman 2001). At first the model is fitted with the original data, then model predictions are formed with the same original dataset and a dataset where one of the predictors is shuffled. Finally, the variable importance score is calculated as:

Variable importance
$$= 1 - \mathrm{corr}\,(\mathrm{Prediction_{original}},\,\mathrm{Prediction_{shuffled}}) \quad (4)$$

Thus, the results settle between 0 and 1: the higher the value, the more influence the shuffled variable has on the model. Variable importance calculations were repeated
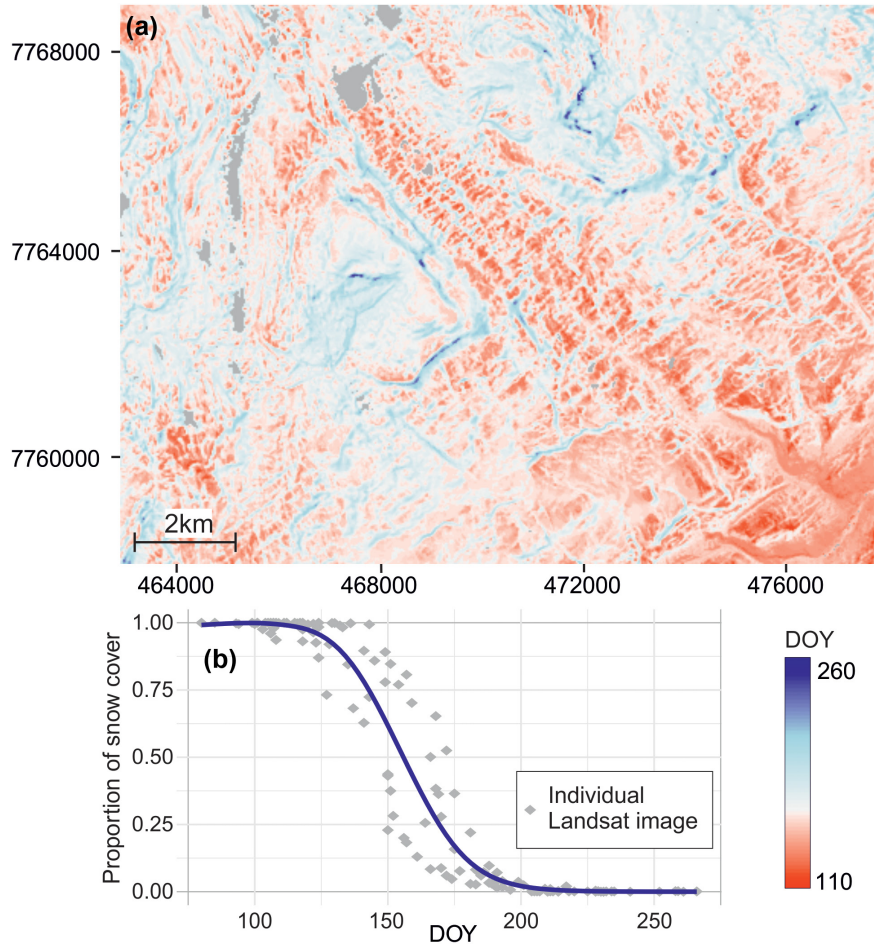

Figure 2. a) The remotely sensed snow persistence map (SNOW) reveals the snow melting day (DOY = day of year) calculated individually for each pixel. Lakes are represented in gray. The map projection is WGS84 UTM35N. b) The proportion of snow cover in the study area plotted against the imaging day of 124 Landsat images. The trend line is based on generalized additive model.
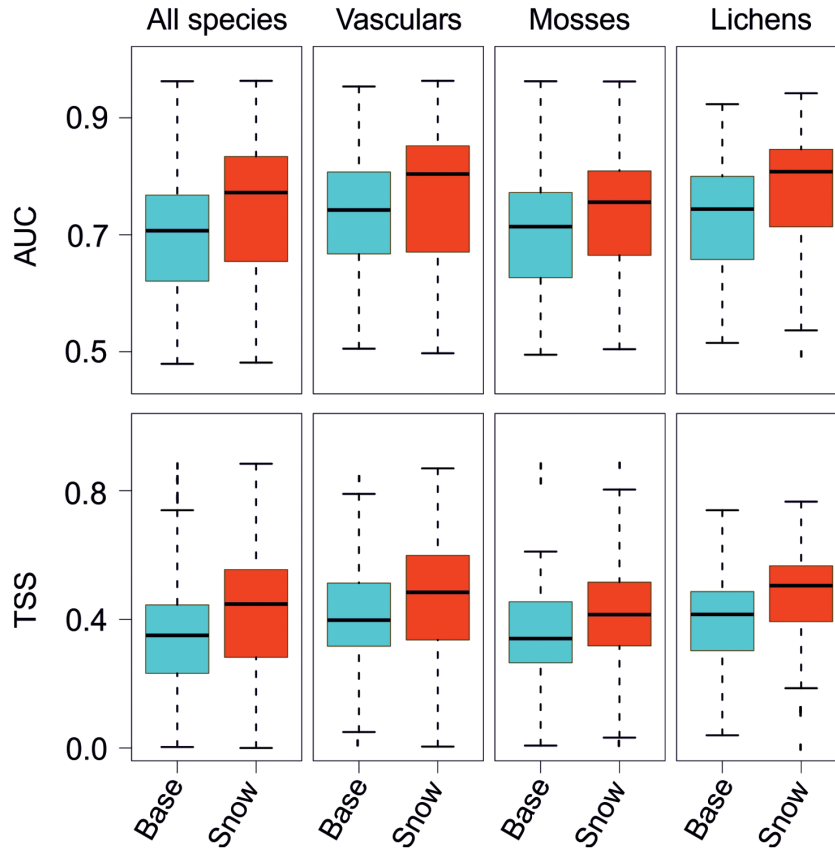
Figure 3. The evaluation metrics (AUC = area under curve; TSS = true skill statistics) for the predictive performance of SDMs for individual species (means of four modelling methods and ten cross-validation rounds). The improvement of snow models compared to base models was highly significant for all species groups and for both evaluation metrics (two-tailed Wilcoxon signed rank test, $p < 0.001$).

10 times for each species with each of the modelling methods and separately for all predictors. Because variable importance is solely based on predicted values, it is suitable for all modelling methods and is fully comparable between them (Thuiller et al. 2009).

Results

The average snow melting date of our study area is 7th June (DOY = 158) (Fig. 2a), ranging from mid-April (DOY = 107) to late September (DOY = 261). The main snow melting season lasts over two months (Fig. 2b). The average TSS-value between two individual binary snow maps from different years with less than two percentage point snow cover proportion difference was 0.62. SNOW variable has low collinearity with all the other predictors ($r_s < |0.38|$).

Snow models provided a better fit than base models based on climate-topography-soil variables only. The mean predictive performance (measured by the TSS) of four modelling methods and 10 cross-validation rounds for 273 species was 0.416 ± 0.012 (mean $\pm$ SE) when we included SNOW, whereas mean TSS of the base model was 0.344 ± 0.010 (two-tailed Wilcoxon signed rank test, V = 3404, $p < 0.001$) (Fig. 3; Supplementary material Appendix 1 Table A1). This improvement was also true when we evaluated predictive performance by AUC (snow model: 0.741 ± 0.007; base

model: 0.697 ± 0.007; V = 3112.5, $p < 0.001$). The significant improvement was consistent for all modelling methods and for vascular plants, mosses, and lichens grouped separately, yet SDMs of lichens showed the most pronounced advantage from SNOW. The statistically highly significant ($p < 0.001$) improvement (both AUC and TSS) was also consistent for species with early (47 species), late (16) or intermediate snow persistence optimum (210) (Supplementary material Appendix 1 Fig. A1).

Additionally, snow information improved the capability of SDMs to reconstruct species community compositions and species richness (Supplementary material Appendix 1 Table A2–A3, Fig. A2–A4). Both Sørensen similarity (average for 1200 sites: base model, 0.514; snow model, 0.566) and Jaccard indices (0.370; 0.418) between the predicted and observed site-scale species assemblages increased significantly with the incorporation of SNOW into the models ($p < 0.001$). The effect was consistent and highly significant for all species groups and for whole communities. SSDMs overpredicted the richness in sites with low observed species richness, but underestimated it where diversity was high. The bias was significantly lower in snow model predictions compared to base models measured by intercept, slope, and R^2 of bootstrapped linear models: slope and R^2 converged toward perfect fit [= 1] and the intercept decreased towards 0 ($p < 0.001$ for all taxonomical groups)
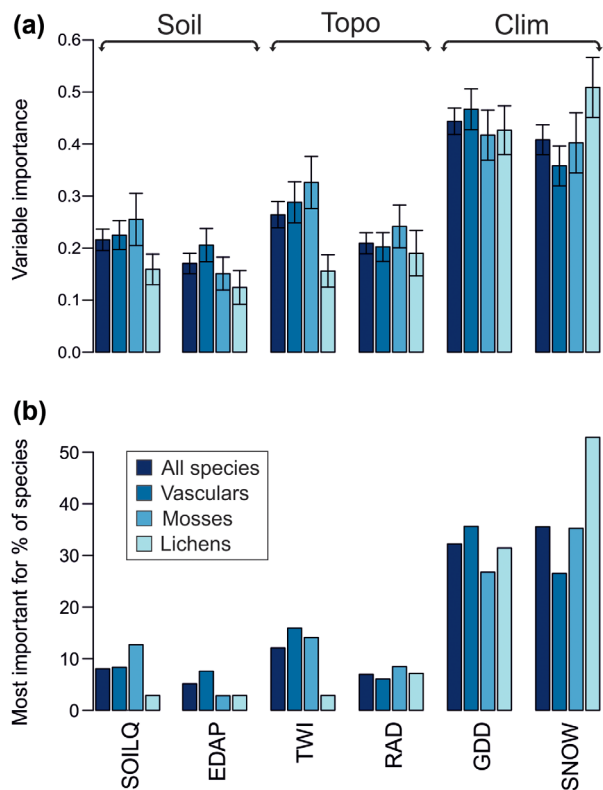
Figure 4. a) The species specific variable importance scores averaged by species groups for each of the predictors. The whiskers represent the 95% confidence intervals of mean from t-test. b) The percentage of species with the specific predictor as the most important predictor. Predictor abbreviations: SOILQ = soil quality; EDAP = soil edaphic conditions; TWI = topographic wetness index; RAD; potential incoming radiation; GDD = growing degree days; SNOW = snow cover duration. Soil, Topo, and Clim indicate the individual predictor comprising the soil, topographic or climatic related factors.

SNOW was the most important predictor for 97 species (36%), followed by GDD for 88 species, and TWI for 33 species (Fig. 4b; Supplementary material Appendix 1 Table A4). On average, SNOW and GDD were the most influential variables well ahead of other predictors, a pattern repeated among all species groups (Fig. 4a). Other predictor variables showed relatively small differences in variable importance scores, except TWI that had a distinct influence on mosses and some vascular plant species especially.

Examination of the response shapes (from GAMs) demonstrated that 16% of the species showed a negative distributional response towards higher snow persistence, 47% had a unimodal response shape, and 7% responded positively. Moreover, 30% of the species did not show any clear trends along the snow persistence gradient. SNOW was an important predictor for species with various snow regime preferences (Supplementary material Appendix 1 Table A5): Chionophilous as well as chionophobous species had strong SNOW responses (Fig. 5). *Saxifraga rivularis*, a small forb (chionophile), and *Flavocetraria cucullata*, a fruticose lichen (chionophobe), showed dissimilar snow responses. Additionally, snow models produced

markedly more refined distribution maps than the base models (Fig. 6).

Discussion

Here, we documented extreme variation in snow persistence over small distances across our study area. This local abiotic heterogeneity clearly affects the fine scale distribution patterns of individual vascular plant, lichen, and moss species. Snow duration also has low collinearity with all the other predictors. Thus, it has its own environmental dimension and exhibits an independent explanatory power that other variables cannot replace.

Our results highlight snow as a key driver of species occurrence patterns in arctic landscapes. Snow does not just improve the predictions of distribution patterns of individual species but enables us to reconstruct the species community assemblages more precisely. The results are in agreement with studies that have observed the strong regulative role of snow conditions on vegetation properties in gradient studies (Heegaard 2002, Odland and Munkejord 2008, Schöb et al. 2009) or in snow manipulation experiments (Wipf and Rixen 2010, Ernakovich et al. 2014). However, in previous species distribution or richness modelling studies, the importance of snow information has been inconsistent. Some authors report snow as a moderately important variable (Guisan and Theurillat 2000, Beck et al. 2005, Carlson et al. 2015) but in some studies snow has not been deemed as influential (Dirnbock et al. 2003, Randin et al. 2009). It is questionable how well the whole snow persistence gradient, from windblown ridges to extreme snowbeds, has been represented in previous studies, and how realistically the various methods to construct snow variables have been able to represent true snow accumulation patterns. Almost all the previous studies have been conducted in the European Alps and, therefore, the geographical coverage of these studies is rather limited. It remains to be answered whether there are differences in the importance of snow between arctic and alpine areas. However, snow manipulation studies have shown the strong regulative role of snow duration on vegetation in many different ecosystems (Wipf and Rixen 2010, Ernakovich et al. 2014), which gives us confidence to state that our methodology and findings are generalizable to other arctic and alpine areas.

Randin et al. (2009) found that the importance of snow varies strongly between species. This pattern was obvious in our study as well, but we also showed that the influence of snow can be very high for species living under very different snow conditions and for species with dissimilar ecological and evolutionary strategies (Fig. 6). These observations agree with Carlson et al. (2015) who modelled species richness of different functional plant groups along a snow persistence gradient and noted clear distributional differences between the groups. The snow response is strong not just for chionophilous snowbed species (Galen and Stanton 1995, Heegaard 2002, Schöb et al. 2009), but also for species with intermediate snow optimum and for species that strictly avoid habitats with long lasting snow cover, e.g. lichens and boreal herbs. We observed high importance of snow for both lichens and mosses. In general, moss species
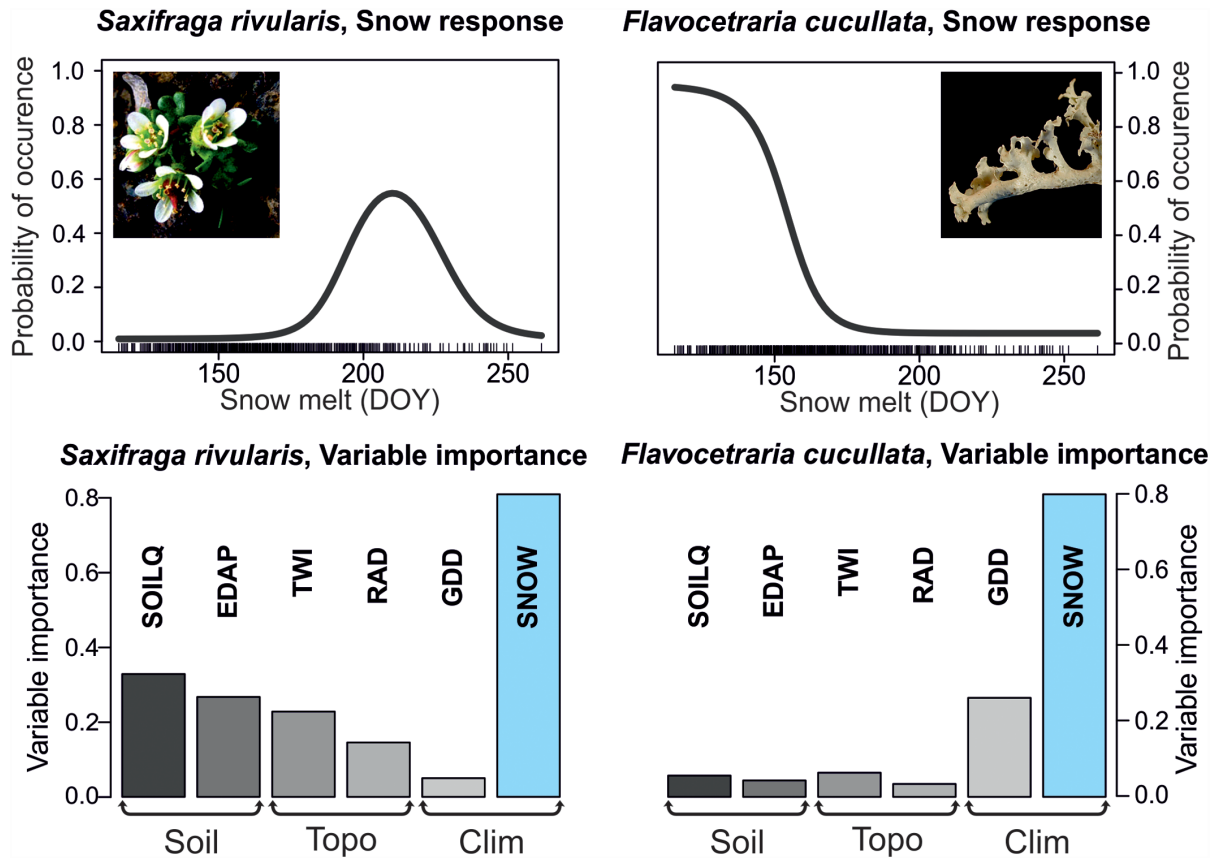
Figure 5. *Saxifraga rivularis*, a small forb, and *Flavocetraria cucullata*, a fruticose lichen, have contrary snow regime preferences but, for both, the influence of SNOW overcame the effect of other variables. The response curves are from generalized additive models. DOY = day of year. The variable importance scores are mean values from all four modelling methods. For an explanation for predictor abbreviations, see Fig. 4.

were more restricted to moist, late melting sites, whereas a majority of the lichens occurred only in early melting habitats that face extremely harsh winter conditions. Our results indicate heterogeneous snow patterns as one of the key reasons for high regional cryptogam diversity in cold climates (Bruun et al. 2006, Mateo et al. 2016).

Many species have evolutionarily adapted to certain length of growing season or to tolerate certain amount of winter stress (Gjaerevoll 1956, Billings and Mooney 1968, Heegaard 2002), but there are many possible, direct and indirect, pathways how snow can affect the species distributions, and this study cannot explicitly weight the relative importance of these factors. Partly, some of the species distribution responses to snow duration can be results of biotic interactions. Although majority of lichens and some moss species are capable to survive in very harsh winter conditions of windblown habitats (Nash and Olafsen 1995, Schlensog et al. 2003), these species are possibly restricted to these extreme habitats by competition by vascular plants in more favorable microclimates (Cornelissen et al. 2001, Lang et al. 2012). Severe shading and litter accumulation may exclude these low- and slowgrowing species from many habitats (Cornelissen et al. 2001). Still, somewhat surprisingly, the greatest improvement in predictive accuracy of SDMs when snow was incorporated in the models, was

among lichens, what promotes the idea of large differences in biotic stress along the snow gradient.

According to global satellite time series, the area of annual snow cover has decreased since the 1970's in the northern hemisphere, indicating the high sensitivity of snow cover to climate change (Liston and Hiemstra 2011, Chen et al. 2016). Global climate models predict that warming will be most pronounced in northern high-latitudes and during the snow season (Hartmann et al. 2013, Bintanja and Andry 2017). However, downscaling global temperature projections to local scales is troublesome and there are even more uncertainties with precipitation predictions (Callaghan et al. 2011a, Trenberth 2011). Thus, it is evident that the evolution of snow cover duration is rather challenging to forecast. Various snow regimes cause local ground surface temperatures decoupled from regional climates (Zhang 2005, Wundram et al. 2010). Therefore, surface and soil conditions may not necessarily respond linearly to regional warming trends with responses varying greatly between different snow accumulation areas. Consequently, snow may act as a buffer for climatic warming and create local microrefugia for arctic species, or, in contrast, have unexpected responses and tipping points where a certain amount of warming has cascading and accelerating impacts on tundra biota mediated by snow (Groffman et al. 2001, Buma et al. 2016).
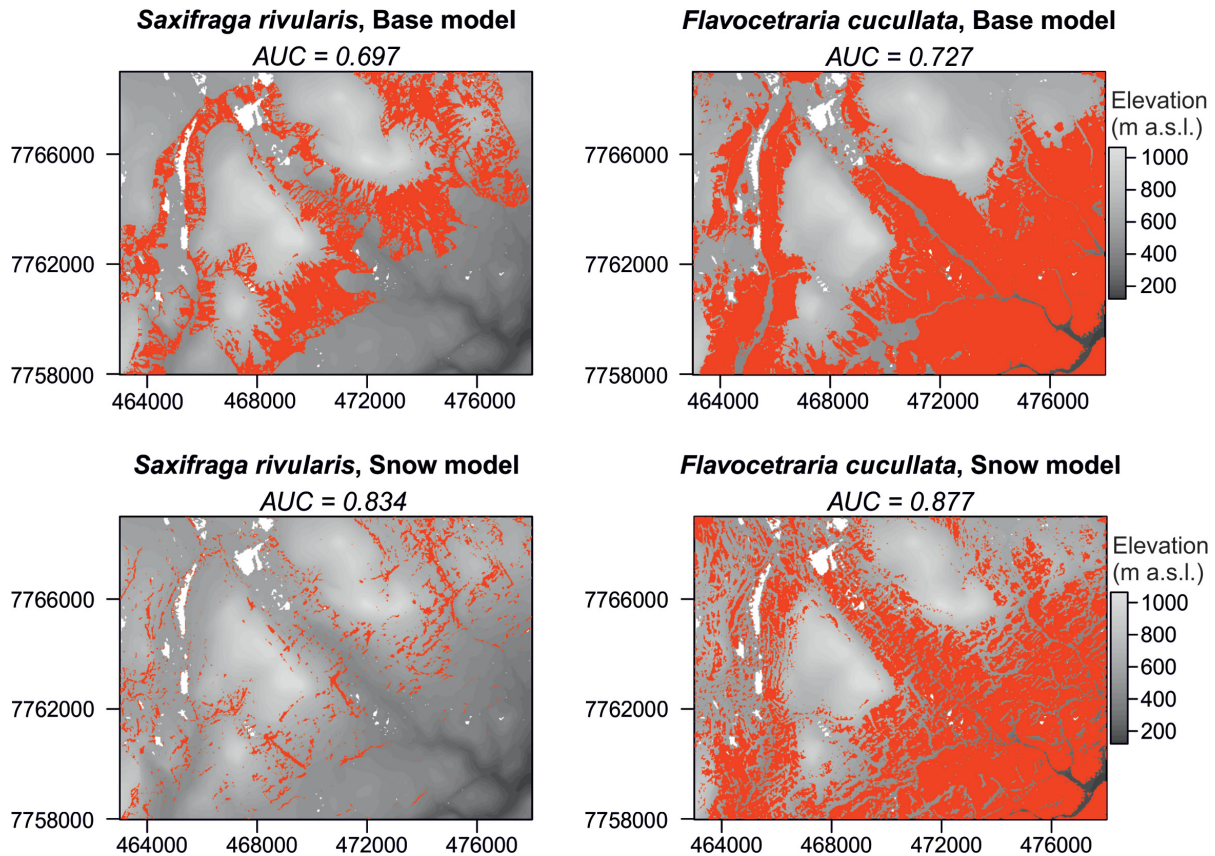
Figure 6. The projected distributions (represented in red) of the base and snow models for two example species: *Saxifraga rivularis* and *Flavocetraria cucullata*. Lakes are represented in white with elevation shown in the background. AUC (area under curve) is an evaluation metric for model predictive performance. A value of 1 represents a perfect accuracy, and 0.5 no better than random.

We are entering the era of efficient mass processing of high-resolution satellite images over large geographical domains and timeframes (Hansen et al. 2013). We are entering an era of efficient mass processing of high-resolution satellite images over large geographical domains and long timeframes (Hansen et al. 2013). We consider that ecologists and biogeographers would greatly benefit from remotely sensed snow variables in all biomes where snow is present. This is especially true in Arctic or mountain tundra, but recent reviews also highlight the importance of winter and snow in temperate and boreal biomes (Kreyling 2010, Williams et al. 2015). Coarse-grain snow data are already available from several decades, but the next generation of vegetation models has an urgent need for snow data at more ecologically relevant scales. One remaining deficiency that obstructs the development of the automated and global snow products, is the poor capability of the cloud detection algorithms to separate the spectral signals between snow and clouds. Many Artic or alpine areas are rather cloudy, and thus the inaccurate snow detection still restricts the quality and quantity of available snow data.

In conclusion, this study demonstrates that the explicit incorporation of snow persistence information improves the accuracy of species distribution and community predictions in high-latitude regions. Based on our results, we recommend the use of snow information in SDMs when modelling the vegetation characteristics of cold climate ecosystems. The high importance of snow is consistent for all studied species groups: vascular plants, mosses, and lichens, although the snow ecology and preferences varied between species. All in all, our findings support snow as an important link between the atmosphere and biosphere. The strong two-way interaction between snow and vegetation influences the albedo and carbon cycling, and therefore the arctic biome - global climate feedback system.

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Supplementary material (Appendix ECOG-03348 at < www.ecography.org/appendix/ecog-03348 >). Appendix 1.