

Water as a resource, stress and disturbance shaping tundra vegetation

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Abstract

Water is crucial for plant productivity and survival as a fundamental resource, but water conditions can also cause physiological stress and mechanical disturbance to vegetation. However, these different influences of water on vegetation patterns have not been evaluated simultaneously. Here, we demonstrate the importance of three water aspects (spatial and temporal variation of soil moisture and fluvial disturbance) for three ecologically and evolutionary distinct taxonomical groups (vascular plants, mosses and lichens) in Fennoscandian mountain tundra. Fine-scale plant occurrence data for 271 species were collected from 378 × 1 m² plots sampled over broad environmental gradients (water, temperature, radiation, soil pH, cryogenic processes and the dominant allelopathic plant species). While controlling all other key environmental variables, water in its different aspects proved to be a crucial environmental driver, acting on individual species and on community characteristics. The inclusion of the water variables significantly improved our models. In this high-latitude system, the importance of spatial variability of water exceeds the importance of temperature for the fine-scale distribution of species from the three taxonomical groups. We found differing responses to the three water variables between and within the taxonomical groups. Water as a resource was the most important water-related variable in species distribution models across all taxonomical groups. Both water resource and disturbance were strongly related to vascular plant species richness, whereas for moss species richness, water resources had the highest influence. For lichen species richness, water disturbance was the most influential water-related variable. These findings demonstrate that water variables are not only independent properties of tundra hydrology, but also that water is truly a multifaceted driver of vegetation patterns at high-latitudes.

Keywords: arctic–alpine, soil moisture, species distribution

Introduction

Water is fundamental for the growth, performance and geographical distribution of vegetation. Water can be a limiting resource for vegetation, but it is also an important stress (both when excessively abundant and scarce) and causes multiple types of disturbances

(such as fluvial erosion and accumulation) (Grime 1977). Individual plant species respond differently to water conditions, i.e. they have unique hydrological niches, which is an important mechanism for species co-existence within vegetation communities (Silvertown et al. 2015). In addition, water shapes species distributions and diversity across gradients from local occurrence patterns to entire biomes (Whittaker 1972, le Roux et al. 2013a, Franklin et al. 2016).

Cold regions are often considered as energy-limited ecosystems, but in a global change context, the role of water has increasingly received attention in the on-going environmental changes experienced in the tundra biome (Bring et al. 2016, Nabe-Nielsen et al. 2017). Tundra plants allocate a large part of their biomass below soil surface, where their roots are relatively shallow rooted (Canadell et al. 1996, Iversen et al. 2015). Consequently, in tundra ecosystems, most plant-available water is restricted to a thin topsoil layer as soil moisture, which is recharged by precipitation, ground-water and meltwaters (Barichivich et al. 2014). Temporal variation of soil moisture, such as occasional water-logging and drought, exposes vegetation to physiological stress (Trahan and Schubert 2016). Furthermore, water-related disturbance posed by fluvial processes provide nutrients from the accumulation of fluvial sediments (Giblin et al. 1991). Fluvial disturbance include also water-induced erosion, which removes soil surface horizons and causes mechanical damage to sessile organisms, such as vascular plants, mosses and lichens (le Roux and Luoto 2014). These evolutionary and ecohydrologically diverse taxonomical groups are key components of tundra ecosystem and presumably have dissimilar tolerances to different water-phenomena (Iturrate-Garcia et al. 2016). Therefore, it is imperative to study how various aspects of water influence fine-scale species distributions, species richness and community composition in the tundra.

The influence of soil moisture variation on vegetation patterns is a pronounced research gap in ecology, particularly at high-elevations and -latitudes (Crimmins et al. 2011, le Roux et al. 2013a, Silvertown et al. 2015), where climate change has greatly impacted both the hydrosphere and cryosphere (Fountain et al. 2012, Bring et al. 2016). These changes have implications for precipitation, evaporation and snow dynamics, all of which alter water conditions experienced by plants (Barichivich et al. 2014, Winkler et al. 2016). Climate simulations project more rainfall in place of snowfall during winter, which combined with earlier snowmelt could lead to extreme drying late in summer and autumn (Bintanja and Andry 2017, Kankaanpää et al. 2018). The increasingly variable weather conditions also affect soil moisture availability and variability (Bring et al. 2016). As a result, soil moisture extremes (i.e. lack of soil oxygen or lack of water) are likely to become more frequent, which will also reflect on vegetation patterns (Silvertown et al. 2015, Franklin et al. 2016). Since no study has simultaneously considered the effects of water on vegetation patterns from its three ecologically-meaningful aspects – a resource (WRE), a stress (WST) and a disturbance (WDI) – this gap in our ecological understanding remains.

High-latitude ecosystems have shown slow responses to short-term experimental manipulations (Blume-Werry et al. 2016). Thus, observational studies along environmental gradients provide us with a valuable approach to investigate tundra vegetation patterns and to predict the consequences of environmental changes (Yuan et al. 2017). Here, we use an observational approach together with species distribution modelling to show how different aspects of water (i.e. soil moisture level, soil moisture change and fluvial disturbance)

influence vegetation patterns, while controlling for eco-physiological factors. We collected fine-scale occurrence data for 271 species from 378 plots surveyed in mountain tundra. In addition to the three water variables, our study setting covered all the key environmental variables (temperature, radiation, soil pH, cryogenic processes and the cover of the dominant allelopathic plant species) that need to be taken into consideration when studying vegetation patterns from a species distribution modelling approach (Austin and Van Niel 2011, Mod et al. 2016).

Our study setting enables a robust assessment of the drivers of tundra vegetation communities, because, firstly, our study is conducted at an ecologically relevant scale, which matches the scale at which water and other factors vary and interact with the plant species (Bramer et al. 2018). Secondly, our setting spans the range of the key environmental gradients within the study system, as well as a relatively large number of species increasing the generalizability of the results (Franklin 1995). Thirdly, our field-quantified observational data comprise the main direct predictors and resource variables relevant to the species being studied (*sensu* Austin 1980). We determined for the first time, how significant are the roles of three different water aspects in shaping fine-scale assemblages of vascular plants, mosses and lichens in tundra.

Material and methods

Study setting

Data were collected on Mount Saana in northwestern Fennoscandia (69°03'N, 20°51'E), with biotic data collected over three consecutive growing-seasons (2011–2013). All abiotic data were collected in the 2013 growing-season. On average, July is the warmest and the wettest month at this site (June: 7.5°C, 42 mm; July: 11.2°C, 73 mm; August: 9.6°C, 47 mm; 1981–2010), as measured 2 m above ground at the nearby Kilpisjärvi meteorological station (69°05'N, 20°79'E; 480 m a.s.l.), which is located 1.5 km from the study area (Pirinen et al. 2012). The landscape is dominated by alternation of minor topographic terrain features, such as hilltops, ridges and small depressions. In addition, there are several soil types ranging from rock outcrops, boulders, glacial till and fluvial deposits to peat deposits. Variation in soil properties together with the fine-scale topographical heterogeneity creates a mosaic of micro-habitats characterized by, for example, fine-scale variation in soil moisture (Kemppinen et al. 2018). Most of the area is covered by a thin organic layer ranging from 0 to 70 cm in depth (Kemppinen et al. 2018). The main vegetation type of the area is dwarf-shrub heath dominated by *Empetrum hermaphroditum* and *Vaccinium* spp., and to a lesser extent by *Betula nana* and *Phyllodoce caerulea* (species list in Supplementary material Appendix 1).

Sampling design and methods

We surveyed 21 study grids on Mount Saana (Fig. 1). The elevation of the study grids ranged from 595 to 810 m a.s.l., with all the grids located above the treeline (comprised of *Betula pubescens* ssp. *czerepanovii*). Each grid contained 18 study plots of 1 m² at 3–4 m intervals and covered a range of environmental conditions (grids were initially orientated to maximize variation in vegetation and mesotopography; le Roux et al. 2013a). In the plots,

we identified 271 species and estimated their percentage cover in all 378 plots (for taxonomy details Supplementary material Appendix 1).

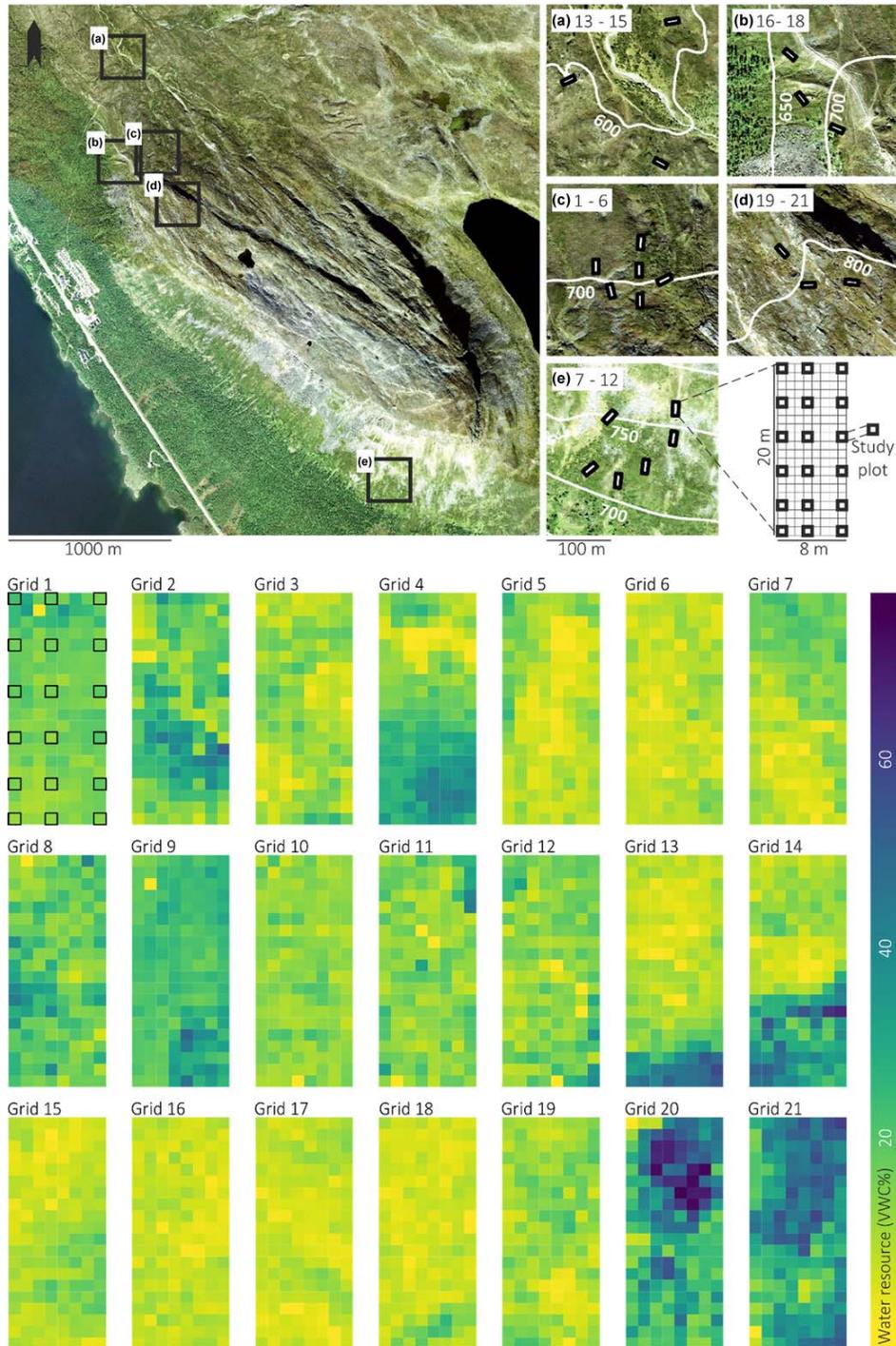


Figure 1. Study design and water resources (volumetric water content; VWC%) across the study grids. To capture the environmental gradients present within the study area, the study grids were located and oriented to sample as diverse conditions as possible, maximizing both environmental variation within (e.g. moisture, topography) and between (e.g. radiation, pH) grids. Water resources were measured within each 1 m² plot (n = 3360), although, in these analyses we used a subset of 378 plots (at 3–4 m intervals; bolded plots) for which observations of the three species groups and in situ measurements of all eight environmental variables were available.

Soil moisture was measured on three occasions during one growing-season (12–13 June; 23–24 July; 9 August 2013). We used a hand-held time-domain reflectometry sensor to measure volumetric water content (VWC%) up to a depth of 10 cm. On each sampling occasion, three measurements were taken within each plot, accounting for possible within-plot moisture variation. Consequently, the mean of the three points was used for calculating WRE and WST. To ensure comparability of measurements, each set of measurements was taken on a day, where there had been no precipitation for at least the preceding 24 h (Bramer et al. 2018). We quantified WRE as soil moisture level (mean over the three sampling occasions VWC%), WST as temporal variability of soil moisture (coefficient of variation of the three sampling occasions [CV]) (Brown 1998), and WDI as the intensity of active fluvial processes (i.e. water-driven processes) occurring in each plot during the growing-season (for more details on the fluvial processes in periglacial environments, French 2007). WDI was visually assessed in situ by a geomorphologist, who surveyed the percentage cover of top-soil surface affected by fluvial erosion caused by small meltwater streams as well as fluvial accumulation (i.e. alluvial deposits) in each plot (following methods of Hjort and Luoto 2009, le Roux and Luoto 2014). All surveys were carried out by the same geomorphologist, who focused only on quantifying geomorphological disturbance to ensure the independence of the vegetation and geomorphological data.

Soil temperature of each plot was measured using miniature temperature loggers. Loggers were buried 10 cm below the soil surface, measuring at 4-h intervals year around. Soil temperature data were then used to calculate the growing degree day (GDD) per plot, using a threshold value of 3°C. Due to malfunctions, the records from 56 loggers were lost. For these plots, we interpolated the GDD values based on the surrounding functioning loggers using inverse distance weighting (IDW) interpolation as implemented in R package *gstat* (Pebesma 2004). IDW predicts values (Z) for unobserved points (S_0) by calculating the weighted average of the known points (S_i ; Eq. 1),

$$\hat{Z}(S_0) = \frac{\sum_{i=1}^n Z(S_i)}{\sum_{i=1}^n w(S_i)} \quad (1)$$

where the weights $w(S_i)$ for observations are calculated based on their distance to the interpolation location (Eq. 2),

$$w(S_i) = \|S_i - S_0\|^{-p} \quad (2)$$

with $\|\cdot\|$ indicating Euclidean distance and p an inverse distance weighting power (Bivand et al. 2008). The optimum p for each grid was bracketed (from 0.5 to 6.0 at 0.5 intervals) to optimize Spearman's correlation coefficient (r_s) between the observed and interpolated values using leave-one-out cross-validation. The cross-validation statistics over the study grids indicated a good agreement between the observed and interpolated GDD ($r_s = 0.81$).

Solar radiation influences species distribution, as light affects several biophysical processes, such as photosynthesis (Rorison et al. 1986, Austin and Van Niel 2011). Incident radiation

(RAD) was calculated as the maximum potential solar radiation per plot (i.e. assuming clear sky conditions) using field-quantified slope and aspect values of each plot (following McCune and Keon 2002). Soil pH (SpH) is an important filter of the local species pool of tundra vegetation, and it may vary strongly over short distances (Gough et al. 2000). It is an ultimate environmental driver (sensu Eskelinen et al. 2009), yet, a cost-efficient proxy for assessing nutrient availability, as soil pH alters various chemical processes between soil and vegetation (Eskelinen et al. 2009). SpH was determined from air-dried soil samples using distilled water in the process in the Laboratory of Geosciences and Geography (Univ. of Helsinki) following the International Organization for Standardization 10390:1994 (E) protocol (le Roux et al. 2013b). Soil frost-related disturbances affect alpine vegetation diversity, peaking at intermediate levels of disturbance (Fox 1981). As the main form of soil disturbance in our study area, we included cryogenic processes (CRY) in our analysis. CRY represents the percentage cover of cryoturbation (frost churning of the topmost soil) and solifluction (French 2007, le Roux and Luoto 2014). CRY was determined in situ following the same protocol as in WDI. To account for the effect of biotic interactions (BIO; le Roux et al. 2013b), we included the percentage cover of *Empetrum hermaphroditum* as a predictor variable (le Roux et al. 2014). This dwarf-shrub is highly competitive, both mechanically and chemically, with the cover of *Empetrum* per plot used as a proxy for the intensity and/or frequency of its interaction with other species (le Roux et al. 2014). *Empetrum* was present in 89% of the plots, with its cover ranging from 0.25 to 95.0%. If the shrub was absent, BIO was assumed to be zero.

Statistical analysis

We investigated the effect of water-related variables on the fine-scale assemblages of vascular plants, mosses and lichen species. Here, we used species distribution modelling, species richness modelling and community composition analysis. We used plot-specific coverage data from all 271 species (116 vascular plant, 68 moss and 87 lichen species) in modelling species richness and analyzing community composition. In modelling the distribution of individual species, we used presence–absence-data on a subset of 152 species, which occurred in ≥ 8 plots (i.e. occurring in $\geq 2\%$ of plots; 68 vascular plant, 30 moss and 54 lichen species).

We used four statistical modelling methods in the species distribution and species richness models to improve the generalizability of our analysis and to reduce uncertainties related to the choice of modelling technique (Marmion et al. 2009). We examined the relationship between predictor variables (GDD, RAD, SpH, CRY, BIO, WRE, WST and WDI) and the distribution of individual species and richness patterns using generalized linear models (GLM), generalized additive models (GAM), generalized boosted regression models (GBM) and random forests (RF). All four techniques are able to incorporate interactions between predictors. As a non-parametric extension of linear regression models, GLM allows the use of non-normally distributed response variables (Nelder and Wedderburn 1972). GAM splits the regression lines into sections and tracks nonlinearity of relationships by using local spline smoothing functions (Hastie and Tibshirani 1987). The user controls the fitting of the smoothing function by appointing the maximum model complexity. GBM is a sequential ensemble modeling method that combines a large number of iteratively fitted classification trees into a single model with improved prediction accuracy (Elith et al. 2008). Random

forest is an ensemble modelling method that generates a large amount of trees, where each tree is built using bootstrap sampling of the data (Breiman 2001). RF uses bagging where predictors are randomly selected for model calibration and the final prediction is the average over all trees in the ensemble.

Species distribution models ('distribution models' from hereafter) were run using the biomod2 R package for fitting GLM, GAM, GBM and RF, assuming a binomial distribution for GLM and GAM, and a Bernoulli distribution for GBM (Thuiller et al. 2016). We assessed the model performance using cross-validation (random 70/30 split with no replacement) with ten repetitions. We used the area under the curve (AUC) and true skill statistic (TSS) for evaluating and comparing the distribution models. For species richness models ('richness models' from hereafter), we used the stats, mgcv, gbm and randomForest R packages, assuming a Poisson distribution for GLM, GAM and GBM (Liaw and Wiener 2002, Wood 2011, Ridgeway 2017). For all GAMs, the maximum degree of smoothing was initially restricted to three, which was further optimized by the model-fitting algorithm. For all GBMs, the number of trees was set to 3000, interaction depth to four, learning rate to 0.001, and bagging fraction to 0.75. For all RF models the number of trees was set to 500. For evaluating the richness models, we used 100 repetitions in cross-validation (70/30). We used the coefficient of determination (R^2) and root mean squared error (RMSE) for evaluating and comparing the richness models. For distribution and richness models, we used Wilcoxon's paired rank test for testing the significance of improvements, when comparing the base model (Eq. 3) to the full model (Eq. 4):

$$\text{Base model}=\text{GDD}+\text{RAD}+\text{SpH}+\text{CRY}+\text{BIO} \quad (3)$$

$$\begin{aligned} \text{Full model}=\text{GDD}+\text{RAD}+\text{SpH}+\text{CRY} \\ +\text{BIO}+\text{WRE}+\text{WST}+\text{WDI} \end{aligned} \quad (4)$$

We assessed the relative influence (0–1) of predictor variables in the models by calculating variable importance following the method of Niittynen and Luoto (2018). First, we fitted the models (all four statistical methods) with the unmanipulated data. Then, we used the models to make two predictions: one using the original data, and another using a dataset in which individual predictor variables were randomly shuffled. Then, we calculated variable importance as (Eq. 5):

$$\text{Variable importance}=1 - \text{cor}_{\text{Spearman}} \left(\text{prediction}^{\text{unmanipulated}} \sim \text{prediction}^{\text{shuffled}} \right) \quad (5)$$

For species richness models, we repeated this procedure 100 times for each response variable, each predictor and each modelling method by bootstrapping the data (random sampling with replacement). For distribution models, we repeated the procedure 10 times for each species. Since the procedure was based on model predictions, it is independent of the modelling methods.

We used non-metric multidimensional scaling (NMDS) to analyze community composition and the changes of species assemblages along environmental gradients (using the metaMDS function from the vegan package) (Oksanen et al. 2017). For examining the community composition based on all three taxonomical groups combined, we set the number of dimensions to three. The first NMDS axis (NMDS1) represents the main axis of variation within the community.

We plotted the relationship between species richness or species community composition (plot scores of NMDS1) in relation to the most important water variable and temperature, to explore how the community composition changes in relation to these fundamental factors controlling tundra vegetation. Here, the NMDS scores were calculated separately for each taxonomical group, with the potential dimensions restricted to four. GAM models fitted to the whole dataset were used to predict species richness and NMDS1 values for an artificial dataset, which consisted all possible WRE and GDD combinations. For species richness predictions, other predictor variables (other than WRE and GDD) were set as constants to their values at plot with maximum species richness (median of those, if there was more than one in a plot). For community composition predictions, other predictors were set to their median value, which were calculated based on all plots in the original dataset. Species-specific WRE and GDD optima were determined for each species as the median WRE and GDD values of all plots, in which the species was present. We used R ver. 3.3.2 for all analyses and models (<www.r-project.org>).

Data deposition

Data available from the Dryad Digital Repository:
<<http://dx.doi.org/10.5061/dryad.km7dc4t>> (Kemppinen et al. 2019).

Results

All three water-related variables showed pronounced variation over the study area: WRE ranged from 5.5 to 64.9 VWC% (mean and standard deviation: 19.6 and 11.3 VWC%), WST from 0.2 to 107.0 CV (24.7 and 15.9 CV), and WDI from 0.0 to 90.0% (3.4 and 10.6%) (Supplementary material Appendix 2). Pair-wise correlations between the water-related predictors were $|r_s| \leq 0.40$ and between all predictors $|r_s| \leq 0.55$ (Supplementary material Appendix 3).

Species distributions

WRE was the most important water-related variable in distribution models across all taxonomical groups (Fig. 2a–c), showing the strongest influence on the occurrences of mosses. The inclusion of the three water-related predictors improved the predictive performance of the distribution models for all taxonomic groups: AUC value increased significantly from 0.733 to 0.754 (two-tailed Wilcoxon signed rank test, $V = 7241.0$, $p = 0.009$) (for TSS values, Supplementary material Appendix 4). For vascular plants, the AUC value increased from 0.807 to 0.836 ($V = 1649.5$, $p = 0.004$), for mosses from 0.687 to 0.727 ($V = 324.0$, $p = 0.061$), and lichens from 0.667 to 0.668 ($V = 697.0$, $p = 0.698$) (Supplementary

material Appendix 4). In addition to WRE, RAD and SpH showed great influence in the distribution models (Fig. 2a–c).

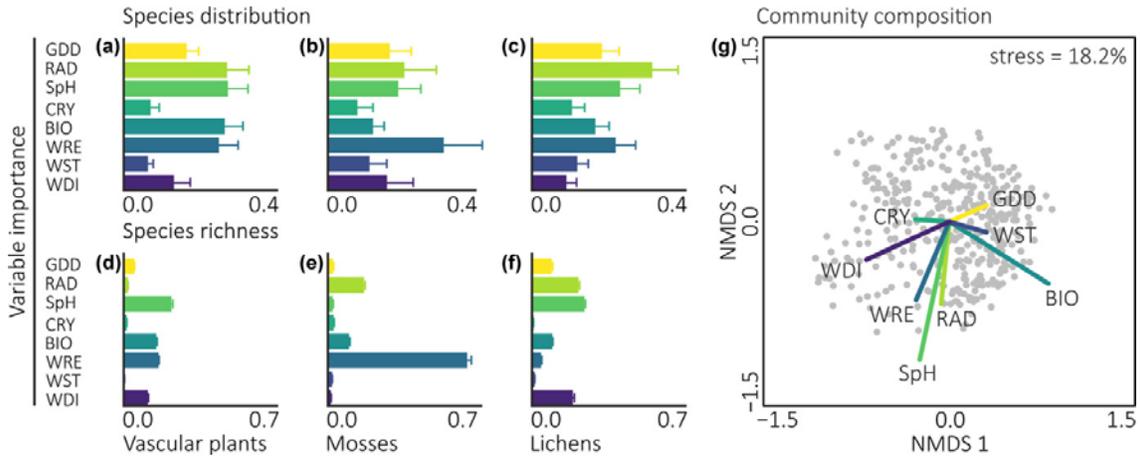


Figure 2. Variable importance (0.0–1.0) in models for species’ distributions (a–c) and species richness (d–f) based on four modelling methods, and an ordination plot of community composition (g) (three dimensions; stress = 18.2%). Water resource (WRE) was the most important water-related variable for species distributions across all taxonomical groups (a–c), also showing the strongest overall influence on the occurrence of mosses (b). For species richness of mosses, the importance of WRE was exceptionally high, compared to all other predictors (e). Water disturbance (WDI) was the most influential water-related predictor for the species richness of lichens (f). Whiskers represent 95% confidence intervals. In the NMDS figure, the study plots are indicated by grey circles. Here, all three water-related predictors had independent influences on community composition (g; Supplementary material Appendix 6 for this same plot, in which individual species are plotted). GDD = growing degree day; RAD = radiation; SpH = soil pH; CRY = cryogenic processes; BIO = biota; WRE = water resources; WST = water stress; WDI = water disturbance.

Most vascular plant and moss species distributions responded positively to WRE, whereas lichen species distributions showed as many positive responses as negative ones (Fig. 3). The majority of vascular plant and lichen species distributions responded negatively to WST and WDI, whereas for most moss species distributions the response to both WST and WDI was positive (Fig. 3).

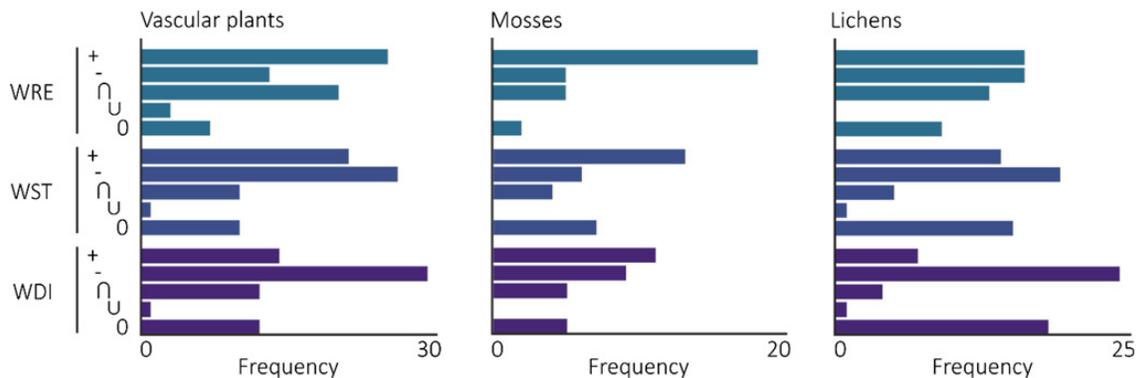


Figure 3. Responses of individual species to the water-related variables as modelled using generalized additive models. The responses vary between species groups, but also within each group, from positive (+) to negative (-) and from unimodal (n) to bimodal (U) and no trend (0) responses. WRE = water resources; WST = water stress; WDI = water disturbance.

Species richness

WRE and WDI were strongly related to vascular plant species richness, with a contribution similar to RAD, SpH and BIO (Fig. 2d–f). WRE was also important in moss richness models, clearly having the highest contribution in models of this response variable (Fig. 2e). In lichen richness models, WDI was the most influential water-related predictor after SpH and RAD (Fig. 2f). The predictive performance of all richness models improved significantly (two-tailed Wilcoxon signed rank test, $p \leq 0.001$), after including the water-related variables (Supplementary material Appendix 5). The R^2 for the richness model based on all species increased from 0.250 to 0.332 ($V = 31.0$), for vascular plants from 0.427 to 0.568 ($V = 1.0$), for mosses from 0.097 to 0.193 ($V = 1.0$), and for lichens from 0.271 to 0.335 ($V = 30.0$) (for RMSE values, Supplementary material Appendix 5).

In general, the relationship between WRE and vascular plant species richness was unimodal, whereas, for moss richness it was positive and for lichen richness negative (Fig. 4). The relationship between WST and taxonomical groups showed similar patterns to WRE, with the exception of vascular plant species richness (negatively related to WST) (Fig. 4). The relationship between WDI and vascular plant species richness was unimodal, whereas for mosses and lichens it was negative (Fig. 4).

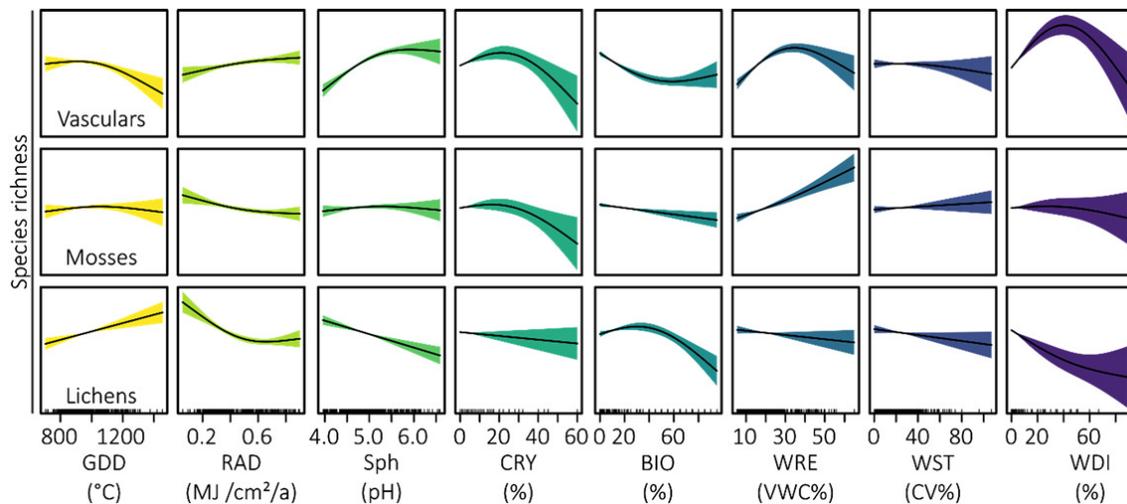


Figure 4. Relationships between species richness and the predictors, presented as generalized additive model response curves. All taxonomical groups have distinct response to the three water-related predictors. The shaded areas represent the 95% confidence intervals. GDD = growing degree day; RAD = radiation; SpH = soil pH; CRY = cryogenic processes; BIO = biota; WRE = water resources; WST = water stress; WDI = water disturbance.

Community composition

Community composition was significantly correlated with all the predictors ($p \leq 0.01$) (Fig. 2g; Supplementary material Appendix 6). SpH and BIO were the variables most strongly related to community composition ($R^2 = 0.506$ and 0.310 respectively), followed by two water variables: WDI and WRE ($R^2 = 0.208$ and 0.183 , respectively) (Supplementary material Appendix 6; see also Supplementary material Appendix 7 for species-specific information).

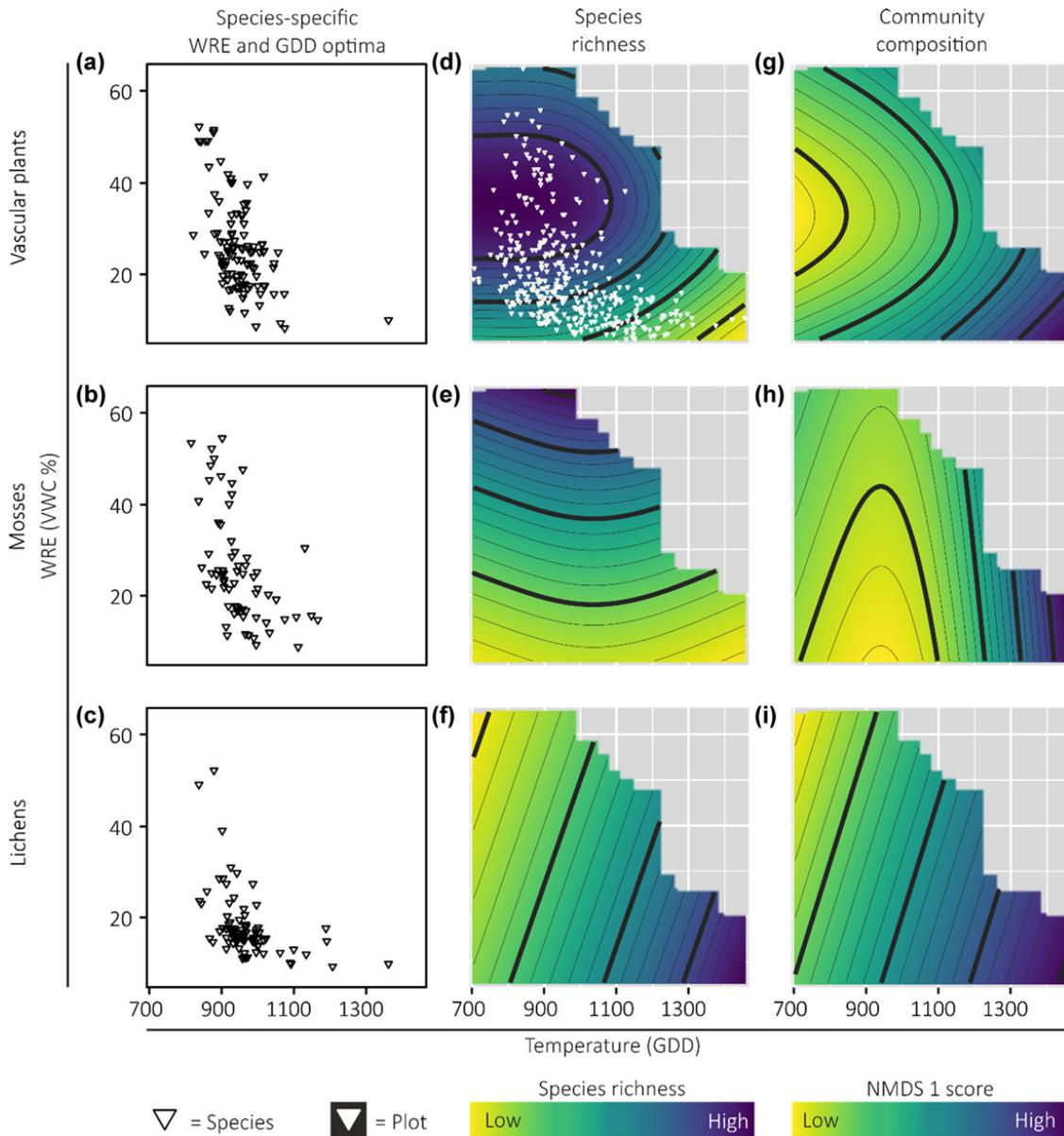


Figure 5. Species-specific water resource (WRE) and temperature (GDD) optima (a–c), and predictions of species richness (d–f) and community composition (g–i) optima in relation to WRE and GDD. Here, species-specific WRE and GDD optima are defined as the median distribution of each species along the WRE and GDD gradients. Species-specific optima shows that vascular plant and moss species exhibits a wide range of WRE optima and a narrow range of GDD optima (a–b). In contrast, optima for lichen species distribution is broader for GDD than for WRE. Prediction of species richness optima revealed that vascular plants chiefly prefer specific (intermediate) GDD conditions, but are more varied with WRE (d). For mosses, high species richness is strongly correlated with high WRE conditions (e), whereas with high GDD for lichens. The community composition optima was based on the scores of the first NMDS axis (Fig. 2g). Vascular plant communities under high GDD conditions are highly correlated with NMDS1 scores, but are very different from communities in intermediate WRE conditions (g). In contrast, for moss community composition, GDD conditions determine the differences between communities. Lichen communities differ strongly between conditions of high WRE with low GDD conditions and in low WRE and high GDD. Triangles with black borders (a–c) represent individual species and white triangles (d) measured plots. GDD = growing degree day; WRE = water resources (measured as mean soil moisture).

Species-specific WRE and GDD optima

As WRE proved to be the most important water variable (Fig. 2a–c), it was chosen for further analysis (Fig. 5). The influence of GDD and WRE on the distribution of species, variation in species richness and community composition showed diverse patterns across the three taxonomical groups (Fig. 5). Distribution optima of vascular plant species spanned a broad range of WRE values (ca 10–50 VWC%), but covered only partially the GDD gradient (ca 800–1000°C) (Fig. 5a). Moss distribution optima showed a similar pattern (Fig. 5b), but optima for lichen distribution was more limited in WRE (ca 10–20 VWC%) and in GDD (ca 900–1000°C, respectively) (Fig. 5c). Vascular plant species richness was highest at ca 20–50 VWC% and with GDD < 1100°C (Fig. 5d). Mosses showed a different pattern, as their richness increased along the WRE gradient showing no response to GDD (Fig. 5e). Lichen species richness was the opposite: it increased with GDD and showed no response to WRE (Fig. 5f). Vascular plant communities in high GDD conditions were strongly correlated with the NMDS1 and were very different from communities in intermediate WRE conditions (Fig. 5g). In contrast, for moss communities, GDD conditions determined the differences between communities (Fig. 5h). Lichen communities differed strongly between high WRE with low GDD conditions and in low WRE and high GDD (Fig. 5i; Supplementary material Appendix 8 for species-specific information).

Discussion

Here, we examined the roles of water-related factors in shaping fine-scale tundra vegetation patterns. Despite water being a vital resource for plants, its impact on vegetation has long been underestimated and overlooked (Silvertown et al. 2015), especially in studies regarding Arctic and alpine areas (Crimmins et al. 2011, le Roux et al. 2013a). Spatial and temporal variation in soil moisture and the intensity of fluvial disturbance were shown to be independent water-related aspects shaping species assemblages, even when controlling for the influences of other key environmental gradients (including, e.g. temperature and soil pH). These different water aspects have crucial impacts on the distribution of individual species, patterns of species richness and community composition of vascular plants, mosses and lichens.

In light of rising temperatures, particularly in high-altitude systems, vascular plant patterns are likely to become more dependent on hydrological conditions (Crimmins et al. 2011, Winkler et al. 2016). Indeed, for high-latitude vegetation, soil moisture may mediate the impacts of changing climatic conditions, including rising temperature and changing snow dynamics (Nabe-Nielsen et al. 2017). Thus, hydrological refugia may occur in high-latitudes, sustaining suitable environmental conditions for threatened species and vegetation types (McLaughlin et al. 2017). However, the future changes in the tundra water cycle and its altered seasonality could eliminate several hydrologically distinct habitats in high-latitude environments, including meltwater streams and snowbeds (Franklin et al. 2016, Bintanja and Andry 2017), which may consequently eliminate a portion of the tundra species pool (Niittynen et al. 2018). It can be particularly challenging to predict the impact of climate change impacts on plant-available water, as soil moisture conditions may not reflect the prevailing microclimate, which may, in turn, be highly decoupled from the macroclimate (Aalto et al. 2018). Therefore, it is critical to focus future research on quantifying plant-

available water resources, and stresses and disturbances related to water at ecologically relevant spatial and temporal scales.

Our results provide evidence on the pivotal role of water in shaping fine-scale spatial patterns of tundra vegetation: species have individual responses and distinct optima to different water aspects. The strong contribution of the water variables in our distribution models and response shapes show that tundra vegetation has species-specific hydrological niches. As water is a key factor for all vegetation, hydrological niche segregation (HNS) occurs in various vegetation types, wherever competing species co-exist, not only in water-limited systems (Silvertown et al. 2015). HNS was evident regarding the diverse responses to water-aspects of our study species within each taxonomic group: all species have a unique response to different water aspects. In general, tundra vascular plants are adapted to a wide range of water conditions, as well as, typically, to relatively low temperatures and a short growing-season. Whereas, the majority of mosses occur in wet conditions regardless of temperature conditions, while lichens show the opposite tendency. Thus, the spatial heterogeneity of tundra water conditions together with other environmental factors, such as temperature, enable the co-occurrence of eco-physiologically distinct species (and higher taxonomic groups), which increases the overall species diversity in tundra (Whittaker 1972). Consequently, instead of focusing on regional averages, more research is needed on local hydrological heterogeneity in the tundra, and how this fine-scale variability in water conditions will be affected in tundra under a changing climate.

Water as a resource proved to be the most important water aspect for the three taxonomic groups. Due to the distinct life histories and physiology of the three taxonomical groups, they have different adaptations to cope with local water conditions (Iturrate-Garcia et al. 2016). Generally, vascular plants are stronger competitors than mosses, but in both extremes of the soil moisture gradient, these roles may be reversed (Iturrate-Garcia et al. 2016). For example, mosses dominate in nearly water-logged conditions, in which the roots of vascular plants may suffer from anoxic conditions. Moreover, lichens and mosses are more tolerant than vascular plants of soil instability in wet environments (e.g. cryoturbation habitats; le Roux and Luoto 2014), due to the lack of a root system, which predisposes vascular plants to damage from mechanical disturbance (Jonasson 1986). However, when soil moisture is low, roots enable better access to soil moisture. Nevertheless, in the driest extreme of the moisture gradient, even extensive roots may not provide sufficient amounts of water for high-demanding vascular plants, thus, only desiccation-tolerant lichen and moss species can survive there.

The changing tundra hydrology may permanently alter entire ecosystems by reshuffling species communities. This is due to the different functional roles of the three taxonomic groups and their diverse responses to different water aspects demonstrated in our results. For example Arctic greening (i.e. shrub encroachment and shrubification) may be exacerbated by changes in local factors, such as soil moisture conditions (Weijers et al. 2018). Indeed, soil moisture is known to impact climate sensitivity of shrub growth, and may therefore mediate how shrub growth responds to warming temperatures (Myers-Smith et al. 2015). Arctic browning (i.e. experiencing plant dieback) is also linked to wetter and warmer climatic conditions (Epstein et al. 2016, Lara et al. 2018). Due to the reduction of photosynthesis during increased water stress (Angert et al. 2005), extreme weather events,

such as droughts, may lead to ‘browning’ as well (Phoenix and Bjerke 2016, Bjerke et al. 2017). The expansion of vascular plants and mosses causes population declines in lichens, however, due to lichen species’ higher tolerance to, e.g. desiccation, extreme conditions may compensate or reverse population declines (Bjerke et al. 2011). This further demonstrates that future vegetation predictions must take into consideration not only the level of plant-available water, but also temporal variability in fine-scale hydrological conditions, which may lead to water stress and disturbance.

Water stress had relatively minor effect on species occurrences. Our water stress factor, based on three measurements over one growing season, could benefit from a more intensive moisture survey (e.g. hourly measurements) or another type of approach (e.g. relative water content of leaves) that could have shown higher significance of water stress over tundra vegetation (Buckland et al. 1997, Dolezal et al. 2016). Thus, our findings call for incorporating temporally comprehensive measurements over the growing season for capturing the entire spectrum of water conditions of extreme stress to stable conditions. Despite these data limitations, our results are highly promising and stress the need of more research on the different aspects affecting tundra ecohydrology.

Our results highlight the essential role of water as a multifaceted driver of tundra vegetation, where in general, water resources are not scarce. In global change context, these fundamental elements of Arctic ecosystems, namely vascular plant, moss and lichen communities, will not only show sensitivity to warming temperatures, but they will also respond to altered water conditions. The changing Arctic hydrology can have pronounced and differing consequences for the three taxonomical groups, which may potentially cascade on other trophic levels and processes as well (Callaghan et al. 2004, Post et al. 2009, Porazinska et al. 2018). Due to uncertainties in projecting future hydrological cycles (Bring et al. 2016), there are possibly ecological surprises ahead for high-latitude ecosystems. Thus, water and its multiple aspects should be considered in future climate change impact assessments.

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References

- Aalto, J. et al. 2018. Biogeophysical controls on soil-atmosphere thermal differences: implications on warming arctic ecosystems. – *Environ. Res. Lett.* 13: 074003.
- Angert, A. et al. 2005. Drier summers cancel out the CO₂ uptake enhancement induced by warmer springs. – *Proc. Natl Acad. Sci. USA* 102: 10823– 10827.
- Austin, M. P. 1980. Searching for a model for use in vegetation analysis. – *Vegetatio* 42: 11– 21.
- Austin, M. P. and Van Niel, K. P. 2011. Improving species distribution models for climate change studies: variable selection and scale. – *J. Biogeogr.* 38: 1– 8.
- Barichivich, J. et al. 2014. Temperature and snow-mediated moisture controls of summer photosynthetic activity in northern terrestrial ecosystems between 1982 and 2011. – *Remote Sens. Basel* 6: 1390– 1431.
- Bintanja, R. and Andry, O. 2017. Towards a rain-dominated arctic. – *Nat. Clim. Change* 7: 263– 267.
- Bivand, R. S. et al. 2008. *Applied spatial data analysis with R*. – Springer.
- Bjerke, J. W. et al. 2011. Contrasting sensitivity to extreme winter warming events of dominant sub-arctic heathland bryophyte and lichen species. – *J. Ecol.* 99: 1481– 1488.
- Bjerke, J. W. et al. 2017. Understanding the drivers of extensive plant damage in boreal and arctic ecosystems: insights from field surveys in the aftermath of damage. – *Sci. Total Environ.* 599–600: 1965– 1976.
- Blume-Werry, G. et al. 2016. Short-term climate change manipulation effects do not scale up to long-term legacies: effects of an absent snow cover on boreal forest plants. – *J. Ecol.* 104: 1638– 1648.
- Bramer, I. et al. 2018. Advances in monitoring and modelling climate at ecologically relevant scales. – *Adv. Ecol. Res.* 58: 101– 161.
- Breiman, L. 2001. Random forests. – *Mach. Learn.* 45: 5– 32.
- Bring, A. et al. 2016. Arctic terrestrial hydrology: a synthesis of processes, regional effects and research challenges. – *J. Geophys. Res. Biogeosci.* 121: 621– 649.
- Brown, C. E. 1998. *Applied multivariate statistics in geohydrology and related sciences*. – Springer.
- Buckland, S. et al. 1997. A comparison of plant responses to the extreme drought of 1995 in northern England. – *J. Ecol.* 85: 875– 882.

- Callaghan, T. V. et al. 2004. Biodiversity, distributions and adaptations of arctic species in the context of environmental change. – *Ambio* 33: 404– 417.
- Canadell, J. et al. 1996. Maximum rooting depth of vegetation types at the global scale. – *Oecologia* 108: 583– 595.
- Crimmins, S. M. et al. 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. – *Science* 331: 324– 327.
- Dolezal, J. et al. 2016. Vegetation dynamics at the upper elevational limit of vascular plants in Himalaya. – *Sci. Rep.* 6: 24881.
- Elith, J. et al. 2008. A working guide to boosted regression trees. – *J. Anim. Ecol.* 77: 802– 813.
- Epstein, H. et al. 2016. *Tundra greenness*. (in Arctic Report Card 2015). – <www.arctic.noaa.gov/reportcard>.
- Eskelinen, A. et al. 2009. Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. – *Oecologia* 161: 113– 123.
- Fountain, A. G. et al. 2012. The disappearing cryosphere: impacts and ecosystem responses to rapid cryosphere loss. – *Bioscience* 62: 405– 415.
- Fox, J. F. 1981. Intermediate levels of soil disturbance maximize alpine plant diversity. – *Nature* 293: 564– 565.
- Franklin, J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. – *Prog. Phys. Geogr.* 19: 474– 499.
- Franklin, J. et al. 2016. Global change and terrestrial plant community dynamics. – *Proc. Natl Acad. Sci. USA* 113: 3725– 3734.
- French, H. M. 2007. *The periglacial environment*. – Wiley.
- Giblin, A. E. et al. 1991. Biogeochemical diversity along a riverside toposequence in arctic Alaska. – *Ecol. Monogr.* 61: 415– 435.
- Gough, L. et al. 2000. Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. – *J. Ecol.* 88: 54– 66.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. – *Am. Nat.* 111: 1169– 1194.

- Hastie, T. and Tibshirani, R.1987. Generalized additive-models – some applications. – *J. Am. Stat. Assoc.* 82: 371– 386.
- Hjort, J. and Luoto, M.2009. Interaction of geomorphic and ecologic features across altitudinal zones in a subarctic landscape. – *Geomorphology* 112: 324– 333.
- Iturrate-Garcia, M. et al. 2016. Interactive effects between plant functional types and soil factors on tundra species diversity and community composition. – *Ecol. Evol.* 6: 8126– 8137.
- Iversen, C. M. et al. 2015. The unseen iceberg: plant roots in arctic tundra. – *New Phytol.* 205: 34– 58.
- Jonasson, S.1986. Influence of frost heaving on soil chemistry and on the distribution of plant growth forms. – *Geogr. Ann. A Phys. Geogr.* 68: 185– 195.
- Kankaanpää, T. et al. 2018. Spatiotemporal snowmelt patterns within a high arctic landscape, with implications for flora and fauna. – *Arct. Antarct. Alp. Res.* 50: e1415624.
- Kemppinen, J. et al. 2018. Modelling soil moisture in a high-latitude landscape using LiDAR and soil data. – *Earth Surf. Process. Landforms* 43: 1019– 1031.
- Kemppinen, J. et al. 2019. *Data from: Water as a resource, stress and disturbance shaping tundra vegetation.*– Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.km7dc4t>>.
- Lara, M. J. et al. 2018. Reduced arctic tundra productivity linked with landform and climate change interactions. – *Sci. Rep.* 8: 2345.
- le Roux, P. C. and Luoto, M. 2014. Earth surface processes drive the richness, composition and occurrence of plant species in an arctic-alpine environment. – *J. Veg. Sci.* 25: 45– 54.
- le Roux, P. C. et al. 2013a. Soil moisture's underestimated role in climate change impact modelling in low-energy systems. – *Global Change Biol.* 19: 2965– 2975.
- le Roux, P. C. et al. 2013b. Horizontal, but not vertical, biotic interactions affect fine-scale plant distribution patterns in a low-energy system. – *Ecology* 94: 671– 682.
- le Roux, P. C. et al. 2014. Incorporating dominant species as proxies for biotic interactions strengthens plant community models. – *J. Ecol.* 102: 767– 775.
- Liaw, A. and Wiener, M.2002. Classification and regression by randomForest. – *R News* 2: 18– 22.
- Marmion, M. et al. 2009. Evaluation of consensus methods in predictive species distribution modelling. – *Divers. Distrib.* 15: 59– 69.

- McCune, B. and Keon, D. 2002. Equations for potential annual direct incident radiation and heat load. – *J. Veg. Sci.* 13: 603– 606.
- McLaughlin, B. et al. 2017. Hydrological refugia, plants and climate change. – *Global Change Biol.* 23: 136– 144.
- Mod, H. K. et al. 2016. What we use is not what we know: environmental predictors in plant distribution models. – *J. Veg. Sci.* 27: 1308– 1322.
- Myers-Smith, I. H. et al. 2015. Climate sensitivity of shrub growth across the tundra biome. – *Nat. Clim. Change* 5: 887– 891.
- Nabe-Nielsen, J. et al. 2017. Plant community composition and species richness in the high arctic tundra: from the present to the future. – *Ecol. Evol.* 7: 10233– 10242.
- Nelder, J. A. and Wedderburn, R. W. 1972. Generalized linear models. – *J. R. Stat. Soc. A* 135: 370.
- Niittynen, P. and Luoto, M. 2018. The importance of snow in species distribution models of arctic vegetation. – *Ecography* 41: 1024– 1037.
- Niittynen, P. et al. 2018. Snow cover is a neglected driver of arctic biodiversity loss. – *Nat. Clim. Change* 8: 997– 1001.
- Oksanen, J. et al. 2017. *vegan: community ecology package*. – *R package ver. 2.4-3*.
- Pebesma, E. J. 2004. Multivariable geostatistics in S: the gstat package. – *Comput. Geosci.* 30: 683– 691.
- Phoenix, G. K. and Bjerke, J. W. 2016. Arctic browning: extreme events and trends reversing arctic greening. – *Global Change Biol.* 22: 2960– 2962.
- Pirinen, P. et al. 2012. *Climatological statistics of Finland 1981–2010*. – Finnish Meteorol. Inst.
- Porazinska, D. L. et al. 2018. Plant diversity and density predict belowground diversity and function in an early successional alpine ecosystem. – *Ecology* 99: 1942– 1952.
- Post, E. et al. 2009. Ecological dynamics across the arctic associated with recent climate change. – *Science* 325: 1355– 1358.
- Ridgeway, G. 2017. *gbm: generalized boosted regression models*. – *R package ver. 1.3 (2006)* 55.
- Rorison, I. et al. 1986. Local climate, topography and plant growth in Lathkill Dale NNR. I. A twelve-year summary of solar radiation and temperature. – *Plant Cell Environ.* 9: 49– 56.

- Silvertown, J. et al. 2015. Hydrological niches in terrestrial plant communities: a review. – *J. Ecol.* 103: 93– 108.
- Thuiller, W. et al. 2016. *biomod2: ensemble platform for species distribution modeling*. – *R package ver. 3.3-7*.
- Trahan, M. W. and Schubert, B. A. 2016. Temperature-induced water stress in high-latitude forests in response to natural and anthropogenic warming. – *Global Change Biol.* 22: 782– 791.
- Weijers, S. et al. 2018. A warmer and greener cold world: summer warming increases shrub growth in the alpine and high arctic tundra. – *Erdkunde* 72: 63– 85.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. – *Taxon* 21: 213– 251.
- Winkler, D. E. et al. 2016. Soil moisture mediates alpine life form and community productivity responses to warming. – *Ecology* 97: 1553– 1563.
- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. – *J. R. Stat. Soc. B* 73: 3– 36.
- Yuan, Z. Y. et al. 2017. Experimental and observational studies find contrasting responses of soil nutrients to climate change. – *eLife* 6: 19.