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1 Snow cover is a neglected driver of Arctic biodiversity loss

2

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14 **Snow has far-reaching effects on ecosystem processes and biodiversity in high-latitude**
15 **ecosystems, but have been poorly considered in climate change impact models^{1,2}. Here, to**
16 **forecast future trends in species occurrences and richness, we fitted species-environment**
17 **models with temperature data from three climate scenarios and simulated up to a 40% decrease**
18 **in snow cover duration (SCD)³. We used plot scale data on 273 vascular plant, moss and lichen**
19 **species in 1200 study sites spanning a wide range of environmental conditions typical for**
20 **mountainous Arctic landscapes (within 165 km²). Based on the models, a rise in temperature**
21 **increased overall species richness and caused only one species to lose all suitable habitat. In**
22 **contrast, a shorter SCD tempered the effect of increasing temperature on species richness and**
23 **led to accelerated rates of species' local extinctions after a tipping point at 20-30% SCD**
24 **decrease. All three species groups showed similar extinction rates but contrasting species**
25 **richness responses. Our simulations indicate that future biodiversity patterns in Arctic regions**
26 **are highly dependent on the evolution of snow conditions. Climate impact models that ignore**
27 **the effects of snow cover change may provide biased biodiversity projections, with potentially**
28 **erratic implications for Arctic nature conservation planning.**

29
30 On-going and projected climate change is most forceful in high latitudes, causing the Arctic to
31 warm up at twice the global rate^{2,4}. Research on Arctic climate change impacts has mostly focused
32 on temperature changes alone, describing the climate change induced turnover of species and the
33 associated ecosystem impacts, such as changes in land-surface albedo and soil carbon balance^{5,6}.
34 However, as the climate change in the Arctic is most prominent for winter months⁴, these regions
35 may face important alterations in snow conditions including a 10-40% decrease in snow cover
36 duration (SCD) by 2050^{2,3}. Recent snow cover dynamics have already led to major changes in
37 Arctic ecosystems^{2,3,7}, and further alterations in snow cover may promote changes in vegetation
38 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.

43

For biotic communities, snow is one of the most important controls on growing conditions⁹ 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 patterns¹⁰. This enables the regional co-occurrence of a wide range of species with different ecological requirements¹¹. 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 Programme². 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}.

54

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 km²; 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.

62

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 years¹². 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 plants¹⁵, 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

82 to 40% decrease in SCD, matching the range of recent snow cover projections³), and all possible
83 combinations between these two groups of scenarios resulting in a total of 36 combinations. The
84 temperatures were projected for period of 2040-2069 and averaged over 23 CMIP5 climate
85 simulations¹⁶. Each species was modelled separately but as a final step we stacked the single-species
86 predictions¹⁷ to examine how changing SCD and temperature affect overall species richness.

87

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

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

108

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

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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.

129

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

136

137

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 season¹⁸. Importantly, the extinction rates in our results were three times higher among Arctic-alpine

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

158

159 Tundra warming experiments have shown a general pattern of vascular plants benefiting from
160 increased temperatures, mosses showing mixed responses, and lichens a declining trend^{19,20}. Our
161 results widely agree with these patterns when considering trends in species richness. Vascular plant
162 and moss richness increase as species expand their ranges upwards, while most lichen species retreat
163 towards the mountain tops probably due to the competition between species groups²¹. The opposite
164 trends in snow-driven extinction rates reflect the fact that the studied vascular plants and mosses
165 include a higher proportion of snowbed species. Contrary, Arctic-alpine lichens mainly inhabit
166 windswept heaths¹¹, where decreasing snow cover has no further important impact on growing
167 conditions.

168

169 The earlier research on the effects of changing snow cover is one-sided because only a few of the
170 tundra experiments have manipulated the snow and temperature conditions in parallel²². Moreover,
171 there is a bias towards studies that have only simulated the increase in snow cover duration, in other
172 words, an unlikely future climate²². However, our results agree with the earlier studies where tundra
173 vegetation has showed high sensitivity to changes in snow regime, manifesting via the direct or
174 indirect alteration of the physical, chemical, or biotic state of local habitat²³⁻²⁷. While manipulation
175 studies usually consider only a small number of species and habitats, our modelling study suggests
176 that strong responses to changes in snow conditions may arise for a large number of species, resulting
177 in rapid changes in species' distributions. This may give rise to development of novel species
178 assemblages and ecological surprises depending on the ratio of temperature and snowpack change

179 (Fig. S6). Furthermore, considering the differing trends of vascular, moss, and lichen richness shown
180 here and knowing their dissimilar functional traits²⁸, shifts in the balance between the species groups
181 can pose significant consequences on the general functioning of Arctic and alpine ecosystems.

182

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

202

203 Our predictions suggest that the future of Arctic vegetation is critically depends on the evolution of
204 snow conditions. However, it should be acknowledged that snow has multiple pathways to alter Arctic
205 biodiversity either by directly affecting the survival of the species or by indirectly modifying the
206 biogeochemical cycles or biotic interactions^{1,7,30}. Thus, other aspects of snow climatology than SCD
207 should be examined as well, because changes in rain-on-snow events and insulating capacity of
208 snowpack, for example, may have important ecological impacts².

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

224 **References (Main text)**

225 1 Callaghan, T. V. *et al.* Multiple Effects of Changes in Arctic Snow Cover. *Ambio* **40**, 32-45
226 (2011).
227 2 AMAP. Snow, Water, Ice and Permafrost in the Arctic (SWIPA) 2017. 269 (Oslo, Norway,
228 2017).

229 3 Callaghan, T. V. *et al.* The Changing Face of Arctic Snow Cover: A Synthesis of Observed
230 and Projected Changes. *Ambio* **40**, 17-31 (2011).

231 4 Hartmann, D. L. *et al.* in *Climate Change 2013: The Physical Science Basis. Contribution of*
232 *Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate*
233 *Change* (eds T.F. Stocker *et al.*) (Cambridge University Press, 2013).

234 5 Pearson, R. G. *et al.* Shifts in Arctic vegetation and associated feedbacks under climate
235 change. *Nat. Clim. Chang.* **3**, 673-677 (2013).

236 6 Hobbie, S. E., Schimel, J. P., Trumbore, S. E. & Randerson, J. R. Controls over carbon storage
237 and turnover in high-latitude soils. *Global Change Biol.* **6**, 196-210 (2000).

238 7 Bokhorst, S. *et al.* Changing Arctic snow cover: A review of recent developments and
239 assessment of future needs for observations, modelling, and impacts. *Ambio* **45**, 516-537
240 (2016).

241 8 Bintanja, R. & Andry, O. Towards a rain-dominated Arctic. *Nature Clim. Change* **7**, 263-267
242 (2017).

243 9 Zhang, T. J. Influence of the seasonal snow cover on the ground thermal regime: An overview.
244 *Rev. Geophys.* **43**, RG4002 (2005).

245 10 Liston, G. E. & Elder, K. A distributed snow-evolution modeling system (SnowModel).
246 *Journal of Hydrometeorology* **7**, 1259-1276 (2006).

247 11 Billings, W. D. & Mooney, H. A. Ecology of Arctic and Alpine Plants. *Biol. Rev. Camb.*
248 *Philos. Soc.* **43**, 481-529 (1968).

249 12 Niittynen, P. & Luoto, M. The importance of snow in species distribution models of arctic
250 vegetation. Preprint at <http://onlinelibrary.wiley.com/doi/10.1111/ecog.03348/full> (2017).

251 13 Bokhorst, S. *et al.* Changing Arctic snow cover: A review of recent developments and
252 assessment of future needs for observations, modelling, and impacts. *Ambio* **45**, 516-537
253 (2016).

254 14 Ernakovich, J. G. *et al.* Predicted responses of arctic and alpine ecosystems to altered
255 seasonality under climate change. *Global Change Biol.* **20**, 3256-3269 (2014).

256 15 Mod, H. K., Scherrer, D., Luoto, M. & Guisan, A. What we use is not what we know:
257 environmental predictors in plant distribution models. *J. Veg. Sci.* **27**, 1308-1322 (2016).

258 16 Taylor, K. E., Stouffer, R. J. & Meehl, G. A. An overview of CMIP5 and the experiment
259 design. *Bull. Amer. Meteorol. Soc.* **93**, 485-498 (2012).

260 17 Guisan, A. & Rahbek, C. SESAM - a new framework integrating macroecological and species
261 distribution models for predicting spatio-temporal patterns of species assemblages. *J.*
262 *Biogeogr.* **38**, 1433-1444 (2011).

263 18 Carlson, B. Z., Choler, P., Renaud, J., Dedieu, J. P. & Thuiller, W. Modelling snow cover
264 duration improves predictions of functional and taxonomic diversity for alpine plant
265 communities. *Ann. Bot.* **116**, 1023-1034 (2015).

266 19 Elmendorf, S. C. *et al.* Global assessment of experimental climate warming on tundra
267 vegetation: heterogeneity over space and time. *Ecol. Lett.* **15**, 164-175 (2012).

268 20 Lang, S. I. *et al.* Arctic warming on two continents has consistent negative effects on lichen
269 diversity and mixed effects on bryophyte diversity. *Global Change Biol.* **18**, 1096-1107
270 (2012).

271 21 Cornelissen, J. H. C. *et al.* Global change and arctic ecosystems: is lichen decline a function
272 of increases in vascular plant biomass? *J. Ecol.* **89**, 984-994 (2001).

273 22 Wipf, S. & Rixen, C. A review of snow manipulation experiments in Arctic and alpine tundra
274 ecosystems. *Polar Res.* **29**, 95-109 (2010).

275 23 Aerts, R., Cornelissen, J. H. C. & Dorrepaal, E. Plant performance in a warmer world: General
276 responses of plants from cold, northern biomes and the importance of winter and spring
277 events. *Plant Ecol.* **182**, 65-77 (2006).

- 278 24 Blume-Werry, G., Kreyling, J., Laudon, H. & Milbau, A. Short-term climate change
279 manipulation effects do not scale up to long-term legacies: effects of an absent snow cover on
280 boreal forest plants. *J. Ecol.* **104**, 1638-1648 (2016).
- 281 25 Bokhorst, S. F., Bjerke, J. W., Tommervik, H., Callaghan, T. V. & Phoenix, G. K. Winter
282 warming events damage sub-Arctic vegetation: consistent evidence from an experimental
283 manipulation and a natural event. *J. Ecol.* **97**, 1408-1415 (2009).
- 284 26 Kreyling, J., Haei, M. & Laudon, H. Absence of snow cover reduces understory plant cover
285 and alters plant community composition in boreal forests. *Oecologia* **168**, 577-587 (2012).
- 286 27 Wipf, S. Phenology, growth, and fecundity of eight subarctic tundra species in response to
287 snowmelt manipulations. *Plant Ecol.* **207**, 53-66 (2010).
- 288 28 Cornelissen, J. H. C., Lang, S. I., Soudzilovskaia, N. A. & During, H. J. Comparative
289 cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry. *Ann.*
290 *Bot.* **99**, 987-1001 (2007).
- 291 29 Mankin, J. S. & Diffenbaugh, N. S. Influence of temperature and precipitation variability on
292 near-term snow trends. *Clim. Dyn.* **45**, 1099-1116 (2015).
- 293 30 Wipf, S., Rixen, C. & Mulder, C. P. H. Advanced snowmelt causes shift towards positive
294 neighbour interactions in a subarctic tundra community. *Global Change Biol.* **12**, 1496-1506
295 (2006).
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297

298 Material & Methods (online-only)

299 The study area (165 km²) is located in Finnmark, northern Norway (N 70°0' E 26°14'). The area
300 consists of two mountain massifs (Rastigaisa, 1064 m a.s.l. and Geidnogaisa 1032 m a.s.l.) with steep
301 valleys in between (lowest point 120 m a.s.l.), resulting in a large elevational gradient from mountain
302 birch forests to almost barren mountain tops. The area provides a suitable study setting in regards to
303 gathering intensive and multifaceted empirical field data along with developing effective species-
304 environment models due to the relatively short Euclidean distances between study sites paired with
305 the areas extensive coverage of climatic space and a spectrum of habitats. Two specific useful features
306 characterize our study area. 1) Considering species dispersal, the compactness of the study area
307 facilitates a study system where the universal dispersal assumption can be plausibly employed as the
308 default condition in the species distribution models. 2) Wide climatic space, in turn, reduces the risk
309 that the projections of species' future distributions extend into non-analogous climates and enables
310 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 biome³². 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 & Luoto¹²).
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 1m² vegetation plots situated

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

342

343 Vegetation sampling was conducted during July-September in three consecutive years (2014 – 2016).
344 Vascular plants are generally gaining most of the research effort in vegetation science, but here we
345 also focused on lichens and mosses (*Bryophyta*, not including liverworts and hornworts) in order to
346 thoroughly model the possible changes in the vegetation community. All the species were identified
347 at the species level with a few exceptions that cannot be distinguished reliably at the species level
348 (*Alchemilla* spp., *Taraxacum* spp., *Cladonia chlorophaea* -section, *Lepraria* spp.). Furthermore,
349 rock-dwelling lichens and mosses were excluded from the data as identification of these species often
350 requires DNA-techniques and these species are not dependent on the resources or physical conditions
351 of the soil, unlike vascular plants. With these exclusions, we ensured the full comparability between
352 the taxonomical groups. Nomenclature and species identification follows Hämet-Ahti et al.³⁴ for
353 vascular plants, Laine et al.³⁵, Hallinback et al.^{36,37}, and Hedenäs and Hallinbäck³⁸ for mosses, and
354 Stenroos et al.³⁹ for lichens.

355

356 We downloaded all available clear sky (less than 50% cloud cover) Landsat TM 5, ETM 7 and OLI
357 8 images covering the whole study area from March to October from 1984 to 2016 (total of 540
358 scenes) from USGS database (<http://earthexplorer.usgs.gov/>). The images were surface reflectance
359 products, which were preprocessed (georeferencing and atmospheric corrections) by USGS^{40,41}. For

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

362

363 In our data, the snow cover duration (SCD) variable reflects the average length of the snow season
364 during the recent 33-year period and is produced pixel by pixel at the native spatial resolution of
365 Landsat (30 m). A time slice as long as this is analogous with the climatological normal period and,
366 moreover, is required to gather a sufficient number of suitable satellite images in an area frequently
367 covered by clouds. The construction of SCD from satellite observations is a two-step process where
368 the snowfall and melting day of years (DOY) were produced separately by generalized linear models
369 (GLM). In general, in producing the pixel-based SCD we followed Macander et al. and Niittynen &
370 Luoto^{12,42} with a few exceptions reported here. All the image processing was performed in statistical
371 software R⁴³ with *Raster* package⁴⁴.

372

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

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

376 Each pixel in an individual image was interpreted as snow if the NDSI value was over 0.4⁴². NDSI
377 is a widely used spectral index in snow-related RS studies and is based on the relative difference in
378 reflectance between green and shortwave infrared (SWIR) spectral bands. Waterbodies, that can also
379 have high NDSI values, were later masked from the snow maps with a water layer digitized from
380 high-resolution satellite images.

381

382 The snow melting DOY was determined pixel by pixel using binomial GLMs. Here all the images
383 from the autumn with new snow cover were excluded from the analysis, resulting in 124 images.

384 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 2050³. 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 $|\rho| > 0.9$). Therefore, we selected
416 only summer (June, July, and August) mean temperature (T_{summer}) to be the representative variable
417 for all climatic factors. The T_{summer} 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 simulations¹⁶.

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 T_{summer} 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 ($\text{MJ}/\text{cm}^2/\text{y}-1$) by using the equations of McCune and Keon

435 assuming clear sky conditions⁴⁸. SAGA Wetness index (hereafter TWI) is a modification of
436 traditional topographical wetness index⁴⁹ and was selected over the traditional as it mimics water flow
437 patterns more realistically in flat areas⁵⁰. The DEM was preprocessed by filling sinks⁵¹ 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

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

461

462 All nine modelling methods produced their own projections for each species and for each climatic
463 scenario. The models provide the probability of the species to be present in a given cell which was
464 then binarized by thresholding the probability with a level that maximizes the TSS-value of the
465 predictions. After the modelling method-specific binary projections were produced, we built an
466 ensemble prediction which judges that the species is present in a certain cell if at least five of the nine
467 methods predicted a local occurrence. This ensemble-building rule is called majority voting and is
468 often utilized in species distribution modelling studies in order to decrease the importance of a single
469 modelling method⁵³. A species was determined as regionally extinct if the ensemble model did not
470 predict any occurrences. All spatial predictions are projected with models using all the 1200 study
471 sites for calibration. In order to check the predictive performance of the models we used cross-
472 validation where the data was randomly split into calibration data (70% of the data) with which the
473 model was fitted and then used to predict species occurrence to the withheld 30% of the data. This
474 procedure was repeated four times for each species, and in each round Area under curve (AUC) and
475 true skill statistics (TSS) were calculated for each species and modelling method separately^{54,55}. These
476 metrics are frequently used in SDM studies to measure and evaluate the predictive accuracy of the
477 binary predictions.

478

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484

485 **Author contributions**

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

488

489 **Competing interests**

490 The authors declare no competing financial interests.

491

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494

495 **Data availability**

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

498

499 **References (Material & Methods)**

500 31 Aalto, J., Riihimäki, H., Meineri, E., Hylander, K. & Luoto, M. Revealing topoclimatic
501 heterogeneity using meteorological station data. *Int. J. Climatol.* **37**, 544-556 (2017).
502 32 Virtanen, R. *et al.* Where do the treeless tundra areas of northern highlands fit in the global
503 biome system: toward an ecologically natural subdivision of the tundra biome. *Ecol. Evol.* **6**,
504 143-158 (2016).
505 33 Ryvarde, L. The vascular plants of the Rastigaissa area (Finnmark, Northern Norway). *Acta*
506 *Borealia* **26**, 1-56 (1969).

507 34 Hämet-Ahti, L., Suominen, J., Ulvinen, T. & Uotila, P. *Retkeilykasvio* (Field Flora of
508 Finland). 3 edn, (Finnish Museum of Natural History, Botanical Museum, Helsinki, 1998).

509 35 Laine, J. *et al.* *The Intricate Beauty of Sphagnum Mosses - a Finnish Guide to Identification*.
510 Vol. 2 1-191 (University of Helsinki, Department of Forest Sciences, 2011).

511 36 Hallinbäck, T., Lönnell, N., Weibull, H., Hedenäs, L. & von Knorring, P. *Nationalnyckeln till*
512 *Sveriges flora och fauna. Bladmossor: Sködmossor - Blåmossor. Bryophyta: Buxbaumia -*
513 *Leucobryum.*, (ArtDatabanken, SLU, 2006).

514 37 Hallinbäck, T. *et al.* *Nationalnyckeln till Sveriges flora och fauna. Bladmossor:*
515 *Kompaktmossor - kapmossor. Bryophyta: Anoetangium - Orthodontium.*, (ArtDatabanken,
516 SLU, 2008).

517 38 Hedenäs, L. & Hallinbäck, T. *Nationalnyckeln till sveriges flora och fauna, Bladmossor:*
518 *Skirmossor-Baronmossor. Bryophyta: Hookeria-Anomodon.* (ArtDatabanken, SLU, 2014).

519 39 Stenroos, S., Ahti, T., Lohtander, K. & Myllys, L. *Suomen jäkäläopas*. (Finnish Museum of
520 Natural History, Botanical Museum, Helsinki, 2011).

521 40 USGS. *Product guide: Landsat 4–7 climate data record (cdr) surface reflectance*.
522 (Department of the Interior U.S. Geological Survey, 2017).

523 41 USGS. *Product guide: Provisional Landsat 8 surface reflectance code (lasrc) product*.
524 (Department of the Interior U.S. Geological Survey, 2016).

525 42 Macander, M. J., Swingley, C. S., Joly, K. & Reynolds, M. K. Landsat-based snow persistence
526 map for northwest Alaska. *Remote Sens. Environ.* **163**, 23-31 (2015).

527 43 R: A language and environment for statistical computing. R Foundation for Statistical
528 Computing (Vienna, Austria, 2016).

529 44 Hijmans, R. J. raster: Geographic data analysis and modeling. – R package ver. 2.5-8. (2016).

530 45 Hall, D. K., Riggs, G. A. & Salomonson, V. V. Development of methods for mapping global
531 snow cover using Moderate Resolution Imaging Spectroradiometer data. *Remote Sens.*
532 *Environ.* **54**, 127-140 (1995).

533 46 Moss, R. H. *et al.* The next generation of scenarios for climate change research and
534 assessment. *Nature* **463**, 747-756 (2010).

535 47 Austin, M. P. & Van Niel, K. P. Improving species distribution models for climate change
536 studies: variable selection and scale. *J. Biogeogr.* **38**, 1-8 (2011).

537 48 McCune, B. & Keon, D. Equations for potential annual direct incident radiation and heat load.
538 *J. Veg. Sci.* **13**, 603-606 (2002).

539 49 Beven, K. J. & Kirkby, M. J. A physically based, variable contributing area model of basin
540 hydrology. *Hydrological Sciences Bulletin* **24**, 43-69 (1979).

541 50 Böhner, J. & Selige, T. in *SAGA - Analysis and Modelling Applications* (eds J. Boehner, K.R.
542 McCloy, & J. Strobl) (Goettinger Geographische Abhandlungen, 2006).

543 51 Wang, L. & Liu, H. An efficient method for identifying and filling surface depressions in
544 digital elevation models for hydrologic analysis and modelling. *Int. J. Geogr. Inf. Sci.* **20**, 193-
545 213 (2006).

546 52 biomod2: Ensemble Platform for Species Distribution Modeling v. R package version 3.3-7
547 (2016).

548 53 Thuiller, W., Lafourcade, B., Engler, R. & Araujo, M. B. BIOMOD - a platform for ensemble
549 forecasting of species distributions. *Ecography* **32**, 369-373 (2009).

550 54 Allouche, O., Tsoar, A. & Kadmon, R. Assessing the accuracy of species distribution models:
551 prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* **43**, 1223-1232 (2006).

552 55 Fielding, A. H. & Bell, J. F. A review of methods for the assessment of prediction errors in
553 conservation presence/absence models. *Environ. Conserv.* **24**, 38-49 (1997).