Title Woody plants constructing tundra soils

Running title Woody plants constructing tundra soils

List of authors Julia Kemppinen¹, Pekka Niittynen¹, Anna-Maria Virkkala¹, Konsta Happonen¹, Henri Riihimäki¹, Juha Aalto^{1,2} & Miska Luoto¹

ORCID

Julia Kemppinen 0000-0001-7521-7229

Pekka Niittynen 0000-0002-7290-029X

Anna-Maria Virkkala 0000-0003-4877-2918

Konsta Happonen 0000-0002-3164-8868

Henri Riihimäki 0000-0002-5727-6492

Juha Aalto 0000-0001-6819-4911

Miska Luoto 0000-0001-6203-5143

Institutional affiliations University of Helsinki¹, Finnish Meteorological Institute²

Contact Information julia.kemppinen@helsinki.fi

Author contributions JK conceived the research and together with PN, A-MV, HR, and ML designed the study setting. JK, PN, and A-MV performed the field research. PN provided the soil temperature calculations, A-MV performed the soil organic carbon stock calculations, and HR provided the calculations on LiDAR-based variables. JK, with support from KH, analysed the data. JK, with support from all of the co-authors, wrote the paper.

26 **Abstract**

27 In tundra, woody plants are expanding towards higher latitudes and altitudes due to increasingly
 28 favourable climatic conditions. Their expansion may also occur through increases in the coverage
 29 and height of the plants. These shifts may cascade further across the ecosystem, such as in the
 30 foundations of tundra: that is, in the soils. Yet, little is known about the effects woody plants have
 31 on local soil conditions. Here, we examined if the coverage and height of woody plants affect the
 32 growing-season soil moisture and temperature as well as soil organic carbon stocks. We carried out
 33 a field observation study in a dwarf shrub–dominated tundra and built a hierarchical model. We
 34 found that, after controlling for other possible factors influencing woody plants and soil conditions
 35 (namely, topography, snow, and the overall plant coverage), the coverage of woody plants inversely
 36 correlated with all three soil conditions. Yet, we found no link between the woody plant height to
 37 the soil variables. This indicates that woody plants affect local soil conditions in various ways,
 38 depending upon whether their expansion occurs through the growth of coverage or their height.
 39 Nevertheless, woody plants likely alter the very ground of the entire tundra system and feedback
 40 into the global climate system through the water, energy, and carbon cycles of tundra.

41 **Key words** dwarf shrubs, shrubification, snow, microclimate, carbon cycle, structural equation
 42 model, tundra, Arctic

43 **Introduction**

44 In tundra regions, climate change has led to an increase in woody plant dominance through, for
 45 instance, shrub expansion and shrubification (Myers-Smith et al., 2011). This results from
 46 increasingly favourable environmental conditions, such as rising growing-season temperatures,
 47 thicker snow cover, and increasing winter precipitation (Carrer, Pellizzari, Prendin, Pividori, &
 48 Brunetti, 2019; Hallinger, Manthey, & Wilmking, 2010). The expanding distribution and increasing
 49 coverage and height of woody plants carry the potential of affecting tundra ecosystems through
 50 species composition and disturbance frequency including fire activity (Jeffers, Bonsall, Watson, &
 51 Willis, 2012; Mod & Luoto, 2016; Scharnagl, Johnson, & Ebert-May, 2019). Moreover, taller
 52 woody plants may decrease the tundra albedo when their top branches reach the snow surface
 53 during winter. In spring, this may further result in earlier snowmelt substantially amplifying surface
 54 warming (Chapin et al., 2005; Rydsaa, Stordal, Bryn, & Tallaksen, 2017).

55 Plants are the key components at the interface between atmospheric and soil processes (Lorant et
 56 al., 2018; Parker, Subke, & Wookey, 2015; Robinson et al., 2019). Changes in tundra ecosystems
 57 are closely linked to the global climate system through water, energy, and carbon cycles (Cahoon et
 58 al., 2012). Through the processes in these cycles, the expansion of woody plants, the largest plant
 59 life form of tundra, is likely to lead to cascading effects across the tundra biome and beyond
 60 (Chapin et al., 2005; Myers-Smith et al., 2011). Yet, a gap in our knowledge exists regarding how
 61 woody plants modify soil conditions on the very substrate upon which they grow. Vegetation can,
 62 in general, influence the amount of vital resources and other soil conditions, such as the soil
 63 moisture, temperature, and carbon stocks, of tundra ecosystems via multiple pathways (Figure 1)
 64 (Aalto, le Roux, & Luoto, 2013). Thus, vegetation can be viewed as a key component in soil
 65 formation, although it remains insufficiently included in tundra soil research (Robinson et al.,
 66 2019).

67 Mountain tundra systems are characterised by a heterogeneous topography and seasonal snow cover
 68 (Billings, 1973). These factors play crucial roles on the spatial and temporal distribution of water
 69 and energy (Ayres et al., 2010; Kemppinen, Niittynen, Riihimäki, & Luoto, 2018; Williams,
 70 McNamara, & Chandler, 2009). Thus, winter conditions should be carefully considered in
 71 vegetation research conducted within seasonally snow-covered ecosystems (Niittynen & Luoto,
 72 2018). Wintertime snow conditions may carry knock-on effects influencing summertime vegetation
 73 and soil properties by affecting the length of the growing season, nutrient availability, and the
 74 hydrothermal condition of soils (Semenchuk et al., 2015; Walker et al., 1999; Williams et al., 2009).
 75 Thus, topography and shrub–snow relations should be considered when investigating the impact of
 76 woody plants on tundra soil conditions (Figure 1) (Beck, Kalmbach, Joly, Stien, & Nilsen, 2005;
 77 Myers-Smith et al., 2011).

78
 79 Figure 1. The mechanisms through which woody plants may affect soil conditions in tundra
 80 ecosystems.

81 Soil hydrothermal conditions (i.e., the soil microclimate) have received increasing attention since
82 they show spatio-temporal variability unrelated to macroclimatic trends (e.g., De Frenne et al.,
83 2019; Gardner, Maclean, & Gaston, 2019; Lembrechts et al., 2019). Biological factors such as
84 plants affect the hydrological and thermal properties of soils (Loranty et al., 2018; Robinson et al.,
85 2019). For instance, vegetation causes drying in soils through transpiration, used for growth and
86 reproduction (Horton & Hart, 1998), although water-use efficiency differs between plant species,
87 functional groups, and ecosystems (Tang et al., 2014). In tundra, woody plants intercept rainfall,
88 which, on a large scale, may decrease the overall water input into the ecosystem (Zwieback, Chang,
89 Marsh, & Berg, 2019). However, vegetation can also cause opposing effects by providing shade,
90 which in turn decreases not only the soil temperature, but also evaporation—that is, water
91 vaporisation at the soil surface (Aalto, Scherrer, Lenoir, Guisan, & Luoto, 2018). Yet, woody plants
92 in particular and their fundamental effects on the soil microclimate, especially on soil moisture,
93 remain insufficiently investigated.

94 The soil and vegetation conditions are integral parts of the tundra carbon cycle (Cahoon et al.,
95 2012). The slow decomposition rate of the cool tundra regions enables high-latitude ecosystems to
96 store a large amount of carbon (Hugelius et al., 2014), roughly 50% of the global belowground
97 organic carbon pool (Tarnocai et al., 2009). The expansion of woody plants is expected to increase
98 the aboveground carbon storage within tundra ecosystems, which may further alter the rate of
99 carbon cycling through changes in litter quality and biomass production (Myers-Smith & Hik,
100 2013). The shifts in vegetation composition towards a higher aboveground productivity may
101 unexpectedly lead to decreasing belowground carbon storage, possibly decreasing the overall
102 carbon storage of tundra ecosystems (Parker et al., 2015). Regardless of the direction of the effect,
103 the expansion of woody plants is likely to affect the tundra carbon cycle carrying possibly
104 consequences for the global carbon cycle (Cahoon et al., 2012). Yet, understanding how local soil

105 organic carbon stocks respond to the expected changes in the expansion of woody plants remains
106 woefully insufficient.

107 Dwarf shrub tundra forms a substantial part of the overall Arctic vegetation (Walker et al., 2017).
108 As a shortcoming, investigations of the effects of woody plant expansion have primarily focused on
109 tall, deciduous shrub species, whilst smaller, albeit more abundant, evergreen dwarf shrubs have
110 received less attention (Vowles & Björk, 2018). Nonetheless, dwarf shrub expansion appears
111 responsive to ongoing climate change (e.g. Buizer et al., 2012; Hallinger et al., 2010; Vuorinen et
112 al., 2017). Here, we carried out an observational study in a dwarf shrub-dominated tundra and built
113 a theory-based hierarchical model. We aimed to quantify the influence of woody plants on topsoil
114 conditions (namely, soil moisture, soil temperature, and soil organic carbon stocks) after controlling
115 for the effects of other factors (namely, the topography, wintertime snow depth, and overall
116 vascular plant abundance). Here, we attempted to answer to the following overarching question: Do
117 woody plants affect multiple soil conditions in tundra?

118

119 **Materials & methods**

120 *Study area*

121 We conducted this research in the Fennoscandian mountain tundra of north-western Finland
122 (69°03'N 20°51'E), in a study area covering 3 km² of a topographically heterogeneous landscape.
123 The study design comprised 171 study plots (1 m²) located above the treeline between two
124 mountains: Mount Saana and Mount Jehkas, which face north and south, respectively (Appendix 1).
125 On average, July is the warmest (11.2°C) and wettest (73 mm) month at the study site according to
126 measurements recorded at the Kilpisjärvi meteorological stations between 1981 and 2010 (Pirinen
127 et al., 2012) (Appendix 2).

128 In Fennoscandia, the expansion of woody plants results from increasing summer temperatures and
129 thicker snow cover during winter (Hallinger et al., 2010). In turn, the abundance and coverage of
130 ground-dwelling dwarf shrubs have increased (Maliniemi, Kapfer, Saccone, Skog, & Virtanen,
131 2018; Wilson & Nilsson, 2009). The main vegetation type in our study area was dwarf shrub–
132 dominated mountain heath with vegetation coverage consisting primarily of woody plant species.
133 The dominant woody plant species are evergreen *Vaccinium vitis-idaea* and *Empetrum nigrum*, and
134 deciduous *Betula nana* and *Vaccinium myrtillus*. Appendix 3 provides a full list of all woody plant
135 species found in our study plots.

136 Topography plays an important role in the distribution of woody plants in tundra systems (Myers-
137 Smith et al., 2011). The landscape in our study area is characterised by a rugged terrain, varying
138 mesotopography, and predominantly thin soils (Bruun et al., 2006). The soil surface is covered by
139 an organic soil layer, with a thickness varying by up to 70 cm (for more details, see Kemppinen et
140 al., 2018). Appendix 1 provides maps describing the topography of the study area.

141

142 *Study design*

143 In tundra, large areas of transition zones between habitats create variability in species composition
144 and ecosystem functions (Fletcher et al., 2012). We selected the location of our study plots using a
145 systematic grid approach covering the study area and its diversity of habitats as well as the
146 transition zones between them (Appendix 1). We recorded the locations of the plots using a hand-
147 held Global Navigation Satellite System receiver with an accuracy of up to ≤ 6 cm under optimal
148 conditions (GeoExplorer GeoXH 6000 Series; Trimble Inc., Sunnyvale, CA, USA).

149 We excluded sites situated in river channels (with the exception of meltwater channels) or boulder
150 fields, or those exposed to anthropogenic disturbance (i.e., trails). In addition to the systematic grid
151 with a 50-m minimum distance between sites, we intentionally situated 25 sites in snow-bank

environments and along windswept ridge tops to maximise the snow accumulation gradient in the data coverage. In all 171 plots, we recorded wintertime snow depth (at the maximum snow-depth timing in April), vegetation conditions (namely, plant coverage, woody plant dominance, and woody plant height), and the soil conditions (namely, soil moisture, soil temperature, and soil organic carbon stock).

Soil data

Soil moisture

We measured the soil moisture during the 2017 growing season (following Kemppinen et al., 2018). We measured the soil moisture using a hand-held time-domain reflectometry sensor (FieldScout TDR 300; Spectrum Technologies Inc., USA). Moisture was measured up to a depth of 7.5 cm as the volumetric water content (VWC%). The resolution of the device is 0.1% with a reported accuracy of ± 3.0 VWC%. We repeated the moisture measurements on five occasions (hereafter, campaigns; see Appendix 2). During each campaign, we took the mean over three measurements per plot to account for possible fine-scale moisture variation within a single plot. In subsequent analyses, we used the mean of these five campaigns to represent the overall soil moisture level during the growing season.

Soil temperature

We measured the soil temperature simultaneously with the soil moisture measurements. We used a hand-held digital temperature device (VWR-TD11; VWR International, USA). The resolution of the device is 0.1°C with a reported accuracy of $\pm 0.8^\circ\text{C}$. Temperature was measured at a depth of up to 7.5 cm. We took the temperature measurement once from the centre of each plot, repeating this

175 on five campaigns during the growing season (Appendix 2). In our analyses, we used the mean over
176 the five campaigns to represent the soil temperature during the growing season. We corrected the
177 possible effects of the timing of the measurements using data from miniature temperature loggers.
178 Details regarding the soil temperature corrections appear in Appendix 4.

179

180 Soil organic carbon stock

181 We measured the depth of the organic soil layer from three points in each plot using a metal probe.
182 In our analysis, we used the mean over the three measurement points per plot to represent the
183 organic layer depth of each plot. We collected soil samples of approximately 1 dl of soil material
184 from the organic and mineral soil layers using metal soil core cylinders (4–6 cm Ø, 5–7 cm in
185 height). Samples from the organic soil layer were collected from the topsoil, with samples from the
186 mineral soil layer taken from directly below the organic soil layer. The samples were collected from
187 the same proximity of each plot between 1 and 31 August 2016 and 2017. A detailed description of
188 the two sampling years appears in Appendix 5.

189 The laboratory analyses were carried out in the Laboratory of Geosciences and Geography and the
190 Laboratory of Forest Sciences at the University of Helsinki. We used a freeze-drying method to
191 remove soil moisture from the samples. The bulk density (kg/m^3) was estimated by dividing the dry
192 weight by the sample volume. The total carbon content (hereafter, C%) analyses were performed
193 using elemental analysers (vario MICRO cube & vario MAX cube; Elementar Analysensysteme
194 GmbH, Germany). Prior to the C% analysis, samples from the mineral soil layer were sieved
195 through a 2-mm plastic sieve. Samples from the organic soil layer were homogenised by
196 hammering the material into smaller particles.

197 Soil organic carbon stocks for the organic and mineral soil layers were estimated using Equation 1
198 (following Parker et al., 2015):

199

200 *Soil organic carbon stock* = $C\%/100 * \text{bulk density (kg/m}^3) * \text{layer depth (m)}$,

201 Equation 1.

202

203 We used the median C% and bulk density of the samples from the mineral soil layer to estimate the
 204 soil organic carbon stocks in all mineral soil layers (3% for C%, n = 54, and 830 kg/m³ for bulk
 205 density, n = 70). We assumed that this would reliably allow us to determine the soil mineral layer
 206 stocks given the relatively low variability in C% (0.4–6.5%) and the bulk density (470–1400
 207 kg/m³). We used the *in situ* measured mineral soil layer depth for each plot (relying on the mean
 208 over three measurements).

209 We did not measure C% from the samples taken from the organic soil layer from all sites. However,
 210 we measured the soil organic matter content (SOM%) using the loss-on-ignition method from the
 211 remaining sites (n = 52) (SFS3008, 1990). We calculated the soil organic matter stocks following
 212 Equation 1 and converted them into soil organic carbon stocks based on a relationship between C%
 213 and SOM% (Appendix 2). For this conversion, we used data from the study plots that had both C%
 214 and SOM% data based on samples from the organic soil layer (n = 118). The carbon fraction in the
 215 soil organic matter was calculated as 0.54 ($R^2 = 0.97$), similar to Parker et al. (2015). This was then
 216 used to estimate the soil organic carbon stock in the organic layer. We arrived at this fraction by
 217 regressing the soil organic carbon stock in the organic soil layer using the soil organic matter stock
 218 in the organic soil layer without the intercept.

219

220 *Vegetation data*

221 Woody plant dominance and height

222 We carried out a survey focusing on woody plants in which we visually estimated the coverage and
223 measured the median height across three measurements of each woody plant species in all plots
224 (Figure 2). Data on woody plants were collected from 23 to 27 July 2016 (146 plots) and completed
225 between 16 and 19 July 2017 (25 plots). The relative coverage of the woody plants was calculated
226 using the absolute coverage of all vascular plant species (hereafter, woody plant dominance).
227 In total, we found 20 woody plant species (Figure 2; Appendix 3). In the height measurements, we
228 excluded possible inflorescence to avoid any bias, particularly regarding the most ground-dwelling
229 species such as *Cassiope hypnoides* and *Linnea borealis*. Besides the prostrate *Salix* species
230 (namely, *Salix herbacea*, *S. polaris*, and *S. reticulata*), we grouped all erect *Salix* species into one
231 category (*Salix* spp.) given the large amount of *Salix* hybridisation. We followed the taxonomy put
232 forth by Hämet-Ahti, Suominen, Ulvinen, and Uotila (1998).

Figure 2. Woody plants of the dwarf shrub-dominated tundra. The relative coverage of the woody plants in relation to the total vascular plant coverage is shown as bars (A). The absolute woody plant coverage data divided between deciduous and evergreen species are presented as a frequency plot (B). The prevalence of the species ranks them from the most common (VACVIT = *Vaccinium vitis-idaea*) to the rarest (DRYOCT = *Dryas octopetala*) species occurring in the data. The hue intensity indicates the local point density. Species-specific coverage and median height data are shown as box plots (C). In the box plots, the notches and hinges represent the 25th, 50th, and 75th percentiles. In addition, the whiskers represent the 95% percentile interval and the points represent the outliers. The variability of coverage and height data in relation to each other are shown in the density plot (D). Full species names appear in Appendix 3.

244

245 Plant coverage

The link between the vegetation and the soil conditions must be acknowledged, particularly in climate–soil–vegetation studies (Porporato & Rodriguez-Iturbe, 2002). In addition to the woody plants, a variety of graminoids and forbs may influence the soil conditions in tundra (Aalto et al., 2013). Thus, we included the effect of the overall vascular plant coverage in the model to separate out the effects of woody plant dominance from the effects of overall plant abundance as well as to distinguish the effects of woody plants on soil moisture from the effects that soil moisture have on vascular plants (Kemppinen, Niittynen, Aalto, le Roux, & Luoto, 2019).

Vascular plant coverage data were collected between 16 July and 8 August 2017. We carried out a vegetation survey, in which we visually estimated the species-specific percentage coverage of each vascular plant species in all plots. In the analysis, we use the plot-specific absolute coverage of all vascular plant species (hereafter, plant coverage). In densely vegetated plots, the plant coverage may exceed 100%, since vegetation may grow in several layers.

258

259 *Snow data*

260 During winter, woody plants effectively capture drifting snow, which may alter the distribution of
261 snow (Lafleur & Humphreys, 2018). Consequently, if trapped, the accumulation of snow may lead
262 to thicker and more insulative snow cover in and around shrub patches compared to shrubless
263 patches (Sturm et al., 2001). Yet, this is unlikely for dwarf shrubs due to their prostrate stature
264 (Vowles & Björk, 2018). Nonetheless, snow cover—or the lack of it—may have consequences for
265 all woody plants regardless of their size (Hallinger et al., 2010; Phoenix & Bjerke, 2016).

266 We measured the snow depth to represent the winter conditions in our study system (Aalto et al.,
267 2018). We collected snow depth data between 13 and 17 April 2017 during the maximum snow
268 depth during the season. We measured the snow depth from the centre of each plot using an
269 aluminium probe.

270

271 *Topographic data*

272 We obtained the LiDAR-based digital terrain model (DTM) at a 2-m resolution from the open file
273 service of the National Land Survey of Finland (NLS, 2019). Based on the 2-m resolution DTM, we
274 calculated the elevation, radiation, the topographic wetness index (TWI), and the topographic
275 position index (TPI) (Appendix 1).

276

277 *Elevation*

278 Elevation represents the macroclimatic conditions of the system, which we assumed were reflected
279 in the snow depth, vegetation, and soil variables for our study system. Differences in the elevation
280 are followed by several environmental gradients, such as air temperature due to a lapse rate (i.e.,

281 general decrease in the air temperature with altitude). This, in turn, affects the coverage and height
282 of the vegetation (Riihimäki, Heiskanen, & Luoto, 2017), as well as the soil formation, soil
283 microclimate, and microbial and cryogenic activity (Amundson, Chadwick, & Sowers, 1989;
284 Dahlgren, Boettinger, Huntington, & Amundson, 1997; Trumbore, Chadwick, & Amundson, 1996).

285

286 Radiation

287 Solar radiation is distributed unevenly across the landscape due to the topographic variability. This
288 creates a strong radiation gradient between the north- and south-facing slopes in the study area (le
289 Roux, Aalto, & Luoto, 2013). We assumed that solar radiation positively correlated with both the
290 coverage and height of the vegetation variables as well as with the soil temperature (Aalto, le Roux,
291 & Luoto, 2014; Winkler et al., 2016).

292 We calculated the potential incoming solar radiation based on the three months of the growing
293 season (June, July, and August) using a tool in SAGA GIS v. 2.3.2 that measures the potential
294 incoming solar radiation. We considered the possible shadow effect of obstructing topographic
295 features using the sky view-factor option (Böhner & Antonic, 2009). We calculated the position of
296 the Sun for every fifth day using a 4-h interval. We used the lumped atmosphere option to calculate
297 the atmospheric transmittance.

298

299 Topographic wetness index

300 The topography controls the surface water flow and the accumulation of it (Beven & Kirkby, 1979).
301 We assumed that the water flow and accumulation for the landscape positively correlated with both
302 the coverage and the height of the vegetation, as well as the soil moisture and soil organic carbon
303 stock (Kemppinen et al., 2018; le Roux et al., 2013).

304 We calculated the topographic wetness index [TWI = $\ln(\text{SCA} / \text{local slope})$], a proxy for the water
 305 flow and accumulation, which can be used to model the variation in the soil moisture at fine-spatial
 306 scales (Kemppinen et al., 2018). The total catchment area (TCA) was calculated from a filled DTM
 307 using the multiple flow–direction algorithm (Freeman, 1991; Wang & Liu, 2006), which performs
 308 best in predicting volumetric water content in mountain tundra (Riihimäki, Kemppinen, Kopecký,
 309 & Luoto, 2019). The specific catchment area (SCA) was calculated assuming that the flow width
 310 equals the grid resolution (2 m) (i.e., $\text{SCA} = \text{TCA}/2$). The local slope was calculated using the
 311 algorithm by Zevenbergen and Thorne (1987).

312

313 Topographic position index

314 Topographic position affects the erosion, transportation, and accumulation of matter and energy in
 315 the landscape. We assumed that the topographic position associates with snow depth specifically in
 316 the study system (Billings & Bliss, 1959).

317 We calculated the topographic position index (TPI), based on the elevation difference between a
 318 plot and the surrounding elevation along a given radius (Agren, Lidberg, Stromgren, Ogilvie, &
 319 Arp, 2014). This describes the position of the plot on a topographic gradient—that is, a plot located
 320 on a ridge top (positive values), in a depression (negative), or on a slope or flat ground (close to
 321 zero). We calculated TPI using 30-m radii based on an unfilled DTM (following Kemppinen et al.,
 322 2018).

323

324 *Statistical analyses*

325 We used structural equation modelling (SEM) to understand the hierarchy of the environmental
 326 variables controlling the soil conditions in tundra systems. SEM is a statistical modelling method

that can be used to understand complex multivariate relationships, such as indirect effects and cascading effects (Grace, Anderson, Olff, & Scheiner, 2010). SEM produces a single causal network in which several response variables and predictors are combined by probabilistic models (Lefcheck, 2016). This enables the testing of hypothesised causal relationships, here presented as arrows. In SEM, a variable can be both a predictor and a response variable. This enables determining if a predictor has a direct or mediating effect—that is, if a variable serves as a mediator. Thus, SEM allows the simultaneous evaluation of several causal structures. Results are expressed as standardised regression coefficients, which allows for the direct comparison of the estimated effects (Lefcheck, 2016). We used the *piecewiseSEM* package in R, version 3.5.1 (Lefcheck, 2016; R Development Core Team, 2016).

We log-transformed all three vegetation variables (plant coverage, woody plant dominance, and woody plant height) as well as the soil moisture and soil organic carbon stock variables to reduce the heteroscedasticity in the component models. This decision was based on the visual interpretation of the histograms of the linear model residuals for each response variable.

We also calculated the bivariate Spearman correlations between all variables. Due to the high correlation (-0.72) between the snow depth and TPI variables (Appendix 6), we excluded TPI from those models that used snow depth as a predictor (i.e., all vegetation and soil models).

We fitted all hypothesised paths (i.e., component models) using a first-order multiple linear regression model. The paths included both the direct pathways from the predictors (topography) and pathways through the mediators (snow depth and vegetation variables) to the response variables (soil variables). We created SEM consisting of seven component models as follows. 1) Snow depth was modelled using elevation and TPI. 2) Plant coverage, 3) woody plant dominance, and 4) woody plant height were modelled using elevation, radiation, TWI, and snow depth. 5) Soil moisture, 6) soil temperature, and 7) soil organic carbon stock were modelled using all predictors and mediators (for a detailed model structure, see Appendix 7).

352 We assumed that correlations might exist between the error terms of the soil and vegetation
353 variables. Thus, we updated the model to account for all possible residual correlations between the
354 vegetation variables and between the soil variables.

355

356 *Data deposition*

357 Field data will be made openly available in Zenodo once this manuscript is accepted, and we will
358 include the link here.

359

360 **Results**

361 The R^2 values for the seven component models ranged from 0.09 to 0.54 (Figure 3; for detailed
362 results of the model, see Appendix 7). According to tests of directed separation, we excluded from
363 the model only one path, which was a link between woody plant height and TPI.

364 Soil temperature was the only soil variable that linked to plant coverage (standardised coefficient =
365 -0.30, $P = 0.00$). Woody plant dominance negatively correlated with all soil conditions: soil
366 moisture, soil temperature, and soil organic carbon stock (standardised coefficients = -0.16; -0.22; -
367 0.27, $P = 0.04$; 0.00; 0.00). None of the soil conditions were affected by woody plant height. The
368 covariance between soil moisture and soil organic carbon stock was positive.

369 We found no significant direct link ($P < 0.05$) for snow depth to the soil conditions. Yet, the snow
370 depth negatively affected plant coverage and woody plant dominance (standardised coefficients = -
371 0.22; -0.17, $P = 0.01$; 0.02), respectively.

Figure 3. Woody plants constructing tundra soils. Results of a structural equation model with seven component models. Here, we only present relationships with $P < 0.05$. The arrows show the standardised regression slopes associated with the links. Double-headed arrows represent

376 correlations between error terms. For further details and relationships with $P \geq 0.05$, see Appendix
377 7.

378

379 **Discussion**

380 We found that woody plants such as dwarf shrubs affect the soil moisture, soil temperature, and soil
381 carbon stock distribution in the tundra ecosystem. In addition to woody plants, we considered the
382 direct and indirect effects of the topography, wintertime snow depth, and overall vascular plant
383 coverage on the tundra soil conditions.

384

385 *Effects of woody plants on the soil moisture*

386 We found that the dominance of woody plants directly related to less soil moisture in the topsoil.
387 However, our results indicated no relationship between woody plant height and soil moisture. This
388 suggests that the expansion of woody plants may carry different consequences on the soil moisture
389 depending upon whether the expansion is realised through the coverage or the height of woody
390 plants.

391 Our findings are relevant in light of previous studies, which found that the expansion of woody
392 plants may lead to an increased evapotranspiration and intercepting precipitation (Bonfils et al.,
393 2012; Pearson et al., 2013; Zwieback et al., 2019). Previous studies reached conclusions similar to
394 our fine-scale investigation: that is, soil moisture is generally lower in woody plant habitats
395 compared to other tundra habitats (Ge, Lafleur, & Humphreys, 2017; Lafleur & Humphreys, 2018).

396 The negative effect of woody plants on the soil moisture could be explained by an increased
397 transpiration. Transpiration also appears sensitive to the height of woody plants, since taller plants
398 transpire more than smaller plants (Bonfils et al., 2012). In tundra, evergreen woody plants may

399 cause less evaporation, since they cast shade on the soil beneath them throughout the growing
400 season. Yet, deciduous woody plant transpiration is affected by phenology, as transpiration may
401 overcome evaporation as soon as buds burst into leaves (Bonfils et al., 2012). The expansion of
402 woody plants can increase water vapour in the atmosphere, because woody plants transpire water
403 more efficiently than barren tundra (Swann, Fung, Levis, Bonan, & Doney, 2010). An increased
404 transpiration, in turn, may amplify the greenhouse effect of woody plants alongside changes in the
405 albedo (Swann et al., 2010).

406 We found no relationship between vascular plant coverage and soil moisture. This shows that we
407 could 1) separate the effects of woody plants from the overall effects of vascular plants and 2)
408 distinguish between the effects of woody plants on the soil moisture from the effects of soil
409 moisture on vascular plants. Thus, the expansion of woody plants may affect the soil moisture
410 beyond that resulting from higher overall vegetation coverage. Therefore, we stress that it is crucial
411 to consider carefully which plant–soil feedbacks are essential in next-generation soil hydrology
412 models (Porporato & Rodriguez-Iturbe, 2002; Robinson et al., 2019).

413

414 *Effects of woody plants on soil temperature*

415 We found that plants in general lower the soil temperatures in tundra, given that both the overall
416 plant coverage and woody plant dominance decreased the soil temperature. In treeless ecosystems
417 (such as tundra), vegetation in general cools the soils below through shading (Aalto et al., 2013;
418 Myers-Smith & Hik, 2013). In addition, both deciduous and evergreen woody plants appear to carry
419 a cooling effect on soil temperatures during the growing season (Lorant et al., 2018).

420 The interactions between the macroclimate, vegetation, and microclimate are strongly linked to
421 each other. Because the macroclimate in tundra regions is warming, woody plants are expected to
422 expand (Myers-Smith et al., 2015). In turn, they alter the microclimate as our results indicate.

423 Woody plants can carry strong effects on the radiation and the mixing of air; thus, abundant
 424 vegetation may create heterogeneous microclimates (De Frenne et al., 2019). Tall, erect species can
 425 potentially cause wind turbulence, and, in turn, enable the release of latent heat from the soil to the
 426 open atmosphere (Bonfils et al., 2012). Small, prostrate species such as cushion plants, however,
 427 grow closer to ground and are aerodynamic compared to taller species, which may lead to less
 428 turbulence at the ground surface.

429

430 *Effects of woody plants on soil organic carbon stock*

431 We found that the dominance of woody plants directly relates to lower soil organic carbon stocks.
 432 Yet, we found no relationship between woody plant height and the soil organic carbon stock (Figure
 433 3), although we did detect a significant positive bivariate correlation between these two variables
 434 (Appendix 6). These findings show that the expansion of woody plants (i.e., increasing coverage or
 435 height) may influence the tundra carbon cycle in various ways. This may explain why no consensus
 436 currently exists regarding how the expansion of woody plants may affect the tundra carbon cycle.

437 Other studies found that the expansion of woody plants may lead to either an increase (Qian,
 438 Joseph, & Zeng, 2010) or decrease (Cahoon et al., 2012) in the soil organic carbon, or carry no
 439 effect at all (Sistla et al., 2013). Woody plants can cycle carbon more rapidly compared to
 440 herbaceous plants (Cahoon et al., 2012; Lafleur & Humphreys, 2018). The expansion of woody
 441 plants in tundra may result in larger, yet less decomposable, litter inputs into the soil (DeMarco,
 442 Mack, & Bret-Harte, 2014). By contrast, in warmer macroclimatic conditions, large-scale expansion
 443 may lead to faster soil decomposition depending upon the type of habitat the woody plant species
 444 expands to (Ge et al., 2017). Plant root properties and rhizosphere processes also influence soil
 445 organic carbon stocks (Parker et al., 2015). For example, root longevity (i.e., age) is lower in
 446 graminoids than in shrubs (Iversen et al., 2015), resulting in slower carbon cycling in soils under

shrub-dominated vegetation. In addition, the roots of woody plants are shallower than those of graminoids; thus, an increase in woody plant coverage may result in smaller carbon inputs from roots to deeper soil layers (Ylänne, Olofsson, Oksanen, & Stark, 2018).

We speculate that our findings can be explained by a combination of all of these factors. Woody plant dominance may lead to decreased soil organic carbon stocks due to a faster decomposition, a more active soil microbiota, and smaller carbon inputs from roots to the soil (Ge et al., 2017). Our results might also be explained by the covariance of soil organic carbon stocks with the soil moisture. In this study, the wettest soils were most often dominated by non-woody plants. Specifically, the plots with tall woody plants had a relatively low coverage, possibly explaining why we found no link between woody plant height and soil organic carbon stock in the model.

Quantifying soil organic carbon may introduce some uncertainties to the model (Hugelius et al., 2014). Some of our study sites were located in tundra meadows (<10%), in which the uppermost part (roughly 0–30 cm) of the soil can in some parts represent a mixture of both organic and mineral layers. Thus, distinguishing the organic layer from the mineral might be reflected in the estimations of the soil organic carbon stocks.

Indirect effects of snow on soil conditions

We found that wintertime snow depth affected summertime soil conditions indirectly through the vegetation properties. These results show that snow depth directly correlated with overall plant coverage and woody plant dominance. Yet, we found no direct effects of snow depth on the soil conditions.

In high-latitude mountainous landscapes, the winter conditions have far-reaching effects long into the summer, since a thick snow cover affects the vegetation through plant development and productivity (Billings & Bliss, 1959), and by affecting plant functional traits, such as the specific

471 leaf area or the dry-matter content (Happonen et al., 2019). Wintertime shrub–snow relationships
 472 affect wintertime soil conditions, such as wintertime soil temperatures, shown to positively
 473 feedback on shrubs (Myers-Smith & Hik, 2013; Sturm et al., 2005). For example, warming winter
 474 conditions are as relevant as summertime changes in the temperature for the growth of *Betula nana*
 475 (Hollesen et al., 2015).

476 Our results regarding snow were unexpected, since previous studies found that wintertime snow
 477 conditions affect multiple soil conditions, particularly the spatio-temporal variability of the
 478 growing-season soil moisture (Ayres et al., 2010), even when controlling for the effects of
 479 topographical variation (Williams et al., 2009). Nevertheless, a careful consideration of snow in
 480 plant–soil interactions remains crucial wherever snow is present (Niittynen, Heikkinen, & Luoto,
 481 2018). In fact, several experimental and observational studies have linked wintertime snow patterns
 482 to ecosystem processes through changing the soil moisture availability (e.g. Ayres et al., 2010;
 483 Barichivich et al., 2014; Plaza et al., 2019).

484

485 *In summary*

486 We investigated the effects of woody plants on multiple soil conditions in tundra. Through this
 487 hierarchical approach, we controlled for the influence of other possible factors—namely, the
 488 topography, wintertime snow depth, and overall vascular plant conditions. Our study benefitted
 489 from a hierarchical framework, since previous studies found it challenging to test whether the
 490 effects found resulted from changing vegetation properties or from, for instance, the underlying
 491 topography (Crofts, Drury, & McLaren, 2018). Thus, we recommend future studies consider SEM
 492 in their analyses when investigating hierarchical systems (Lefcheck, 2016).

493 Our results suggest that the dominance of woody plants negatively affects the soil moisture, soil
 494 temperature, and soil organic carbon stocks. Yet, the height of woody plants did not affect the soil

conditions in our model when considering the coverage of woody plants. These findings indicate that the effects of woody plants on tundra soil conditions depend upon whether expansion occurs in terms of the coverage or height. Thus, future studies should consider quantifying multiple dimensions of woody plants to describe their expansion in tundra ecosystems.

Acknowledgements

The authors thank all past and present members of the BioGeoClimate Modelling Lab and the Arctic Microbial Ecology group at the University of Helsinki for their assistance during field and laboratory work, and the staff at the Kilpisjärvi Biological Station for their support. Dr. Aleksandra M. Lewandowska and Dr. Dorothee Hodapp are greatly acknowledged for their help and encouragement regarding SEM. We are also grateful to Vanessa Fuller for assistance with English-language revision. We also thank Professor Gustaf Olsson for sharing his knowledge of scientific writing. The National Land Survey of Finland and the Finnish Meteorological Institute gratefully provided the LiDAR and meteorological data.

Funding

JK and HR were funded by the Doctoral Programme in Geosciences at the University of Helsinki. PN was funded by the Kone Foundation. A-MV was funded by Societas pro Fauna et Flora Fennica, the Otto Malm Foundation, and the Väisälä Fund. KH was funded by the Doctoral Programme in Wildlife Biology Research at the University of Helsinki. JA was funded by the Academy of Finland (project no. 307761). Field campaigns were funded by the Academy of Finland (project no. 286950).

Permissions

Permission to carry out fieldwork was granted by Metsähallitus.

References

- Aalto, J., le Roux, P. C., & Luoto, M. (2013). Vegetation Mediates Soil Temperature and Moisture in Arctic-Alpine Environments. *Arctic Antarctic and Alpine Research*, 45(4), 429-439. doi:10.1657/1938-4246-45.4.429
- Aalto, J., le Roux, P. C., & Luoto, M. (2014). The meso-scale drivers of temperature extremes in high-latitude Fennoscandia. *Climate Dynamics*, 42(1-2), 237-252. doi:10.1007/s00382-012-1590-y
- Aalto, J., Scherrer, D., Lenoir, J., Guisan, A., & Luoto, M. (2018). Biogeophysical controls on soil-atmosphere thermal differences: implications on warming Arctic ecosystems. *Environmental Research Letters*, 13(7), 074003. doi:ARTN 074003 10.1088/1748-9326/aac83e
- Agren, A. M., Lidberg, W., Stromgren, M., Ogilvie, J., & Arp, P. A. (2014). Evaluating digital terrain indices for soil wetness mapping - a Swedish case study. *Hydrology and Earth System Sciences*, 18(9), 3623-3634. doi:10.5194/hess-18-3623-2014
- Amundson, R. G., Chadwick, O. A., & Sowers, J. M. (1989). A comparison of soil climate and biological activity along an elevation gradient in the eastern Mojave Desert. *Oecologia*, 80(3), 395-400. doi:10.1007/BF00379042
- Ayres, E., Nkem, J. N., Wall, D. H., Adams, B. J., Barrett, J. E., Simmons, B. L., . . . Fountain, A. G. (2010). Experimentally increased snow accumulation alters soil moisture and animal community structure in a polar desert. *Polar Biology*, 33(7), 897-907. doi:10.1007/s00300-010-0766-3
- Barichivich, J., Briffa, K. R., Myneni, R., van der Schrier, G., Dorigo, W., Tucker, C. J., . . . Melvin, T. M. (2014). Temperature and Snow-Mediated Moisture Controls of Summer Photosynthetic Activity in Northern Terrestrial Ecosystems between 1982 and 2011. *Remote Sensing*, 6(2), 1390-1431. doi:10.3390/rs6021390
- Beck, P. S. A., Kalmbach, E., Joly, D., Stien, A., & Nilsen, L. (2005). Modelling local distribution of an Arctic dwarf shrub indicates an important role for remote sensing of snow cover. *Remote Sensing of Environment*, 98(1), 110-121. doi:10.1016/j.rse.2005.07.002
- Beven, K. J., & Kirkby, M. J. (1979). A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Bulletin*, 24:1, 43-69.
- Billings, W. D. (1973). Arctic and Alpine Vegetations - Similarities, Differences, and Susceptibility to Disturbance. *Bioscience*, 23(12), 697-704. doi:Doi 10.2307/1296827
- Billings, W. D., & Bliss, L. C. (1959). An Alpine Snowbank Environment and Its Effects on Vegetation, Plant Development, and Productivity. *Ecology*, 40(3), 388-397. doi:Doi 10.2307/1929755
- Bonfils, C. J. W., Phillips, T. J., Lawrence, D. M., Cameron-Smith, P., Riley, W. J., & Subin, Z. M. (2012). On the influence of shrub height and expansion on northern high latitude climate. *Environmental Research Letters*, 7(1), 015503. doi:Artn 015503 10.1088/1748-9326/7/1/015503

- Bruun, H. H., Moen, J., Virtanen, R., Grytnes, J. A., Oksanen, L., & Angerbjorn, A. (2006). Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of Vegetation Science*, 17(1), 37-46. doi:DOI 10.1111/j.1654-1103.2006.tb02421.x
- Buizer, B., Weijers, S., van Bodegom, P. M., Alsos, I. G., Eidesen, P. B., van Breda, J., . . . Rozema, J. (2012). Range shifts and global warming: ecological responses of *Empetrum nigrum* L. to experimental warming at its northern (high Arctic) and southern (Atlantic) geographical range margin. *Environmental Research Letters*, 7(2), 025501. doi:Artn 025501 10.1088/1748-9326/7/2/025501
- Böhner, J., & Antonic, O. (2009). *Land surface parameters specific to topo-climatology*. Amsterdam: Elsevier.
- Cahoon, S. M., Sullivan, P. F., Shaver, G. R., Welker, J. M., Post, E., & Holyoak, M. (2012). Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. *Ecology Letters*, 15(12), 1415-1422. doi:10.1111/j.1461-0248.2012.01865.x
- Carrer, M., Pellizzari, E., Prendin, A. L., Pividori, M., & Brunetti, M. (2019). Winter precipitation - not summer temperature - is still the main driver for Alpine shrub growth. *Science of the Total Environment*, 682, 171-179. doi:10.1016/j.scitotenv.2019.05.152
- Chapin, F. S., 3rd, Sturm, M., Serreze, M. C., McFadden, J. P., Key, J. R., Lloyd, A. H., . . . Welker, J. M. (2005). Role of land-surface changes in arctic summer warming. *Science*, 310(5748), 657-660. doi:10.1126/science.1117368
- Crofts, A. L., Drury, D. O., & McLaren, J. R. (2018). Changes in the understory plant community and ecosystem properties along a shrub density gradient. *Arctic Science*, 4(4), 485-498. doi:10.1139/as-2017-0026
- Dahlgren, R. A., Boettinger, J. L., Huntington, G. L., & Amundson, R. G. (1997). Soil development along an elevational transect in the western Sierra Nevada, California. *Geoderma*, 78(3-4), 207-236. doi:Doi 10.1016/S0016-7061(97)00034-7
- De Frenne, P., Zellweger, F., Rodriguez-Sanchez, F., Scheffers, B. R., Hylander, K., Luoto, M., . . . Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nat Ecol Evol*, 3(5), 744-749. doi:10.1038/s41559-019-0842-1
- DeMarco, J., Mack, M. C., & Bret-Harte, M. S. (2014). Effects of arctic shrub expansion on biophysical vs. biogeochemical drivers of litter decomposition. *Ecology*, 95(7), 1861-1875.
- Fletcher, B. J., Gornall, J. L., Poyatos, R., Press, M. C., Stoy, P. C., Huntley, B., . . . Phoenix, G. K. (2012). Photosynthesis and productivity in heterogeneous arctic tundra: consequences for ecosystem function of mixing vegetation types at stand edges. *Journal of Ecology*, 100(2), 441-451. doi:10.1111/j.1365-2745.2011.01913.x
- Freeman, T. G. (1991). Calculating Catchment-Area with Divergent Flow Based on a Regular Grid. *Computers & Geosciences*, 17(3), 413-422. doi:Doi 10.1016/0098-3004(91)90048-I
- Gardner, A. S., Maclean, I. M., & Gaston, K. J. (2019). Climatic predictors of species distributions neglect biophysiological meaningful variables. *Diversity & Distributions*.
- Ge, L., Lafleur, P. M., & Humphreys, E. R. (2017). Respiration from soil and ground cover vegetation under tundra shrubs. *Arctic Antarctic and Alpine Research*, 49(4), 537-550. doi:10.1657/Aaar0016-064
- Grace, J. B., Anderson, T. M., Olff, H., & Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. *Ecological Monographs*, 80(1), 67-87. doi:Doi 10.1890/09-0464.1
- Hallinger, M., Manthey, M., & Wilmking, M. (2010). Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytol*, 186(4), 890-899. doi:10.1111/j.1469-8137.2010.03223.x
- Happonen, K., Aalto, J., Kempainen, J., Niittynen, P., Virkkala, A.-M., & Luoto, M. J. B. (2019). Snow is an important control of plant community functional composition. 564583.

- Hollesen, J., Buchwal, A., Rachlewicz, G., Hansen, B. U., Hansen, M. O., Stecher, O., & Elberling, B. J. G. C. B. (2015). Winter warming as an important co-driver for *Betula nana* growth in western Greenland during the past century. *21*(6), 2410-2423.
- Horton, J. L., & Hart, S. C. (1998). Hydraulic lift: a potentially important ecosystem process. *Trends Ecol Evol*, *13*(6), 232-235.
- Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J. W., Schuur, E. A. G., Ping, C. L., . . . Kuhry, P. (2014). Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. *Biogeosciences*, *11*(23), 6573-6593. doi:10.5194/bg-11-6573-2014
- Hämet-Ahti, L., Suominen, J., Ulvinen, T., & Uotila, P. (1998). Retkeilykasvio (Field Flora of Finland, in Finnish). *Finnish Museum of Natural History, Botanical Museum*. 656p.
- Iversen, C. M., Sloan, V. L., Sullivan, P. F., Euskirchen, E. S., McGuire, A. D., Norby, R. J., . . . Wullschleger, S. D. (2015). The unseen iceberg: plant roots in arctic tundra. *New Phytol*, *205*(1), 34-58. doi:10.1111/nph.13003
- Jeffers, E. S., Bonsall, M. B., Watson, J. E., & Willis, K. J. (2012). Climate change impacts on ecosystem functioning: evidence from an *Empetrum* heathland. *New Phytol*, *193*(1), 150-164. doi:10.1111/j.1469-8137.2011.03907.x
- Kemppinen, J., Niittynen, P., Aalto, J., le Roux, P. C., & Luoto, M. (2019). Water as a resource, stress and disturbance shaping tundra vegetation. *Oikos, Accepted Author Manuscript*. doi:10.1111/oik.05764
- Kemppinen, J., Niittynen, P., Riihimäki, H., & Luoto, M. (2018). Modelling soil moisture in a high-latitude landscape using LiDAR and soil data. *Earth Surface Processes and Landforms*, *43*(5), 1019-1031. doi:10.1002/esp.4301
- Lafleur, P. M., & Humphreys, E. R. (2018). Tundra shrub effects on growing season energy and carbon dioxide exchange. *Environmental Research Letters*, *13*(5), 055001. doi:ARTN 055001
- 10.1088/1748-9326/aab863
- le Roux, P. C., Aalto, J., & Luoto, M. (2013). Soil moisture's underestimated role in climate change impact modelling in low-energy systems. *Glob Chang Biol*, *19*(10), 2965-2975. doi:10.1111/gcb.12286
- Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573-579. doi:10.1111/2041-210x.12512
- Lembrechts, J. J., Lenoir, J., Roth, N., Hattab, T., Milbau, A., Haider, S., . . . Biogeography. (2019). Comparing temperature data sources for use in species distribution models: From in-situ logging to remote sensing.
- Loranty, M. M., Abbott, B. W., Blok, D., Douglas, T. A., Epstein, H. E., Forbes, B. C., . . . Malhotra, A. (2018). *Reviews and syntheses: Changing ecosystem influences on soil thermal regimes in northern high-latitude permafrost regions* (1810-6285). Retrieved from
- Maliniemi, T., Kapfer, J., Saccone, P., Skog, A., & Virtanen, R. (2018). Long-term vegetation changes of treeless heath communities in northern Fennoscandia: Links to climate change trends and reindeer grazing. *Journal of Vegetation Science*.
- Mod, H. K., & Luoto, M. (2016). Arctic shrubification mediates the impacts of warming climate on changes to tundra vegetation. *Environmental Research Letters*, *11*(12), 124028. doi:Artn 124028
- 10.1088/1748-9326/11/12/124028
- Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S. A., Wilmsking, M., Hallinger, M., Blok, D., . . . Vellend, M. (2015). Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, *5*(9), 887-891. doi:10.1038/nclimate2697

- Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., . . . Hik, D. S. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, 6(4), 15. doi:Artn 045509
- 10.1088/1748-9326/6/4/045509
- Myers-Smith, I. H., & Hik, D. S. (2013). Shrub canopies influence soil temperatures but not nutrient dynamics: An experimental test of tundra snow-shrub interactions. *Ecol Evol*, 3(11), 3683-3700. doi:10.1002/ece3.710
- Niittynen, P., Heikkinen, R. K., & Luoto, M. (2018). Snow cover is a neglected driver of Arctic biodiversity loss. *Nature Climate Change*, 8(11), 997-+. doi:10.1038/s41558-018-0311-x
- Niittynen, P., & Luoto, M. (2018). The importance of snow in species distribution models of arctic vegetation. *Ecography*, 41(6), 1024-1037. doi:10.1111/ecog.03348
- NLS. (2019). National Land Survey of Finland. <https://www.maanmittauslaitos.fi/en/maps-and-spatial-data/expert-users/product-descriptions/elevation-model-2-m>, Access date: 19.4.2019.
- Parker, T. C., Subke, J. A., & Wookey, P. A. (2015). Rapid carbon turnover beneath shrub and tree vegetation is associated with low soil carbon stocks at a subarctic treeline. *Global Change Biology*, 21(5), 2070-2081. doi:10.1111/gcb.12793
- Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S. A., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, 3(7), 673-677. doi:10.1038/Nclimate1858
- Phoenix, G. K., & Bjerke, J. W. (2016). Arctic browning: extreme events and trends reversing arctic greening. *Glob Chang Biol*, 22(9), 2960-2962. doi:10.1111/gcb.13261
- Pirinen, P., Simola, H., Aalto, J., Kaukoranta, J.-P., Karlsson, P., & Ruuhela, R. (2012). *Climatological statistics of Finland 1981–2010*. Retrieved from Helsinki:
- Plaza, C., Pegoraro, E., Bracho, R., Celis, G., Crummer, K. G., Hutchings, J. A., . . . Salmon, V. G. (2019). Direct observation of permafrost degradation and rapid soil carbon loss in tundra. *Nature Geoscience*, 12(8), 627.
- Porporato, A., & Rodriguez-Iturbe, I. (2002). Ecohydrology - a challenging multidisciplinary research perspective. *Hydrological Sciences Journal-Journal Des Sciences Hydrologiques*, 47(5), 811-821. doi:Doi 10.1080/02626660209492985
- Qian, H. F., Joseph, R., & Zeng, N. (2010). Enhanced terrestrial carbon uptake in the Northern High Latitudes in the 21st century from the Coupled Carbon Cycle Climate Model Intercomparison Project model projections. *Global Change Biology*, 16(2), 641-656. doi:10.1111/j.1365-2486.2009.01989.x
- R Development Core Team. (2016). The R Project for Statistical Computing, Vienna, Austria. R Development Core Team. Retrieved from <<https://www.r-project.org/>>
- Riihimäki, H., Heiskanen, J., & Luoto, M. (2017). The effect of topography on arctic-alpine aboveground biomass and NDVI patterns. *International journal of applied earth observation geoinformation*, 56, 44-53.
- Riihimäki, H., Kemppinen, J., Kopecký, M., & Luoto, M. (2019). Modelling performance of the Topographic Wetness Index is affected by grid resolution and flow-routing algorithm. *Under review*.
- Robinson, D. A., Hopmans, J. W., Filipovic, V., van der Ploeg, M., Lebron, I., Jones, S. B., . . . Tuller, M. (2019). Global environmental changes impact soil hydraulic functions through biophysical feedbacks. *Glob Chang Biol*, 25(6), 1895-1904. doi:10.1111/gcb.14626
- Rydsaa, J. H., Stordal, F., Bryn, A., & Tallaksen, L. M. (2017). Effects of shrub and tree cover increase on the near-surface atmosphere in northern Fennoscandia. *Biogeosciences*, 14(18), 4209-4227. doi:10.5194/bg-14-4209-2017
- Scharnagl, K., Johnson, D., & Ebert-May, D. (2019). Shrub expansion and alpine plant community change: 40-year record from Niwot Ridge, Colorado. *Plant Ecology & Diversity*, 1-10.

- Semenchuk, P. R., Elberling, B., Amtorp, C., Winkler, J., Rumpf, S., Michelsen, A., & Cooper, E. J. (2015). Deeper snow alters soil nutrient availability and leaf nutrient status in high Arctic tundra. *Biogeochemistry*, 124(1-3), 81-94. doi:10.1007/s10533-015-0082-7
- SFS3008. (1990). SFS 3008, Determination of total residue and total fixed residue in water, sludge and sediment. *Finnish Standards Association, Helsinki, Finland*, 3.
- Sistla, S. A., Moore, J. C., Simpson, R. T., Gough, L., Shaver, G. R., & Schimel, J. P. (2013). Long-term warming restructures Arctic tundra without changing net soil carbon storage. *Nature*, 497(7451), 615-+. doi:10.1038/nature12129
- Sturm, M., Holmgren, J., McFadden, J. P., Liston, G. E., Chapin III, F. S., & Racine, C. H. J. J. o. C. (2001). Snow–shrub interactions in Arctic tundra: a hypothesis with climatic implications. *14*(3), 336-344.
- Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., . . . Romanovsky, V. E. (2005). Winter biological processes could help convert arctic tundra to shrubland. *Bioscience*, 55(1), 17-26. doi:Doi 10.1641/0006-3568(2005)055[0017:Wbpchc]2.0.Co;2
- Swann, A. L., Fung, I. Y., Levis, S., Bonan, G. B., & Doney, S. C. (2010). Changes in Arctic vegetation amplify high-latitude warming through the greenhouse effect. *Proceedings of the National Academy of Sciences of the United States of America*, 107(4), 1295-1300. doi:10.1073/pnas.0913846107
- Tang, X., Li, H., Desai, A. R., Nagy, Z., Luo, J., Kolb, T. E., . . . Kutsch, W. J. S. r. (2014). How is water-use efficiency of terrestrial ecosystems distributed and changing on Earth? , 4, 7483.
- Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., & Zimov, S. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, 23(2). doi:Artn Gb2023
- 10.1029/2008gb003327
- Trumbore, S. E., Chadwick, O. A., & Amundson, R. (1996). Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science*, 272(5260), 393-396. doi:DOI 10.1126/science.272.5260.393
- Walker, D. A., Daniëls, F. J., Matveyeva, N. V., Šibík, J., Walker, M. D., Breen, A. L., . . . Hennekens, S. (2017). Circumpolar Arctic Vegetation Classification. *Phytocoenologia*.
- Walker, M. D., Walker, D. A., Welker, J. M., Arft, A. M., Bardsley, T., Brooks, P. D., . . . Turner, P. L. (1999). Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrological Processes*, 13(14-15), 2315-2330. doi:Doi 10.1002/(Sici)1099-1085(199910)13:14/15<2315::Aid-Hyp888>3.0.Co;2-A
- Wang, L., & Liu, H. (2006). An efficient method for identifying and filling surface depressions in digital elevation models for hydrologic analysis and modelling. *International Journal of Geographical Information Science*, 20(2), 193-213. doi:10.1080/13658810500433453
- Williams, C. J., McNamara, J. P., & Chandler, D. G. (2009). Controls on the temporal and spatial variability of soil moisture in a mountainous landscape: the signature of snow and complex terrain. *Hydrology and Earth System Sciences*, 13(7), 1325-1336. doi:DOI 10.5194/hess-13-1325-2009
- Wilson, S. D., & Nilsson, C. (2009). Arctic alpine vegetation change over 20 years. *Global Change Biology*, 15(7), 1676-1684. doi:10.1111/j.1365-2486.2009.01896.x
- Winkler, M., Lamprecht, A., Steinbauer, K., Hulber, K., Theurillat, J. P., Breiner, F., . . . Pauli, H. (2016). The rich sides of mountain summits - a pan-European view on aspect preferences of alpine plants. *Journal of Biogeography*, 43(11), 2261-2273. doi:10.1111/jbi.12835
- Vowles, T., & Björk, R. G. J. J. o. E. (2018). Implications of evergreen shrub expansion in the Arctic.

757 Vuorinen, K. E., Oksanen, L., Oksanen, T., Pyykönen, A., Olofsson, J., & Virtanen, R. J. G. c. b.
758 (2017). Open tundra persist, but arctic features decline—Vegetation changes in the warming
759 Fennoscandian tundra. *23*(9), 3794-3807.

760 Yläanne, H., Olofsson, J., Oksanen, L., & Stark, S. (2018). Consequences of grazer-induced
761 vegetation transitions on ecosystem carbon storage in the tundra. *Functional Ecology*, *32*(4),
762 1091-1102.

763 Zevenbergen, L. W., & Thorne, C. R. (1987). Quantitative-Analysis of Land Surface-Topography.
764 *Earth Surface Processes and Landforms*, *12*(1), 47-56. doi:DOI 10.1002/esp.3290120107

765 Zwieback, S., Chang, Q., Marsh, P., & Berg, A. J. E. R. L. (2019). Shrub tundra ecohydrology:
766 rainfall interception is a major component of the water balance. *14*(5), 055005.