OIKOS

Research article

Root trait variation along a sub-arctic tundra elevational gradient

Clydecia M. Spitzer[1], **Maja K. Sundqvist**[1], **David A. Wardle**[2], **Michael J. Gundale**[1] **and**
Paul Kardol[1]

[1]Dept of Forest Ecology and Management, Swedish Univ. of Agricultural Sciences, Umeå, Sweden
[2]Asian School of the Environment, Nanyang Technological Univ., Singapore, Singapore

Correspondence: Clydecia M. Spitzer (clydecia.spitzer@slu.se)

Oikos
2023: e08903
doi: 10.1111/oik.08903
Subject Editor:
Monique Weemstra
Editor-in-Chief:
Gerlinde B. De Deyn
Accepted 9 April 2022

Elevational gradients are useful for predicting how plant communities respond to global warming, because communities at lower elevations experience warmer temperatures. Fine root traits and root trait variation could play an important role in determining plant community responses to warming in cold-climate ecosystems where a large proportion of plant biomass is allocated belowground. Here, we investigated the effects of elevation-associated temperature change on twelve chemical and morphological fine root traits of plant species and plant communities in a Swedish subarctic tundra. We also assessed the relative contributions of plant species turnover and intraspecific variation to the total amount of community-level root trait variation explained by elevation. Several root traits, both at the species and whole community levels, had significant linear or quadratic relationships with elevation, but the direction and strength of these relationships varied among traits and plant species. Further, we found no support for a unidirectional change from more acquisitive root trait values at the lower elevations towards trait values associated with greater nutrient conservation at the higher elevations, either at the species or community level. On the other hand, root trait coefficients of variation at the community level increased with elevation for several root traits. Further, for a large proportion of the community-level traits we found that intraspecific variation was relatively more important than species turnover, meaning that trait plasticity is important for driving community-level trait responses to environmental factors in this tundra system. Our findings indicate that with progressing global warming, intraspecific trait variation may drive plant community composition but this may not necessarily lead to shifts in root resource–acquisition strategy for all species.

Keywords: arctic, community ecology, elevational gradient, root traits, trait variation, tundra

Introduction

Elevational gradients are useful space-for-time substitution tools (Pickett 1989) that can be used to increase our understanding of responses of plant species and communities to global warming. This is because high elevations experience lower temperatures than do low elevations, with consequences for individual species, plant- and soil microbial communities, and plant-available nutrients (Sundqvist et al. 2013,

NORDIC SOCIETY OIKOS

www.oikosjournal.org

Mayor et al. 2017). Spatial temperature gradients, including elevational gradients, have been used in several recent studies in plant trait-based ecology to understand species and community responses to long-term changes in climate (Read et al. 2014, Ostonen et al. 2017, Bjorkman et al. 2018, Roos et al. 2019, Laughlin et al. 2021). Such studies have shown that leaf mass:area ratio and nitrogen (N) content per unit area often increase with increasing elevation (Körner 2013, Read et al. 2014). However, most studies have focused on aboveground traits, and we know little about the corresponding responses of belowground plant traits, although such knowledge is critical for understanding plant responses to climate change. This is especially important since roots take up nutrients and water from the soil that are essential to plant growth.

Fine root traits potentially play a more important role than aboveground traits in determining plant species and community responses to global change in arctic ecosystems, because a substantial proportion of plant biomass (i.e. up to 70%) is allocated belowground in these systems (Körner 2013, Iversen et al. 2015). As such, fine root traits are increasingly being examined in the context of plant resource investment for nutrient acquisition (Freschet et al. 2010, Spitzer et al. 2021). Acquisitive fine root trait values (e.g. smaller diameter, lower dry matter content and C:N ratios) are related to fast plant growth and a lower dependence on mycorrhizal fungi for nutrient uptake, while conservative trait values are related to slower growth, higher investment in defence compounds, and a stronger dependence on mycorrhizal fungi for nutrient acquisition (Bardgett et al. 2014, Eissenstat et al. 2015, Bergmann et al. 2020, Carmona et al. 2021). Some recent studies have found that root traits at both the species- and community-level become more acquisitive (e.g. higher specific root length and lower root dry matter content) at colder temperatures (Defrenne et al. 2019, Laughlin et al. 2021), and others become more conservative (e.g. higher root tissue density) (Ostonen et al. 2017, Laughlin et al. 2021). But, it has also been found that root trait responses of plant species and communities to elevation can be idiosyncratic (Weemstra et al. 2021).

A better understanding of fine root trait relationships to elevation would aid our knowledge about how responsive different plant species and communities may be to environmental change. Generally, a low trait variability across environments that vary in climate (such as elevational gradients), may indicate slower responsiveness of plants to climate change (Henn et al. 2018). There is evidence that trait variation can be substantial not only among plant species (Kumordzi et al. 2014) but also within plant species (Albert et al. 2010, Messier et al. 2010), and within plant communities (Stark et al. 2017, Zanzottera et al. 2020). Acknowledging both inter- and intra-specific sources of trait variation that emerge as a result of plant plasticity (Holdaway et al. 2011, Bruelheide et al. 2018) can thus contribute to a more realistic and complete understanding of how different plant species contribute to community responses to environmental and global change factors.

Trait studies at the plant community level along environmental gradients are increasing rapidly (Joel et al. 1994, Holdaway et al. 2011, Prieto et al. 2015, Ostonen et al. 2017, de la Riva et al. 2018, Kühn et al. 2020, Thomas et al. 2020). However, many of these studies are focused on aboveground traits and few studies have focused on root trait responses at the intraspecific level or at the whole community level (Weemstra et al. 2021). Mean root trait values and trait variation at the species and community level may however respond to different factors than do aboveground traits (Freschet et al. 2015), given that roots are exposed to different biotic and abiotic drivers than are aboveground plant structures. Aboveground community level trait means along elevational gradients have been observed to result from both plant species turnover (Descombes et al. 2017, Gebrehiwot et al. 2019) and intraspecific trait variation (Pescador et al. 2015), both of which may reflect plant species responses to biotic and abiotic conditions (Bach et al. 2007). In a recent study exploring intraspecific root trait variation with elevation in a French alpine system, Weemstra et al. (2021) found that only a small proportion of across-species trait variation was explained by intraspecific variation, indicating that species turnover could likely be a more important mechanism in their study system. However, no study on intraspecific and community level root trait variation of a large number of chemical and morphological root traits in response to elevation has been carried out in the Arctic, which is notable given that arctic environments are predicted to experience extreme environmental change over the next century (IPCC 2013).

Ambient mean air temperature is rising rapidly in the Arctic and is projected to increase by up to 3.5°C by the end of this century (Collins et al. 2013). Warmer temperatures are already resulting in changes in plant community composition (Elmendorf et al. 2012), aboveground plant functional traits (Bjorkman et al. 2018) and increased shrub growth and expansion into tundra (Myers-Smith et al. 2011, García Criado et al. 2020). Future warming in the Arctic is likely to further influence tundra plant communities. Here, we investigated the impact of elevation-associated temperature change on plant traits within species, across species and at the community-level by investigating root trait variation in subarctic tundra heath of northern Sweden. We measured twelve fine root traits, of which six are chemical root traits and six are morphological root traits (Table 1), for a large proportion of the heath plant species present along a subarctic elevational gradient. We assessed root trait relationships with elevation within and between individual species, and at the whole community level, and used these data to test the following hypotheses: 1) with increasing elevation, plant species- and community-level root trait values will change from those more associated with faster nutrient acquisition (e.g. higher specific root length) to those associated with higher conservation of nutrients (e.g. thicker average diameters) (Table 1). We also expect chemical root traits, and notably root phosphorus (P), to show the strongest decline with elevation, and this will be associated with an increase in root C:P and N:P ratios (Table 1). This is because nutrient availability

Table 1. Chemical and morphological root traits measured in this study and their units, as well as their ecological relevance. The expected relationship with elevation is predicted based on leaf traits shifting from resource-acquisitive to resource-conservative at this site and P availability declining relative to N availability as elevation increases (Sundqvist et al. 2011a, b, Vincent et al. 2014).

	Root trait	Unit	Ecological relevance	Expected relationship with elevation
Chemical	carbon (C) content	%	tissue quality	increase
	nitrogen (N) content	%	nitrogen acquisition	decrease
	C:N ratio	–	tissue quality	increase
	phosphorus (P) content	%	phosphorus acquisition	decrease
	C:P ratio	–	tissue quality	increase
	N:P ratio	–	nutrient acquisition	increase
Morphological	average diameter	mm	collaboration with mycorrhizal fungi	increase
	dry matter content	mg mg^{-1}	resource conservation	increase
	forks per root length	forks cm^{-1}	soil exploration	decrease
	specific root area	cm^2 mg^{-1}	nutrient absorption	decrease
	specific root length	cm mg^{-1}	soil exploration	decrease
	specific root tip abundance	tips mg^{-1}	soil exploration and foraging	decrease

often declines with elevation, with P availability declining more than N availability in our study system (Sundqvist et al. 2011a, b, Vincent et al. 2014). 2) Shifts in community-level root traits with elevation will be best explained by intraspecific trait variation rather than by species turnover. This is because plant species turnover in these subarctic tundra heaths is relatively low, with several of the dominant species occurring across most elevations (Sundqvist et al. 2011a, b). In this context, we also explored intraspecific variation within elevations versus intraspecific variation along elevations. Testing these hypotheses in combination will contribute to our ability to understand and better predict how tundra plant species and communities will respond to future climate change in the Arctic.

Material and methods

Study system

The study was conducted along an elevational gradient on the north-east facing slope of Mount Suorooaivi, approximately 15 km south-east of Abisko, Sweden (68°21′N, 18°49′E). Along this elevational gradient, air temperature declines by approximately 2.5°C from 500 to 1000 m a.s.l. (Sundqvist et al. 2011a). This temperature range across this gradient is roughly on par with the expected magnitude of temperature increase through climate warming in the region over the next 80 years (Collins et al. 2013) and can therefore be used as a proxy to help inform about changes that may occur under future warming (Sundqvist et al. 2013). Precipitation ranges from 230 to 290 mm from June to October and does not change along the elevational gradient (Sundqvist et al. 2014). The parent material consists of salic igneous rocks and quartic and phyllitic hard schists. The tree line, formed by *Betula pubescens* ssp. *czerepanovii* , is located at approximately 550 m. The heath vegetation is dominated by ericaceous shrubs and the dwarf shrub *Betula nana* ssp. *nana*, but also contains some graminoids and forbs. Several plant species in our study (e.g. *Vacciunium vitis-idaea* and *Empetrum hermaphroditum*) have ericoid mycorrhizal associations, but one of the dominant shrub species (*Betula nana*) has ectomycorrhizal associations (Deslippe and Simard 2011, Deslippe et al. 2012). Further information about this gradient is presented in Sundqvist et al. (2011b), Vincent et al. (2014), De Long et al. (2016a) and Blume-Werry et al. (2018).

Plot establishment and vegetation recording

We established five plots (1 × 1 m) at each of six elevations on 25–26 June 2018 within heath vegetation at the following elevations: 500, 600, 700, 800, 900 and 1000 m. Plots were randomly established with similar slopes and aspects and positioned to ensure adequate independence among plots at each elevation. In these tundra systems, there is a high level of spatial heterogeneity in microtopography, hydrology and soil fertility over short distances (Björk et al. 2007). To account for this, plots were established at a minimum distance of 10 m and a maximum distance of 25 m of each other, which represents a scale at which soil processes should be spatially independent among plots (Baldrian 2014). To assess the density of each species within the plots when root production peaks in late summer (Blume-Werry et al. 2016), we conducted a point quadrat analysis during 13–16 August 2018, by recording the total number of times (i.e. hits) that each plant species in each plot is intercepted by each of 100 downwardly projecting pins (Goodall 1952). We used this data to calculate relative abundances of plant species. We recorded soil temperatures every 4 h at 3 cm depth with DS1921G-F5 Thermochron i-buttons in three of the five plots at each elevation from 18 August 2018 to 22 July 2019 to gain an understanding soil temperature decline along the gradient. The average soil temperature ranged from +1.0°C at the lowest site to −2.1°C at the highest site (Supporting information).

Root sampling

We sampled roots of all plots over 16–28 August 2018. We used a shovel to cut down to the bedrock in the perimeter of each plot and carefully excavated the intact vegetation and soil. The intact excavated vegetation was subsequently subdivided into four quadrats of 50 × 50 cm and transferred to a tarpaulin. We removed the mineral soil and sampled roots within the organic soil. Except for the 500 m elevation, where the average depth was 9.2 cm, the organic soil depth was similar at all elevations (i.e. average depth of 5.69 cm ± 1.13). We sampled roots from all plant species in each plot, by first identifying the shoot of any individuals of each plant species beginning at the edge of each quadrat and then towards the centre of the plots. Beginning at the base of the shoot, we carefully used our fingers to follow and disentangle the roots and/or rhizomes of each plant species. After removal of the roots of each plant, we clipped off most of the aboveground biomass of the plant, but kept some to allow for species identification. To preserve root moisture and to avoid damaging the fine roots, we left some soil on the roots until further sample processing. Thereafter, plants were placed into separate plastic bags for each plant species in each plot. We sampled roots from each plot quadrat and stopped sampling roots when we had filled three 5-l ziploc bags with roots of each species, or all roots of less abundant species. Therefore, several individuals or ramets of the same species were bulked into each bag. This was necessary since most species are clonal and it is difficult to distinguish between individuals. In total, we collected roots from sixteen plant species. Samples were stored in coolers and then transported to SLU in Umeå, Sweden and stored at 4°C until further processing.

Root washing and fine root trait measurements

To enable similar storage times for the harvested roots from each plot, we processed samples in the order that plots were harvested. For each sample, we first carefully pre-washed the roots in a 2 mm sieve over a 1 mm sieve under a showerhead tap and thereafter transferred each sample to a tray filled with water. Using tweezers, we removed large pieces of litter and/or mosses from the root system, and the smaller fragments of organic matter. After the roots were sufficiently clean, they were washed in a slightly tilted tray, and we used spray bottles with a mist spray to remove remaining soil particles. We clipped off all of the fine roots (< 1 mm diameter) of all the individuals of the same species or from along ramets (for clonal species) within each plot and bulked them. A subsample of roots was then placed onto a large scanning tray (15 × 20 cm) with cold tap water.

Prior to scanning, roots were disentangled to avoid overlapping roots that could distort root diameter classification, branching patterns and number of tips. We scanned roots using WinRhizo 2016 with a flatbed scanner using the following image acquisition parameters: speed priority and dust removal; 800 dpi; intact root axes; root and background detection (100 pixels); roots darker than background; and detect 'very pale roots'. We obtained the following morphological measurements from scanning each root sample: total root length, average diameter, number of root tips, root surface area and the number of root forks. It is possible that the value of the number of root tips and forks could be slightly higher than what we measured due to roots being clipped along the rhizomes for clonal species. After scanning, we recorded the sample fresh weights and thereafter placed each scanned root sample in a small paper bag. Samples were dried in an oven at 60°C for 48 h and their biomass was recorded. These sample biomass data were used to calculate the following root traits: root dry matter content (i.e. dry mass per fresh mass), root forks per root length (i.e. number of forks per dry mass), specific root area (i.e. root area per dry mass), specific root length (i.e. root length per dry mass) and specific root tip abundance (i.e. number of tips per dry mass). The remaining roots that were not scanned were ground using a ball mill and analysed for total carbon, nitrogen and phosphorus by dry combustion using an elemental analyser. This was used to calculate the ratios of carbon to nitrogen, carbon to phosphorus and nitrogen to phosphorus.

Statistical analyses

All statistical analyses were performed using R ver. 3.4.0 (www.r-project.org). We used community-weighted means of each root trait for our analyses because dominant species play an important role in driving the responses of communities to the environment (Ackerly et al. 2002). For each root trait, we calculated community-weighted means in each plot using the following formula:

$$\text{Weighted plot average} = \sum_{i=1}^{n} \left(\mathrm{p}_i \times \text{trait}_{i\_\text{plot}}\right)$$

where p_i is the relative abundance (i.e. percentage cover) of the i-th species in a plot, n is the total number of species in the plot and $\text{trait}_{i\_\text{plot}}$ is the measured root trait of the i-th species in the plot.

Hypothesis 1

For both species and community level data, we used general linear models to assess the relationships between elevation and mean values of each of the twelve fine root traits for each plot (n = 5) at each elevation, using the weighted plot averages. To fulfil the model assumptions for linear models we either log-transformed or Tukey power-transformed the trait data, where necessary. In cases where the relationships between elevation and the root traits were not linear and data transformation was not suitable for fulfilling linear model assumptions, we fit second order polynomial models. Partial F-tests were then used to compare the model fits (i.e. linear versus polynomial). We further assessed the relationship between elevation and fine root traits across plots for each of the plant species that was present at a minimum of five of the six elevations (i.e. for five of the sixteen species). Model fitting was conducted as above. Prior to all the analyses, two outliers (i.e. larger than 3 standard deviations from the mean), both for specific root area, were removed.

Elevation in our study is used as a proxy for temperature, in line with many previous studies (Sundqvist et al. 2013). However, we further tested whether soil temperature could better explain mean community trait values than elevation by fitting general linear models with average growing season (i.e. 1 June – 31 August) soil temperature at each elevation as the explanatory variable. Here, average growing season soil temperature was calculated using soil temperature data that we recorded from three out of five plots at each elevation.

Trait variation with elevation

We used general linear models to assess the relationship between root trait variation (i.e. coefficients of variation) at the plant community level and elevation. First, we used the R package Weighted.Desc.Stat (Parchami 2016) to calculate the weighted coefficient of variation (i.e. the weighted standard deviation divided by the weighted mean) among all species for each plot at each elevation. Within the package, this was done by first multiplying the relative abundances of each plant species in the plot by their respective trait values prior to calculating the weighted standard deviation and weighted mean. We then conducted separate general linear models for each root trait with the weighted coefficient of variation as a response variable and elevation as an explanatory variable. We obtained p-values and F-values for the above models with the type III ANOVA function from the car package (Fox and Weisberg 2019).

Hypothesis 2

To assess the relative contributions of intraspecific variation and species turnover in response to elevation for each root trait, we used the variance partitioning method developed by Lepš et al. (2011). Briefly, prior to variance partitioning two types of plot averages were calculated:

1) Fixed plot average $= \sum_{i=1}^{n} \left(\mathrm{p}_i \times \mathrm{trait}_i \right)$

   where p_i is the relative abundance of the i-th species in a plot, n is the total number of species in the plot and trait_i is the mean root trait value of i-th species across all thirty plots.
2) Weighted plot average (calculated as above).

Hence, fixed plot averages therefore remove the intraspecific variation across the elevational gradient and the remaining variation of trait values reflect the effects of changes in plant species turnover. However, weighted plot averages across the elevational gradient include the variation caused by intraspecific variability and species turnover (Lepš et al. 2011). The contribution of intraspecific variation, species turnover and their covariance to the total variance explained by elevation was then partitioned for each root trait using R code provided by Lepš et al. (2011). This code calculates intraspecific trait variation by taking the difference between the specific average and fixed average, i.e. intraspecific variability effect = weighted average − fixed average.

We further assessed whether intraspecific trait variation of each of the five most abundant species was larger across the whole elevational gradient than within elevations. Here, we determined intraspecific trait variation across the gradient for each of the five most abundant species, as their traits are likely to have the greatest influence on overall patterns at the community level (Lepš et al. 2011). For all twelve traits we used average trait values at each of the six elevations and calculated the coefficient of variation (i.e. the standard deviation divided by the mean) among them. Intraspecific trait variation within elevation was calculated as the coefficient of variation among the five plots within each elevation.

Results

Sixteen plant species were present within the plots along the elevational gradient (Fig. 1). Four of those species were found at all elevations, i.e. *Betula nana*, *Empetrum hermaphroditum*, *Vaccinium vitis-idaea* and *Vaccinium uliginosum*, while *Arctostaphylos alpina* was found at all elevations except 800 m. Across the elevational gradient and plots, *Empetrum hermaphroditum* was the most abundant species (56.0%), followed by *Betula nana* (20.2%), *Vaccinium vitis-idaea* (13.4%) and *Cassiope tetragona* (4.2%), with the latter being found only at the three highest elevations (Fig. 1).

Community mean root trait value relationships with elevation

Six root traits at the whole community level had significant relationships with elevation, but the direction of those relationships varied among traits (Fig. 2). Linear declines with elevation were found for root C content ($R^2 = 0.14$; $F = 5.89_{1,28}$; $p = 0.02$), specific root area ($R^2 = 0.26$; $F = 11.28_{1,28}$; $p = 0.002$) and root forks per root length ($R^2 = 0.16$; $F = 6.83_{1,28}$; $p = 0.01$). Meanwhile, root P content, root N to P ratio and specific root length had significant quadratic relationships with elevation respectively (adjusted $R^2 = 0.19$; $F = 4.31_{2,27}$; $p = 0.02$, adjusted $R^2 = 0.26$; $F = 6.20_{2,27}$; $p = 0.006$ and adjusted $R^2 = 0.21$; $F = 4.95_{2,27}$; $p = 0.01$, respectively). There was no significant relationship between elevation and average root diameter ($F = 0.13_{1,28}$; $p = 0.72$), root N content ($F = 2.92_{1,28}$; $p = 0.10$), root C to N ratio ($F = 3.80_{1,28}$; $p = 0.06$), root C to P ratio ($F = 3.29_{1,28}$; $p = 0.05$), root dry matter content ($F = 0.04_{1,28}$; $p = 0.85$) or specific root tip abundance ($F = 1.73_{1,28}$; $p = 0.20$). Only two of the twelve measured traits could be explained by the average growing season soil temperature at each elevation, i.e. specific root area ($F = 10.25_{1,28}$; $p = 0.003$) and root P content ($F = 4.31_{1,28}$; $p = 0.047$) (Supporting information).

Species-level root trait relationships with elevation

Out of 60 species by trait combinations, only twelve showed statistically significant ($p < 0.05$) responses to elevation. Interestingly, two of the community mean root trait relationships with elevation that we found were also found for *Betula*

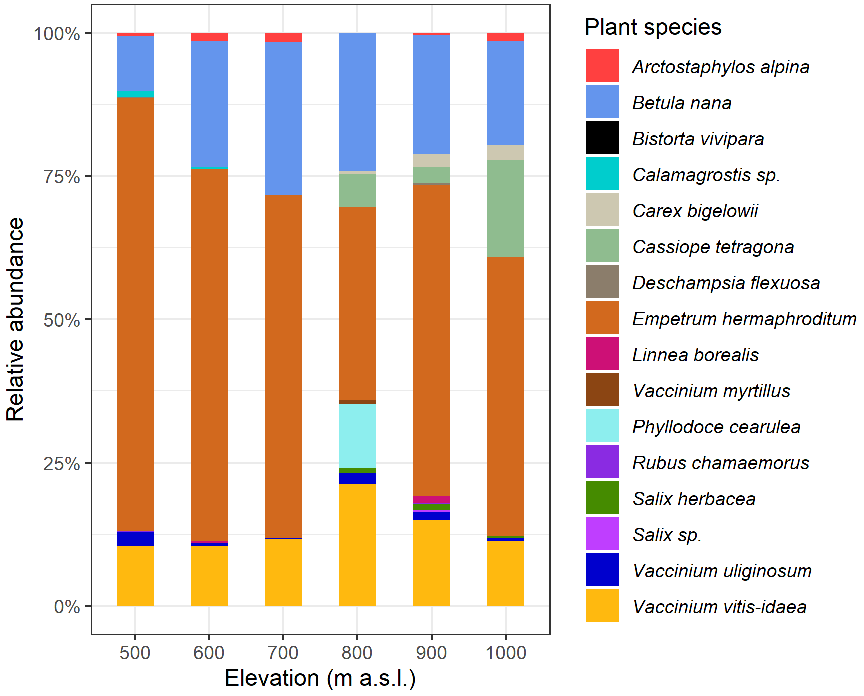

Figure 1. Relative abundance of plant species in subarctic tundra heath vegetation at each elevation. Data show the average of five plots at each elevation.

nana (Fig. 3), but none occurred for any of the other plant species. As such, for *B. nana*, root C content decreased linearly with elevation ($R^2=0.22$; $F=9.34_{1,28}$; $p=0.005$) and specific root length had a positive quadratic relationship with elevation ($R^2=0.17$; $F=4.08_{2,27}$; $p=0.03$). Meanwhile, root C to N ratio decreased linearly with elevation for *Betula nana* and *Vaccinium vitis-idaea* ($R^2=0.22$; $F=9.39_{1,28}$; $p=0.005$ and $R^2=0.17$; $F=6.38_{1,28}$; $p=0.01$, respectively), while root N content increased linearly for both species ($R^2=0.23$; $F=8.46_{1,28}$; $p=0.007$ and $R^2=0.17$; $F=6.85_{1,28}$; $p=0.01$, respectively). In addition, root C to P ratio decreased linearly with elevation for *Betula nana* ($R^2=0.10$; $F=4.21_{1,28}$; $p=0.05$).

However, some root trait relationships with elevation varied among the plant species (Fig. 3). For example, root forks per root length had a significant positive linear relationship with elevation for *Vaccinium vitis-idaea* ($R^2=0.17$; $F=6.11_{1,28}$; $p=0.02$), but a significant positive quadratic relationship with elevation for *Empetrum hermaphroditum* ($R^2=0.17$; $F=3.96_{2,27}$; $p=0.03$). Further, *Vaccinium vitis-idaea* was the only plant species with a significant negative relationship between elevation and average diameter ($R^2=0.13$; $F=4.27_{1,28}$; $p=0.05$) and a significant positive quadratic relationship between elevation and specific root tip abundance ($R^2=0.25$; $F=5.97_{2,27}$; $p<0.01$). Likewise, only *Arctostaphylos alpina* had a significant positive quadratic relationship between elevation and specific root area ($R^2=0.53$; $F=7.31_{2,27}$; $p=0.01$). None of the five species had a significant relationship between elevation and root P content or root dry matter content.

Plot scale coefficients of variation in root traits in response to elevation

There were significant positive relationships between elevation and the community-weighted coefficients of variation for six root traits (Fig. 4), i.e. average diameter ($R^2=0.25$; $p=0.004$; $F=9.57_{1,28}$), root C to N ratio ($R^2=0.41$; $p<0.001$; $F=19.38_{1,28}$), root C to P ratio ($R^2=0.10$; $p=0.048$; $F=4.27_{1,28}$), root N to P ratio ($R^2=0.37$; $p=0.044$; $F=4.45_{1,28}$) and root N content ($R^2=0.36$; $p<0.001$; $F=16.01_{1,28}$) and specific root length ($R^2=0.20$; $p=0.013$; $F=7.06_{1,28}$). Coefficients of variation of the other traits remained invariant with elevation.

Species turnover versus intraspecific variation in response to elevation

Overall, the contribution of intraspecific variation to the total community level root trait variation explained by elevation ranged from 12.4% to 63.1% depending on the trait, whereas the contribution of species turnover ranged from 0.4% to 15.1% (Fig. 5). Further, intraspecific variation contributed more than species turnover to the variation explained by elevation for all fine root traits except root N content (Fig. 5). For example, intraspecific variation contributed 63.1% to the total variation for root dry matter content, whereas the contribution of species turnover was only 0.5%. For the chemical root traits, species turnover contributed the least to the total variation for root N to P ratio (i.e. 0.4%), and the most for root N content (i.e. 15.1%). For the morphological root traits, species turnover contributed the least for root dry matter content

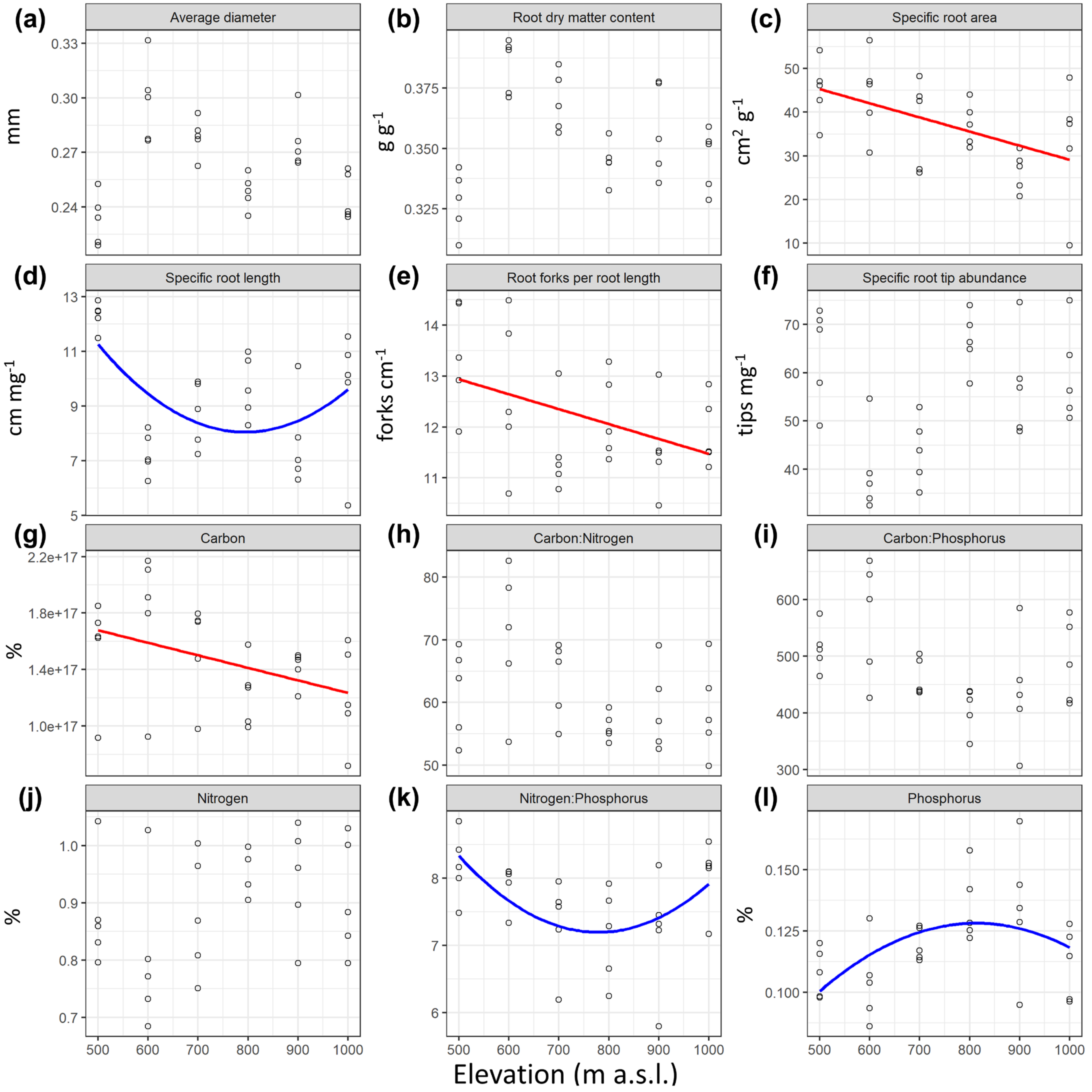

Figure 2. Community level root trait relationships for subarctic heath vegetation with elevation. Coloured lines are significant relationships between root traits and elevation at $p = 0.05$. Red lines are linear model fits and blue lines are polynomial model fits. Circles are community-weighted average root trait values in each plot ($n = 5$). Note that data for root carbon content were transformed using Tukey's power transformation ($\lambda = 9.9$).

(i.e. 0.5%) and the most for specific root tip abundance (i.e. 15.0%).

Intraspecific variation along versus within elevation

Intraspecific trait variation (measured as the coefficient of variation) for all chemical traits except root C content was larger within elevation than the mean coefficient of variation across the whole elevational gradient for all species (Supporting information). For example, for root P content, the coefficient of variation within elevation for the most abundant species, *E. hermaphroditum*, was 17.2% within elevation versus 8.9% across the gradient. However, for specific root area, a morphological trait, the variation along the gradient was higher than within elevation for three of the five dominant plant species (i.e. *A. alpina*, *E. hermaphroditum* and *V. uliginosum*). For all remaining traits, the intraspecific trait variation was

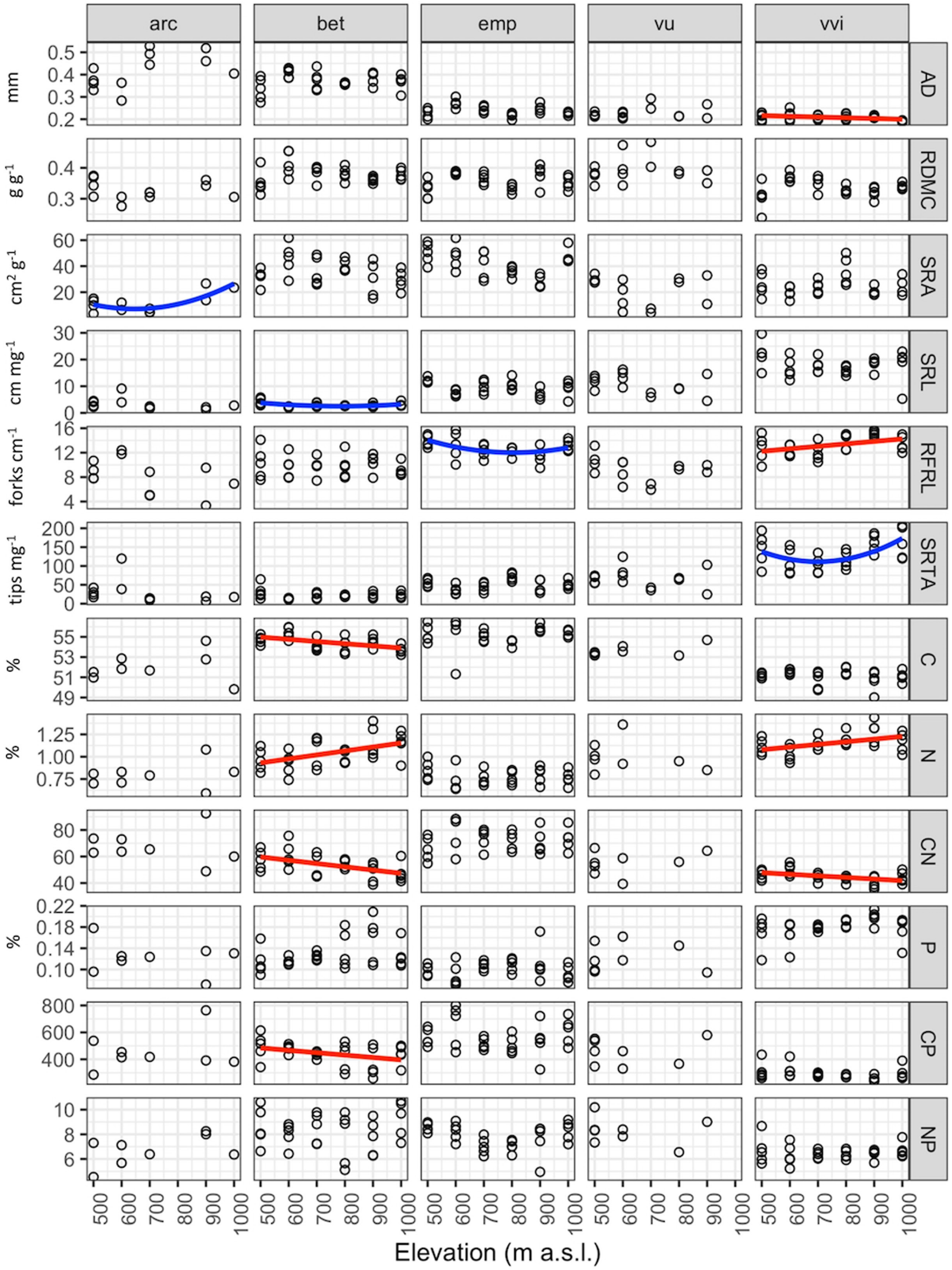

Figure 3. Root trait relationships with elevation for plant species occurring at a minimum of five elevations. The five plant species are *Arctostaphylos alpina* (arc), *Betula nana* (bet), *Empetrum hermaphroditum* (emp), *Vaccinium uliginosum* (vu) and *Vaccinium vitis-idaea* (vvi). Coloured lines are significant relationships between root traits and elevation at $p = 0.05$. Red lines are linear model fits and blue lines are polynomial model fits. Circles are root trait values for each plot ($n = 5$ at each elevation), except for *Arctostaphylos alpina* and *Vaccinium uliginosum* where n ranges from 1 to 5. In all other cases, where fewer than five circles are visible at a specific elevation, the trait values for two or more plots strongly overlap at that elevation. The twelve fine root traits are average diameter (AD), root carbon content (C), root carbon to nitrogen ratio (CN), root carbon to phosphorus ratio (CP), root nitrogen content (N), root nitrogen to phosphorus ratio (NP), root phosphorous content (P), root dry matter content (RDMC), root forks per root length (RFRL), specific root area (SRA), specific root length (SRL) and specific root tip abundance (SRTA).

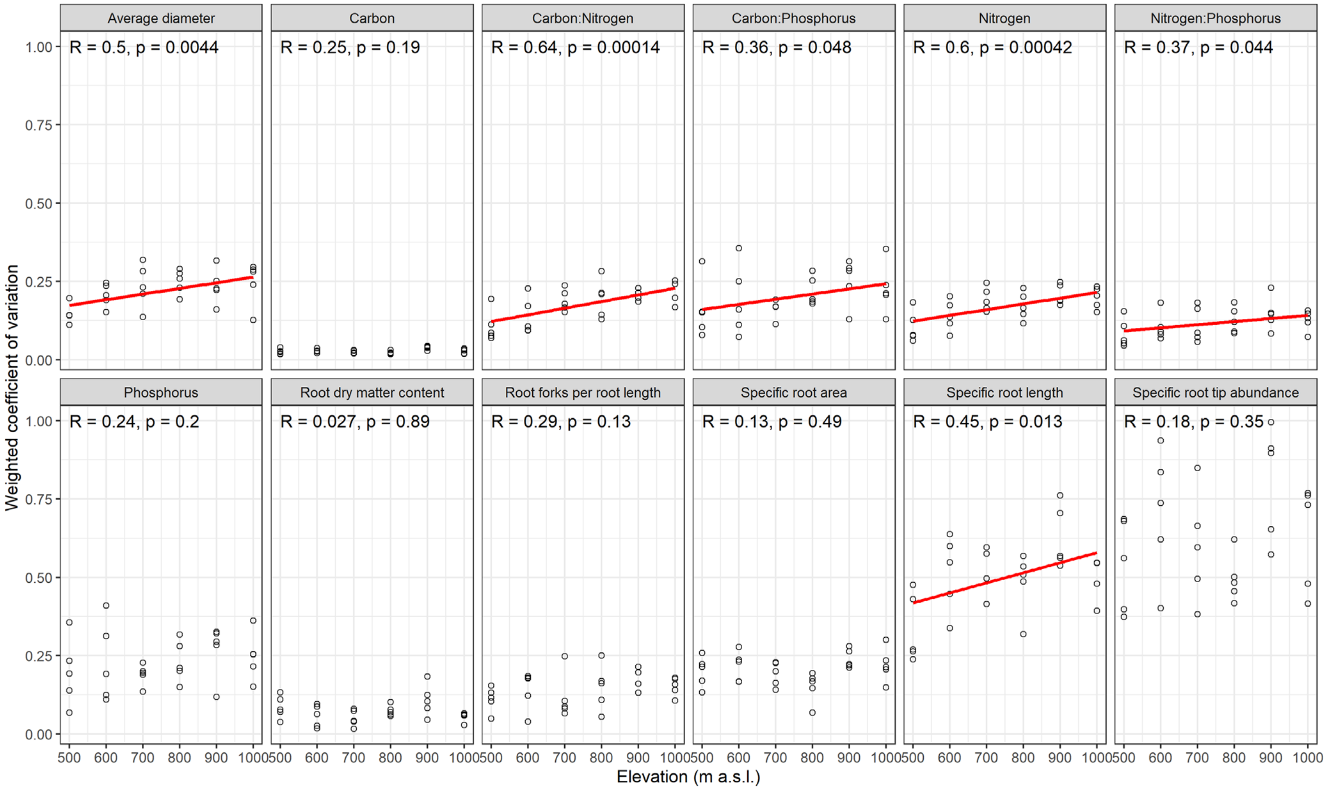

Figure 4. Relationships of community-weighted coefficients of variation with elevation (i.e. the weighted standard deviation divided by the weighted mean). Red lines are statistically significant relationships based on linear model fits between weighted coefficients of variation and elevation ($p < 0.05$). Circles are community-weighted coefficients of variation for root trait values in each plot ($n=5$).

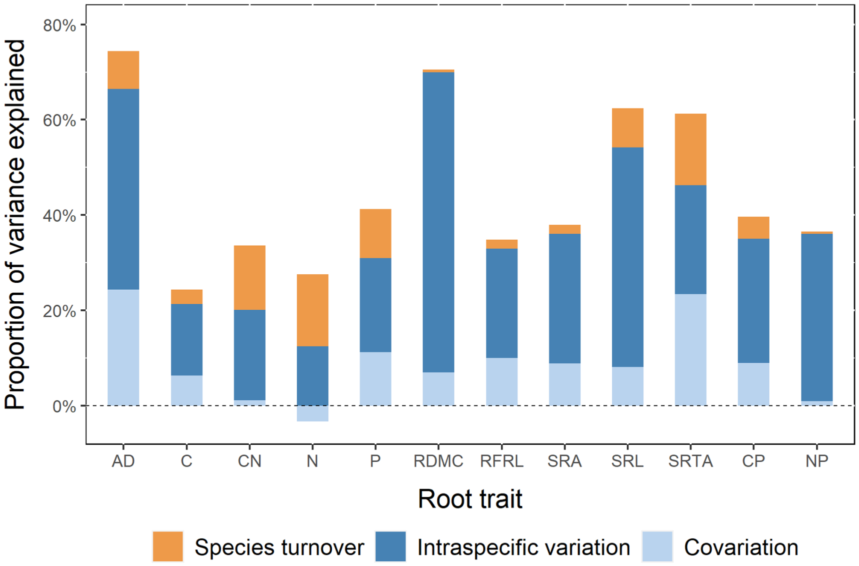

Figure 5. Variance decomposition of community-weighted means for each trait across an elevational gradient. Bars are the proportions of total community-level variation explained by elevation for each root trait. The fine root traits are average diameter (AD), root carbon content (C), root carbon to nitrogen ratio (CN), root nitrogen content (RNC), root phosphorous content (P), RDMC (root dry matter content), root forks per root length (RFRL), specific root area (SRA), specific root length (SRL) and specific root tip abundance (SRTA), root carbon to phosphorus ratio (CP) and root nitrogen to phosphorus ratio (NP).

either similar within and along the elevational gradient, or was either larger or smaller within versus along the elevational gradient for the dominant species.

Discussion

In this study, we investigated the relationships between elevation (as a proxy for temperature) and fine root traits of sub-arctic tundra species across an elevational gradient in northern Sweden. We found no overall support for a unidirectional change from more acquisitive root trait values at the lower elevations to trait values associated with greater nutrient conservation at the higher elevations, either at the species or at the whole community level. Instead, we found that at both levels, only some morphological and chemical root traits had significant relationships with elevation, and the direction and strength of these relationships varied both among traits and among species. In addition, we show that coefficients of variation of root traits at the community level increased with elevation for several root traits, and that a larger proportion of the community level variation in root trait values explained by elevation was due to intraspecific variation rather than due to species turnover in this arctic tundra study system. Below, we discuss these findings in relation to our hypotheses.

Root trait relationships with elevation at the species level

In contrast to our first hypothesis, we found no evidence that species spanning a wide range of elevations at our study site have more conservative root traits at higher elevations. Instead, we found strong idiosyncrasies both in how different traits varied with elevation and how the same trait varied with elevation among different species. Such idiosyncratic trait relationships with elevation were also observed by Weemstra et al. (2021). Notably, for three of the five dominant species we studied, we found no significant linear responses to elevation for any of the measured root traits. In fact, the only trait that was responsive to elevation for the most abundant species in our system (*E. hermaphroditum*) was root forks per root length, which indicates branching intensity, and the relationship was quadratic with maximal values at both ends of the elevational gradient. Hence, although foliar N:P ratios have previously been shown to increase with elevation for *E. hermaphroditum* at our study site (Sundqvist et al. 2011b), such a response is not coupled with a corresponding change in root chemical traits for this species. Overall, our findings instead show that for the majority of species in our system, including the abundant species *E. hermaphroditum*, elevation-associated changes in temperature are not associated with any consistent or linear response in root resource acquisition strategies.

Interestingly, root trait values shifted to more acquisitive values with increasing elevation for four of the twelve measured traits for *Vaccinium vitis-idaea* and three of the twelve measured traits for *Betula nana*. This suggests a shift in resource investment strategy at least with regard to some traits for these two species. For both species, root N content increased with increasing elevation, while root C to N ratios decreased, and root C content decreased with elevation for *B. nana*. While shifts towards more acquisitive root trait values have indeed been observed with decreasing temperatures in forested ecosystems (Zadworny et al. 2016, Defrenne et al. 2019, Laughlin et al. 2021), our results further contrast with previous findings for foliar chemical traits in our study system (Sundqvist et al. 2011b). They also indicate a faster root growth strategy at higher elevations, suggesting a faster return on investment, but a shorter lifespan for these two species (Bergmann et al. 2020, Weigelt et al. 2021). Although this strategy has commonly been observed in fertile environments (Eissenstat et al. 2000, Wang et al. 2017), one potential explanation could be that it is also advantageous in colder environments, where the growing season and the period for plant nutrient uptake is short. Another potential explanation is that higher root N content can be associated with a higher affinity for uptake of ammonium (Grassein et al. 2015) whereby increased root N content with elevation for both species would provide an advantage, given that soil ammonium concentrations in this system can be lowest at the highest elevations (Sundqvist et al. 2011a).

Further, for *V. vitis-idaea* we also found a shift towards lower average diameters and higher numbers of root forks per root length which may indicate increased root absorptive and soil exploration capacity, and potentially less dependence on mycorrhizal symbionts for nutrient uptake at high elevations (Eissenstat et al. 2015). For example, there is some evidence of responses of mycorrhizal colonization rates to temperatures within the range of our gradient (Li et al. 2015, Wilson et al. 2016), with warming resulting in lower mycorrhizal colonization rates, although most studies have higher experimentally elevated temperatures. However, further research examining the relationship between fine root diameters of ericaceous shrubs and mycorrhizal colonization is needed, particularly in response to temperature, as existing knowledge is based only on species with arbuscular and ectomycorrhizal relationships.

Root trait relationships with elevation at the community level

Similar to our findings at the species level, we found no consistent coordinated response to elevation of root resource acquisition strategy at the whole community level. For example, values of root forks per root length and specific root area declined (i.e. were less acquisitive) with increasing elevation, while root C content decreased (i.e. were more acquisitive) at higher elevations. Similarly, Pérez-Ramos et al. (2012) found that specific root area of plant communities increased with soil fertility along a natural gradient in southern France. However, we found no response of root dry matter content to elevation, although other studies have shown shifts to conservative trait values at colder temperatures (Prieto et al. 2015). Meanwhile, root P content, root N to P ratio and specific root length had quadratic relationships with elevation, indicating an inflection point along the elevational gradient where the direction of the relationship changes. Hence, these findings are in contrast to our first hypothesis, and they differ from previous findings from our study system on leaf traits showing that foliar C to P and N to P ratios at the community level increase with increasing elevation (Sundqvist et al. 2011b, De Long et al. 2016b) while soil P availability declines (Vincent et al. 2014). Further, linear shifts in trait relationships with elevation towards more acquisitive values that were observed for some measured traits at the individual species level for *B. nana* and *V. vitis-idaea* were not observed at the whole community level. The lack of trait patterns at the community level may be because these relationships were not observed for the most abundant species in our study (*E. hermaphroditum*) that would have driven whole community level measurements.

To our knowledge, previous studies have not examined whole community level root trait relationships with elevation, but our findings suggest that whole community level responses do not appear to be related to a shift in overall plant resource–acquisition strategy. Here, we note that if we would have excluded our lowest elevation site (i.e. 500 m) which was in treeless heath vegetation situated just below the treeline, we might have observed a shift towards more acquisitive values with increasing elevation at the whole community for a greater number of root traits (Fig. 2). This points to a potential role of environmental factors associated with the treeline ecotone for certain root traits (Clemmensen et al. 2021). Further, we did find a linear response of specific root area and root P content to the growing season soil temperature at the whole community level, showing that at least for these traits a decline in temperature with elevation is important for driving a shift in resource acquisition strategy in these tundra heath communities. Overall, however, we found no support for a unidirectional shift in root traits associated with resource acquisitive strategies towards higher elevations for tundra heath communities.

While community level root trait values were not unidirectionally responsive to elevation, we found differences in within-community variability in fine root traits among elevations. Specifically, we found that fine root trait variation at the whole community level (measured as the weighed coefficient of variation within plots) increased with increasing elevation for six of the twelve measured traits: average diameter, specific root length, root N content, root C to N ratio, root C to P ratio and root N to P ratio. Interestingly, except for specific root length, none of the mean trait values for these four root traits were related to elevation at the community level. It has been shown that within-community variation in aboveground traits among species is driven both by environmental means and environmental heterogeneity (Stark et al. 2017), and it is likely that at higher elevations there is a larger variation in microtopographic factors at the within-plot scale than at lower elevations (Lampei et al. 2019). Therefore, our findings could rather reflect increased spatial heterogeneity of resources or microclimatic conditions at higher elevations that promote within-community variability for certain root traits.

Variance partitioning – species turnover and intraspecific variation along the elevational gradient

We found support for our second hypothesis that intraspecific variation of all traits except root N content contributing more than plant species turnover to the total community-level trait variation explained by elevation. This result is inconsistent with a recent study in the French Alps (Weemstra et al. 2021), where they identified interspecific root trait variation as relatively more important than intra-specific variation in driving the community morphological root trait response to elevation, although that study did not assess whole plant communities and therefore could not examine species turnover. An explanation for this difference could be that our study consisted of a single vegetation type across the whole elevational gradient, whereas the gradient in Weemstra et al. (2021) consisted of different vegetation types at different elevations, and hence, species turnover in their study system was possibly relatively large in comparison to ours. It is notable that heath plant species composition changes little across our elevational gradient, and that three dominant species comprise the majority of the cover and biomass at all elevations (Fig. 1). It also aligns with studies on foliar traits that have found a larger contribution of intraspecific variability than species turnover to plant community trait responses along environmental gradients (Albert et al. 2010, Messier et al. 2010). However, the relative contribution of intraspecific variation is likely to be context-dependent (Lajoie and Vellend 2015), and previous research has also shown mixed support for its role in explaining the overall community trait variation explained by environmental heterogeneity for various aboveground plant traits (Lepš et al. 2011, Roos et al. 2019).

Further, intraspecific trait variation within elevation was found to be larger than intraspecific trait variation along the whole elevational gradient for some traits, and specifically most chemical traits. These findings are similar to those of Weemstra et al. (2021), although chemical root traits were not examined in their study. These large intraspecific variations in root trait values may explain the lack of clear linear relationships between root trait values and elevation. This points to the considerable importance of small-scale local heterogeneity in environmental conditions in driving root traits, which is likely to be as important as large scale heterogeneity along the whole gradient. Taken together, our results suggest that intraspecific rather than interspecific root trait variability in arctic tundra heath plays an important role in driving plant root community responses to long-term climatic changes.

Conclusions

Our results show that several root traits, both at the species and whole plant community level, responded to elevation. Further, we show that within-plot root trait variation of plant communities increased with elevation for some root traits at our subarctic tundra study site. We also demonstrate that intraspecific trait variation contributed more than plant species turnover to the root trait variation explained by elevation in these plant communities for almost all the measured root traits. This study provides insights into responses of plant species and communities to climate warming within a sub-arctic tundra ecosystem, as the temperature range along our elevational gradient (Sundqvist et al. 2011a, Supporting information) is on par with the predicted increase in temperature for arctic ecosystems by the end of the century, i.e. approximately 2.5–3°C (ACIA 2005).

Our results indicate that with progressing global warming, intraspecific root trait variation is likely to be a major means by which plant communities adjust to new environmental conditions, at least in the next decades. Our results further suggest that while elevation-associated declines in temperature can be important for some root traits, it is not likely to lead to linear directional shifts towards a resource-acquisitive strategy for all root traits. In addition, most research related to trait–environment relationships at the community level has largely focused on aboveground traits. However, in arctic ecosystems a large proportion of plant biomass is allocated belowground (Iversen et al. 2015, Blume-Werry et al. 2016), and we found that root trait responses to warming may not necessarily align with leaf trait responses. Hence, understanding root trait responses to increasing temperatures may enable improved predictions of plant community stability or change in response to global warming.

Finally, the greater contribution of intraspecific plasticity compared to species turnover to community-level trait variation in our study system suggests that these communities may maintain a stable species composition with changing environmental conditions, at least with regards to root relationships with soils. However, longer-term observational and experimental studies that expose plants and their associated above- and belowground consumers to more variable and extreme environmental conditions are needed to further improve our understanding of plant community responses to global warming. Of particular importance will be to discern to what extent species are able to adjust their root traits to higher temperatures and when they will be pushed beyond their ecological tolerance and risk being outcompeted by other species.

Acknowledgements – We thank the staff at Abisko Scientific Research station and the Climate Impacts Research Centre, Leonardo Capoani (RIP †) and Alice Trotel for their help during field work, as well as Morgan Karlsson and Ilse van Duuren for their assistance in the laboratory. CMS, PK, MS and DAW formulated the research idea. Field methodology was formulated by CMS, MS, PK and DAW, and field work was conducted by CMS. Lab work and data analysis was conducted by CMS. CMS lead the writing of the manuscript. All authors contributed to all versions of the manuscript.

Funding – This work was conducted with a grant (no. 2015-04214) from the Swedish Research Council (Vetenskapsrådet) to PK. PK also acknowledges funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement no. 864287 – THRESHOLD – ERC-2019-COG).

Author contributions

Clydecia M. Spitzer: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Maja K. Sundqvist**: Conceptualization (supporting); Methodology (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **David A. Wardle**: Conceptualization (supporting); Methodology (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Michael J. Gundale**: Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Paul Kardol**: Conceptualization (lead); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.c866t1g7m (Spitzer et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Ackerly, D. D. et al. 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. – Oecologia 130: 449–457.

ACIA 2005. Arctic climate impact assessment. – Cambridge Univ. Press.

Albert, C. H. et al. 2010. A multi-trait approach reveals the structure and the relative importance of intra- vs interspecific variability in plant traits. – Funct. Ecol. 24: 1192–1201.

Bach, K. et al. 2007. A simulation approach to determine statistical significance of species turnover peaks in a species-rich tropical cloud forest. – Divers. Distrib. 13: 863–870.

Baldrian, P. 2014. Distribution of extracellular enzymes in soils: spatial heterogeneity and determining factors at various scales. – Soil Sci. Soc. Am. J. 78: 11–18.

Bardgett, R. D. et al. 2014. Going underground: root traits as drivers of ecosystem processes. – Trends Ecol. Evol. 29: 692–699.

Bergmann, J. et al. 2020. The fungal collaboration gradient dominates the root economics space in plants. – Sci. Adv. 6: 1–10.

Björk, R. G. et al. 2007. Linkages between N turnover and plant community structure in a tundra landscape. – Plant Soil 294: 247–261.

Bjorkman, A. D. et al. 2018. Plant functional trait change across a warming tundra biome. – Nature 562: 57–62.

Blume-Werry, G. et al. 2016. The hidden season: growing season is 50% longer below than above ground along an arctic elevation gradient. – New Phytol. 209: 978–986.

Blume-Werry, G. et al. 2018. Proportion of fine roots, but not plant biomass allocation below ground, increases with elevation in arctic tundra. – J. Veg. Sci. 29: 226–235.

Bruelheide, H. et al. 2018. Global trait–environment relationships of plant communities. – Nat. Ecol. Evol. 2: 1906–1917.

Carmona, C. P. et al. 2021. Fine-root traits in the global spectrum of plant form and function. – Nature 597: 683–687.

Clemmensen, K. E. et al. 2021. A tipping point in carbon storage when forest expands into tundra is related to mycorrhizal recycling of nitrogen. – Ecol. Lett. 24: 1193–1204.

Collins, M. et al. 2013. Long-term climate change: projections, commitments and irreversibility. – In: Stocker, T. F. et al. (eds), Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge Univ. Press, pp. 1029–1136.

de la Riva, E. G. et al. 2018. Root traits across environmental gradients in Mediterranean woody communities: are they aligned along the root economics spectrum? – Plant Soil 424: 35–48.

De Long, J. R. et al. 2016a. Contrasting responses of soil microbial and nematode communities to warming and plant functional group removal across a post-fire boreal forest successional gradient. – Ecosystems 19: 339–355.

De Long, J. R. et al. 2016b. Effects of elevation and nitrogen and phosphorus fertilization on plant defence compounds in subarctic tundra heath vegetation. – Funct. Ecol. 30: 314–325.

Defrenne, C. E. et al. 2019. Intraspecific fine-root trait–environment relationships across interior Douglas fir forests of western Canada. – Plants 8: 52–117.

Descombes, P. et al. 2017. Uneven rate of plant turnover along elevation in grasslands. – Alp. Bot. 127: 53–63.

Deslippe, J. R. and Simard, S. W. 2011. Below-ground carbon transfer among *Betula nana* may increase with warming in Arctic tundra. – New Phytol. 192: 689–698.

Deslippe, J. R. et al. 2012. Long-term warming alters the composition of Arctic soil microbial communities. – FEMS Microbiol. Ecol. 82: 303–315.

Eissenstat, D. M. et al. 2000. Building roots in a changing environment: implications for root longevity. – New Phytol. 147: 33–42.

Eissenstat, D. M. et al. 2015. Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. – New Phytol. 208: 114–124.

Elmendorf, S. C. et al. 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. – Nat. Clim. Change 2: 453–457.

Fox, J. and Weisberg, S. 2019. An R companion to applied regression. – Sage.

Freschet, G. T. et al. 2010. Evidence of the 'plant economics spectrum' in a subarctic flora. – J. Ecol. 98: 362–373.

Freschet, G. T. et al. 2015. Integrated plant phenotypic responses to contrasting above- and below-ground resources: key roles of specific leaf area and root mass fraction. – New Phytol. 206: 1247–1260.

García Criado, M. et al. 2020. Woody plant encroachment intensifies under climate change across tundra and savanna biomes. – Global Ecol. Biogeogr. 29: 925–943.

Gebrehiwot, K. et al. 2019. Elevational changes in vascular plants richness, diversity and distribution pattern in Abune Yosef mountain range, northern Ethiopia. – Plant Divers. 41: 220–228.

Goodall, D. W. 1952. Some considerations in the use of point quadrats for the analysis of vegetation. – Aust. J. Biol. Sci. 5: 1–41.

Grassein, F. et al. 2015. Relationships between functional traits and inorganic nitrogen acquisition among eight contrasting european grass species. – Ann. Bot. 115: 107–115.

Henn, J. J. et al. 2018. Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. – Front. Plant Sci. 9: 1548.

Holdaway, R. J. et al. 2011. Species- and community-level patterns in fine root traits along a 120 000-year soil chronosequence in temperate rain forest. – J. Ecol. 99: 954–963.

IPCC 2013. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. – In: Stocker, T. F. et al. (eds), Climate change 2013: the physical science basis. Cambridge Univ. Press, pp. 1539.

Iversen, C. M. et al. 2015. The unseen iceberg: plant roots in arctic tundra. – New Phytol. 205: 34–58.

Joel, G. et al. 1994. Leaf morphology along environmental gradients in Hawaiian *Metrosideros polymorpha*. – Biotropica 26: 17.

Körner, C. 2013. Alpine plant life – functional plant ecology of high mountain ecosystems. – Springer.

Kühn, P. et al. 2020. Contrasting patterns of intraspecific trait variability in native and non-native plant species along an elevational gradient on Tenerife, Canary Islands. – Ann. Bot. 127: 565–576.

Kumordzi, B. B. et al. 2014. Changes in local-scale intraspecific trait variability of dominant species across contrasting island ecosystems. – Ecosphere 5: art26.

Lampei, C. et al. 2019. Microclimate predicts frost hardiness of alpine Arabidopsis thaliana populations better than elevation. – Ecol. Evol. 9: 13017–13029.

Lajoie, G. and Vellend, M. 2015. Understanding context dependence in the contribution of intraspecific variation to community trait-environment matching. – Ecology 96: 2912–2922.

Laughlin, D. C. et al. 2021. Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological tradeoffs. – Nat. Ecol. Evol. 5: 1123–1134.

Lepš, J. et al. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. – Ecography 34: 856–863.

Li, Y. et al. 2015. Effects of warming on ectomycorrhizal colonization and nitrogen nutrition of *Picea asperata* seedlings grown in two contrasting forest ecosystems. – Sci. Rep. 5: 17546.

Mayor, J. R. et al. 2017. Elevation alters ecosystem properties across temperate treelines globally. – Nature 542: 91–95.

Messier, J. et al. 2010. How do traits vary across ecological scales? A case for trait-based ecology. – Ecol. Lett. 13: 838–848.

Myers-Smith, I. H. et al. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. – Environ. Res. Lett. 6: 045509.

Ostonen, I. et al. 2017. Adaptive root foraging strategies along a boreal–temperate forest gradient. – New Phytol. 215: 977–991.

Parchami, A. 2016. Weighted.Desc.Stat: weighted descriptive statistics. – https://cran.r-project.org/package=Weighted.Desc.Stat.

Pérez-Ramos, I. M. et al. 2012. Evidence for a 'plant community economics spectrum' driven by nutrient and water limitations in a Mediterranean rangeland of southern France. – J. Ecol. 100: 1315–1327.

Pescador, D. S. et al. 2015. Plant trait variation along an altitudinal gradient in mediterranean high mountain grasslands: controlling the species turnover effect. – PLoS One 10: 1–16.

Pickett, J. T. 1989. Space-for-time substitution as an alternative to long-term studies. – In: Likens, G. E. (ed.), Long-term studies in ecology. Springer, pp. 110–135.

Prieto, I. et al. 2015. Root functional parameters along a land-use gradient: evidence of a community-level economics spectrum. – J. Ecol. 103: 361–373.

Read, Q. D. et al. 2014. Convergent effects of elevation on functional leaf traits within and among species. – Funct. Ecol. 28: 37–45.

Roos, R. E. et al. 2019. Contrasting drivers of community-level trait variation for vascular plants, lichens and bryophytes across an elevational gradient. – Funct. Ecol. 33: 2430–2446.

Spitzer, C. M. et al. 2021. Root trait–microbial relationships across tundra plant species. – New Phytol. 229: 1508–1520.

Spitzer, C. M. et al. 2022. Data from: Root trait variation along a sub-arctic tundra elevational gradient. – Dryad Digital Repository, https://doi.org/10.5061/dryad.c866t1g7m.

Stark, J. et al. 2017. Does environmental heterogeneity drive functional trait variation? A test in montane and alpine meadows. – Oikos 126: 1650–1659.

Sundqvist, M. K. et al. 2011a. Interactive effects of vegetation type and elevation on aboveground and belowground properties in a subarctic tundra. – Oikos 120: 128–142.

Sundqvist, M. K. et al. 2011b. Within- and across-species responses of plant traits and litter decomposition to elevation across contrasting vegetation types in subarctic tundra. – PLoS One 6: e27056.

Sundqvist, M. K. et al. 2013. Community and ecosystem responses to elevational gradients: processes, mechanisms and insights for global change. – Annu. Rev. Ecol. Evol. Syst. 44: 261–280.

Sundqvist, M. K. et al. 2014. Plant and microbial responses to nitrogen and phosphorus addition across an elevational gradient in subarctic tundra. – Ecology 95: 1819–1835.

Thomas, H. J. D. et al. 2020. Global plant trait relationships extend to the climatic extremes of the tundra biome. – Nat. Commun. 11: 1351.

Vincent, A. G. et al. 2014. Bioavailable soil phosphorus decreases with increasing elevation in a subarctic tundra landscape. – PLoS One 9: e92942.

Wang, R. et al. 2017. Different phylogenetic and environmental controls of first-order root morphological and nutrient traits: evidence of multidimensional root traits. – Funct. Ecol. 32: 29–39.

Weemstra, M. et al. 2021. Patterns in intraspecific variation in root traits are species-specific along an elevation gradient. – Funct. Ecol. 35: 342–356.

Weigelt, A. et al. 2021. An integrated framework of plant form and function: the belowground perspective. – New Phytol. 232: 42–59.

Wilson, H. et al. 2016. Experimental warming decreases arbuscular mycorrhizal fungal colonization in prairie plants along a Mediterranean climate gradient. – PeerJ 2016: 1–22.

Zadworny, M. et al. 2016. Scots pine fine roots adjust along a 2000-km latitudinal climatic gradient. – New Phytol. 212: 389–399.

Zanzottera, M. et al. 2020. Community-level variation in plant functional traits and ecological strategies shapes habitat structure along succession gradients in alpine environment. – Community Ecol. 21: 55–65.