

## RESEARCH ARTICLE

# How does spatial heterogeneity affect inter- and intraspecific growth patterns in tundra shrubs?

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## Abstract

1. Arctic and alpine ecosystems are strongly affected by rapidly changing environmental conditions, resulting in profound vegetation shifts, which are highly heterogeneous and hard to predict, yet have strong global impacts. Shrubs have been identified as a key driver of these shifts. In this study, we aim to improve the understanding of how such broad-scale vegetation changes are locally impacted by inter- and intraspecific plasticity and topographically driven heterogeneity in microsite conditions.
2. We assessed continuous stem diameter variation of three dominant tundra shrub species at daily resolution during 5 years, using high-precision dendrometers, thus bridging the gap between classical dendroecology and plant physiology. From this data, we identified distinct growth patterns which we linked to microsite environmental drivers.
3. The observed patterns appeared highly variable depending on site and species, strongly influenced by characteristics of the individual plant. As the main driver of this variability, we identified fine-scale topographic complexity, causing the sampled specimens to adjust locally by developing distinct growth strategies. We found these strategies strongly related to snow-cover variation and associated freezing and thawing. Predicted changes in winter conditions and associated snow regimes will therefore have strong effects on shrub growth and community structure, yet, these effects are highly complex and not uniform in direction.
4. *Synthesis.* The ability to adapt in a heterogeneous environment appeared highly differentiated between species and closely connected to intraspecific plasticity. Here, we identified spatial variability related to local topography as a main indicator for potential future redistribution and niche shifts in response to environmental change.

## KEYWORDS

arctic–alpine vegetation change, climate–growth relations, dendrometer, ecophysiology, growth variation, linear mixed effect models, partial least squares regression

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## 1 | INTRODUCTION

In a rapidly changing climate, there is an increasing need to understand how communities and ecosystems respond to environmental change. With tundra ecosystems experiencing temperatures rising at thrice the global rate (AMAP, 2021; Post et al., 2019), massive changes in vegetation structure and ecosystem functioning are taking place already (Bjorkman et al., 2018; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe-Henry, et al., 2012; Epstein et al., 2017; IPCC, 2014). In the past decades, an increased biomass and coverage of shrubs in response to changes in climate has led to major vegetation shifts. The observed greening of wide areas of the circumpolar Arctic has profound implications for the global climate system (Bjorkman & Gallois, 2020; Carlson et al., 2016; Collins et al., 2021; Forbes et al., 2010; Fraser et al., 2014; Myers-Smith et al., 2011). In recent years, however, this trend has been recognized as highly heterogeneous and complex, with the direction of change still poorly understood (Abbott et al., 2016; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Macias-Fauria et al., 2020; Myers-Smith et al., 2020; Nielsen et al., 2017; Phoenix & Bjerke, 2016). As growing seasons are lengthening (Epstein et al., 2017), snow-cover conditions are changing (Xu et al., 2013) and extreme winter warming events are more frequently causing snowmelt in midwinter (Bjerke et al., 2017), questions are rising about the ability of dominant tundra species to adapt within the necessary timeframe to survive under these changing conditions.

An individual plant's ability to thrive in a changing environment has been linked to multiple factors, including its evolutionary history, genetic constraints, environmental influences and plasticity, both on an inter- and intraspecific level (Funk et al., 2017; Henn et al., 2018; Matesanz et al., 2012; Violle et al., 2012). Phenotypic plasticity, the ability of a species to alter its phenotype in response to environmental variation (Kingsolver & Huey, 1998), as well as genetic adaptation (Hoffmann & Sgrò, 2011), play a key role in determining the individual plant's ability to shift optimal trait values with changing environmental conditions. In ecology, plasticity is therefore closely linked to range size and climatic niche breadth (Callaway et al., 2003; Duputié et al., 2015; Graae et al., 2018; Henn et al., 2018; Malyshev et al., 2016). Inter- and intraspecific variability have long been recognized as a key element of community ecology with strong implementations on ecosystem-level processes in response to environmental change (Firn et al., 2019; Hendry, 2016; Violle et al., 2012). This fact has led numerous studies (e.g. Duputié et al., 2015; Firn et al., 2019; Pfennigwerth et al., 2017; Valladares et al., 2014) to look at inter-plant variability in response to climate change research, where species are challenged to cope with modified environmental drivers, that may lead to range and niche shifts. In this context, variation in functional traits is often used as indicator for this variability, while physiological adjustment and consequent variation in growth patterns have not yet been utilized in this context. Furthermore, models of species distribution and range limits still rarely consider plasticity and

such models are often restricted by small datasets. How plasticity, in response to heterogeneous environments, connects with the factors determining a species niche, remains poorly understood (Pérez-Ramos et al., 2019).

In this context, we examined variations in stem diameter across three dominant shrub species within a heterogeneous oroarctic (Virtanen et al., 2016) setting along steep geographical gradients. We derived fine-scale growth curves from continuous stem diameter measurements using high-precision dendrometers, thus bridging the gap between classical dendroecology and plant physiology. We expected to discern distinct growth patterns from these curves, adapted to site-specific environmental conditions, and reflected by inter-site variability in stem diameter change. Our objectives were to specify this variability within growth patterns, answering (a) how these patterns differ between species and along topographic gradients, (b) how they are linked to site- and topography-specific environmental drivers and (c) how growth variance between individual specimens is affected. We assumed that answering those questions will allow us to infer conclusions about drivers of radial growth in shrubs and derive valuable information regarding the overall plasticity of the examined shrub species, which would facilitate predictions of possible range and niche shifts in response to future climate change.

## 2 | MATERIALS AND METHODS

### 2.1 | Species and specimens

For this study, we selected three shrub species abundant across the tundra, two evergreen (*Empetrum nigrum* ssp. *hermaphroditum* (Hagerup), crowberry, and *Phyllodoce caerulea* (Linnaeus), blue mountain heath), and one deciduous species (*Betula nana* (Linnaeus), dwarf birch). All three species have a near circumpolar distribution (Büntgen et al., 2015; Hultén, 1968), exert considerable effects on tundra communities (Bell & Tallis, 1973; Bret-Harte et al., 2001; Coker & Coker, 1973), and play a key role in the 'greening of the Arctic' (Crawford, 2008; Myers-Smith et al., 2015). Regarding interspecific interaction, *B. nana* commonly surpasses both *E. hermaphroditum* and *P. caerulea* in height (Coker & Coker, 1973; de Groot et al., 1997), and is thus likely to influence growth of its competitors by restricting their exposure to solar radiation (Bär et al., 2007; Bret-Harte et al., 2001). At higher elevations (>1,100–1,300 m a.s.l.), *B. nana* and *P. caerulea* cease to exist while *E. hermaphroditum* remains within a matrix consisting of debris and graminoids (Bär et al., 2007). While *B. nana* and *E. hermaphroditum* occur across a broad range of micro-habitats and are able to tolerate comparatively low winter temperatures (Andrews et al., 1980; de Groot et al., 1997; Ögren, 2001; Stushnoff & Junttila, 1986), *P. caerulea* usually grows best at habitats with prolonged snow cover (more than 100 days annually) and primarily prefers slopes (Coker & Coker, 1973; Kameyama et al., 2008).

## 2.2 | Study sites

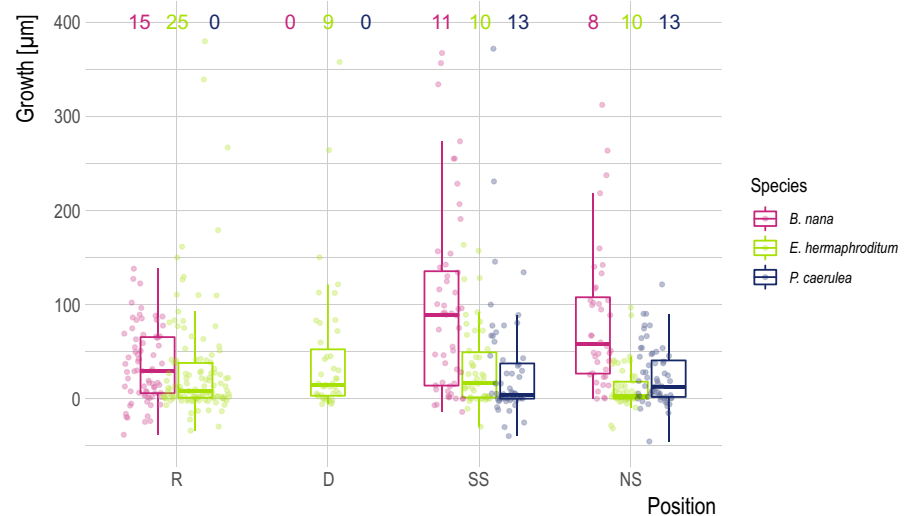
Our study is based on long-term monitored specimens from two study regions located in two contrasting alpine regions of central Norway. To the east, the Vågå/Innlandet region (61°53'N; 9°15'E) is located within the continental climatic section (C1; Moen & Lillethun, 1999). With a total annual precipitation of approximately 300–500 mm in the valleys, this area experiences the highest aridity found in Norway (Kleiven, 1959). Mean annual ambient air temperature is  $-1.2^{\circ}\text{C}$  (range:  $-29.2$  to  $+16.7^{\circ}\text{C}$ ) (measured between 1991 and 2002, Löffler, 2003). Our second study region to the west, the Geiranger/Møre og Romsdal region (62°03'N; 7°15'E), is located within the slightly to markedly oceanic climatic section (O1–O2; Moen & Lillethun, 1999) of the inner fjords. It is characterized by humid conditions, with total annual precipitation of 1,500–2,000 mm in the valleys (Aune, 1993) and a mean annual ambient air temperature of  $1.9^{\circ}\text{C}$  (range:  $-23.2$  to  $+17.2^{\circ}\text{C}$ ) (measured between 1991 and 2002, Löffler, 2003). Additionally, our own measurements within the studied regions (in the alpine parts) and within the study period indicated an annual liquid precipitation of 900 mm in the west and 375 mm in the east. The additional amount of snow and its water equivalent remains unknown, but snowdrift leads to an uneven distribution of the snowpack within the complex alpine topography (Löffler, 2007). The study sites within the regions were stratified-randomly chosen to cover the elevational gradient, following the framework of our long-term alpine ecosystem research project (LTAER; e.g. Frindte et al., 2019; Hein et al., 2014; Löffler et al., 2021; Löffler & Finch, 2005). They were placed to represent the different elevational bands at 100-m intervals from the tree line upwards, shifted by approximately 100 height-metres between the Western and Eastern study region to account for the depression of the elevational zonation towards the west. The tree line, defined as the upper elevational limit of the occurrence of subalpine birch trees (*Betula pubescens* ssp. *czerepanovii*), and, as such, the lower limit of the alpine belt (Dahl, 1986), is located at approximately 1,000 m a.s.l. in the Eastern study region and at approximately 750 m a.s.l. in the

Western region. In accordance with the local micro-topography, we chose sites from four distinct micro-topographical positions at each of the elevational bands: (a) exposed ridge positions (R), (b) positions within local depressions (D), (c) south-facing slopes (SS) and (d) north-facing slopes (NS). For a detailed depiction of the study design see Figure S1. Because of the topographic preferences of the studied species, we measured *P. caerulea* at the slopes (SS and NS) only. Additionally, a small proportion of the measurements contained missing data, resulting in gaps in the dendrometer curves. This was attributed to technical errors, and we therefore discarded the affected specimens from the study. This resulted in a lack of data for *B. nana* within local depressions (D). All chosen specimens were monitored for five consecutive years, resulting in a total of 570 annual dendrometer curves. For the total number of sampled specimens at each position, see Figure 1.

## 2.3 | Data collection

To monitor stem diameter variations, we used high-precision dendrometers (type DRO; Ecomatik, Dachau/Germany) mounted on one major above-ground stem horizontal to the ground surface for each specimen, as close to the assumed root collar as possible (approximately 1–5 cm above the ground). As addressed by Bär et al. (2006 and 2007), this major stem is thought to represent the whole plant at least partly. We tried to account for this variation between stems of the same plant by sampling a high number of individual specimens. During the mounting process of the dendrometers, we removed the dead outer bark to place the sensor as close to the living tissue as possible, following a common practice for dendrometer measurements of trees (e.g. Grams et al., 2021; Oberhuber et al., 2020; Wang et al., 2020). This ensures that hygroscopic shrinkage and swelling of dead tissues from the outer bark does not influence the diameter measurements. The sensor used had a temperature coefficient of  $<0.2 \mu\text{m}/\text{K}$ . Measurements were taken at 1 min intervals and aggregated, averaging dendrometer data into time series of daily

**FIGURE 1** Summary of radial stem growth at the monitored topographical positions, showing the median and the 25th and 75th percentiles (box), as well as the smallest and largest value no further than 1.5\*interquartile range from the hinge respectively (whiskers). Each value within the plot represents one annual value derived from stem diameter measurements (see Section 2). Numbers at the top show the number of specimens of each focal species, which were monitored at the respective position



mean values, using the R statistical software (R Core Team, 2020). When choosing microsites, we avoided positions near stones and small depressions, inside the radius of other larger shrub species, and near patches of wind erosion. At each site, we sampled one or more specimens of each species, if available, and took additional measures of microsite environmental parameters. These included soil temperatures ( $^{\circ}\text{C}$ ) at a depth of 15 cm below the ground surface (within the root zone; hereafter 'Trz') and air temperatures at 15 cm above the ground surface (within the shoot zone; hereafter 'Tsz'), measured at 1 min intervals and recorded as hourly means. For these recordings, we used ONSET's HOBO loggers (type H21-002) in combination with type S-TMB-002 temperature sensors ( $\pm 0.2^{\circ}\text{C}$  accuracy). For measurements of Tsz, the sensors were equipped with passively ventilated radiation shields. Based on this setup, we were able to accurately capture near-ground thermal conditions, which are often decoupled from the governing macro-climatic temperature signal (Körner, 2021; Körner & Hiltbrunner, 2018; Löffler et al., 2006). Additionally, we measured the volumetric soil water content (soil moisture,  $\text{m}^3 \text{ water} / \text{m}^3 \text{ soil}$ ) 15 cm below the soil surface (hereafter SMrz) at all sites. The uncalibrated SMrz was measured at 1 min intervals and recorded as hourly means using ONSET's type S-SMD-M005 soil moisture sensors ( $\pm 3\%$  accuracy). Those measurements proved especially valuable in the final analysis, as they, apart from the intended assessment of soil moisture, allowed for the fine-scaled analysis of freezing and thawing conditions within the root zone as derived from the availability of liquid water. To complement these data, we additionally inferred snow cover estimates from daily temperature amplitude. We assumed that a daily Tsz amplitude of less than 5K indicated that a layer of snow restricted daily air temperature fluctuations at the measured height of 15 cm. The respective periods were therefore defined as snow covered. The threshold of 5K was carefully chosen in accordance with the data. All the collected data covered a period of five full calendar years from 1 January 2015, to 31 December 2019, with some additional data collected in 2014. Missing data did not occur at any of the chosen sites.

## 2.4 | Statistical analysis

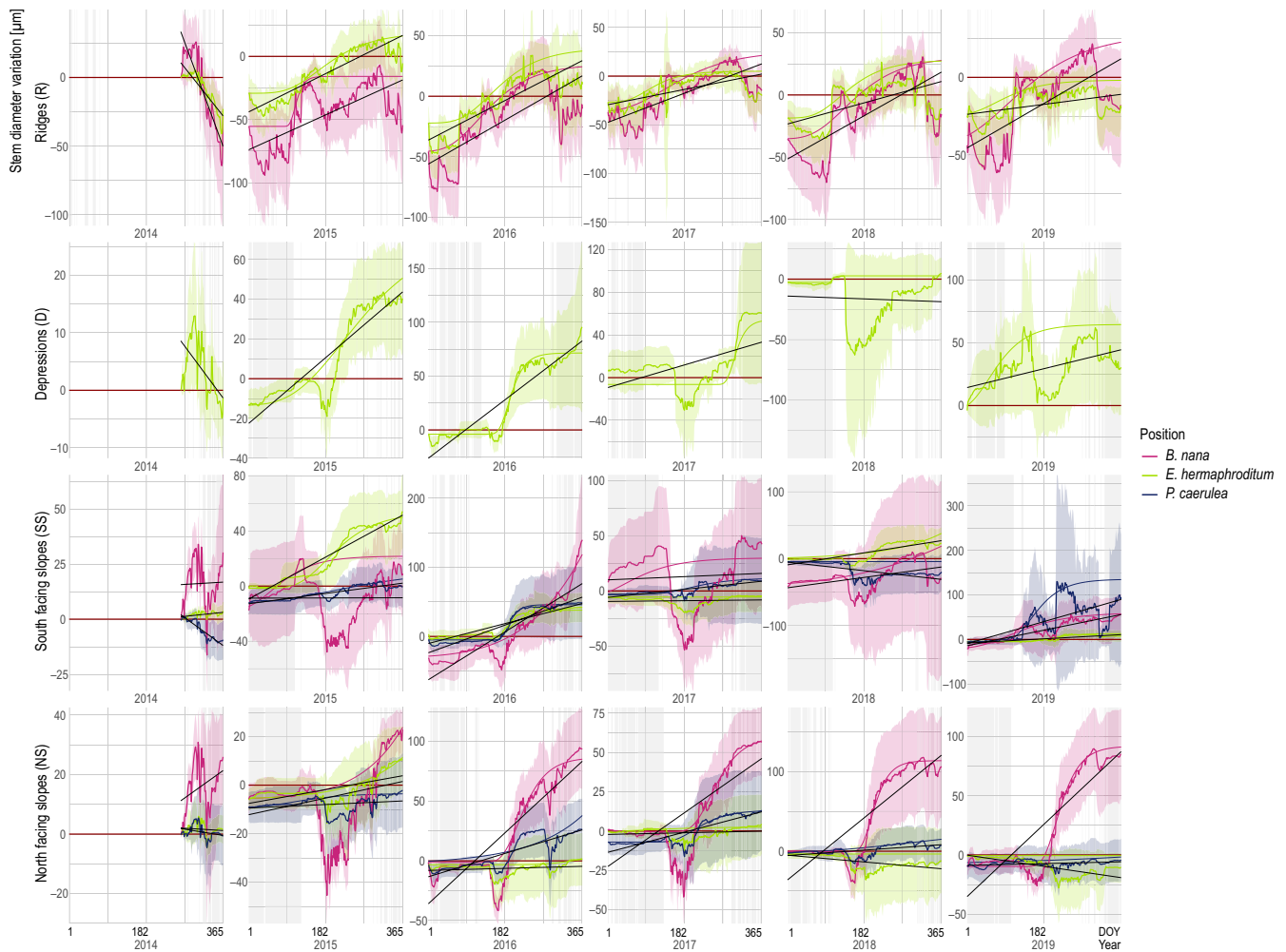
All statistical analyses were conducted using R v. 4.0.3 (R Core Team, 2020). For all analyses, significance levels were set at  $\alpha = 0.05$ . The stem diameter curves produced from the continuous dendrometer measurements were split by calendar years and the resulting annual stem diameter curves were normalized through subtraction of the previous year's maximum to exclude year-related growth trends and to maximize the separation of growth-related expansion from water-related swelling and shrinking of the stem. This necessity arises because dendrometers are not measuring the absolute stem diameter, but rather changes in stem diameter relative to the start of the measurement cycle. Additionally, singular outliers, which might occur due to mechanical influence to the sensor, were removed, by defining cut-off ranges, using the interquartile range (IQR) and the 25th (Q1) and 75th (Q3) percentile ( $(Q1/Q3) \mp 1.5 * \text{IQR}$ ; Figure 2).

Finally, for each year, a set of complementary growth characteristics was derived from the raw data: (a) growth, defined as the amount of stem diameter increase within 1 year, compared to the previous year (maximum stem diameter – maximum stem diameter of the previous year), (b) increment, defined as the total stem diameter increase (maximum stem diameter – minimum stem diameter) and (c) (annual) stem diameter change, defined as the absolute stem diameter increase within the span of the year (stem diameter at the end of the year – stem diameter at the beginning of the year) (Figure 2; Figure S2). While annual growth describes growth-related stem diameter expansion, the two latter include potentially reversible stem diameter shrinking, which is commonly associated with hydrological processes (Zweifel, 2016; Zweifel et al., 2014). In this way, we differentiated between growth-induced stem expansion (growth), which is most likely visible in the anatomical structure of the plant and thus directly comparable to classic measurement methods of radial stem growth in shrubs, and additional processes causing radial stem change (e.g. temporary water deficits), which are uniquely captured by our dendrometer measurements. In addition, we derived (d) the maximum annual stem diameter (including the initial stem diameter at the start of the year) from the dendrometer curves.

To assess whether there are governing trends or patterns in variation between individually measured sites and plants, depending on elevation or topographical position, we first performed a principal component analysis (PCA), using the R package *VEGAN* (Oksanen et al., 2020). In this analysis we included growth characteristics (annual growth, annual increment and annual stem change), as defined above. PCAs were computed for each species separately. The results (Figure S3) revealed no clear governing patterns between elevational bands and between the two study sites. The clearest distinctions were visible between topographical positions. For this reason, we chose to focus on this parameter for most of the subsequent analysis.

To understand the influence of microsite environmental drivers on growth, we then calculated Pearson's correlation coefficients and determined the significance of the coefficient through 500 bootstrapped iterations using the R package *wBOOT* (Weiss, 2016). Correlation coefficients were calculated between annual growth and monthly, as well as seasonal, mean values for our environmental parameters Tsz, Trz and SMrz. To account for possibly time-lagged effects of the previous year's conditions, we included monthly mean values for the period June (of the previous year) to December (of the current year) into the correlation analyses, similar to the analysis of growth chronologies as derived from ring-width series (e.g. Bär et al., 2008). Data from each topographical position, and from each species, entered into the analysis separately.

In addition, we applied partial least squares regression (PLSR; Wold, 1975) with the aim to use variable selection methods to assess the relative importance of certain environmental parameters in promoting or hindering growth and to thus substantially expand on the results of the correlation analysis. Developed for multidisciplinary problems (Wold, 1980), PLSR has found application in ecological studies during the past decade (Carrascal et al., 2009; Frindt et al., 2019; Löffler & Pape, 2020), yet the approach described here is



**FIGURE 2** Annual stem diameter variations relative to previous years maximum or start of the measuring period (for 2014), as derived from dendrometer measurements and aggregated to daily mean values. Measurements of individual specimens were averaged for each focal species and topographical position. Black lines indicate linear trends. Additional lines show fitted sigmoid Gompertz models derived from the original data. Grey areas indicate snow cover, derived from the daily amplitude in air temperature measurements (see Section 2)

comparatively novel. Main advantages include that it works without distributional assumptions (Dijkstra, 1983; Vinzi, 2010; Wold, 1980) and deals efficiently with unreliability and heteroscedasticity issues (Frindte et al., 2019; Martens & Næs, 1989). Moreover, the method is not limited, if the number of predictors exceeds the number of observations, or if the predictors are highly correlated, which makes PLSR highly suitable for our data (Carrascal et al., 2009; Frindte et al., 2019; Geladi & Kowalski, 1986). Following the approach successfully applied by Löffler and Pape (2020) to determine species thermal niches, we aggregated our environmental data, rounding to 0.2°C for temperatures and 0.01 m<sup>3</sup>/m<sup>3</sup> for soil moisture values. Subsequently, we counted and totalled the frequency of each value occurring within the time series. These calculations were performed for each meteorological season separately, resulting in sets of predictor variables, which were subsequently scaled and centred. Annual growth served as the associated response variable. For final single response model estimation, we used the SIMPLS algorithm (de Jong, 1993), implemented in the R package *MDATOOLS*

(Kucheryavskiy, 2020). The optimal number of components in the PLSR model was found using Wold's R criterion (Wold, 1978) and 10-fold cross-validation was used to assess the explained variance during model calibration and validation. From the numerous methods available to assess the relevance of each independent variable from the created models (reviewed by Mehmood et al., 2012), we chose the selectivity ratio (SR), based on assessments by Farrés et al. (2015) and Frindte et al. (2019). This parameter is defined as the ratio of explained to residual (unexplained) variance for each variable in the target projection vector. From the SR, we derived the explained variance ( $SR/abs(SR + 1)$ ) for more contrastable results. In the results, the variables with highest SR represent the explanatory variables with the highest influence on growth (Rajalahti et al., 2009). We increased the interpretability of these results by multiplying the SR of each variable by the sign of its corresponding regression coefficient, making it easy to identify which variables were positively or negatively related to the dependent variable (Löffler & Pape, 2020; Rajalahti et al., 2009). Like the correlations,

the analysis was conducted for each of the topographic positions and for each species separately.

Finally, we aimed to explore the variation in the stem diameter change patterns captured by the dendrometers, as well as the effects of environmental influences on this variation. We ran a set of linear mixed effects models, using the lmer function from the lme4 R package (Bates et al., 2015). This modelling approach has found wide application in ecological settings in recent years as it is an excellent tool to decompose the variability within grouped, complex data (Aller et al., 2019; Bolker et al., 2009; Firn et al., 2019; Henn et al., 2018). First, we fitted linear mixed effect models to the previously aggregated total annual growth values (dependent variable) and seasonally aggregated environmental parameters (independent variable), to further explore climate–growth relations. In contrast to the approaches described above, our complex study design can be implemented into this modelling approach by including species and topographical position as random effects, controlling variation in slope and intercept of the resulting models. In all created models, our response variables were log transformed. Models were created for each of the growth characteristics defined above, which entered as response variables. For total annual growth, years with negative values (net stem diameter shrinking) were defined as not growing and set to zero. After selecting these response variables, we grouped our data by a set of characteristics, that is, species, topographical position, year and site (including both elevation and study region). Furthermore, we included the initial stem diameter at the beginning of the year, rounded to the nearest decimal, as a grouping variable. By including these grouping factors as random effects into the models, we investigated the percentage of variance explained by each factor, which was derived from the models using the VarCorr function (Bates et al., 2015) in R. To represent the study design (Figure S1) within the model structure, we nested topographical position within the site parameter and species within position and site. The final models included no fixed effects and thus had the form  $\text{Growth} \sim (1 | \text{site/position/species}) + (1 | \text{year}) + (1 | \text{initial stem diameter})$ , as implemented into the lmer function of the lme4 R package (Bates et al., 2015). Aside from the full models, we created additional models for each species separately, removing the variable species from the random effects. Following this statistical exploration of spatial and temporal variability, we tested the role of microsite environmental variation within and between the grouping characteristics defined above and how this variation influenced annual growth. Therefore, we included seasonal means of measured environmental parameters (Tsz, Trz and SMrz) as fixed effects, creating one full model including all fixed and random effects and the response variable growth:  $\text{Growth} \sim \text{environmental parameters} + (\text{environmental parameters} | \text{position}) + (\text{environmental parameters} | \text{site}) + (\text{environmental parameters} | \text{year}) + (\text{environmental parameters} | \text{species}) + (1 | \text{initial stem diameter})$ , as implemented into the lmer function of the lme4 R package (Bates et al., 2015). From this model we then derived explained variance estimates (conditional,  $R^2_c$ , and marginal,  $R^2_m$ ), as well as the partitioned variance, using the R package MuMIn (Barton, 2020; Nakagawa & Schielzeth, 2013). In that way,

we quantified the percentage of variance in growth, which can be explained by environmental variation between sites, years and topographical position. More importantly, we quantified the proportion of variance in growth, which cannot be explained by those factors and can therefore probably be partly attributed to specimen-specific internal biology and/or other biotic/abiotic factors not accounted for by the study. All environmental data were standardized (scaled by means and standard deviations) prior to model fitting to make coefficients comparable (Grace & Bollen, 2005).

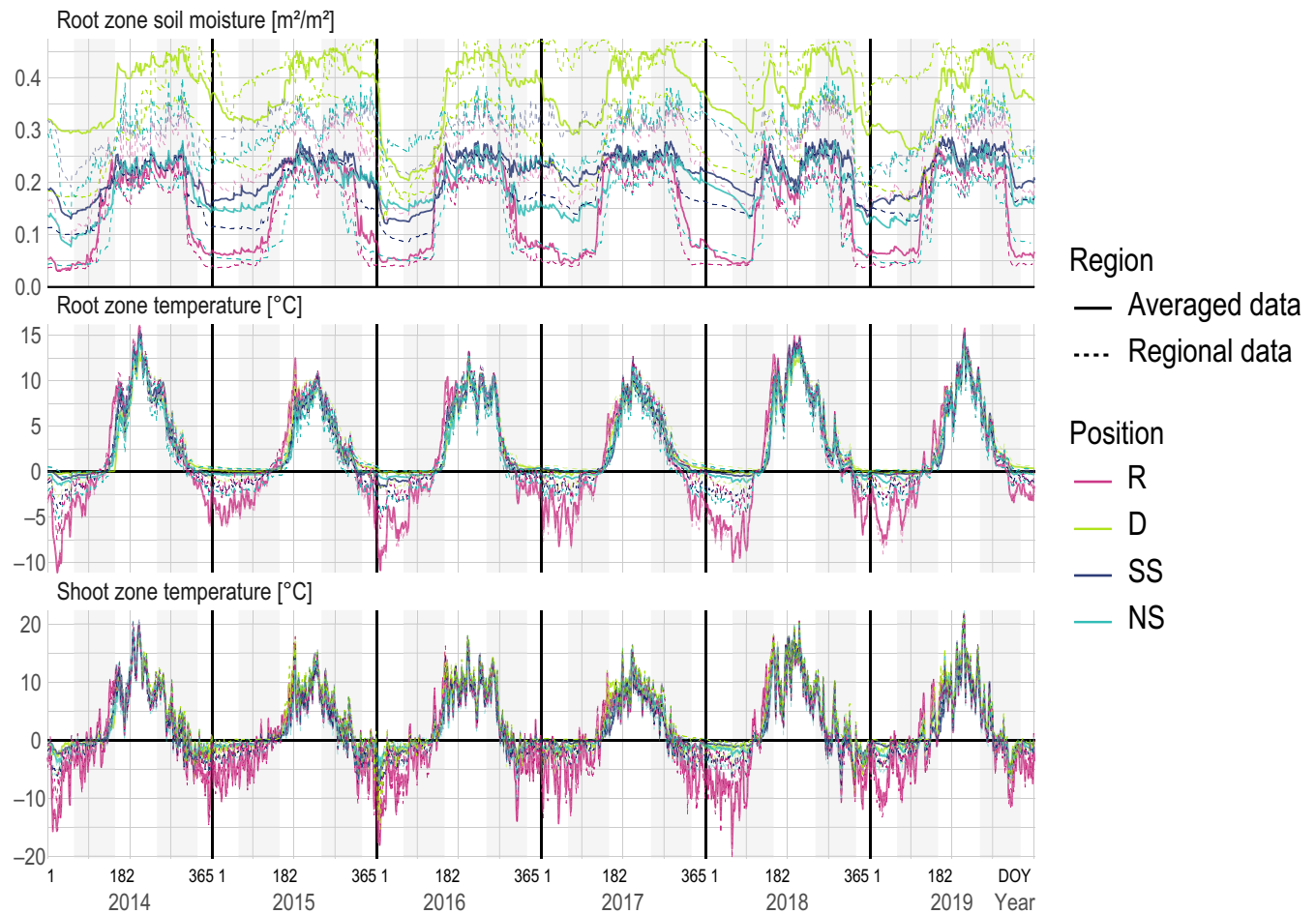
The full analysis thus consisted of four different statistical approaches to assess variation in growth–environment relations across species and positions. Combined, our results should provide a clear understanding of how the chosen three species are influenced by their respective local environment.

### 3 | RESULTS

#### 3.1 | How do microsite environmental conditions vary within the study area?

Each of the four sampled topographical positions was characterized by distinct regimes of near-surface environmental conditions (Tsz, Trz and SMrz) with different degrees of variation between the positions (Figure 3; Figure S4). However, a number of subordinate trends in inter- and intra-annual environmental variation were present at all sites: Temperatures usually started rising in spring (April or May). Lowest mean temperatures were measured in 2017, highest in 2018, with shoot and root zone conditions following, expectedly, a similar regime throughout all years. The year 2015 stands out because of a comparatively long winter, with lasting low temperatures throughout the meteorological spring and soil moisture rising only gradually, indicating reoccurring freezing conditions. However, according to our calculations regarding snow cover, snowmelt did not occur unusually late in 2015. In contrast, the years 2019 and 2018 were characterized by relatively short, cold winters with an early rise in spring temperatures, followed by considerable spring cold snaps (as evident by drops in the SMrz regimes), indicating renewed soil freezing. The successive winters 2015/2016 and 2016/2017 were characterized by comparatively little snow cover at all positions.

In terms of variability between the positions (Figure S3), a number of microsite environmental variations were represented in our data, resulting from the complex topographical conditions given in the studied alpine region. Here, we found differences in snow cover caused by snowdrift and timing of snowmelt to be most crucial. Extremely low winter temperatures and severe ground freezing, with high exposure to global radiation and only periodic snow cover, resulting in a slightly earlier temperature rise in spring (Figure 3), characterized the exposed ridge positions (R). In contrast, the positions within depressions (D) experienced no ground freezing in winter due to an isolating and mostly continuous snow cover during these months, coupled with little exposure to global radiation and very wet conditions, resulting in SMrz measurements



**FIGURE 3** On-site environmental data. Shoot zone temperature ( $T_{sz}$ ), root zone temperature ( $T_{rz}$ ) and root zone soil moisture ( $SM_{rz}$ ) regimes (daily means, derived from hourly measurements) averaged over all studied sites, aggregated by topographical position. Shaded areas indicate meteorological seasons

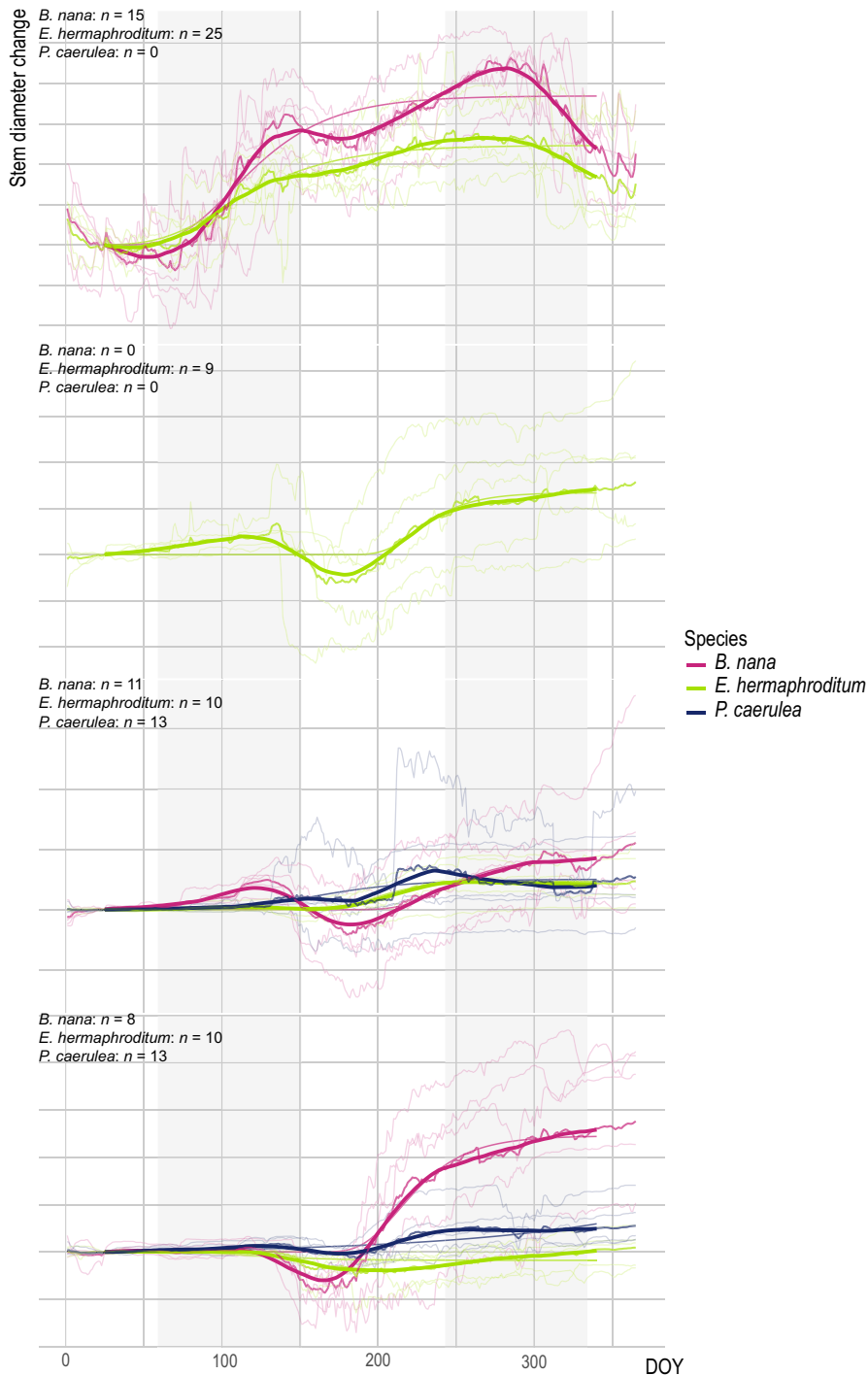
surpassing all other positions throughout the studied period. South- and north-facing slopes (SS and NS) showed very similar regimes. Here, snow protection leads to only moderate ground freezing in winter, whereas the slightly differentiated soil moisture regimes are most likely caused by differing exposure to global radiation, leading to differences in snowmelt timing (Figures 2 and 3). In addition to this variation between micro-topographical positions, soil moisture also varied between the two study regions, with markedly higher soil moisture values in the oceanic region in the west, compared to the continental region in the east. Here, it is worth noting that despite this high environmental variability, variation patterns between topographical positions were very similar in both regions (Figure 3).

### 3.2 | How do inter- and intra-annual growth patterns differ between species and along topographic gradients?

At each of the sampled topographical positions, stem diameter variability followed a distinct pattern of stem expansion and contraction (Figures 2 and 4). These patterns were surprisingly similar between species, even

though total realized growth varied considerably, with *B. nana* on average surpassing the evergreen species at all positions, yet thriving especially at the slopes. In contrast, *E. hermaphroditum* showed the highest annual stem diameter increase within the depressions (D), and both evergreen species showed little annual growth at the north-facing slopes (NS), with an especially prominent contrast to the south-facing slopes (SS) for *E. hermaphroditum*, which was not visible in *P. caerulea* (Figure 1; Figure S5). Thus, interspecific variability in annual stem diameter expansion was highest at the slopes. Overall mean growth ( $148 \mu\text{m}$ ,  $SE = 56$ ) was highest in 2016 for *B. nana* at south-facing slopes and lowest ( $2.5 \mu\text{m}$ ,  $SE = 1$ ) in 2019 for *E. hermaphroditum* at the north-facing slopes.

The main growth phase usually started during the meteorological spring at the exposed ridge positions (R) and in early to late summer at all other positions. The ridge positions showed a distinct phase of radial stem contraction during winter, which was missing at most of the other positions and which can therefore be attributed to the unique winter conditions experienced at the mostly snow-free ridges (Figure 4). In contrast, some specimens at the slopes (SS and NS) and within the depressions (D), all of which are mostly snow covered throughout the winter months, showed additional winter stem expansion, mostly during the winter 2016/2017. This phenomenon



**FIGURE 4** Schematic representation of annual stem diameter variation for each focal species at each topographical position. Curves were derived from dendrometer measurements. Thin lines represent the average across all available individual annual curves with the day of the year (DOY) on the x-axis, while thick lines represent smoothed versions of these curves. Numbers at the top show the number of included specimens. For each specimen, five annual curves were included. Additional lines show fitted sigmoid Gompertz models derived from the original data. Since the curves show schematic representations derived from the original data, there are no absolute values or units given (y-axis)

was present in *E. hermaphroditum* and *B. nana* and can most likely be attributed to hydrological processes within the stem and additional water uptake (Figure 2). Additionally, at these snow-covered positions, the winter was usually followed by a more or less pronounced phase of stem contraction in May or June, sometime after snowmelt and preceding the summer growth phase (Figure 4). Length and magnitude of this phase varied considerably between years and species, with *B. nana* usually showing a higher amplitude in stem contraction and expansion than the evergreen species (Figure 2).

Year-to-year variability in growth characteristics was high at all positions, obscuring a clear temporal growth trend over the studied

period of 5 years (Figure S6). Because this inter-annual variability showed no synchrony across species, it can most likely be attributed to interspecific variation in response patterns to environmental conditions.

### 3.3 | How are growth patterns linked to site- and topography-specific environmental drivers?

Our analysis of growth response to microsite environmental conditions revealed complex patterns and highly differentiated response

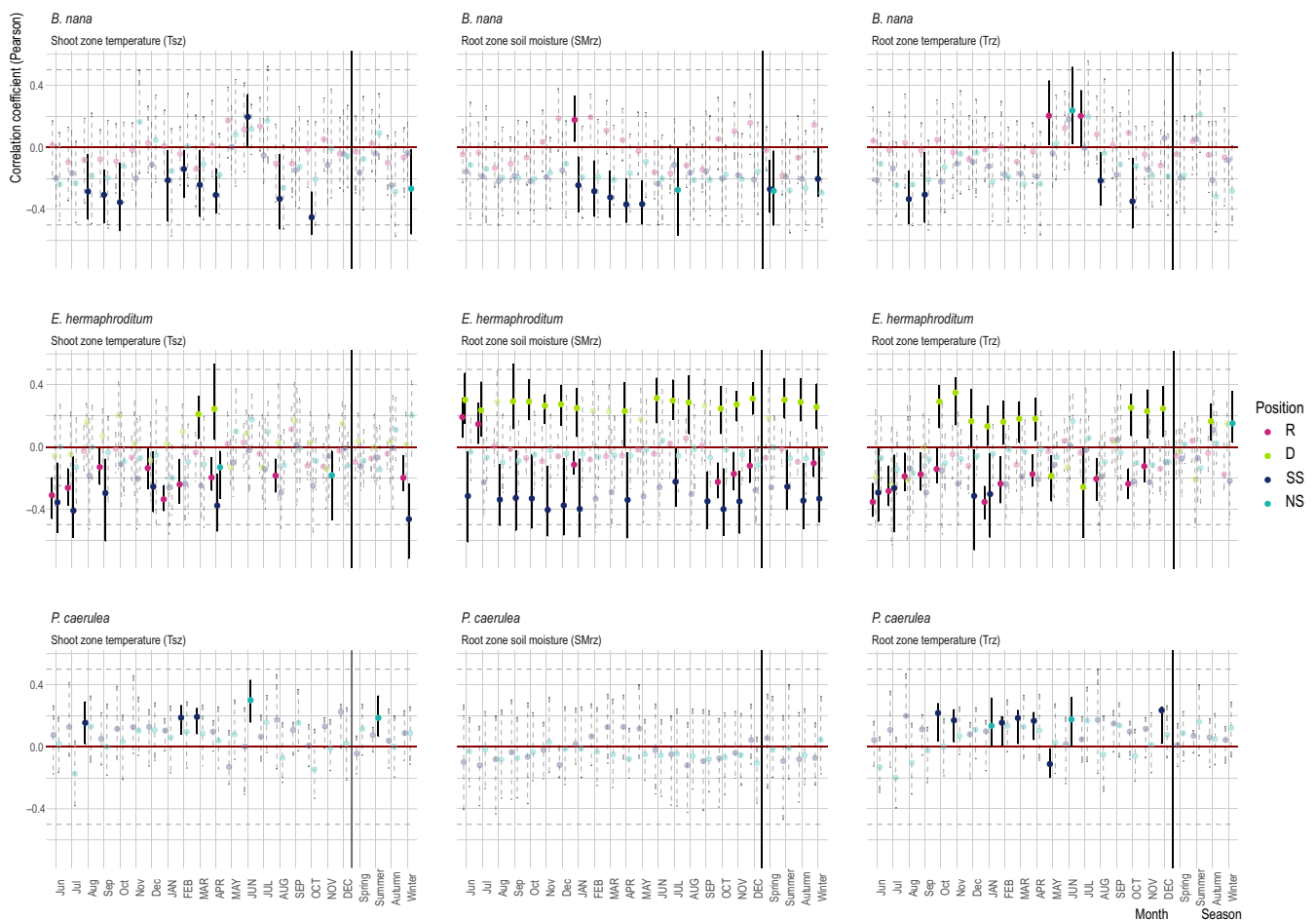


patterns, depending on species and topographical position. At the exposed ridge positions (R), for instance, *E. hermaphroditum* showed a strong response to temperatures, especially during winter, profiting from cold winters, associated with high global radiation (Figure 5; Figures S7–S9). For *B. nana*, on the other hand, warm summers and high soil moisture during winter, the latter indicating wet and snowy conditions, were most influential.

In the depression (D), our correlation analysis indicated a clear positive effect of soil moisture on *E. hermaphroditum* growth throughout the year, which was, however, not significantly reflected in PLSR analysis, indicating fine-scale complexity. The effect might be less pronounced in the PLSR analysis, because the depressions experience comparatively high levels of soil moisture at all times, thus showing a reduced range. In this context, it is worth noting that none of our analysis showed a negative effect of soil moisture at these positions, which is in strong contrast with the south-facing slopes (SS), where high soil moisture had negative impacts throughout the year, especially for *E. hermaphroditum* (Figure 5). Additionally, linear mixed effect models and correlation analyses revealed a negative effect of unusually high spring soil temperatures

on total annual growth in the depressions, especially during May (Figures S9; Figure 5), while the PLSR analysis revealed a negative effect of subzero temperatures, associated with soil freezing, during spring. As such, when growing at positions within local depressions, *E. hermaphroditum* thrived during years of prolonged spring cold and associated snow cover (e.g. 2015, 2016), showing a shorter and less pronounced shrinking phase in early summer and an earlier growth start under these conditions (Figure 2). Because the depressions are usually frost protected by an isolating snow cover, this indicates that *E. hermaphroditum* might rely on this protection until well into the spring and responds to unexpected cold spells and soil freezing later in the year after an early temperature rise with contraction of the stem, as shown in 2018 (Figure 2).

A similar pattern existed at the slopes (SS and NS), where *E. hermaphroditum* followed the severe late frost spell in 2018 with prolonged stem shrinking at most of the monitored sites, possibly caused by cell damage (Figure 2). Furthermore, annual growth measured at the slopes showed the least pronounced relation to microsite environmental parameters, indicating that an interaction of multiple factors is influencing growth here. Still, for *E. hermaphroditum*, our



**FIGURE 5** Pearson's correlation coefficient for annual growth derived from stem diameter measurements (see Section 2) and monthly, as well as seasonally, aggregated environmental parameters. Significance is indicated by non-transparency and lines show 95% confidence intervals, with dotted lines additionally indicating significance. Lowercase months on the x-axis correspond to previous year months

analysis revealed a stronger (and mostly negative) impact of soil moisture in comparison to temperatures, which might be attributed to the complex patterns of snow coverage present at these positions (Figure 5).

Across all topographical positions, *B. nana* showed more positive relations to temperatures throughout the year, compared to the evergreen species (Figure S9). Optimum temperatures revealed by the PLSR analysis were in general higher for *B. nana* as well, especially during summer (Figures S8 and S9). In general, all species were driven by soil moisture availability, including a high influence of winter and spring freezing conditions.

### 3.4 | How is growth variance between individual specimens affected?

Linear mixed effect models revealed high variation of growth between sites, species, positions and years, as well as high variability in growth response to microsite environmental conditions. This variation was to some extent reflected in the PCAs (Figure S3), which showed distinctions between the topographical positions, yet no clear patterns in growth variation related to elevation or study region. Through linear mixed effects modelling, we were able to attribute 94% of variance in total annual growth to temporal and spatial environmental variation and initial stem diameter (Figure 6b), leaving 6% of growth variance unexplained. We identified soil moisture, related to seasonal soil freezing, as the strongest contributor to this variation, and, accordingly, winter and spring conditions most influential. Because of the highly complex topography found in the studied regions, these conditions varied considerably between positions, explaining most of the observed differences in annual growth patterns. Inter-annual temporal variation in climate and environmental variation associated with the elevational gradient, as well as the overall regional climate signal had considerably less explanatory power (Figure 6). Directly comparing the sources of variance in growth parameters (Figure 6a) confirmed this result. Here, it is worth noting that the initial stem diameter at the start of the study period played a significant role for overall radial growth and that variance in maximum stem diameter, which in turn strongly linked to this initial stem diameter, was highly dependent on topographical position, elevation and region and thus almost completely explainable by these parameters. Furthermore, the percentage of variance in growth parameters explained by variation between species was comparatively small (Figure 6a).

Collectively, our results indicate that radial stem growth and its response to local microsite conditions are closely linked to local topography, which is the strongest contributor to microsite environmental heterogeneity.

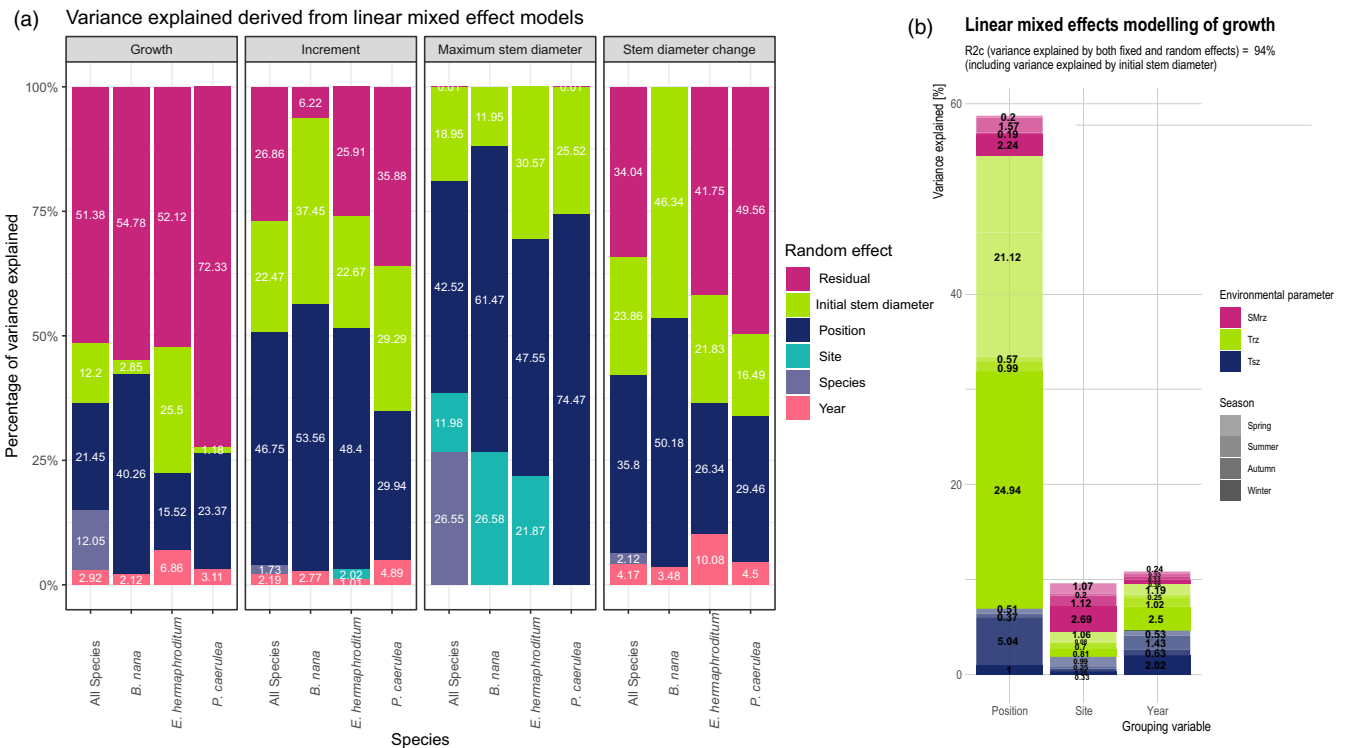
## 4 | DISCUSSION

Our results clearly show that patterns of stem change in shrubs are closely linked to microsite environmental conditions, with this

link evidently present across temporal scales (i.e. intra- and inter-annually). In trees, such patterns of stem diameter change have been interpreted as the result of irreversible stem increment, associated with cambial activity (Rossi et al., 2008; Steppe et al., 2015; Zweifel, 2016), as well as reversible expansion or shrinking, attributed to underlying changes in water relations (Lindfors et al., 2019). As such, these processes have been strongly linked to the overall physiology of the individual plant, which results both from physiological constraints and from adaptive strategies (Duputié et al., 2015; Zweifel, 2016). Our results can therefore be interpreted as an indication of physiological adjustments of the individual plants, controlling shrub growth at the monitored sites (Martin et al., 2017). Further studies using experimental or modelling approaches to directly target these ecophysiological adjustments might be of help in further defining the underlying processes of climate-growth relationships.

We found the observed patterns of stem change strongly variable, depending on species, location and associated microsite environmental conditions. The main factor contributing to this variability was local topography, with species playing a surprisingly small role in explaining variation in growth patterns, indicating that multiple species might develop similar growth strategies in response to site-specific local environmental conditions. In general, we found a high variability of overall radial growth, which might be a result of physiological plasticity, or a remodelling of the plant's physiology to meet local environmental conditions (Callaway et al., 2003; Seebacher et al., 2015). To what extent genetic structure and varying genotypes play a role here, requires further studies (Chevin et al., 2010; Hoffmann & Sgrò, 2011). However, given the wide genetic variation found for example in *E. hermaphroditum* across three populations in northern Sweden (Szmíd et al., 2002), it can be assumed that both genotypic adaptation and phenotypic plasticity play a major role in contributing to the observed intraspecific variation. In general, our results emphasize the importance of topographically driven heterogeneity in environmental conditions for understanding and predicting vegetation shifts, including distribution and redistribution of species in response to climate change, which has been recognized in recent years (Graae et al., 2018; Körner, 2016; Ropars et al., 2015; Young et al., 2016).

Furthermore, our results indicate a high complexity in temperature-growth relationships. All three studied species showed high variation across seasons and topographical positions, with especially *E. hermaphroditum* exhibiting negative responses at specific positions. Consequently, there was no clear relation between high temperatures and growth in our data, contrasting the prominent assumption of temperatures being the key driver of plant life in arctic and alpine environments (Graae et al., 2018; Körner, 2021; Raunkjær, 2015). Accordingly, the increase in shrub growth currently observed in these regions is commonly linked to a rise in temperatures (e.g. Bär et al., 2008; Hollesen et al., 2015; Liang & Eckstein, 2009). Conversely, our results highlight the importance of topography-controlled soil moisture, snow conditions and associated freeze-thaw cycles (Dobbert et al., 2021).



**FIGURE 6** Partitioned variance in growth parameters explained by variation in spatial and temporal grouping variables (a). For each growth parameter (growth, stem increment, maximum stem diameter and stem diameter change) four models were fitted, one including all data, and one for each focal species. The models included no fixed effects and thus had the form  $\text{Growth} \sim (1 | \text{site/position/species}) + (1 | \text{year}) + (1 | \text{initial stem diameter})$ , as implemented into the lmer function of the lme4 R package (Bates et al., 2015). (b) Includes micro-environmental parameters and shows variance in total annual growth explained by variation in seasonally aggregated environmental conditions between topographical position, site (including region and elevation) and year. All results for (b) are derived from a singular model of the form  $\text{Growth} \sim \text{environmental parameters} + (\text{environmental parameters} | \text{position}) + (\text{environmental parameters} | \text{site}) + (\text{environmental parameters} | \text{year}) + (\text{environmental parameters} | \text{species}) + (1 | \text{initial stem diameter})$ , as implemented into the lmer function of the lme4 R package (Bates et al., 2015). This model is thus able to explain variance in total annual growth to a large extend

At most monitored positions, freezing after snowmelt, caused by spring cold spells, resulted in stem contraction, reduced growth or stem shrinkage during the rest of the growing season. In some cases, stem shrinkage even lasted into the following year, indicating cambial cell damage (Choler, 2018; Weijers et al., 2018). This proved especially dangerous for our evergreen species on the north-facing slopes, where the individual plants are highly adapted to the protective snow cover and are usually able to start growth activity directly after snowmelt, as soon as liquid water becomes available in the root zone (Bråthen et al., 2018). Unusually discontinuous snow cover and early snowmelt during this crucial phase might have left our specimens vulnerable to spring cold spells and many seemed unable to recover from such conditions during 2018 and consequently showed less overall growth during the following growing season. At positions where protective snow cover is usually present, a reduced snow cover during the winter months (clearly expressed during the winter 2016/2017) resulted in rapid stem expansion and reduced growth during the following years, possibly attributed to freezing processes and cell damage. Through isolating effects, mitigating the influence of extreme temperatures, as well as shielding from global radiation, snow cover is altering the thermal

conditions at the micro-scale. Predicted changes in snow conditions (AMAP, 2017; Bjerke et al., 2017; Xu et al., 2013) are therefore likely to significantly alter species composition across all topographical positions. However, current studies aiming to predict these changes have found them highly complex and spatial variable (AMAP, 2017; Niittynen et al., 2018; Rizzi et al., 2018). Our data suggest that snow protected the plant from negative effects of soil freezing and extreme temperatures (Blok et al., 2015; González et al., 2019; Körner, 2012). Consequently, a reduction in isolating snow cover duration (Callaghan et al., 2011), for instance, might mitigate the effects of winter warming and a prolonged growing season for deciduous species like *B. nana* and increase the risk of growth-inhibiting spring cold spells and soil freezing for *E. hermaphroditum* at positions where the species is currently adapted to frost protection. Here, an increase in frequency of winter warming events and associated snowmelt (Bjerke et al., 2017) would expose the plants to unfamiliar and potentially fatal freeze-and-thaw stress, forcing the individual plant to adopt coping strategies.

We found indications for such coping strategies at the ridge sites, for both *B. nana* and *E. hermaphroditum*, with *E. hermaphroditum* showing a positive growth response to cold winter conditions,

possibly using the associated high solar radiation input for additional photosynthetic activity (Bråthen et al., 2018; Löffler & Pape, 2020). At the same time, *P. caerulea* was limited to those positions where snow cover provides protection from extreme temperatures until well into spring, when the growth processes begin. For both *E. hermaphroditum* and *B. nana*, our measurements revealed a distinct phase of stem contraction at the ridge positions, presumably an active response mechanism protecting the plant from frost damage by reducing cell water content to avoid frost-induced cavitations (Fonti et al., 2010). Such dehydration processes, alongside ice nucleation and ice forming in the apoplast causing additional dehydration stress, have shown to lead to xylem diameter shrinkage in other woody plants (Améglio et al., 2001; Charra-Vaskou et al., 2016; Lindfors et al., 2019; Lintunen et al., 2016). Both *B. nana* and *E. hermaphroditum* are generally considered frost-hardy species (González et al., 2019; Hollesen et al., 2015). They are able to withstand extreme winter conditions with prolonged soil freezing at the exposed ridges. As such, our findings suggest that the ability to adopt coping strategies in response to extreme environmental conditions is highly species dependent. For instance, *P. caerulea* indicated comparatively low adaptive or maladaptive plasticity in response to frost. This might leave the species vulnerable to predicted future climate changes.

In contrast, our results suggest that *B. nana* and *E. hermaphroditum* have developed adaptive growth strategies to varying degrees, which are in accordance with the microsite environmental conditions at their respective topographical positions and strongly related to the snow regime. Our sampled *E. hermaphroditum* specimens were able to thrive at both of the most extremes of the sampled topographical positions (ridges and depressions), indicating a high plasticity and capacity to adapt in diverse environments. However, at the same time, *E. hermaphroditum* showed high sensitivity to spring cold spells at the north-facing slopes and no positive response to warming conditions. *B. nana*, on the other hand, was similarly adapted to local microsite conditions at the ridges, but, at the same time, able to profit from rising temperatures and to thrive at all monitored positions simultaneously. Such an acclimatization has been interpreted as an indicator for the species' capacity to tune their physiological characteristics to changing conditions, which in turn is linked to their ability to avoid migration or extinction under climate change (Matesanz et al., 2010; Nicotra et al., 2010; Valladares et al., 2014). We here support the assumption that the individual plant's physiology can vary considerably within populations, in response to the local environment (Banta et al., 2012; Graae et al., 2018; Leimu & Fischer, 2008; Savolainen et al., 2007) and further highlight the importance of integrating physiological plasticity into our understanding of species distribution and niche shifts (Valladares et al., 2014). Following this mechanistic understanding for our three focal species, we suggest that *P. caerulea* is likely to show the least persistence in a changing environment, as the species currently inhabits a comparatively narrow niche (Graae et al., 2018; Wasof et al., 2013), predominantly caused by limited adaptive thermal plasticity. Both *E. hermaphroditum* and *B. nana*

are likely to show higher resilience to changing conditions than *P. caerulea*, based on their more pronounced plasticity towards thermal conditions. At an interspecific level, we argue that deciduous species, like *B. nana*, are most likely to profit from the predicted environmental changes, thus further contributing to the ongoing greening trend. However, on a broader scale, other factors might additionally affect species composition. For example, both our studied regions are not majorly affected by reindeer grazing, whereas grazing was generally shown to be a major influencing factor on shrub growth in other areas, with highly species-specific effects (Grellmann, 2002; Pape & Löffler, 2016, 2017; Weijers & Löffler, 2020). Furthermore, our study illustrates how growth trends are usually not uniform in space and time, and generalization across sites consequently might result in a too simplistic view of future vegetation changes in the highly relevant ecosystems of the tundra regions.

## 5 | CONCLUSIONS

Overall, our findings demonstrate that species in heterogeneous environments adapt locally by adjusting their growth strategies to fine-scale microsite conditions, in accordance with their physiological plasticity. This allows them to potentially occupy wide ecological niches and is closely linked to the adaptive capacity of the species as a whole. Physiological plasticity can, thus, be directly linked to a species ability to cope with potentially rapid climate change (e.g. Pérez-Ramos et al., 2019; Seebacher et al., 2015). However, this plasticity varies a great deal between species and we found no clear link to leaf habit here (e.g. Funk et al., 2017; Lavorel & Garnier, 2002). On an intraspecific level, our results support principal findings by Pfennigwerth et al. (2017), suggesting that multiple populations and individuals within a species may not exhibit a single, universal response to climatic variation. While past studies have emphasized the role of the elevational gradient in this context (Henn et al., 2018; Pfennigwerth et al., 2017), our results conversely show no clear evidence of a strong connection between elevation or larger-scale climatic region and radial growth (Figure S3). Instead, we identified environmental variation associated with micro-topography as the main driver of the variability in response patterns. Thus, our findings highlight fine-scale spatial complexity as a main indicator for a species' adaptive capacity, which is, in turn, strongly linked to local topography. Therefore, intraspecific variability in physiological characteristics has the potential to yield highly relevant information on future niche shifts, and might even be used to predict changes in a species' geographical range in the face of environmental change. Regarding the broad-scale vegetational changes observed across the arctic and alpine regions, our findings highlight the fine-scale complexity of these developments, and elevate the importance of locally differentiated microsite conditions and species-specific response patterns in determining future community development. We thus stress the importance of a fine-scale perspective in arctic and alpine tundra ecosystem research.

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## CONFLICT OF INTEREST

Svenja Dobbert, Roland Pape and Jörg Löffler declare that they have no conflict of interest.

## AUTHORS' CONTRIBUTIONS

J.L. had the idea, designed the research platform, conducted the fieldwork and together with R.P. ran the long-term project; S.D. analysed the data, led the writing of the manuscript and arranged the figures, with contributions from R.P. and J.L.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13784>.

## DATA AVAILABILITY STATEMENT

All underlying data pertinent to the results were recently published in 'ERDKUNDE---Archive for Scientific Geography' (<https://www.erdkunde.uni-bonn.de>) under the following <https://doi.org/10.3112/erdkunde.2021.dp.01>.

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