SPECIAL FEATURE: MACROECOLOGY OF VEGETATION

Annual air temperature variability and biotic interactions explain tundra shrub species abundance

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Abstract

Questions: Shrub vegetation has been expanding across much of the rapidly changing Arctic. Yet, there is still uncertainty about the underlying drivers of shrub community composition. Here, we use extensive vegetation surveys and a trait-based approach to answer the following questions: which abiotic and biotic factors explain abundance of shrub species and functional groups in the Arctic tundra, and can we interpret these relationships using plant traits related to resource acquisition?

Location: Nuup Kangerlua (Godthåbsfjord), western Greenland.

Methods: We tested the power of nine climatic, topographic and biotic variables to explain the abundances of nine shrub species using a Bayesian hierarchical modelling framework.

Results: We found highly variable responses among species and functional groups to both abiotic and biotic environmental variation. The overall most important abiotic explanatory variable was annual air temperature variability, which was highly correlated with winter minimum air temperature. Functional community composition and graminoid abundance were the most influential biotic factors. While we did not find systematic patterns between shrub abundances and abiotic variables with regard to resource acquisition traits, these traits did explain relationships between shrub abundances and biotic variables.

Conclusions: Shrub abundance responses to abiotic variables rarely aligned with expectations based on plants' resource acquisition traits or functional groups. Our results, therefore, indicate that approaches exclusively based on resource acquisition traits might be limited in their ability to predict abundances of individual groups and species, particularly in response to complex abiotic environments. However, integrating community theory and functional trait concepts represents a promising pathway to better predict biotic interactions and ultimately responses of dominant shrub vegetation to rapid environmental changes across the arctic tundra biome.

KEYWORDS

Arctic tundra, biotic interactions, gradient, moisture predictors, plant functional groups, plant functional traits, shrubs, species-specificity, temperature variability, vegetation change

1 | INTRODUCTION

Substantial warming has been documented for the Arctic over the past decades, indicating severe amplification relative to lower latitudes (Serreze & Barry, 2011; IPCC, 2014; Post et al., 2019). In the Arctic tundra, this has resulted in alterations of other abiotic variables such as precipitation and snow cover, as well as biophysical parameters, including phenological shifts and altered nutrient cycling (Post et al., 2009, 2019; Box et al., 2019). As a response to these climatic and environmental changes, widespread changes in vegetation composition have been reported from across the biome (e.g., Myers-Smith et al., 2011; Elmendorf et al., 2012; Bjorkman et al., 2020), particularly increases in shrub abundance and height (Elmendorf et al., 2012; Pearson et al., 2013; García Criado et al., 2020), as well as shrub range expansion (Tape et al., 2006). These changes could substantially alter the structure and composition of plant communities (Pajunen et al., 2011; Bråthen & Lortie, 2016), and ecosystem functioning (Myers-Smith et al., 2011; Cahoon et al., 2012; McLaren et al., 2017) and provide feedbacks to global and Arctic warming (Chapin et al., 1995; Pearson et al., 2013). Therefore, understanding the drivers of patterns of shrub species abundance is crucial for predicting the future impacts of climate change on Arctic tundra ecosystems.

Several abiotic and biotic drivers have been found to influence shrub growth and abundance across the Arctic tundra (Martin et al., 2017; García Criado et al., 2020). Summer temperature is generally identified as the most important climatic driver (e.g., Hallinger et al., 2010; Blok et al., 2011; Büntgen et al., 2015; Myers-Smith et al., 2015; Young et al., 2016; Forchhammer, 2017; Gamm et al., 2018; Maliniemi et al., 2018; Weijers et al., 2018; Buchwal et al., 2019), but some studies have also found relationships of growth or cover with winter temperature (Hollesen et al., 2015; Maliniemi et al., 2018) or summer precipitation (Blok et al., 2011; Maliniemi et al., 2018). Topography can also influence these shrub responses, e.g., through its impact on solar radiation (Albert et al., 2011), snow cover (Young et al., 2016; Niittynen et al., 2020b), or soil moisture (Elmendorf et al., 2012; Ackerman et al., 2017), which can crucially mediate the

effects of temperature changes on shrub growth (Myers-Smith et al., 2015). Fewer studies have tested the influence of biotic factors on shrub growth and abundance. These studies suggest that interspecific competition for nutrients (Dormann et al., 2004; Wilson & Nilsson, 2009), browsing (Olofsson et al., 2009; Bråthen et al., 2017; Vowles et al., 2017; Maliniemi et al., 2018), and insect herbivory (Lund et al., 2017; Prendin et al., 2019) can influence shrub responses. Additionally, interactions between abiotic and biotic factors have the potential to shape the species and functional composition of plant communities (Dormann et al., 2004; Little et al., 2015; Boulanger-Lapointe et al., 2016; Cahoon et al., 2016). Yet, few studies have investigated multiple abiotic and biotic drivers at the same time, thus impeding reliable predictions of tundra shrub expansion (Martin et al., 2017).

To predict climate change effects on tundra ecosystems we need to understand community-level responses (Wookey et al., 2009). Many previous studies on shrub expansion have focussed on a single or few species (Martin et al., 2017), limiting their generalisability as they only represent part of the community. At the same time, previous attempts to generalise responses across species based on functional groups (e.g., evergreen vs deciduous shrubs; Chapin et al., 1996) may not have accurately represented the variety of responses among species (Dorrepaal, 2007; Bret-Harte et al., 2008; Little et al., 2015; Saccone et al., 2017), likely because they mask crucial variation in functional traits (Thomas et al., 2019). Instead, using functional traits directly to predict shrub community responses could allow us to obtain a better understanding of future vegetation changes in the tundra.

Plant functional traits describe the relationship between plants and both their abiotic and biotic environment, and can thus be used to assess biotic interactions along abiotic gradients (McGill et al., 2006; Kunstler et al., 2016). Generally, ecological strategies linked to plant functional traits range from resource-acquisitive (competitive) to resource-conservative (stress-tolerant; Reich, 2014). The individual ecological strategies of different plant species will affect the outcome of their interactions across abiotic gradients (Maestre et al., 2009). For example, a resource-conservative species would be

expected to perform relatively well in harsh (e.g., cold) environments, but less well under benign conditions due to competition with other species, especially when interacting with more resource-acquisitive species. In contrast, due to their higher competitive ability, resource-acquisitive species should benefit from more benign environments, and this effect should be more pronounced with higher trait dissimilarity (Maestre et al., 2009). Assessing biotic interactions across ecological gradients is vital for understanding tundra shrub dynamics (Wookey et al., 2009; Gilman et al., 2010; Martin et al., 2017; Myers-Smith et al., 2019b) and a functional traits-based approach predicting the outcomes of such biotic interactions could help elucidate the role of shrubs in a changing Arctic.

Here, we present an integrated framework to bridge trait- and species-based approaches to identify important environmental variables explaining abundance of tundra shrub species and functional groups. We recorded the abundance of nine locally dominant shrub species along a 95-km coastal–inland gradient in west Greenland, including both resource-acquisitive (e.g., *Salix glauca*) and -conservative species (e.g., *Empetrum nigrum*; Thomas et al., 2020; Figure 1; Appendix S1). We gathered information on 15 environmental variables that represent climatic (air temperature, precipitation, annual air temperature variability), topographical (solar radiation, terrain ruggedness, wetness), and biological (functional dissimilarity from the community, abundance of other shrub species, graminoid abundance) variation. We used Bayesian hierarchical models to predict shrub abundances based on the environmental variables and test the following hypotheses:

1. Shrub species with more acquisitive traits (Figure 1) should be more abundant where environmental conditions are more benign, i.e. warmer summer temperatures, lower temperature variability, and wetter conditions
2. All shrub species, but especially more drought-sensitive ones with acquisitive traits, should be more abundant with warmer temperatures under wet but not dry conditions
3. All shrub species should be more abundant in communities with relatively more resource-conservative, or less resource-acquisitive, species

4. The abundance–temperature relationship should be more positive for shrub species which have more acquisitive traits than their community, than for those with more conservative strategies (Figure 1)

The outcomes of this study contribute to a better understanding of the abiotic and biotic factors that shape the current distribution of tundra shrub species, and thus improve our ability to predict shrub vegetation dynamics under climate change in Greenland and across the Arctic.

2 | METHODS

2.1 | Study area and sampling design

We collected plant abundance data across a climatic gradient along Nuup Kangerlua (Godthåbsfjord) in west Greenland, from 64.23 N, −51.81 W to 64.69 N, −50.04 W, spanning about 95 km (Figure 2a). The fjord is characterised by a steep west–east continentality gradient, resulting in high variation in air temperature and precipitation patterns (Appendix S2, see section 2.3 for a detailed description). In addition, the heterogeneous topography creates spatially variable water flow. This regional variation in abiotic factors was overall well captured in our study (Appendix S3).

Data collection followed a stratified design and was conducted in five different sampling sites (Figure 2b), in areas that were located as far apart as possible to cover the entire east–west climatic gradient in the fjord. Sites 1, 2, and 4 were sampled in 2011, site 3 in 2012, and site 5 in 2013. Using the sampling approach of Nabe-Nielsen et al., (2017), we laid out 414 vegetation plots in groups of six plots (Figure 2c, d) that were distributed along isoclines on an altitudinal gradient within each study site. We placed three plot groups on each of the isoclines 20 m, 100 m, 200 m, 300 m, 400 m and 500 m above sea-level (Figure 2c). The position of the first plot group was chosen by walking until the isocline was reached (as indicated by a hand-held GPS), while the second and third plot group were placed with 500-m distance in between where the slope was < 45°, or slightly further apart when this was
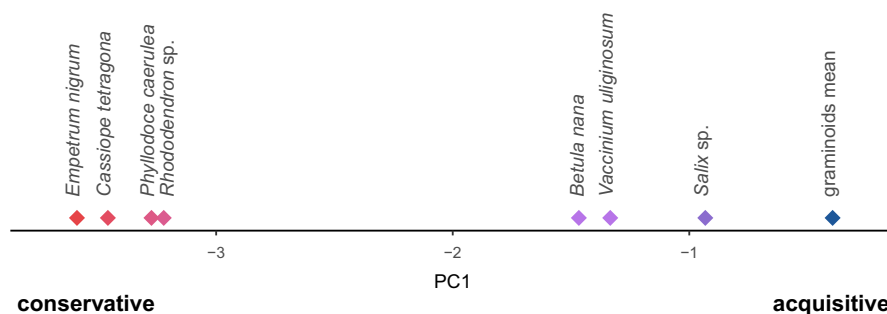
FIGURE 1 Position of the study species along the resource economics spectrum (PC1 = principal component axis 1 in Figure 2b in Thomas et al., 2020). More blue colours represent more resource-acquisitive strategies, while more red colours indicate more resource-conservative strategies. Values for grouped *Rhododendron* and *Salix* species represent proxies, as *Rhododendron groenlandicum* and *S. arctophila* were not represented in our database, but species within the respective genera are highly similar and closely related. See Appendix S1 for more detailed information on the study species, and Appendix S2 for more details on the extraction of values

FIGURE 2 Overview of the study area and sampling design. (a) Location of the study area in southwestern Greenland (red box, enlarged) and (b) sites along the Nuuk Fjord. (c) Within each site (her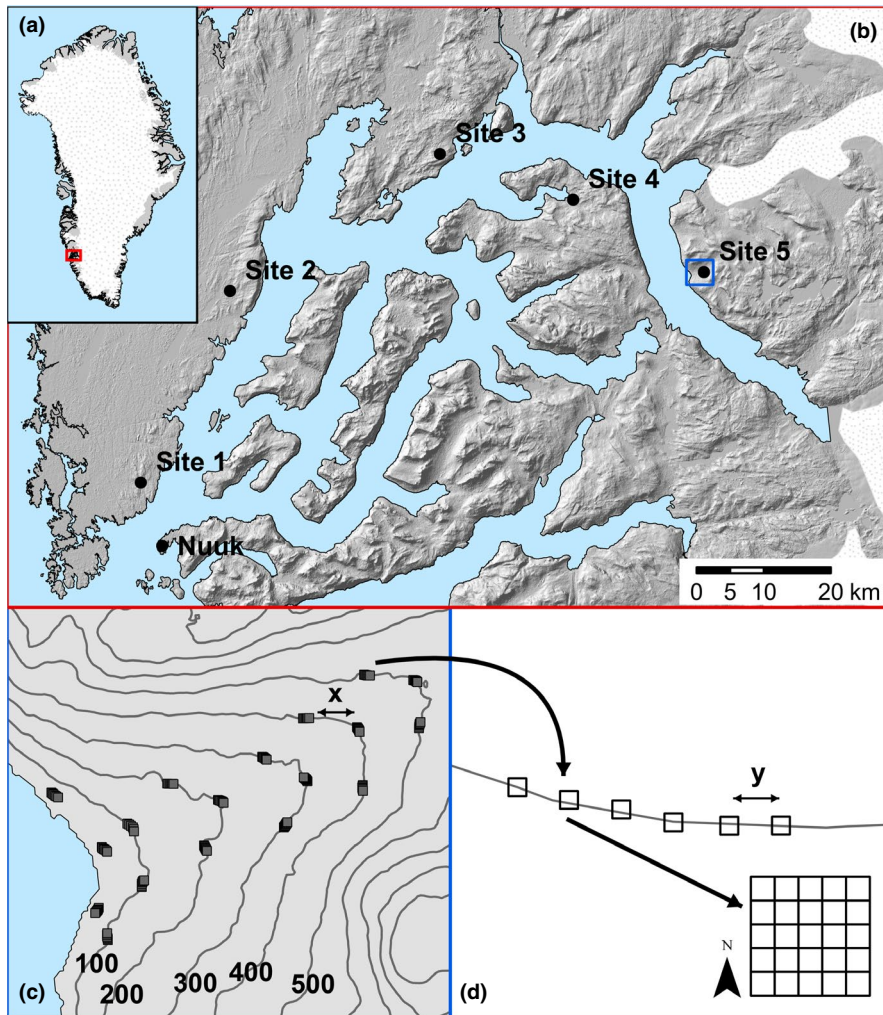e, site 5, blue box), plots were placed in a stratified manner along 20-m, 100-m, and 200-m isoclines and in groups of six, with $x = 500$ m between plot groups. (d) Plots within plot groups were $y = 10$ m apart and consisted of a 0.7 m × 0.7 m square, divided into 5 × 5 grid cells used for pinpoint vegetation surveys

necessary to avoid steep cliffs. If the length of a particular isocline did not allow placement of three plot groups, we did not place any plots on that isocline or higher up at the given study site. Therefore, fewer plots could be established towards the coast where the slopes did not reach altitudes up to 500 m. Within plot groups, we placed plot centres 10 m apart on the same altitude (Figure 2d), or slightly further apart when this was necessary to prevent that the plot landed entirely in water or that the average slope of the plot was > 45°. Plots on rocks and plots that partly covered swamps, creeks, or lakes were included.

Each plot consisted of a square with a side length of 0.7 m. We assessed plant abundance using the pin-point method, dividing the plot into 5 × 5 squares, and recording the presence of the focal species (see below) for each of the 25 grid intersects. A pin with a diameter of 2 mm was vertically lowered into the vegetation at each intersect and all species touched by the pin were recorded. Dead plants (including dry grass leaves) were not included in the analysis.

2.2 | Study species and response variable

We focussed the study on shrubs as ecosystem dominants, and specifically on the following nine shrub species that occurred across all study sites: *Betula nana*, *Cassiope tetragona*, *Empetrum nigrum*, *Phyllodoce caerulea*, *Rhododendron groenlandicum*, *Rhododendron tomentosum*, *Salix glauca*, *Salix arctophila*, and *Vaccinium uliginosum* (Appendix S1). Taxonomy follows the Panarctic Flora (http://www.panarcticflora.org/).

As our response variable, we quantified the abundance of each target species as the proportion of the grid intersects where the species occurred. We calculated abundance of functional shrub groups (evergreen, deciduous, or all shrubs) as the sum of the abundances of individual species within each group (Appendix S1).

2.3 | Explanatory variables

2.3.1 | Climatic variables

We retrieved monthly air temperature and precipitation data from the CHELSA data set at 30 arc-second resolution (Karger et al., 2017), which we then downscaled to 90-m resolution based on the MEaSUREs Greenland Ice Mapping Project (GIMP) Digital Elevation Model v1 (Howat et al., 2014, 2015). To better account for variation due to topography and elevation, downscaling involved the following

steps: (a) refining minimum and maximum land surface temperature by combining CHELSA climatology, temperature lapse rates calculated from the ERA5 dataset (Hersbach et al., 2018), and solar radiation corrected for cloud cover using the EarthEnv dataset (Wilson & Jetz, 2016); and (b) refining precipitation by applying geographically weighted regression in combination with the digital elevation model. For a detailed description of the downscaling process, see Appendix S2. From the downscaled data, we obtained the following calculated variables (from N. Chardon) for each plot, averaged over a 30-year period prior to the year of observation: arctic summer (June–August) mean temperature, summer maximum and winter (January–March) minimum monthly mean temperatures, annual temperature variability (summer maximum–winter minimum monthly mean temperature), cumulative summer precipitation, cumulative winter-spring (January–May) precipitation, and cumulative spring (March–May) precipitation.

2.3.2 | Topographic variables

Tundra topography often varies on very small spatial scales below metres, complicating accurate estimates of plant-relevant conditions (Lenoir et al., 2013). The variables chosen here are, therefore, proxies specifically selected to take this fine-scale variation into account.

For each plot, we recorded the following topographical parameters in the field: geographic position, using a hand-held GPS device (GPSmap 62s, Garmin Ltd., Schaffhausen, Switzerland; accuracy approx. multiple to a few tens of metres, depending on terrain), and angle as well as direction of the slope (both in degrees), using a hand-held clinometer of approx. 2-degree accuracy. Slope angle was included as an explanatory variable to reflect erosion potential at a given plot. Based on these locally measured parameters, we computed the Solar Radiation Index (SRI; Keating et al., 2007) per plot.

In addition, we calculated terrain ruggedness (Terrain Ruggedness Index, TRI; Riley et al., 1999) based on the 2-m resolution ArcticDEM (Porter et al., 2018). We also derived two proxies of local wetness for the plots: the Topographic Wetness Index (TWI; Beven & Kirkby, 1979), which is based on models of terrain-based water flow, and the Tasselled-Cap Wetness Index (TCWS; Crist & Cicone, 1984), which is calculated from satellite-derived surface reflectance measures. Both indices have been used in tundra ecological research (e.g., TWI: le Roux et al., 2012; Greaves et al., 2016; TCWS: Raynolds & Walker, 2016; Bartsch et al., 2020). TWI computation was done in SAGA GIS 7.8.2 (Conrad et al., 2015), based on the 30-m resolution GIMP MEaSUREs DEM (Howat et al., 2017) and following the workflow and parameters recommended by Kopecký et al., (2020). TCWS was calculated from a 30-m resolution Landsat 8 composite (Surface Reflectance Tier 1) of the study area for 19 August 2013 using the Google Earth Engine (Gorelick et al., 2017). For each plot, the TRI, TWI and TCWS values were extracted as the weighted mean of all cells overlapping a circle with a 5-m radius centred on the plot. Cell values were weighted by the proportion of the circle overlapping each cell. TRI, TWI, and TCWS values hold some uncertainty, as they are based on locations recorded using hand-held GPS devices with accuracy in the range of multiple metres to a few tens of metres. For further details, see Appendix S2. Since TCWS is potentially more confounded by standing vegetation, we focussed on TWI as our wetness variable.

2.3.3 | Biotic variables

To assess the role of biotic influences on shrub species distribution, we included an estimate of resource competition intensity between shrub species. We assumed that, under benign conditions, species that are more resource-acquisitive than their local community should have a competitive advantage. In contrast, we expected more resource-conservative species to have an advantage under harsh conditions. To quantify this effect, we extracted principal component axis 1 (representing the leaf economics spectrum) scores for the focal tundra shrub species from Thomas et al., (2020) to quantify species' acquisitiveness. We then scaled the scores from zero (minimum) to one (maximum) and calculated

$$\mathrm{dCWA}_{j,x} = a_j - \sum_k \rho_k \cdot a_k$$

where dCWA is the difference to community-weighted mean (CWM) acquisitiveness for each focal species j in plot x, a is the scaled acquisitiveness score, and ρ is the relative abundance of each other shrub species k co-occurring in the plot. The concept is similar to "weighted mean distance to native species" when predicting invasion dynamics (Thuiller et al., 2010). A positive dCWA indicates that the focal species is relatively more resource-acquisitive than its community, while a negative value indicates that it is relatively more resource-conservative. Index values were below −1 or above 1 in some instances if multiple shrub species formed overlapping vegetation layers. In plots with none of the species present, dCWA was set to 0 for all species as in this case none is experiencing either a negative or positive community effect.

In addition, as a measure of vegetation structure that each species is experiencing in each plot, we summed the total relative abundance of other shrubs excluding each respective focal species. Abundance values for shrubs could exceed 1 if multiple species formed overlapping vegetation layers.

We also included graminoid abundance as an explanatory variable, as parallel increases in both shrub and graminoid abundance will likely lead to stronger competition between these two groups in the future (Myers-Smith et al., 2019a). Since graminoid abundance was not highly correlated with total shrub cover (Appendix S4), any relationship with individual shrub groups or species abundance should indicate an interactive effect rather than a statistical artefact representing exclusion due to limited physical space in the plot (i.e. it is theoretically possible for both shrub and graminoid abundance to increase).

2.4 | Statistical analyses

We ran two parallel analyses which were identical in the procedures described below except for one using TWI and the other TCWS as a

wetness variable. Analysis and results based on TCWS are presented in Appendix S5.

To select the final set of variables, we calculated the Pearson correlation between all potential variables across the 414 plots, using the correlate function from the *corrr* R package (Kuhn et al., 2020; Appendix S4), and calculated variance inflation factors (VIF) among variables with the vif function from the *usdm* R package (Naimi et al., 2014). Highly correlated variables were removed sequentially, eliminating the variable with the highest VIF in each iteration until all VIF values were < 3 (Zuur et al., 2010; Appendix S6). As the only exception, we retained summer precipitation instead of spring precipitation, as this increases comparability to other studies (e.g., Blok et al., 2011; Maliniemi et al., 2018) and the two variables were highly correlated ($r = 0.92$; Appendix S4). All remaining variables were scaled by standard deviation and centred on zero.

Variables were incorporated on different hierarchical levels: as plot groups spanned up to approx. 50 m, several plots within a plot group fell into the same climate grid cell of 90-m resolution. Therefore, all climate variables were averaged within a given plot group. Topographic and biotic variables varied at the plot level. As dCWA and other shrub abundances represent species-specific variables, we only included them in single-species models.

We ran two sets of models, each using a Bayesian hierarchical modelling framework: abundance of shrub groups was assessed based on a log-normal distribution, as cover values were not bound to a specific upper limit (due to overlapping vegetation layers), while species abundance was modelled using a beta-Bernoulli mixture model to account for both continuous and integer (0 and 1) values in proportion data. All models were computed in JAGS (v. 4.3.0) called from R through the packages *rjags* (Plummer, 2019) and *R2jags* (Su & Yajima, 2015). All models included a random effect for plot group to account for spatial non-independence of plots within plot groups, and used weakly informative normal priors centred on zero for all coefficients, except for the variance parameters (sigmas) where we used uniform priors instead. Models were run with three chains for 100,000 iterations each (burn-in = 70,000, thinning factor = 2). We assessed model convergence visually by examining trace plots and by ensuring that values of $\hat{R}$ (Gelman–Rubin convergence statistic; Gelman & Rubin, 1992) were ≪1.1 for all parameters (Appendix S7). Models did not converge for *Cassiope tetragona*, *Phyllodoce caerulea*, *Rhododendron tomentosum*, and *Salix arctophila* (Appendix S7) due to low abundance of these species (only present in 16, 10, 13, and 13 out of the 69 plot groups, respectively; Appendix S1). Hence, we report results only for the remaining five species, though the presence of these species is still reflected in the calculation of dCWA values and total shrub abundance. Bayesian approaches do not assess "significance" of parameters in the model. However, in order to improve clarity and readability of the results, we refer to any parameter as "significant" (or "marginal"), if the 95% credible interval (marginal: 90% CI) for that parameter estimate did not overlap zero. If the quadratic terms of summer temperature, summer precipitation, and temperature variability did not have significant or marginally significant influence on abundance of the five species, we excluded the respective quadratic terms from models before re-running.

All data processing as well as analyses were performed using R v. 4.0.3 (R Core Team, 2020).

3 | RESULTS

The direction and magnitude of shrub abundance relationships with climatic, topographic, and biotic variables differed strongly among species and functional groups (Figure 3). Moreover, functional group responses only partially reflected responses of individual species (Figure 3). Annual air temperature variability was the most common (four of five species) and influential (two of five species) variable explaining abundance across individual species, while graminoid cover consistently explained abundance of all three functional groups (Figure 3). Also, for three shrub species and both evergreen and deciduous functional groups, summer temperature effects on abundance were slightly, yet not significantly, dependent on wetness (Figure 4b–e, g). Difference to CWM acquisitiveness explained abundance of resource-acquisitive, but not -conservative shrub species, as all deciduous species were more abundant in relatively more conservative communities (Figure 3). However, the exact relationship varied slightly among species along the temperature gradient (Figure 5).

We found no consistent benefit of warmer, wetter, or less variable climate for the abundance of more resource-acquisitive species (hypothesis 1; Figure 3). In fact, for many of the variables, most species and groups showed opposite trends. Higher annual temperature variability, occurring mainly towards the inland (Appendix S3), was correlated with higher abundance of acquisitive deciduous *Betula nana* and *Salix glauca*, even though modelled abundance of deciduous shrubs overall decreased sharply at the most variable sites (Appendix S7). Neither any individual deciduous species nor deciduous shrubs combined showed a particular trend with higher summer precipitation (Figure 3). Abundance of the resource-conservative species *Empetrum nigrum* and *Rhododendron groenlandicum* showed differing relationships to the same climatic variables, weakening possible trends across the functional group (Figure 3).

Topography explained even less of the abundance of individual species and functional groups (Figure 3). Higher topographic wetness was related to higher abundance of resource-acquisitive *Salix glauca* (Appendix S7). *Betula nana* and *Vaccinium uliginosum* as well as deciduous shrubs overall showed a similar, yet non-significant trend (Appendix S7), but abundance of evergreen shrubs or total shrub abundance showed no such relationship (Figure 3).

Furthermore, the interaction between wetness and temperature did not significantly affect the abundance of any species or group, irrespective of acquisitiveness (hypothesis 2; Appendix S7). While mean parameter estimates for evergreen and deciduous shrubs as well as *Empetrum nigrum* and *Vaccinium uliginosum* deviated notably
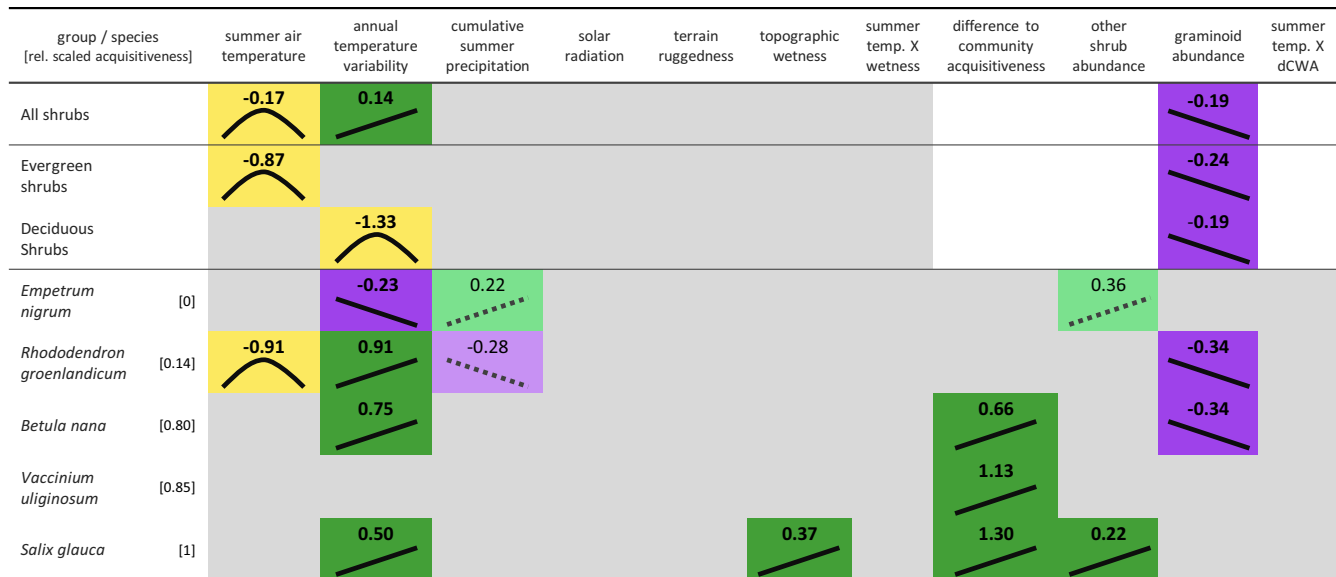
group / species [rel. scaled acquisitiveness]	summer air temperature	annual temperature variability	cumulative summer precipitation	solar radiation	terrain ruggedness	topographic wetness	summer temp. X wetness	difference to community acquisitiveness	other shrub abundance	graminoid abundance	summer temp. X dCWA
All shrubs	-0.17	0.14								-0.19	
Evergreen shrubs	-0.87									-0.24	
Deciduous Shrubs		-1.33								-0.19	
Empetrum nigrum [0]		-0.23	0.22						0.36		
Rhododendron groenlandicum [0.14]	-0.91	0.91	-0.28							-0.34	
Betula nana [0.80]		0.75						0.66		-0.34	
Vaccinium uliginosum [0.85]								1.13			
Salix glauca [1]		0.50				0.37		1.30	0.22		

FIGURE 3 Schematic overview of how abundance of shrub functional groups and species was related to climatic, topographic, and biotic variables, as obtained from individual hierarchical Bayesian models, with Topographic Wetness Index (TWI) as the wetness variable. Colours and sketched trend lines indicate relationships as positive (green, ascending line), unimodal (yellow, curved line), or negative (purple, descending line). Colour saturation and line appearance indicate 95% (saturated, solid lines) or 90% (half-saturated, dotted lines) credible intervals of coefficient posterior distributions not overlapping zero. Grey fields indicate relationships with credible intervals overlapping zero. Difference to community-weighted mean (CWM) acquisitiveness and shrub cover was not included in functional group models as they are species-specific estimates. Species are arranged according to their ecological strategy, from resource-conservative (*Empetrum nigrum*) to -acquisitive (*Salix glauca*; see also Figure 1). See also Appendix S7 for modelled abundances and model coefficients, as well as Appendix S5 for comparison with models including Tasselled-Cap Wetness instead of TWI

from zero, uncertainties in those estimates were high across all species and groups (Figure 4). Neither solar radiation nor terrain ruggedness explained abundance of any shrub species or functional group.

All deciduous species were significantly more abundant in less resource-acquisitive communities (hypothesis 3). Difference to CWM acquisitiveness best explained abundance of *Salix glauca* and *Vaccinium uliginosum*, while it was not reflected in abundance of any evergreen species (Figure 3). This varied along the temperature gradient for some deciduous species, but none of these relationships was statistically significant (hypothesis 4; Appendix S7), due to generally high uncertainty in model parameters (Figure 5). In addition, higher abundance of other shrubs was correlated with higher abundance of both the most resource-conservative (*Empetrum nigrum*) and the most resource-acquisitive species (*Salix glauca*). Similarly, evergreen *Rhododendron groenlandicum*, deciduous *Betula nana*, and all functional groups were less abundant in the presence of more graminoids (Figure 3).

The general importance of temperature variability as well as graminoid abundance for explaining shrub abundance was consistent across model frameworks, regardless of the wetness variable included (Figure 3; Appendix S5). However, unlike TWI, higher TCWS was significantly and positively correlated to abundance of all functional groups as well as *Empetrum nigrum*, *Rhododendron groenlandicum*, and *Vaccinium uliginosum*, but not *Betula nana* or *Salix glauca*. TCWS was even the most important explanatory variable for abundance in all shrubs, evergreen shrubs, and both evergreen species *Empetrum nigrum* and *Rhododendron groenlandicum*. Including TCWS instead of TWI lowered the importance of other variables, particularly summer temperature and other shrub abundance, though TCWS was not highly correlated with either of these variables (Appendix S4).

4 | DISCUSSION

Shrub vegetation is expanding in many regions of the Arctic, but there is uncertainty about the underlying drivers of shrub expansion and their relative importance (Martin et al., 2017). We found that the abundance of different tundra shrub species showed contrasting relationships to variation in multiple climatic, topographical, and biotic variables across the study area, both within and among functional groups (Figure 3). Explanatory power of functional traits was limited, especially for shrub species' relationships with the abiotic environment. These results indicate that predicting future dynamics of tundra vegetation will be challenging, as species are likely to respond individualistically based on the local interplay of warming with wetness conditions, other abiotic factors, and their biotic interactions.

4.1 | Temperature variability was the most important abiotic variable

We found annual temperature variability to be the most influential abiotic variable for explaining shrub abundance across all groups and species. However, like for all tested abiotic variables, the magnitude and direction of the relationships varied considerably among species,
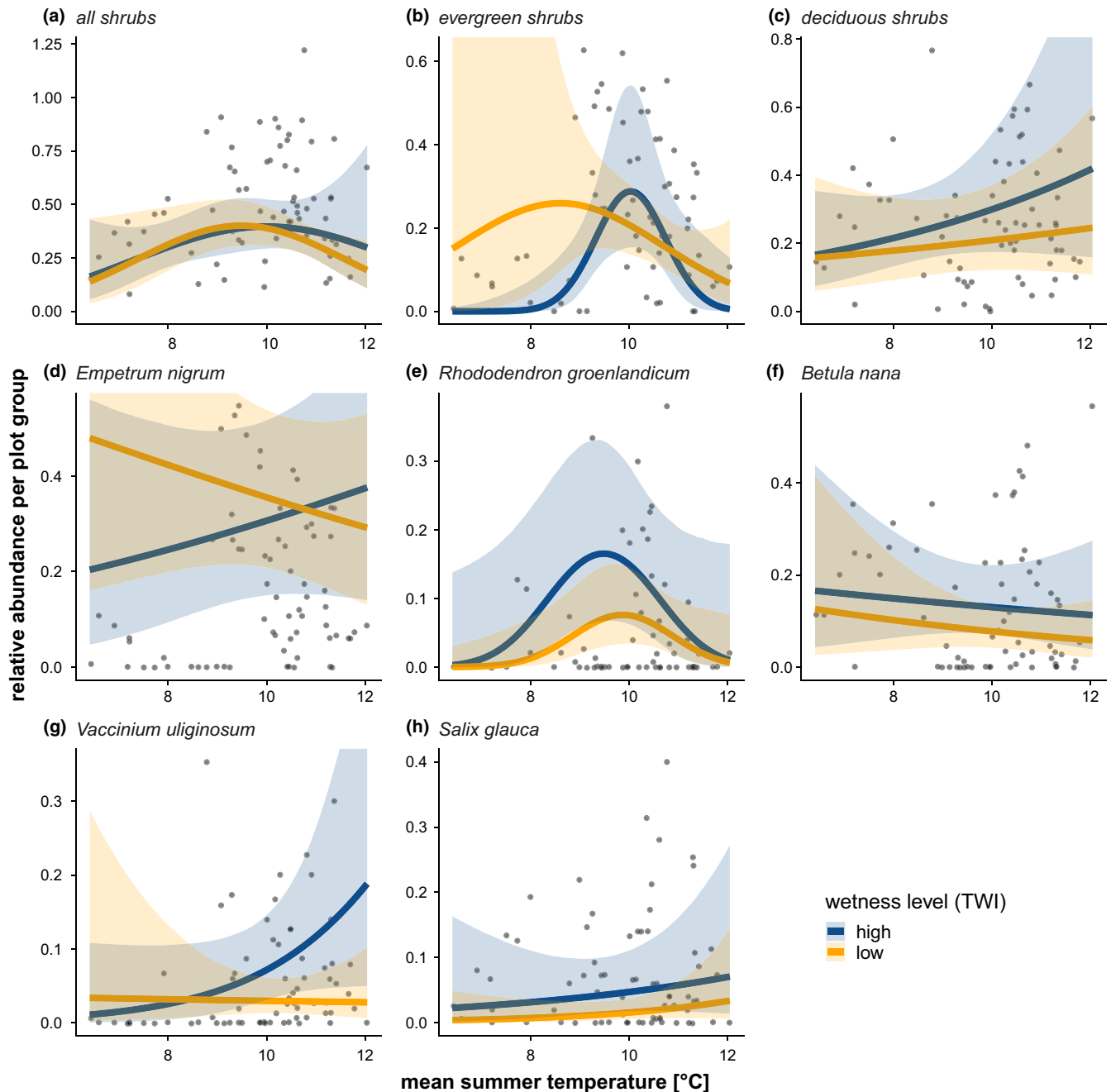
FIGURE 4 Interactive effects of mean summer temperature and wetness (Topographic Wetness Index) on modelled abundance of different shrub functional groups (a–c) and species (d–h). Low (orange) and high (blue) moisture levels represent 5 and 95% quantiles of wetness values across all study locations, respectively. Trend lines are based on derived predictions from individual hierarchical Bayesian models per group or species, and ribbons represent the corresponding 95% credible intervals. Abundance values > 1 for all shrubs can occur due to overlapping vegetation layers. Note that lines extrapolating beyond point ranges (e.g., d) should be interpreted with care. See also Appendix S5 for comparison with models including Tasselled-Cap Wetness instead of TWI

across and within functional groups. This finding often contradicted our first hypothesis suggesting higher abundance of more resource-acquisitive species towards less variable temperatures by the coast. Temperature variability along our study gradient was strongly and negatively correlated to winter temperature ($r = -0.83$), which has recently been highlighted as an important control of tundra vegetation (Niittynen et al., 2020a) and a major component of arctic

warming (Boisvert & Stroeve, 2015; Graham et al., 2017). Our results could, therefore, reflect different cold tolerances among the studied shrub species, and further research along large-scale temperature variability gradients could help explain the underlying mechanisms.

Contrasting to our expectations, the relationships with summer temperature were unimodal or absent for most shrub groups and species (Figure 3). The unimodal responses could indicate that
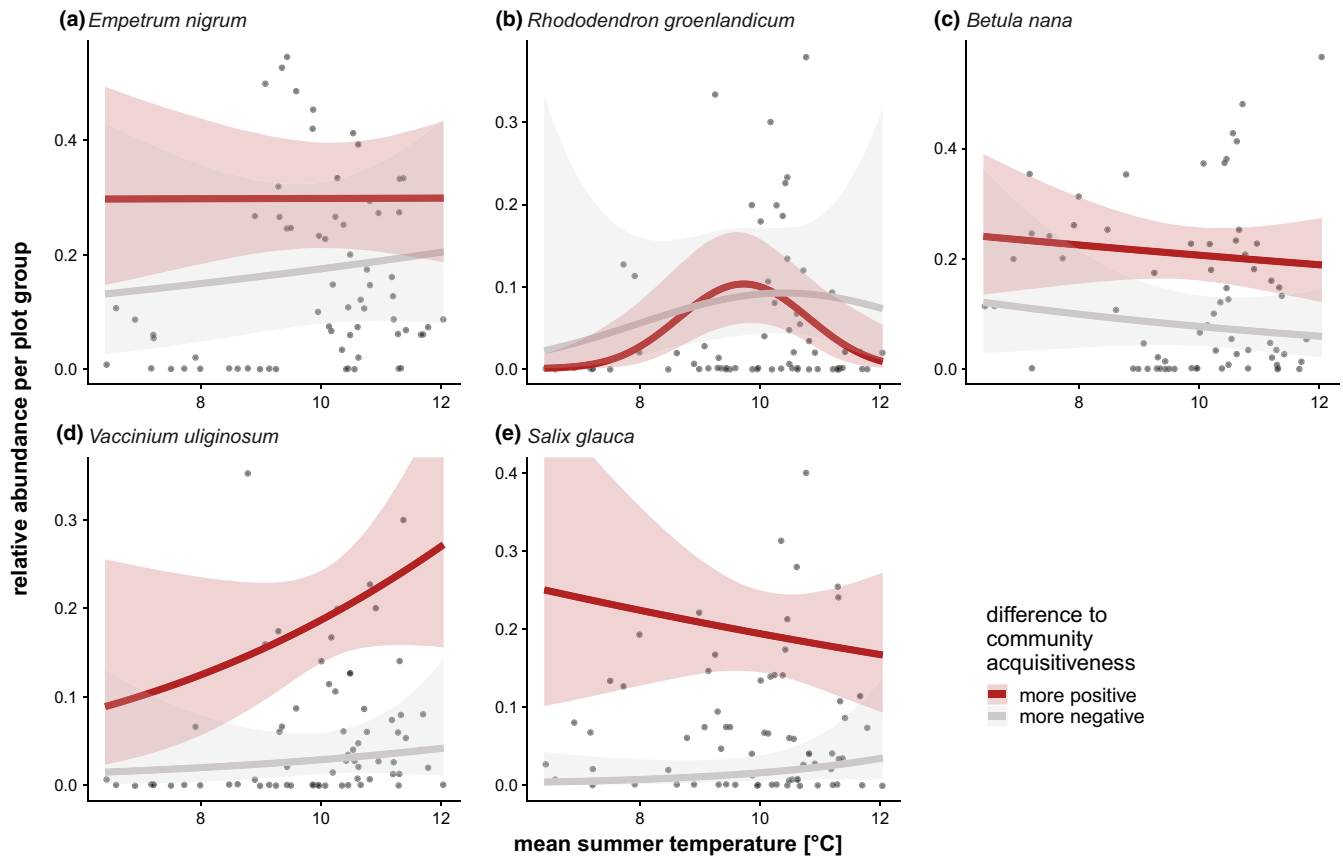
FIGURE 5 Interactive effects of mean summer temperature and biotic interactions (difference with community-weighted mean acquisitiveness) on modelled abundance of different shrub species. Low (light grey) and high (red) acquisitiveness levels represent 5 and 95% quantiles of respective community acquisitiveness values. Species are arranged from least (a) to most acquisitive (e; see also Figure 1). Trend lines are based on derived predictions from individual hierarchical Bayesian models per species, and ribbons represent the corresponding 95% credible intervals. Note that lines extrapolating beyond point ranges (e.g., d, e) should be interpreted with care

abundance of these species is limited by drought at the warm end of the gradient (Myers-Smith et al., 2015). However, our wetness measure did not reveal this interaction (Figure 4; see section 4.2). Generally, we found no systematic patterns in the relationships of abiotic variables and shrub abundance with regard to acquisitiveness. The only exception was *Salix glauca*, the most resource-acquisitive shrub species. Meeting our expectations, *Salix glauca* was more abundant in wetter sites (Figure 3), reflecting the advantages this acquisitive species has when resource stress is low (Maestre et al., 2009) and demonstrating the influence of moisture availability on shrub growth (Myers-Smith et al., 2015; Ackerman et al., 2017; Gamm et al., 2018) and abundance (Elmendorf et al., 2012) across the Arctic. Similarly, precipitation only showed weak relationships with shrub abundance, potentially due to the relatively small differences between the study sites (Appendix S3). Variation in solar radiation and terrain ruggedness did not explain shrub abundances, suggesting that they did not accurately capture the relevant environmental processes as intended. In the case of terrain ruggedness, the scale of the underlying terrain model might be too coarse to represent important local factors such as snow cover (Niittynen et al., 2020b). To achieve reliable predictions of tundra shrub dynamics, it will be essential to thoroughly capture small-scale abiotic variation,

especially during winter, while replicating across large spatial gradients (Lembrechts et al., 2020).

4.2 | Uncertainties limit conclusions on wetness–temperature interactions

We did not find support for our second hypothesis predicting a positive effect of combined warmer and wetter conditions, regardless of acquisitiveness (Figure 3). Reliable predictions were impeded by large uncertainty in the model estimates (Figure 4) and our limited ability to accurately capture variation in plant-relevant wetness in the absence of in situ soil moisture measurements (see detailed discussion below). To overcome issues related to large model uncertainties, future studies should aim for sampling a wide range in moisture and temperature conditions, and ensure many spatially independent samples that match the spatial resolution of explanatory variables reflecting the relevant small-scale environmental variation. Combined with coordinated monitoring initiatives (Lembrechts et al., 2020), this will contribute to a better understanding of how shrub vegetation will respond to the interacting changes of temperature and moisture in the arctic tundra.

4.3 | Trait-mediated biotic interactions can shape tundra shrub dynamics

Biotic variables explained a considerable amount of variation in the abundance of shrub species in our models, highlighting the importance of accounting for biotic interactions when assessing mechanisms of tundra shrub expansion. In line with our third hypothesis, we identified higher abundances for all deciduous shrub species in more conservative communities, and more so for more resource-acquisitive species, reflecting their potential advantages in nutrient acquisition over relatively more conservative species. Also, the most acquisitive species (*Salix glauca*) could benefit from high cover of any other shrubs and the resulting protective structure (Bråthen & Lortie, 2016). The abundance of resource-conservative species did not show the expected negative relationship with higher dissimilarity from more acquisitive shrub communities. Yet, resource-conservative *Rhododendron groenlandicum* and the least acquisitive deciduous species *Betula nana* were less abundant with higher cover of graminoids (Figure 3), which represent the most acquisitive strategies in the study system (Figure 1). This relationship indicates a potential limitation of shrub expansion if large-scale abundance of graminoids will increase as observed at regional scales (Myers-Smith et al., 2019a).

In connection to our fourth hypothesis, our mean parameter estimates for the statistical interaction terms also indicate that a species' relative acquisitiveness can influence their relationship with the abiotic environment (Maestre et al., 2009; Figure 5). However, due to high uncertainties in our model estimates we cannot draw firm conclusions about these relationships (Figures 3 and 5), indicating that a higher sample size and spatial resolution of temperature data points could be desirable. Furthermore, our acquisitiveness score might not fully reflect relative differences in acquisitiveness between species, for instance, due to a general "hardiness" in tundra organisms, or multiple interacting trait "axes" (e.g., plant size, sensu Thomas et al., 2020) that we did not capture. There is much potential for future studies to expand our trait-based approach, and a general need to improve measures of biotic interactions and consider their role in mediating vegetation changes (Mod et al., 2014).

4.4 | Divergence of environmental relationships between species and groups

Surprisingly, except for biotic interactions, our results did not reflect the hypothesised links between resource economic traits and shrub abundance. We identified several cases where trends visible in functional groups did not correspond to responses of the individual species in the group (Figure 3). This highlights that functional group-level responses to altered environmental variables do not necessarily apply to all individual species, and, inversely, responses of a few particular species should not readily be extrapolated to functional group level (Dorrepaal, 2007; Bret-Harte et al., 2008; Little et al., 2015). Also, resource economic traits had little explanatory power

in relation to abiotic parameters, despite functional groups representing differences in leaf economic traits between species well (Figure 1; Thomas et al., 2019). Here, our findings suggest a limitation of approaches exclusively based on resource acquisition traits to predict species abundances and community structure, particularly in response to multiple abiotic variables (McGill et al., 2006; Kunstler et al., 2016). Future approaches should incorporate various conceptual paths when assessing how the interplay of abiotic and biotic environment shapes vegetation developments in the tundra.

4.5 | We need more accurate moisture variables

While most results were consistent across the models using the two contrasting wetness proxies, TCWS explained much more variation in abundances of species or groups than TWI (Figure 3; Appendix S5), yet neither method can satisfy the need to accurately represent in-situ plant-available water. TCWS is a surface reflectance-based measure and is, therefore, inherently influenced by vegetation cover, which could lead to circularity in the model predictions and explain the higher explanatory power of the wetness proxy in the TCWS models (Appendix S5). In turn, TWI estimates might also represent plant-available moisture only to a limited extent (Kemppinen et al., 2018; Kopecký et al., 2020) and its success in doing so depends on the algorithm used to model water flow in the landscape (Kopecký & Čížková, 2010), and the scale and quality of the underlying digital elevation model. Nevertheless, to avoid the potential circularity associated with the TCWS models, we chose to focus on the results based on TWI. Given the widely recognised importance of soil moisture for tundra vegetation (e.g., Elmendorf et al., 2012; Kemppinen et al., 2019), there is a pressing need to collect more in situ soil moisture observations and to develop better wetness proxies based on remote-sensing data (Kemppinen et al., 2018). Recent advancements in logging technology (e.g., Wild et al., 2019) and data availability (e.g., Lembrechts et al., 2020) represent promising first steps forward.

4.6 | Implications for understanding future changes in shrub abundances

As much of the Arctic tundra is located along coastlines, and many of the species included in our study occur throughout the biome, the patterns we observed here are likely relevant for many Arctic regions. Due to the observed high heterogeneity in responses, applying our findings to predictions for future shrub-dominated tundra vegetation is challenging, but some trends are still visible. First, continued winter warming and the accompanying decrease of annual temperature variability (Boisvert & Stroeve, 2015; Graham et al., 2017) can potentially support expansion of some evergreen, resource-conservative species, particularly *Empetrum nigrum*, by tipping the otherwise adverse interaction balance with more resource-acquisitive deciduous species to their favour. Second, specific

interactions within local communities will be crucial for determining future species composition as well as the effects of abiotic changes, though this will generally depend on which species will actually take advantage of the altered conditions (Myers-Smith et al., 2019a). Third, the outcome of these interactions and resulting local dominance of certain species can greatly influence shrub dynamics, which might deviate considerably from large-scale shrub responses (Bret-Harte et al., 2008; Saccone et al., 2017; Vowles & Björk, 2019), especially to changes in the abiotic environment.

In remote areas such as the Arctic, much research is relying on remotely-sensed variables, yet most of these fail to capture environmental variation at spatial and temporal scales relevant for the organisms (Lembrechts et al., 2019, 2020; Myers-Smith et al., 2020). Downscaled climate data increase the relevance compared to large-scale gridded variables, but still come with numerous caveats, including relatively high uncertainty, particularly in remote areas (Wilby & Wigley, 1997), dependence on the underlying terrain model, missing verification, and spatial and temporal aggregation beyond plant-relevant scales (Lembrechts et al., 2019). Local abiotic variation can crucially influence arctic plant communities (e.g., Niittynen et al., 2020b) and local vegetation structure is likely to feed back on abiotic conditions as well, for example on soil temperatures and moisture (Myers-Smith & Hik, 2013; Kemppinen et al., 2021). These points further stress the importance of in situ measurements of abiotic conditions for predicting tundra species distributions (Lembrechts et al., 2019). In addition, future studies should consider biotic interactions across trophic levels such as browsing (Olofsson et al., 2009; Vowles et al., 2017) or insect herbivory (Prendin et al., 2019), and temporal dynamics, for instance, to include different successional stages and abundance changes, as well as effects of intra-specific trait variation on the outcome of biotic interactions among shrubs (e.g., Violle et al., 2012; Westerband et al., 2021). Addressing these knowledge gaps could further improve understanding of long-term tundra shrub responses to changing abiotic and biotic environments.

5 | CONCLUSION

We observed highly individualistic relationships of tundra shrub species and functional groups' abundances with nine abiotic and biotic variables across the coastal–inland gradient studied. Functional traits connected to resource economics explained responses of some species, mainly to biotic variables. Yet, much of the variation in responses to abiotic factors was not related to economic traits of the species investigated, thus demanding a wider focus than exclusively trait-based approaches to explain responses to multiple interacting variables of both abiotic and biotic origin. We found that annual temperature variability explained much variation in shrub abundance, suggesting that future changes in temperature variability, caused for example by stronger winter than summer warming, could alter shrub communities in the tundra. Biotic interactions, as considered in our study, will likely affect the outcome of these changes to a large

degree, but specific analyses of biotic influences on shrub species' responses to abiotic variation are needed. Increasing the availability of fine-resolution, plant-relevant environmental information will be crucial to capture this abiotic variation, and incorporating these data into integrative approaches like our analysis will improve our understanding and ability to predict ecosystem changes in a rapidly changing Arctic.

AUTHOR CONTRIBUTIONS

SN, MF, and JNN designed the study and performed the field sampling. MG downscaled the climate data, and JJA extracted data on topographic variables. JvO analysed the data with help from ADB, ABO and JJA, and input from SN and JNN. JvO drafted the paper in collaboration with all co-authors. The final version of the manuscript was read and approved by all co-authors.

DATA AVAILABILITY STATEMENT

Data and code for this study are available at https://github.com/jonathanvonoppen/nuuk_shrub_drivers.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Study species

Appendix S2. Patterns of explanatory variables across the study gradient

Appendix S3. Calculation of explanatory variables

Appendix S4. Correlation between explanatory variables

Appendix S5. Summary of results from Tasselled-Cap Wetness Index (TCWS) models

Appendix S6. Variable selection and model code for Topographic Wetness Index (TWI) models

Appendix S7. Coefficient estimates and modelled abundances from Topographic Wetness Index (TWI) models