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Nature Research
2018-10-22

Niittynen, P, Heikkinen, R K & Luoto, M 2018, 'Snow cover is a neglected driver of Arctic biodiversity loss', Nature Climate Change, vol. 8, no. 11, pp. 997-1001. https://doi.org/10.1038/s41558-018-0311-x

http://hdl.handle.net/10138/322024
10.1038/s41558-018-0311-x

acceptedVersion

Snow cover is a neglected driver of Arctic biodiversity loss

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Snow has far-reaching effects on ecosystem processes and biodiversity in high-latitude ecosystems, but have been poorly considered in climate change impact models[1,2]. Here, to forecast future trends in species occurrences and richness, we fitted species-environment models with temperature data from three climate scenarios and simulated up to a 40% decrease in snow cover duration (SCD)[3]. We used plot scale data on 273 vascular plant, moss and lichen species in 1200 study sites spanning a wide range of environmental conditions typical for mountainous Arctic landscapes (within 165 km^2). Based on the models, a rise in temperature increased overall species richness and caused only one species to lose all suitable habitat. In contrast, a shorter SCD tempered the effect of increasing temperature on species richness and led to accelerated rates of species' local extinctions after a tipping point at 20-30% SCD decrease. All three species groups showed similar extinction rates but contrasting species richness responses. Our simulations indicate that future biodiversity patterns in Arctic regions are highly dependent on the evolution of snow conditions. Climate impact models that ignore the effects of snow cover change may provide biased biodiversity projections, with potentially erratic implications for Arctic nature conservation planning.

On-going and projected climate change is most forceful in high latitudes, causing the Arctic to warm up at twice the global rate[2,4]. Research on Arctic climate change impacts has mostly focused on temperature changes alone, describing the climate change induced turnover of species and the associated ecosystem impacts, such as changes in land-surface albedo and soil carbon balance[5,6]. However, as the climate change in the Arctic is most prominent for winter months[4], these regions may face important alterations in snow conditions including a 10-40% decrease in snow cover duration (SCD) by 2050[2,3]. Recent snow cover dynamics have already led to major changes in Arctic ecosystems[2,3,7], and further alterations in snow cover may promote changes in vegetation with substantial feedbacks on global climate[5,7]. However, the uncertainties included in the global

climate models lead to high spatial heterogeneity in the projected trends for precipitation and snow[2,7,8]. Furthermore, topographical heterogeneity causes strong local decoupling of SCD from regional climate[9,10] suggesting that snow responses to climate warming may diverge notably in rugged terrain.

For biotic communities, snow is one of the most important controls on growing conditions[9] and Arctic and alpine plant species are strongly affected by snow cover[11,12]. Snow accumulates unevenly in topographically complex landscapes, resulting in heterogeneous snow cover duration patterns[10]. This enables the regional co-occurrence of a wide range of species with different ecological requirements[11]. Despite the fundamental importance of snow, the consideration of the impacts of snow cover change is surprisingly lacking in climate impact models of tundra vegetation and is a major research gap acknowledged by the Arctic Monitoring and Assessment Programme[2]. By ignoring the changes in snow cover alongside temperature, most species-climate impact models dismiss an obvious mechanistic pathway of how climate change will alter Arctic and alpine ecosystems[1,13,14].

Here, in order to improve the understanding of the sensitivity of Arctic ecosystems to both snow cover and temperature changes, we utilized fine-scale observational information of snow cover dynamics linked with summer temperature data and the plot-scale occurrences of 273 vascular plant, moss, and lichen species in a comprehensively studied landscape (165 km^2; 1200 study sites; Fig. 1). We examined the role of snow on biodiversity change under a warming climate by modelling the responsiveness and vulnerability of the study species to the separate and joint changes in temperature and snow cover duration.

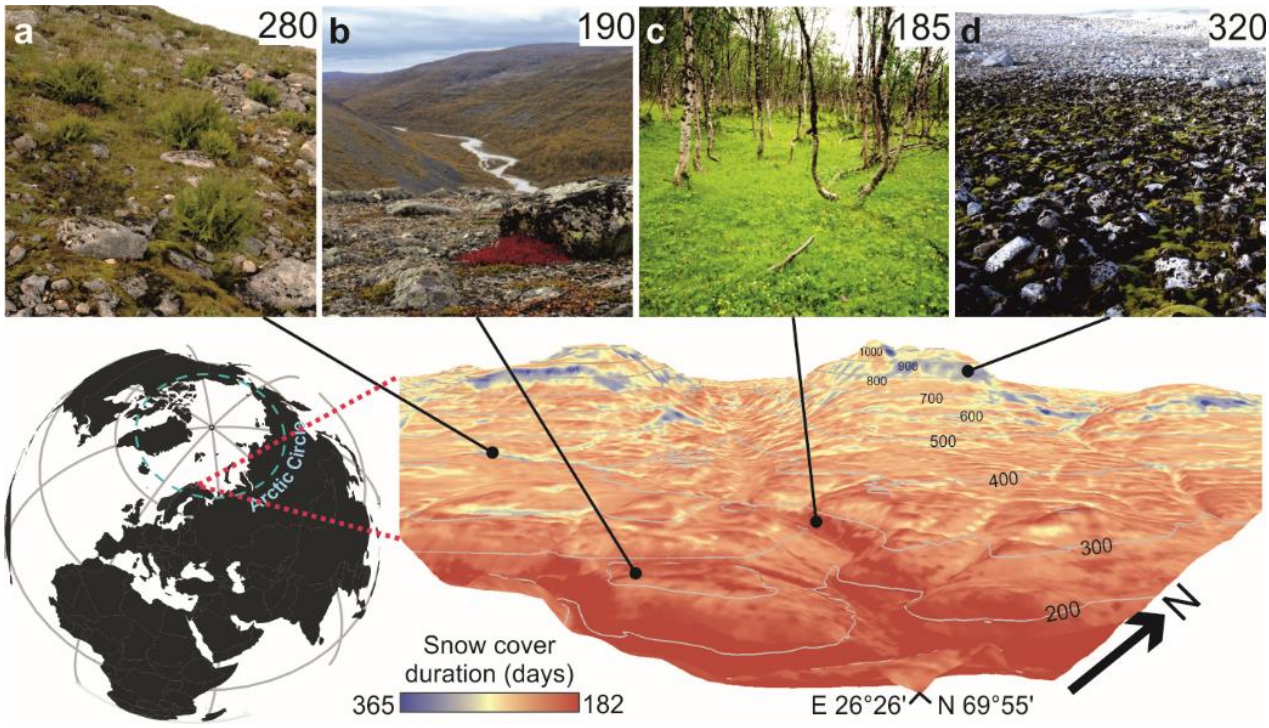

Figure 1. The study area and example habitats along the snow cover duration gradient. The study area in Northern Norway contains large elevational and snow cover duration gradients providing a wide spectrum of different habitats from early melting sub-arctic birch forests (c) and wind-blown lichens heaths (b) to forb-rich meadows (a) and moss-dominated snowbeds (d). Numbers in photographs indicate the length of snow cover duration in current climate for each of the habitats.

We mapped SCD and modelled the distributions of the 273 studied species at a 30-m spatial resolution sufficient to capture the patchy nature of Arctic snow cover and vegetation patterns in our study area (Note S1). A spatially continuous and temporally comprehensive snow cover duration map was constructed based on in-depth analysis of 135 fine-scale satellite images (Landsat TM5, ETM7, and OLI8) spanning over 33 years[12]. To determine the key species-environment relationships, we used species distribution models (SDM) including the current temperature (baseline climate of 1981-2010) and snow conditions, while also controlling for the effects of five other environmental predictors known to be important for plants[15], namely potential incoming radiation, topographic wetness index, slope angle, surface soil quality, and soil edaphic conditions. Using the SDMs calibrated for present-day relationships, we projected the species distributions for the year 2050 by developing four temperature projections (no change, and forced by Representative Concentration Pathway (RCP) scenarios 2.6, 4.5, and 8.5), nine SCD scenarios (no change and eight descending steps from 5% down

to 40% decrease in SCD, matching the range of recent snow cover projections[3]), and all possible combinations between these two groups of scenarios resulting in a total of 36 combinations. The temperatures were projected for period of 2040-2069 and averaged over 23 CMIP5 climate simulations[16]. Each species was modelled separately but as a final step we stacked the single-species predictions[17] to examine how changing SCD and temperature affect overall species richness.

The species distribution models showed good average model fit (AUC = 0.873; TSS = 0.645) and cross-validated predictive performance (AUC = 0.756; TSS = 0.450) across the 273 studied species and nine modelling methods. Separate impacts of decreasing SCD (Fig. 2, column at the far left) and, in particular, increasing temperature (Fig. 2, upper row) both led to a higher average total species richness. However, with respect to projected species extinctions (i.e. total loss of suitable SCD-temperature space), notable differences emerged. Projections based on temperature increase alone show only one species to go extinct even with the highest greenhouse gas emissions scenario (RCP8.5). In contrast, decreasing snow cover led to a rapid acceleration of species extinctions when decrease in SCD exceeds 20%, revealing a potentially important (and under current conditions hidden) tipping point in the Arctic biodiversity-climate change relationship (Fig. 3a-b). When the impacts of SCD and temperature change are considered jointly, asymmetric trends emerged. Most importantly, major decreases in SCD counteracted temperature effects and tempered the increases in total species richness resulting from warming summers (Fig. 2). In contrast, accelerating species extinction trends along the SCD gradient were relatively insensitive to increasing temperature; the projected trends were of largely similar magnitude irrespective of the greenhouse gas emissions scenario (Fig. 3a). Moreover, projected trends were similar for each of the taxonomic groups resulting in ca. 15% extinction rate among the study species under the most extreme SCD scenario (Fig. 2). However, responses in species' biogeographic groups differed (Note S2). Extinction rate was higher

in Arctic-alpine than boreal species (32% and 12%, respectively), and the difference was particularly clear in vascular plants (36% and 7%).

The projected trends of average species richness differed also between vascular plants, mosses, and lichens. Vascular plant richness was promoted by higher temperatures but somewhat tempered by the concurrent change in SCD (Fig 3c; Supplementary Fig S1 and S3). The moss species richness was projected to increase in most of the 36 scenario combinations, reaching its maximum under conditions where both temperature and SCD show maximal change (Fig 3d; Supplementary Fig S1 and S4). In contrast to vascular plants and mosses, lichen species richness showed weaker response to decrease in SCD. However, lichens appeared sensitive to the effects of temperature increase, showing the most drastic decreases under the greatest changes in snow cover and temperature conditions of RCP8.5 (Fig 3e; Supplementary Fig S1 and S5).

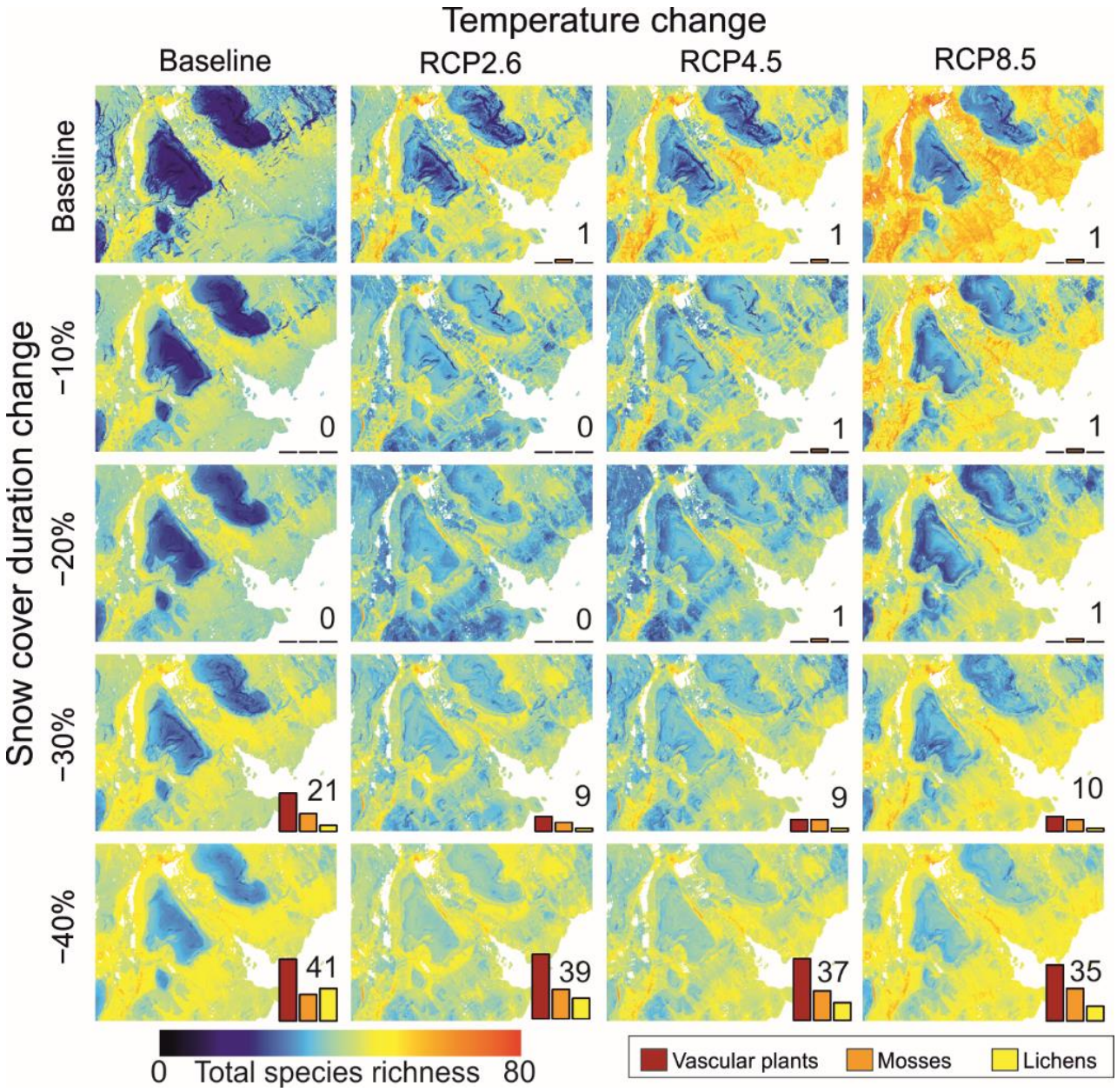

Figure 2. Projected species richness patterns (maps) and number of local extinctions (bars and numbers). Predicted local species richness (summed probabilities of 273 individual species distribution models) and number of extinctions (species losing all suitable habitat) by taxonomical groups when conditions change from current climate to 19 different scenario combinations projected to the year 2050. Areas below 400 m a.s.l. were excluded from the scenario maps to avoid prediction to non-analogue climate space and extrapolation outside the model calibration data.

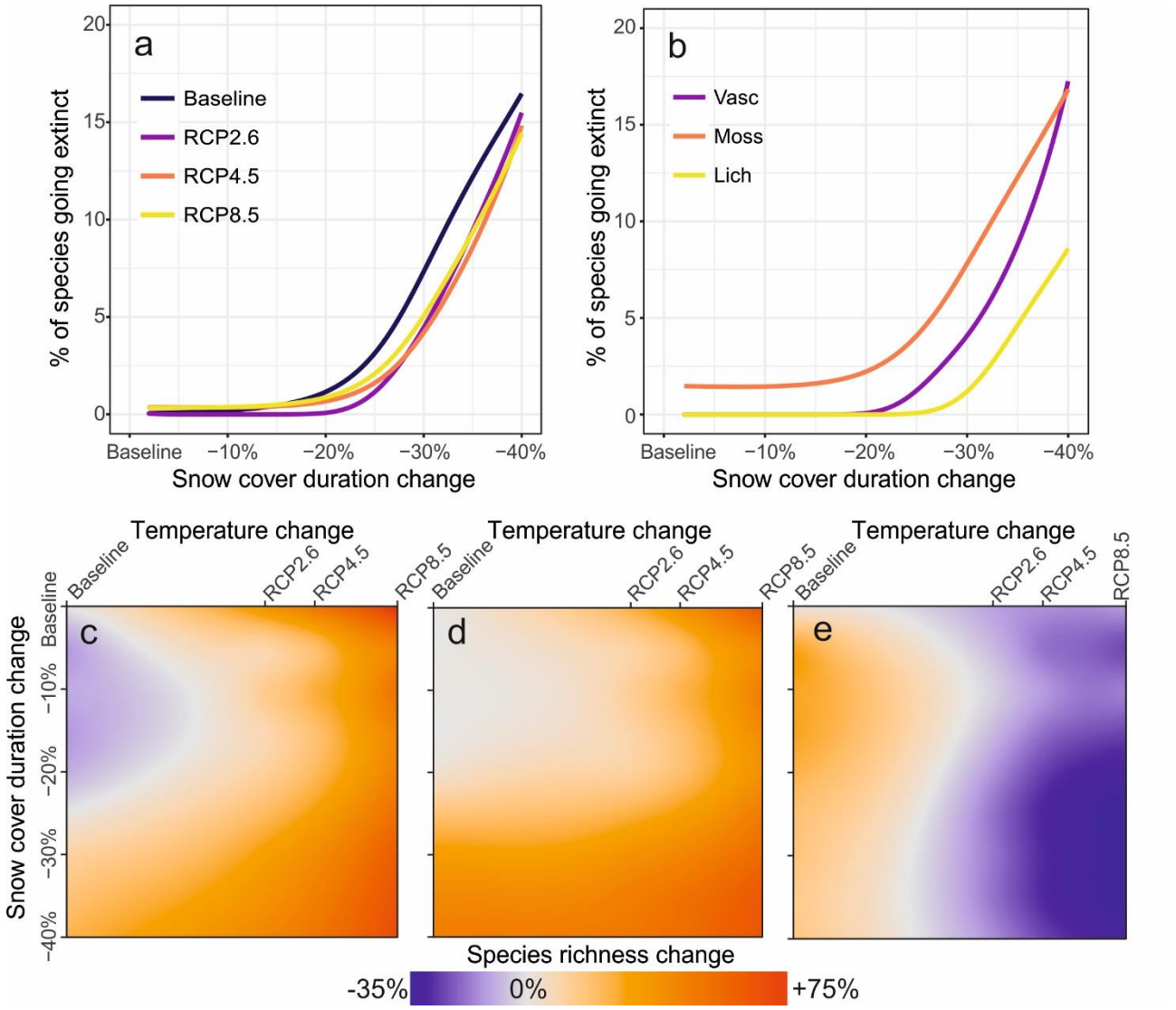

Figure 3. The evolution of the rate of extinctions and average species richness. The rate of local extinction against changing snow cover duration under different temperature scenarios (a) and in the three different taxonomic groups (b; greenhouse gas emissions scenario = RCP4.5). The evolution of the average change in local species richness against changing snow cover duration and warming summer temperatures (warming in RCP2.6 = 1.76; RCP4.5 = 2.19; RCP8.5 = 2.89) for vascular plants (c), mosses (d), and lichens (e).

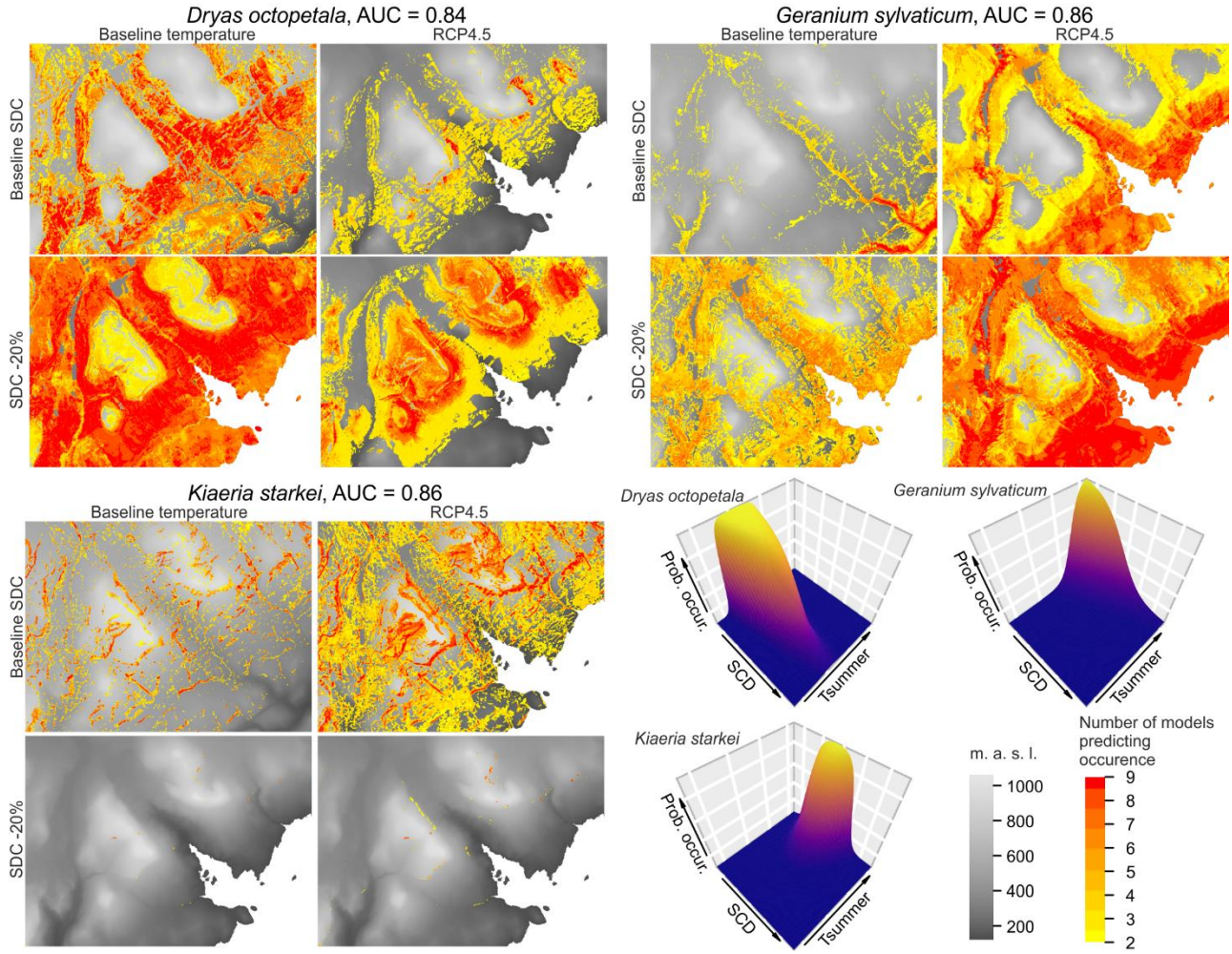

Fig 4. The occurrence predictions for three example species under current and future snow and summer temperature conditions. *Dryas octopetala* (Mountain avens) is a dwarf shrub inhabiting early melting dry mountain heaths; *Geranium sylvaticum* (Wood cranesbill) is a tall forb of relatively warm meadows; *Kiaeria starkei* (Starke's kiaeria moss) is a small moss and a snowbed specialist. The yellow-to-red color scale indicates the number of different modelling methods predicting an occurrence. The 3D response plots are constructed from generalized additive models. AUC (Area under curve) is an evaluation metric for binary models, with AUC = 1 indicating perfect predictive performance.

Our models suggest that species with the highest modelled local extinction risk are threatened by a shortening of the snow season rather than solely temperature rise. In fact, many Arctic and alpine species may even benefit from the warming climate if the SCD remains stationary whereas other species show contrasting responses (see example species in Fig 4). Thus, species that are favored by warmer ambient temperatures are not always the same that can take advantage of a shorter snow season[18]. Importantly, the extinction rates in our results were three times higher among Arctic-alpine

than boreal species. Most likely, boreal species projected to go extinct in our study area can survive in other low productivity habitats. In contrast, snow-dependent Arctic-alpine species face the challenge of losing significant portions of their suitable habitats, not only in our study area, but also within their global distributions.

Tundra warming experiments have shown a general pattern of vascular plants benefiting from increased temperatures, mosses showing mixed responses, and lichens a declining trend[19,20]. Our results widely agree with these patterns when considering trends in species richness. Vascular plant and moss richness increase as species expand their ranges upwards, while most lichen species retreat towards the mountain tops probably due to the competition between species groups[21]. The opposite trends in snow-driven extinction rates reflect the fact that the studied vascular plants and mosses include a higher proportion of snowbed species. Contrary, Arctic-alpine lichens mainly inhabit windswept heaths[11], where decreasing snow cover has no further important impact on growing conditions.

The earlier research on the effects of changing snow cover is one-sided because only a few of the tundra experiments have manipulated the snow and temperature conditions in parallel[22]. Moreover, there is a bias towards studies that have only simulated the increase in snow cover duration, in other words, an unlikely future climate[22]. However, our results agree with the earlier studies where tundra vegetation has showed high sensitivity to changes in snow regime, manifesting via the direct or indirect alteration of the physical, chemical, or biotic state of local habitat[23-27]. While manipulation studies usually consider only a small number of species and habitats, our modelling study suggests that strong responses to changes in snow conditions may arise for a large number of species, resulting in rapid changes in species' distributions. This may give rise to development of novel species assemblages and ecological surprises depending on the ratio of temperature and snowpack change

(Fig. S6). Furthermore, considering the differing trends of vascular, moss, and lichen richness shown here and knowing their dissimilar functional traits[28], shifts in the balance between the species groups can pose significant consequences on the general functioning of Arctic and alpine ecosystems.

Drawing implications from our results to a wider context requires careful attention to at least three questions: (i) the uncertainties embedded in climate models, (ii) the high spatial variability of the snow projections, and (iii) topographical heterogeneity. Firstly, Callaghan et al.[3] reviewed the progress in the development of global and regional snow cover change scenarios. They concluded that the limitations in General Circulation Models (GCM) may often hinder the construction of high-quality projections for the Arctic snow cover change and that ensembles of the best performing GCMs are required to develop as realistic as possible regional projections (see also [2,8,29]). Thus, modelling many levels of potential SCD change is recommended to develop understanding of the alternative future directions of biodiversity change and potential tipping points. Secondly, observed snow trends and global snow projections hold remarkable spatial heterogeneity and thus exploiting our results requires consideration of predicted regional levels of SCD change. Shortening of the SCD is especially strong in maritime climates (up to 40%), such as Fennoscandia, which are shifting from snow to rain dominated climate systems, even during the winters. In contrast, the predicted change is much lower in the most continental parts of Arctic Eurasia and America (< 10%) due to a combination of increasing winter precipitation and extremely cold winter temperatures. Thirdly, regions of complex topography contain a wide range of snow accumulation positions. Such landscapes may thus have an effective buffering capacity against the impacts of climate change. In turn, for relatively flat areas that do not have this safeguarding feature or harbor many snow-dependent species, the extinction rates may be different.

Our predictions suggest that the future of Arctic vegetation is critically depends on the evolution of snow conditions. However, it should be acknowledged that snow has multiple pathways to alter Arctic biodiversity either by directly affecting the survival of the species or by indirectly modifying the biogeochemical cycles or biotic interactions[1,7,30]. Thus, other aspects of snow climatology than SCD should be examined as well, because changes in rain-on-snow events and insulating capacity of snowpack, for example, may have important ecological impacts[2].

The recent climate record of northernmost Fennoscandia shows a minor warming trend and a decrease in SCD (Note S3). These changes may be considered indicative of the changes to be expected during the 21st century. On one hand, while changes in temperature and snow conditions have the potential to increase plot-scale species richness, the shortening of the snow season may wipe out a remarkable proportion of the Arctic-alpine species pool. On the other hand, if changes in snow cover duration remain moderate, landscapes characterized by a wide SCD gradient may buffer the species loss induced by rising temperatures, even under the most severe warming. Future study efforts should be invested into examining snow-species-interactions and the climate sensitivity of snow cover. Increased attention should also be targeted to the relatively high uncertainty in snow projections as this vagueness is further transmitted into models of Arctic and alpine ecosystems. Our study offers a strong remark on how insufficient acknowledgement of the diverse impacts of spatio-temporally varying snow cover have more critical consequences for climate change-biodiversity models than has previously been considered.

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Material & Methods (online-only)

The study area (165 km^2) is located in Finnmark, northern Norway (N 70°0’ E 26°14’). The area consists of two mountain massifs (Rastigaisa, 1064 m a.s.l. and Geidnogaisa 1032 m a.s.l.) with steep valleys in between (lowest point 120 m a.s.l.), resulting in a large elevational gradient from mountain birch forests to almost barren mountain tops. The area provides a suitable study setting in regards to gathering intensive and multifaceted empirical field data along with developing effective species-environment models due to the relatively short Euclidean distances between study sites paired with the areas extensive coverage of climatic space and a spectrum of habitats. Two specific useful features characterize our study area. 1) Considering species dispersal, the compactness of the study area facilitates a study system where the universal dispersal assumption can be plausibly employed as the default condition in the species distribution models. 2) Wide climatic space, in turn, reduces the risk that the projections of species’ future distributions extend into non-analogous climates and enables the comprehensive modelling of species’ niches. The main climatic characteristics of the study area

311 (based on fine-scale gridded climate data set described in Aalto et al.[31]) are listed in supplementary
312 material table S1.
313
314 The climate station record from northern Fennoscandia (>68°N) shows a significant increasing trend
315 for 3 out of 25 stations in summer temperature and a significant decreasing trend for 6 out of 16 in
316 snow cover duration during the 33-year study period (See supplementary materials Note S3 for more
317 details). On average, the snow cover duration has decreased by 17.3 days and summer temperature
318 increased by 0.76°C between 1984 and 2016.
319
320 The study area lies at the southern margin of the circumpolar Arctic biome[32]. The forest line is formed
321 by mountain birch (*Betula pubescens* ssp. *chzerepanovii*) and it reaches elevations of 250-350 m a.s.l.
322 depending on slope aspect. The most dominant vegetation type is xeric tundra heath characterized by
323 several dwarf-shrub species such as crowberry (*Empetrum nigrum* ssp. *hermaphroditum*) and dwarf
324 birch (*Betula nana*) as the most dominant species. Depressions, small water channels, and other moist
325 habitats maintain forb-rich vegetation types and most water-logged wetlands are dominated by rushes
326 and willow thickets. In addition, snow cover duration creates its own gradient from lichen-covered
327 exposed sites to extremely late moss-dominated snowbeds (for more details, see Niittynen & Luoto[12]).
328 The majority of the area is acidic Precambrian crystalline rock covered by glacial till, but the
329 mountain massifs are fringed by a thin layer of easily weathering shales (Hyolithus zone) that provide
330 a good substratum for more nutrient demanding or calcicolous species (e,g, *Saxifraga* ssp., *Dryas*
331 *octopetala*, *Ranunculus sulphureus*)[33]. The species pool consists of Arctic, alpine, and boreal species,
332 which makes it an interesting mix of species between the main biomes of the northern high-latitudes.
333
334 The vegetation dataset consists of occurrence records for 460 vascular plant, moss, and lichen taxa
335 observed in 1200 study sites. Each of the study sites consists of four $1m^2$ vegetation plots situated

five meters from the center of the site. Study sites were chosen in a semi-random manner in the field or beforehand using stratified sampling along the main environmental gradients. We aimed for a uniform spatial coverage and thus, every square kilometer of the study area includes at least four study sites. To reduce the risk of the effects of spatial autocorrelation in the modelling results, the minimum distance between study sites was 50 meters. The co-ordinates of the study sites were noted using hand-held GPS-device in the field.

Vegetation sampling was conducted during July-September in three consecutive years (2014 – 2016). Vascular plants are generally gaining most of the research effort in vegetation science, but here we also focused on lichens and mosses (*Bryophyta*, not including liverworts and hornworts) in order to thoroughly model the possible changes in the vegetation community. All the species were identified at the species level with a few exceptions that cannot be distinguished reliably at the species level (*Alchemilla* spp., *Taraxacum* spp., *Cladonia chlorophaea* -section, *Lepraria* spp.). Furthermore, rock-dwelling lichens and mosses were excluded from the data as identification of these species often requires DNA-techniques and these species are not dependent on the resources or physical conditions of the soil, unlike vascular plants. With these exclusions, we ensured the full comparability between the taxonomical groups. Nomenclature and species identification follows Hämet-Ahti et al.[34] for vascular plants, Laine et al.[35], Hallinback et al.[36,37], and Hedenäs and Hallinbäck[38] for mosses, and Stenroos et al.[39] for lichens.

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 (*http:\\earthexplorer.usgs.gov*). The images were surface reflectance products, which were preprocessed (georeferencing and atmospheric corrections) by USGS[40,41]. For

analysis, we selected images that were georeferenced correctly and cloudless over the whole study area. The total number of suitable images was 135.

In our data, the snow cover duration (SCD) variable reflects the average length of the snow season during the recent 33-year period and is produced pixel by pixel at the native spatial resolution of Landsat (30 m). A time slice as long as this is analogous with the climatological normal period and, moreover, is required to gather a sufficient number of suitable satellite images in an area frequently covered by clouds. The construction of SCD from satellite observations is a two-step process where the snowfall and melting day of years (DOY) were produced separately by generalized linear models (GLM). In general, in producing the pixel-based SCD we followed Macander et al. and Niittynen & Luoto[12,42] with a few exceptions reported here. All the image processing was performed in statistical software R[43] with *Raster* package [44].

The individual cloud-free images were first converted to binary snow cover maps by calculating and thresholding a spectral index *normalized difference snow index* (NDSI; equation 1)[45].

Equation 1: NDSI = (Green - SWIR) / (Green + SWIR)

Each pixel in an individual image was interpreted as snow if the NDSI value was over 0.4 [42]. 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. Waterbodies, that can also have high NDSI values, were later masked from the snow maps with a water layer digitized from high-resolution satellite images.

The snow melting DOY was determined pixel by pixel using binomial GLMs. Here all the images from the autumn with new snow cover were excluded from the analysis, resulting in 124 images. Every pixel had two strings of information that were passed as inputs for pixel-based GLMs: 1) a

385 string of binary scores of snow occurrence (one score from each of the 124 images), and 2) a string
386 of the corresponding DOY values. In the pixel-based GLMs, the binary snow scores were treated as
387 a dependent variable and the DOYs as the predictor. After the model was fitted, it was used to predict
388 the probability of snow occurrence for every possible DOY value from day 1 (January 1st) to day 273
389 (September 30th). We estimated the average snowmelt date to be the DOY in which the probability
390 breaks the 0.5 probability threshold. If the probability stayed above the 0.5 for the whole sequence of
391 DOYs, the pixel was determined as ever-snow.
392
393 The snowfall DOY was determined using the same principles as in determining the melting DOY.
394 For the modelling, we selected the images from mid-August (DOY >= 230) to October (n = 25) from
395 which 11 images had a new snow cover. Then the GLM was fitted and used for predictions similarly
396 as the melting DOY above. If the probability of snow occurrence stays above the 0.5 for the string of
397 DOYs the pixel was determined as ever-snow. After the DOY_{melt} and DOY_{new_snow} were determined
398 the total snow cover duration was calculated as:
399 Equation 2: $SCD = DOY_{melt} + (365 - DOY_{new\_snow})$
400
401 The SCD variable employed here has a good agreement with snow cover duration constructed with
402 year-around soil temperature data from 175 microloggers (linear correlation = 0.873) and snow
403 patches observed from one fine scale (6-m resolution) satellite image (SPOT6; True skill statistics =
404 0.91). See supplementary materials Note S1 for further details of SCD validation process.
405
406 The Arctic snow cover duration is predicted to decrease by 10-40% before 2050 [3]. Therefore, we
407 simply reduce the observed pixel-based SCD by 5, 10, 15, 20, 25, 30, 35 and 40%. Thus, the absolute
408 change is smaller in sites with short SCD and bigger in late lying snow-beds.
409

410 Summer temperatures were extracted from a gridded climate dataset that is presented by Aalto et al.[31].
411 The dataset is based on monthly records of 942 climate stations in Fennoscandian countries (Finland,
412 Sweden and Norway) covering the period of 1981–2010, which were then interpolated with
413 generalized additive models using altitude, relative elevation, potential incoming radiation, and cover
414 of sea and lakes as predictors. Due to our relatively compact study area, different climatic factors are
415 strongly correlated with each other (Spearman correlation coefficient |>0.9|). Therefore, we selected
416 only summer (June, July, and August) mean temperature (Tsummer) to be the representative variable
417 for all climatic factors. The Tsummer variable was then projected for period of 2040-2069 forced by
418 three Representative Concentration Pathway (RCP) scenarios 2.6, 4.5, and 8.5 [16,46]. The projected
419 temperatures were averaged over 23 CMIP5 climate simulations[16].
420
421 As we wanted to construct reasonable and ecological models for the study species we also included
422 environmental predictors – in addition to temperature and SCD variables – that are known to have
423 important effects on vegetation in our study area[15,47]. No model-selection was made, i.e. all models
424 were forced to have the same predictor variables, ensuring that the models were fully comparable. To
425 capture the impacts of local environment, we employed five environmental predictors to represent
426 the main physical and chemical gradients: potential incoming radiation (RAD), topographic wetness
427 index (TWI), slope (SLOPE), surface soil quality (SOILQ), and soil edaphic conditions (EDAP).
428 Summary statistics for predictor variables are provided in supplementary materials (Table S2 and
429 Table S3). The nine SCD and four Tsummer scenarios combined produced a total number of 36
430 different models.
431
432 RAD, TWI, and SLOPE were derived from a 10-m resolution digital elevation model (DEM) [data
433 portal of Norwegian Mapping Authority (http://data.kartverket.no/download/)]. The potential annual
434 direct solar radiation was calculated (MJ/cm-2/y-1) by using the equations of McCune and Keon

435 assuming clear sky conditions[48]. SAGA Wetness index (hereafter TWI) is a modification of
436 traditional topographical wetness index[49] and was selected over the traditional as it mimics water flow
437 patterns more realistically in flat areas[50]. The DEM was preprocessed by filling sinks[51] and then used
438 to calculate the specific catchment area and slope required by the TWI algorithm. SLOPE is the local
439 slope angel in degrees. SOILQ represents the surface soil quality with five soil classes: peat, fluvial
440 sediments, glacial till, bolder field, and bare rock. SOILQ is based on interpretation of fine-scale
441 aerial and satellite images (resolutions of 0.5–1.4 m) verified with field surveys. EDAP represents
442 the nutritional status of the bedrock and was calculated as the downhill Euclidean distance to the shale
443 belt (the only base-rich rock type in the area) scaled from zero to 100. Areas located on the shale belt
444 were valued at 100 and areas uphill from shale belt or outside the area where the shale belt drains
445 were set to zero. The geological data were downloaded from the bedrock geology database maintained
446 by Geological Survey of Norway (http://geo.ngu.no/kart/berggrunn/). Values of predictors were
447 extracted for study points from original rasters but spatial predictions were conducted at 30 m spatial
448 resolution (as in Landsat images), and thus, variables were resampled to 30 m resolution using bilinear
449 interpolation (with the exception of the nominal variable SOILQ, in which case class with maximum
450 area aggregation was used).
451
452 Only species with at least 8 presence sites were included in the analyses: 273 species in total (132
453 vascular plants, 71 mosses, and 70 lichens). The binary distributions of individual species were
454 modelled using nine modelling methods implemented in *Biomod2* modelling framework in R
455 modelling environment (generalized linear model = GLM; generalized additive models = GAM;
456 multiple adaptive regression splines = MARS; flexible discriminant analysis = FDA; classification
457 tree analysis = CTA; generalized boosted method = GBM, random forest = RF; maximum entropy =
458 MAXENT; artificial neural network = ANN)[52]. The model parameterization is described in the

supplementary materials (Note S4). By using nine modelling methods we decreased the algorithm based error as the methods handle the data in fundamentally different manners.

All nine modelling methods produced their own projections for each species and for each climatic scenario. The models provide the probability of the species to be present in a given cell which was then binarized by thresholding the probability with a level that maximizes the TSS-value of the predictions. After the modelling method-specific binary projections were produced, we built an ensemble prediction which judges that the species is present in a certain cell if at least five of the nine methods predicted a local occurrence. This ensemble-building rule is called majority voting and is often utilized in species distribution modelling studies in order to decrease the importance of a single modelling method[53]. A species was determined as regionally extinct if the ensemble model did not predict any occurrences. All spatial predictions are projected with models using all the 1200 study sites for calibration. In order to check the predictive performance of the models we used cross-validation where the data was randomly split into calibration data (70% of the data) with which the model was fitted and then used to predict species occurrence to the withheld 30% of the data. This procedure was repeated four times for each species, and in each round Area under curve (AUC) and true skill statistics (TSS) were calculated for each species and modelling method separately[54,55]. These metrics are frequently used in SDM studies to measure and evaluate the predictive accuracy of the binary predictions.

Acknowledgements

The authors are grateful for research support provided by the Academy of Finland (project no. 1286950), Kone foundation, and Societas pro Fauna et Flora Fennica. We thank A. Niskanen for her

language check and all members of the Biogeoclimate modelling Lab for assistance with the field work.

Author contributions

P.N., M.L., and R.K.H. designed the research. P.N. collected the field and satellite data, performed the analysis and wrote the first draft of the paper. All the authors contributed to writing the paper.

Competing interests

The authors declare no competing financial interests.

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Data availability

The data that support the findings of this study are available from the corresponding author upon request.

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