Decreased soil moisture due to warming drives phylogenetic diversity and community transitions in the tundra

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Abstract

Global warming leads to drastic changes in the diversity and structure of Arctic plant communities. Studies of functional diversity within the Arctic tundra biome have improved our understanding of plant responses to warming. However, these studies still show substantial unexplained variation in diversity responses. Complementary to functional diversity, phylogenetic diversity has been useful in climate change studies, but has so far been understudied in the Arctic. Here, we use a 25 year warming experiment to disentangle community responses in Arctic plant phylogenetic β diversity across a soil moisture gradient. We found that responses varied over the soil moisture gradient, where meadow communities with intermediate to high soil moisture had a higher magnitude of response. Warming had a negative effect on soil moisture levels in all meadow communities, however meadows with intermediate moisture levels were more sensitive. In these communities, soil moisture loss was associated with earlier snowmelt, resulting in community turnover towards a more heath-like community. This process of ‘heathification’ in the intermediate moisture meadows was driven by the expansion of ericoid and "Betula" shrubs. In contrast, under a more consistent water supply "Salix" shrub abundance increased in wet meadows. Due to its lower stature, palatability and decomposability, the increase in heath relative to meadow vegetation can have several large scale effects on the local food web as well as climate. Our study highlights the importance of the hydrological cycle as a driver of vegetation turnover in response to Arctic climate change. The observed patterns in phylogenetic β diversity were often driven by contrasting responses of species of the same functional growth form, and could thus provide important complementary information. Thus, phylogenetic diversity is an important tool in disentangling tundra response to environmental change.

1. Introduction

High-latitude climate change, characterized by above-average warming and increases in precipitation (Stocker et al 2013, Pithan and Mauritsen 2014, Vihma et al 2016), has drastic consequences for high-latitude ecosystems and their biodiversity (Post et al 2009, Elmendorf et al 2012b). However, what we mean by biodiversity is not always clear since biodiversity is a broad term referring to any type of living variation, from the ecosystem level to genetic variation within organisms (Faith 2015). As a consequence, biodiversity is quantified in a number of fundamentally different ways. Facets of biodiversity
include the richness and abundance of species (taxonomic diversity), the diversity of evolutionary lineages (phylogenetic diversity), and that of the traits related to resource use strategy (functional diversity) (Le Bagousse-Pinguet et al 2019). Depending on the scientific question at hand, different measures of quantifying biodiversity will vary in their explanatory value.

In the context of the Arctic, one of the main concerns of plant diversity changes is their feedback on the global climate through effects on carbon cycling, albedo, and ecosystem energy balance (Elmendorf et al 2012a, Bjorkman et al 2018). Measures of functional diversity, such as the diversity of growth forms and functional traits, have received significant scientific attention as they provide more readily interpretable mechanistic drivers for plant community feedback (Chapin et al 1995, Myers-Smith et al 2011, Elmendorf et al 2012a, 2012b, Bjorkman et al 2018). Biome-wide syntheses (Elmendorf et al 2012a, 2012b, Bjorkman et al 2018) of plant functional responses to experimental and ambient warming have shown increases in shrub abundance and in vegetation height, effects that lower the surface albedo (Sturms et al 2001). Moreover, a shift to more resource acquisitive leaves has been found in moist and wet communities (Myers-Smith et al 2015, Bjorkman et al 2018). Thus, soil moisture has emerged as an important factor modulating plant functional type and trait response to warming (Elmendorf et al 2012a, 2012b, Bjorkman et al 2018), though plot-scale soil moisture changes are rarely considered as potential drivers of community change.

In current studies of functional diversity there is still considerable residual variation, both in the degree that functional traits explain underlying ecosystem functions of interest (Diaz et al 2016, Remy et al 2019, Van Der Plas et al 2020), and in observed variation in functional trait and growth form responses to environmental change within and among study sites (e.g. Walker et al 2006, Elmendorf et al 2012a, Bjorkman et al 2018). Studies that have included multiple facets of biodiversity have shown complementary effects on their provision of ecosystem functions (Roger et al 2016, Craven et al 2018). Within the Arctic, variation in plant traits is not fully predicted by plant growth forms, which suggests that growth forms and trait measurements can be of complementary value (Thomas et al 2019). In a global assessment of drylands, Le Bagousse-Pinguet et al (2019) showed that both functional and phylogenetic diversity drove multifunctionality (e.g. carbon, nitrogen, and phosphorus cycles), whereas specific traits among the dominant species only modulated individual cycles. Thus, considering multiple biodiversity facets when investigating long-term climate change effects on Arctic vegetation can capture a larger variation of co-occurring processes in the ecosystem.

Of the facets of biodiversity discussed above, phylogenetic diversity has received the least amount of scientific attention in the context of long-term vegetation monitoring in the Arctic. Phylogenetic diversity assumes that shared features among species are explained by their shared ancestry and thereby represents an estimate of the diversity of traits between species (Faith 1992, 2015). Phylogenetic diversity thus increasingly correlates with functional diversity as more functional traits are considered (Tucker et al 2018). A challenge of working with phylogenetic diversity is that it does not identify the actual traits, and thus is not as readily interpretable as a driver of specific ecosystem functions compared to functional traits. However, the associated benefit of the more general nature of phylogenetic diversity is that it captures interspecific variation in traits that are not typically measured (e.g. plant-pathogen or mycorrhizal interactions; Gilbert and Webb 2007, Montesinos-Navarro et al 2015). Thus, besides the complementary information it can provide to the analysis of specific ecosystem functions, phylogenetic diversity has the potential to identify unknown variation (Faith et al 2010). Therefore, even though phylogenetic diversity is important in the context of its predictive value of known ecosystem functions, it is also important to study phylogenetic diversity for its own sake and to understand how it is affected by climate warming.

Here, we examine the effect of 25 years of experimental warming on the phylogenetic diversity of five tundra plant communities, with a focus on the differentiation between communities (β diversity). Our study site in northern Scandinavia is an experimental warming setup using open-top chambers within five plant communities that occur within 600 m of each other along a natural moisture gradient (Molau 2001). The experimental design ensures constant climate conditions over the study area. Four of these communities fall within the two dominant community types, heath and meadow, that occur at all elevations up to about 1250 m a.s.l. (Sundqvist et al 2011). Relative to the heath communities, the meadows are richer in soil nitrogen (N) and species diversity, and have a higher N turnover rate (Sundqvist et al 2011). The fifth community is a tussock tundra found on the same nitrogen-poor soil as the heath (Molau 2010). The community is located at the southern margin of its ecosystem range, and it is dependent on permafrost for its persistence. As permafrost at the site degraded during the 1990s, the local community is undergoing rapid change (Molau 2010). Using this experimental setup, together with plot-scale soil moisture measurements, we assess the effects of time and warming on phylogenetic β diversity and whether these responses vary over the soil moisture gradient and between communities.

The phylogenetic diversity measure we introduce here (netMPD), is a corrected version of the β mean pairwise distance (MPD; Webb et al 2008). The MPD
refers to the mean of all pairwise distances within the phylogeny. The use of a phylogeny dated to absolute time defines the distances as the mean amount of time since two different species within a given plot diverged from each other (Webb et al 2002). The most commonly used MPD between plots (β diversity) aims to recover the average phylogenetic distance (or time) separating two individuals or taxa drawn randomly from different communities (Webb et al 2008, Miller et al 2017). This means that if plots are identical, the β MPD value will be the same as the MPD within a plot (α diversity). This fact reveals a flaw in the method, because not only is the distance between identical plots non-zero, it is also variable depending on the α diversity of a given plot (Ricotta et al 2015). This issue has been addressed in methods for inferring variation in total branch length (e.g. using total tree length; Bryant et al 2008), but has not been considered in the context of the MPD.

We hypothesize that experimental warming will alter the phylogenetic β diversity as both taxonomic and functional diversity have been shown to respond to warming (Elmendorf et al 2012a). Furthermore, since climate change has accelerated during the 25 years the study has proceeded, we hypothesize that the ambient plots have also experienced changes in the phylogenetic β diversity. We expect these responses to increase in magnitude over the soil moisture gradient and vary among community types as these have been found to be important factors in modulating plant functional type and trait responses to warming (Elmendorf et al 2012a, 2012b, Bjorkman et al 2018). Thus, using this improved measure of phylogenetic β diversity we aim to improve our understanding of how warming influences Arctic plant community structure over soil moisture gradients, and disentangle some of the hitherto masked responses within growth forms seen in biome-wide Arctic syntheses (e.g. Elmendorf et al 2012a, 2012b, Bjorkman et al 2018).

2. Material and methods

2.1. Site description

The study site is located in the valley of Latnjavagge close to the Latnjajaure Field Station (LFS; 68°21′N, 18°30′E; Sweden), located at 980 m a.s.l. Latnjavagge is a U-shaped glacial valley in the mid-alpine region with cool summers, relatively mild, snow-rich winters, and snow cover for most of the year. Mean annual temperature ranges from −1 to −3 °C and the total annual precipitation from 600 to 1100 mm (figure 1). The vegetation is typical of the Low Arctic, but with higher diversity (Molau 2001), owing to high variation in local soil properties and moisture regimes.

The five targeted plant communities (table 1) are distributed along a nutrient and moisture gradient. The three nutrient-rich meadow communities are found on calcareous bedrock while the dry heath and tussock tundra communities are found on nutrient-poor acidic glacial moraine ridges and flats (Molau et al 2003). The meadow communities cover dry, mesic, and wet moisture regimes while the nutrient-poor communities cover both mesic (tussock tundra) and dry (dry heath) regimes. This moisture gradient is mainly caused by wind-mediated redistribution of the winter snow and continuous meltwater from higher-elevation snow patches after initial snowmelt. Moreover, the tussock tundra is the only community known to have had permafrost during the start of the study period—known to be important for the persistence of the community type (Molau 2010). The permafrost in the tussock tundra was lost between 1993

![Figure 1](image-url) Mean air temperature ($P = 0.12, R^2 = 0.11$) and annual precipitation ($P = 0.53, R^2 = 0.02$) measured at the Latnjajaure field station during the growing season (May–September; 1993–2016).
Table 1. The five most common vascular plant species in the ambient plots for each of the studied plant communities, with species listed in decreasing abundance.

| Dry heath          | Tussock tundra                  | Dry meadow            | Mesic meadow          | Wet meadow          |
|--------------------|--------------------------------|-----------------------|-----------------------|---------------------|
| Cassiope tetragona | Eriophorum vaginatum            | Dryas octopetala      | Dryas octopetala      | Carex bigelowii     |
| Betula nana        | Phyllocladus caerulea           | Vaccinium vitis idaea | Carex bigelowii       | Bistorta vivipara   |
| Salix herbacea     | Vaccinium vitis idaea           | Festuca ovina         | Carex vivipara        | Carex lachenalii    |
| Vaccinium vitis idaea | Salix herbacea            | Carex bigelowii       | Bistorta vivipara     | Calamagrostis stricta |
| Empetrum nigrum    | Betula nana                    | Bistorta vivipara     | Vaccinium uliginosum  | Poa arctica        |

and 2001 (Beylich et al. 2004). The dominant vegetation differs markedly between community types as outlined in table 1.

2.2. Experimental warming and sampling

Experimental warming was performed using year-round open-top chambers which warmed the soil surface and air (up to 15 cm) temperatures by 0.6 and 1.6 °C, respectively, compared to ambient plots (Molau and Mølgaard 1996, Marion et al. 1997). The warming treatment was replicated five times in each of the communities, initiated between 1993 and 1994 (depending on the community). Thus, we used a total of 50 plots: five ambient and five experimental warming plots per community. Mapping of plant abundance was performed using the standardized 1 m² point frame method of the International Tundra Experiment manual (Molau and Mølgaard 1996). Plant abundance measurements were repeated three to five times between 1993 and 2016; sampling dates between and within communities did not always align (supplementary table S1 (available online at stacks.iop.org/ERL/16/064031/mmedia)). Soil moisture (top 6 cm) was measured every second week (six times per season; May–August) in each plot with a minimum of three replicates per date during both 2017 and 2018 using a Delta ML2x Theta probe (Delta-T Devices Ltd, Cambridge, U.K.).

2.3. Phylogenetic inference

Leaf material of vascular plant species sampled in our plots was sequenced for the plant DNA barcodes rbcl. and matK (Group et al. 2009). To alleviate issues with divergent sampling across the plant tree of life, we added our samples to an existing angiosperm-wide alignment (Magallón et al. 2015) reduced to a single representative for each plant order using the multiple sequence alignment in MAFFT v7 (Katoh and Standley 2013). Since the angiosperm data contained additional markers (atpB, S18, and S26), we supplemented our sequence data with GenBank (Sayers et al. 2020) sequences where possible (supplementary table S2).

We conducted phylogenetic analyses using RAxML v8.2.1 (Stamatakis 2014) with 1000 bootstrap replicates at the CIPRES web portal (Miller et al. 2010). To enable the calculation of phylogenetic diversity measures based on time rather than the number of mutations, we calculated divergence times using penalized likelihood as implemented in TreePL v1.0 (Sanderson 2003, Smith and O’Meara 2012). We used the fossil constraints outlined by Magallón et al. (2015) for angiosperms and by Magallón (2010) for deeper nodes of non-angiosperm lineages (supplementary table S3). The optimal smoothing value was determined using random subsampling and replicate cross-validation testing values between $1 \times 10^{-7}$ and $1 \times 10^{-2}$, separated by an order of magnitude (Sanderson 2002, Smith and O’Meara 2012). After this, the tree was pruned into a site-specific tree containing only species found on the site using the R v3.5.3 package ape v5.3 (Paradis et al. 2004, R Core Team 2018).

2.4. Phylogenetic diversity measures

In order to measure variation between plots, we calculated a ‘net’ version of the between-plot MPD. We first calculated the within-plot intraspecific abundance-weighted MPD, hereafter referred to as intra MPD (Miller et al. 2017), which measures the distance between any two individuals present in a plot. Weighting by species abundance transforms distances into the average time species occurrence were separated from one another, while ‘intra’ refers to the fact that two individuals of the same species have zero separation (see inter MPD among species; Miller et al. 2017). We used this measure of intra MPD as it is robust to the misidentification of closely related species and captures increases and decreases of phylogenetic dispersion caused by selective processes such as habitat filtering and competitive exclusion (Miller et al. 2017). We then used intra MPD to calculate net differences between plots as follows: in any two given plots A and B, we deconstructed their abundance-weighted intra MPD into the proportion that each branch in the phylogeny contributes to the total value. For any given branch (any line connecting a species to its ancestor) in the phylogeny, we multiplied the branch length with the proportion of pairwise distances it contributes to. This was done using the following formula:

$$bc = bl \times 2(d \times o)$$  

where $bc$ is the branch contribution to the MPD, $bl$ is the branch-length, $d$ is the summed relative abundance of its descendants, and $o$ is the summed relative
abundance of other taxa in the tree. Then we subtracted the branch contributions of plot B from that of plot A, giving the net difference in contribution to the local intra MPD of each branch. The summed absolute value of all branches in the phylogeny is the net intra MPD between the two plots. We refer to the ‘abundance weighted net $\beta$ intra MPD’ as netMPD.

2.5. Statistical analysis
To assess the effect of passive warming on soil moisture, we used a generalizable Bayesian modelling approach using the rjags (v4-10; Plummer 2016) and r2jags (v0.6-1; Su and Yajima 2015) packages in R. We used two models: a factorial model focusing on the overall treatment effect, and a continuous model where we aimed to separate out whether warming affects soil moisture through the timing of snowmelt (differences in intercept) or whether warming affects the rate of soil moisture change over time (differences in slope). As soil moisture content is a proportional type of data (bound between 0 and 1), we used a beta error distribution to model it. The factorial model included the log-transformed soil moisture content as dependent variable and community, treatment, year, and their interactions as fixed effects. Plot identity and day of year (as a factor) were included and as random effects. In the continuous model, day of year was included as a continuous independent variable rather than as a random effect, but the model was otherwise identical. We defined a treatment response to be ‘significant’ when the difference between control and treated plots did not overlap with 0 in its 95% credible interval.

We used the betadisper function in vegan (v2.5-4; Anderson 2006, Oksanen et al 2016) to calculate and compare within-community dispersion in netMPD among available sampling times for each community. We then compared taxonomic community composition through time using permutational multivariate analysis of variance (PerMANOVA) implemented with the Adonis function in vegan, constraining the permutations to each unique plot to account for repeated sampling through time (Anderson 2001). Although PerMANOVA assumes homogeneity of variances, the effect of violating this assumption is minimal as long as sampling is balanced (Anderson & Walsh 2013).

We used non-metric multidimensional scaling (NMDS) to identify community-level diversity based on the netMPD between plots. Confidence interval ellipses and community centroids were extracted using the ordiellipse function in vegan (v2.5-4; Kruskal 1964; Minchin 1987, Oksanen et al 2016). To understand which taxa were driving differences in the phylogenetic diversity, we then inferred the correlation between plant families and netMPD through vector fitting (Oksanen et al 2016).

3. Results
3.1. Soil moisture
Plot-scale soil moisture data from the two growing seasons after the vegetation was last sampled showed a consistent moisture gradient, with dry heath and tussock tundra being the driest, dry and mesic meadow intermediate, and the wet meadow highest in soil moisture. In all meadow communities, experimentally warmed plots had lower soil moisture than ambient plots (figures 2 and S1(a)). Experimental plots were significantly drier during both measured years in the dry and mesic meadows (the communities with intermediate soil moisture), while in the wet meadow they were only significantly drier in 2018. The lower soil moisture observed in the dry and mesic meadows was driven by differences in the intercept between treatments, while slopes did not differ significantly for any of the communities (figures S1(b) and (c)). The tussock tundra and dry heath did not show any treatment differences in soil moisture.

3.2. Phylogenetic diversity
Indices of netMPD varied within and among communities and treatments through time (figures 3(a) and (b)). Meadow communities responded the most strongly to warming in comparison with other community types, and showed a significant temporal response ($R^2 = 0.24–0.34$, $P < 0.05$; table 2). We observed a significant increase in dispersion in phylogenetic $\beta$ diversity over time in warmed mesic ($F_{3,15} = 4.62$, $P = 0.02$) and wet ($F_{3,16} = 7.2$, $P = 0.01$) meadow communities (figure 4; supplementary table S1), as is also shown in the NMDS plots (figures 3(a) and (b)). In the warmed mesic meadow, this increase in dispersion is clearly visible along the first NMDS axis (figure 3(b)). As the change over time in this community is also the most pronounced along this axis, it is likely that the observed difference in dispersion is due to variability in the speed at which the mesic meadow plots responded to the warming treatment.

Although all meadow plots showed a strong treatment response, the direction of these changes differed between the dry, mesic, and wet meadows. The former two became more similar to the dry heath, while the latter became more distinct from all other communities. Vector fitting showed that these differences in the direction of response to experimental warming coincide with increases in Betulaceae and Ericaceae shrubs in the dry and mesic meadows, whereas community shifts in the wet meadow correlated with increases in Salicaceae shrubs and Cyperaceae (sedges; figure 3(c)).

Ambient dry and mesic meadow communities showed similar temporal patterns to communities in the warmed plots, though only significantly so in the mesic meadow ($F_{3,18} = 0.99$, $P = 0.02$; table 2).
There was no significant temporal response in the wet meadow’s ambient plots.

The tussock tundra showed a significant shift in phylogenetic β diversity towards the dry heath community between 1996 and 2006. This shift was observed in both the ambient ($F_{2,12} = 1.46, P = 0.01$) and treatment ($F_{2,15} = 1.42, P = 0.01$) plots with similar strength (table 2). The ambient tussock tundra also showed a significant decrease in dispersion (figures 2 and 3; table S4), though this appears to be minor and did not show a clear pattern. The ambient dry heath showed significant shifts in phylogenetic β diversity ($F_{3,12} = 0.78, P = 0.02$), but these shifts did not have any clear directionality (figures 3(a) and (b)).

4. Discussion

We found that phylogenetic β diversity responded to warming, and that the response and its magnitude varied across the five plant communities. In agreement with our hypotheses and the general pattern observed in functional diversity studies (Elmendorf et al 2012a, Bjorkman et al 2018), the responses varied over the soil moisture gradient. Ambient plots showed similar patterns to warmed plots, however, except for in the mesic meadow and tussock tundra, these patterns were insignificant at current levels of climate change. Warming responses were the strongest in the meadow communities, where the wet meadow became more distinct from other warmed communities, whereas the dry and mesic meadows became increasingly similar to the dry heath in phylogenetic β diversity. These transitions from meadow to heath communities, or ‘heathification’, have wide-reaching consequences as heath communities tend to be less productive and have lower species diversity (Löffler and Pape 2008). Furthermore, trophic interactions will also be affected as the heath vegetation tends to be less palatable for herbivores (Post et al 2009). For instance, many of the most common heath shrubs, such as Empetrum nigrum, are usually not preferred by reindeer which in itself can enhance the heathification process (Vowles et al 2017). Heathification could also pose different feedback to climate: since heath vegetation is lower in height, the negative effects of protruding branches and snow depth on snow albedo and soil warming are less pronounced compared to meadow communities (Sturm et al 2001). This albedo effect combined with the lower palatability and decomposability of ericoid shrubs and their associated mycorrhiza are suggested to have less a positive, or even a negative, feedback on climate warming (Langley and Hungate 2003, Aerts 2006, Vowles and Björk 2019). Thus, if warming is the dominant driver for vegetation change in the...
Figure 3. Non-metric multidimensional scaling ($s = 0.17, k = 2$) based on netMPD of all five plant communities on control and treatment plots (a, b). Each community's development through time is indicated by a color gradient from 1993 (light) to 2016 (dark). Lines colored by the same gradient connect the community centroids through time while community dispersion is shown by ellipses representing community standard deviations. Original plot positions are shown in the background colored grey. (c) The original control plots were fitted with vectors representing plant family contributions to plot intra MPD. The length of the arrows is proportional to the correlation between variables and the ordination of the plots. Only families with a vector fit of $R^2 > 0.2$ and $P > 0.05$ were plotted to preserve figure legibility.

Table 2. Results of PerMANOVA, examining the effect of time in each treatment per community. $P$ values shown are adjusted using Bonferroni correction.

| Community       | Treatment | df  | $F$   | $R^2$ | $P$  |
|-----------------|-----------|-----|-------|-------|------|
| Dry heath       | Ambient   | 3.12| 0.73  | 0.155 | 0.02 |
| Tussock tundra  | Ambient   | 2.12| 1.48  | 0.198 | 0.01 |
| Dry meadow      | Ambient   | 1.8 | 0.81  | 0.092 | 0.625|
| Mesic meadow    | Ambient   | 3.18| 0.99  | 0.142 | 0.02 |
| Wet meadow      | Ambient   | 4.20| 0.6   | 0.107 | 1    |
| Dry heath       | Warmed    | 2.9 | 0.64  | 0.125 | 1    |
| Tussock tundra  | Warmed    | 2.12| 1.42  | 0.191 | 0.01 |
| Dry meadow      | Warmed    | 3.16| 1.7   | 0.242 | 0.01 |
| Mesic meadow    | Warmed    | 2.15| 3.93  | 0.344 | 0.01 |
| Wet meadow      | Warmed    | 3.16| 1.79  | 0.252 | 0.02 |

Arctic, meadow communities will respond differently due to their inherent soil moisture conditions, which will have a detrimental effect on Arctic ecosystems.

In addition, we found that only the warmed meadow plots had a lower soil moisture content compared to their ambient counterparts, which could explain why these were the communities responding to warming. In the dry and mesic meadows, the lower soil moisture was driven by the intercept differences in our linear models, which suggests that differences in the timing of meltout in the plots drove the soil moisture differences between warmed and ambient plots. Meltout at the site has further been noted to occur up to two weeks earlier in open top chambers at the site (Marion et al 1997). Therefore, it is likely that snowmelt is an important factor driving the observed patterns in plant communities with intermediate soil moisture conditions. While the use of phylogenetic diversity indices is not common in studies of the Arctic tundra biome, some of the patterns we observed are nonetheless consistent with previous findings regarding functional diversity indices. For instance, decreased soil moisture favoring shrub species over graminoids and sedges was found in both dry (Klein et al 2004, 2007, Wahren et al 2013) and wet communities (Hinzman et al 2005, Leffler et al 2016). Moisture limitation has even been linked to increased plant invasive success into alpine systems (Winkler et al 2016). Within mesic sites in particular, decomposition has been shown to be sensitive to the drying effects of soil warming (Robinson et al 1995, Aerts 2006). In addition, mesic sites also tended to lose species richness under experimental warming across the tundra biome (Elmendorf et al 2012a), reflecting...
Figure 4. Effect of time on community dispersion measured in netMPD. Only communities that showed a significant dispersion are shown. Letters indicate treatments that differ significantly at $P < 0.01$, using a Tukey HSD (honestly significant difference) test. Color gradients show community identity and time of sampling reflecting those in figure 2. Boxplot hinges represent first and third quartile ranges, and the bar in each box represents the median. An asterisk (*) denotes a trend with $P < 0.1$.

the transition from high-diversity meadow to low-diversity heath communities, as we observed here. Similar to our observations, short-term decreases in sedges have been observed in a four-year warming experiment on a mesic meadow community in the Norwegian Scandes tundra (Klanderud 2008). Taken together, we conclude that soil moisture limitation due to warming is an important driver behind community transition within this study and across the Arctic. Communities experiencing earlier snowmelt may become especially restricted by soil moisture as meltwater becomes more limiting throughout the lengthened growing season. In this context, assessment of future changes in timing and amount of precipitation are imperative for predicting plant response to climate change.

Furthermore, we found that community responses within the meadows, as well as the tussock tundra, were driven by an increase in abundance in shrub species. This response corroborates the pattern of climate-driven shrub expansion found in the Low Arctic (Chapin III et al 1995, Tape et al 2006, Harte et al 2015). However, here we show that shrubification is driven by different plant lineages in the different communities. The pattern within the dry meadow, mesic meadow, and tussock tundra—which experienced reductions in their soil moisture—was driven by heather (Ericaceae), rose (Rosaceae) and birch (Betulaceae). In contrast, willow shrubs (Salicaceae) drove the pattern in phylogenetic $\beta$ diversity within the wet meadow, which maintained high levels of soil moisture. If these species would have been grouped by their functional types (‘evergreen shrub’ for most Ericaceae and the dominant Rosaceae, and ‘deciduous shrub’ in the case of Betulaceae and Salicaceae), these changes would have been masked, as the pattern in the dry and mesic meadows was driven by both evergreen and deciduous shrub species. Consequently, the use of phylogenetic diversity not only provides complimentary information, but also allows us to detect strong variability within the shrubification response. This variability would have been missed by studies relying on the use of plant functional types, and highlights the fact that phylogenetic diversity-driven approaches increases our understanding of plant response to climate change.

The tussock tundra at Latnjajaure is unique both regionally and among Arctic research sites since it lost its permafrost within the study duration (1992–2001; Beylich et al 2004, Molau 2010). In terms of phylogenetic $\beta$ diversity, this loss has led to a shift towards dry heath conditions during the first decade of the study driven by the invasion of ericoid shrubs.
more commonly found on well-drained soils (Molau 2010). This shift is common between the ambient and treatment plots and appears to be a stronger driver of phylogenetic β diversity than experimental warming. However, since this initial shift, phylogenetic β diversity has remained relatively constant, indicating that the rate of transition is slowing down. Tussock grasses (Eriophorum vaginatum) are quite long-lived, and ages ranging between 70 and 120 years have been recorded in northern Alaska (Mark et al 1985). Thus, it is possible that invasion was limited to unoccupied soil that became available with the disappearance of the permafrost and lowered water table. In addition, the observed loosening of the tussocks could have provided more open ground, further facilitating the fast initial response (Molau 2010). Thus, even though community turnover in the tussock tundra is undoubtedly underway, the longevity of the dominant species likely diminishes the rate of transition beyond the initial response.

5. Conclusions

Our study identified the importance of the hydrological cycle as a driver of vegetation turnover in response to Arctic climate change, both in terms of response to long-term warming and as an event-based driver such as the disappearing permafrost in this study. In a warmer Arctic, decreased soil moisture can lead to community turnover from meadow to heath communities. Communities with intermediate soil moisture conditions experiencing earlier snowmelt can be especially sensitive to heathification as meltwater becomes restrictive throughout the lengthened growing season. In contrast, a more consistent water supply would instead promote the development of Salix (willow)-dominated meadows. Thus, changes in the source, amount, and/or timing of soil moisture input could partially explain the site-specific responses found in Arctic-wide studies. Another important driver of community changes that we identified is the disappearance of permafrost in tussock tundra, leading to a drop in soil moisture and a rapid initial community response. However, a long-term change was inhibited by the longevity of the local tussocks. Our use of phylogenetic diversity detected patterns not found by commonly used plant functional types and can thus be an important tool in assessing plant response to warming.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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Author contributions (statement of authorship)

R S, R G B, R H N, and A A conceived the idea for the paper; U M established the original experiment; R S, R G B, C J L, J M A, A A and U M collected the plant abundance data; C D B generated the molecular data; M B collected the soil moisture and climatic data. R S and R G B led the writing of the paper, with contributions from all authors.

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References

Aerts R 2006 The freezer defrosting: global warming and litter decomposition rates in cold biomes J. Ecol. 94 713–24
Anderson M J 2001 A new method for non-parametric multivariate analysis of variance Austral Ecol. 26 32–46
Anderson M J 2006 Distance-based tests for homogeneity of multivariate dispersions Biometrics 62 245–53
Anderson M J and Walsh D C 2013 Pernanova, Anosim, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecol. Monogr. 83 557–74
Beylich A A, Kolstrup E, Thyrrsted T, Linde N, Pedersen L B and Dynesius I 2004 Chemical denudation in arctic-alpine Latjnvagge (Swedish Lapland) in relation to regolith as assessed by radio magnetotelluric-geophysical profiles Geomorphology 57 303–19
Bjorkman A D et al 2016 Plant functional trait change across a warming tundra biome Nature 562 57
Bryant J A, Lamanna C, Morlon H, Kerkhof A J, Enquist B J and Green J I 2008 Microbes on mountaintop: contrasting elevational patterns of bacterial and plant diversity Proc. Natl Acad. Sci. 105 11505–11
Chapin III F S, Shaver G R, Giblin A E, Nadelhoffer K J and Laundre J A 1995 Responses of Arctic tundra to experimental and observed changes in climate Ecology 76 694–711
Craven D et al 2018 Multiple facets of biodiversity drive the diversity–stability relationship Nat. Ecol. Evol. 2 1379–87
Díaz S et al 2016 The global spectrum of plant form and function Nature 529 167–71
Elmendorf S C et al 2012a Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time Ecol. Lett. 15 164–75
Elmendorf S C et al 2012b Plot-scale evidence of tundra vegetation change and links to recent summer warming Nat. Clim. Change 2 453
Faith D P 1992 Conservation evaluation and phylogenetic diversity Biological Conservation, 61 1–10
Faith D P 2015 Phylogenetic diversity, functional trait diversity and extinction: avoiding tipping points and worst-case losses Phil. Trans. R. Soc. B 370 20140011
Faith D P, Magallon S, Hendry A P, Conti E, Yahara T and Webb C O 2007 Phylogenetic signal in plant pathogen–host range Proc. Natl Acad. Sci. 104 8975–83
Group C P W et al 2009 A DNA barcode for land plants Proc. Natl Acad. Sci. 106 12794–7
Harte J, Saleska S R and Levy C 2015 Convergent ecosystem responses to 23-year ambient and manipulated warming link advancing snowmelt and shrub encroachment to transient and long-term climate–soil carbon feedback Glob Change Biol. 21 2549–56
Hinzman L D et al 2005 Evidence and implications of recent climate change in northern Alaska and other Arctic regions Clim. Change 72 251–98
Katoh K and Standley D M 2013 MAFFT multiple sequence alignment software version 7: improvements in performance and usability Mol. Biol. Evol. 30 772–80
Klander K 2008 Species-specific responses of an alpine plant community under simulated environmental change J. Veg. Sci. 19 363–72
Klein J A, Harte J and Zhao X Q 2004 Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau Ecol. Lett. 7 1170–9
Klein J A, Harte J and Zhao X-Q 2007 Experimental warming, not grazing, decreases rangeland quality on the Tibetan Plateau Ecol. Appl. 17 541–57
Kruskal J B 1964 Nonmetric multidimensional scaling: a numerical method Psychometrika 29 115–29
Langley J A and Hungate B A 2003 Mycorrhizal controls on belowground litter quality Ecology 84 2302–12
Le Bagousse-Pinguet Y, Soliveres S, Gross N, Torices R, Berdugo M and Maestre F T 2019 Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality Proc. Natl Acad. Sci. 116 8419–24
Leffler A J, Klein E S, Oberbauer S F and Welker J M 2016 Coupled long-term summer warming and deeper snow alters species composition and stimulates gross primary productivity in tussock tundra Oecologia 181 287–97
Löffler J and Pepe R 2008 Diversity patterns in relation to the environment in alpine tundra ecosystems of northern Norway Antarct. Antarct. Alp. Res. 40 573–81
Magallón S 2010 Using fossils to break long branches in molecular dating: a comparison of relaxed clocks applied to the origin of angiosperms Syst. Biol. 59 384–99
Magallón S, Gómez-Acevedo S, Sánchez-Reges Y L and Hernández-Hernández T 2015 A meta-calibrated time-tree examines the early rise of flowering plant phylogenetic diversity New Phytol. 207 437–53
Marion G et al 1997 Open-top designs for manipulating field temperature in high-latitude ecosystems Glob. Change Biol. 3 20–32
Mark A, Fetcher N, Shaver G and Chapin III F 1985 Estimated ages of mature tussocks of Eriophorum vaginatum along a latitudinal gradient in central Alaska, USA Arctic Alpine Res. 17 1–5
Miller E T, Farine D R and Trisos C H 2017 Phylogenetic community structure metrics and null models: a review with new methods and software Ecography 40 461–77
Miller M A, Pfeiffer W and Schwartz T 2000 Creating the CIPRES Science Gateway for inference of large phylogenetic trees 2010 Gateway Computing Environments Workshop (GCE) (IEEE) pp 1–8
Minchin P R 1987 An evaluation of the robustness of techniques for ecological ordination Vegetatio 69 89–107
Molau U 2001 Tundra plant responses to experimental and natural temperature changes Second Int. Symp. Environmental Research in the Arctic (Tokyo: National Institute of Polar Research) pp 445–66
Molau U 2006 Long-term impacts of observed and induced climate change on tussock tundra near its southern limit in northern Sweden Plant Ecol. Divers. 3 29–34
Molau U, Kling J, Lindblad K, Björk R, Dänhardt J and Liess A 2003 A GIS assessment of alpine biodiversity at a range of scales Alpine Biodiversity in Europe (Berlin: Springer) pp 221–9
Molau U and Møglaard P 1996 ITEX Manual II (Copenhagen: Danish Polar Center) p 29
Montesinos-Narváez A, Segarra-Moragues J G, Valiente-Banuet A and Verdú M 2015 Evidence for phylogenetic correlation of plant–AMF assemblages Ann. Bot. 115 171–7
Myers-Smith I H et al 2015 Methods for measuring Arctic and alpine shrub growth: a review Earth Sci. Rev. 140 1–13
Myers-Smith I H et al 2011 Shrubs expansion in tundra ecosystems: dynamics, impacts and research priorities Environ. Res. Lett. 6 045009
Oksanen J, Blanchet F, Kindt R, Legendre P and O'Hara R 2016 Vegan: community ecology package. R Package 2.3–3 (https://CRAN.R-project.org/package=vegan)
Paradis E, Claude J and Strimmer K 2004 APE: analyses of phylogenetics and evolution in R language Bioinformatics 20 289–90
Pithan F and Mauritsen T 2014 Arctic amplification dominated by temperature feedbacks in contemporary climate models Nat. Geosci. 7 181
Plumlee E 2016 jags: Bayesian graphical models using MCMC (available at: http://mcmc-jags.sourceforge.net
Post E et al 2009 Ecological dynamics across the Arctic associated with recent climate change Science 325 1355–8
R Core Team 2018 R: a language and environment for statistical computing R Foundation for Statistical Computing (Vienna) (available at: https://www.R-project.org
Rerry C, Krollcheck D J, Keyser A B, Litvak M E, Collins S L and Harteau M D 2019 Integrating species-specific information in models improves regional projections under climate change Geophys. Res. Lett. 46 6554–62
Ricotta C, Bacaro G and Pavoine S 2015 A cautionary note on some phylogenetic dissimilarity measures J. Plant Ecol. 8 12–6
Robinson C H, Wooley P, Parsons A, Potter J A, Callaghan T V, Lee J A, Press M C and Welker J M 1995 Responses of plant litter decomposition and nitrogen mineralisation to simulated environmental change in a high Arctic polar semi-desert and a subarctic dwarf shrub heath Oikos 73 503–12

Roger F, Bertilsson S, Langenheder S, Osman O A and Gamfeldt L 2016 Effects of multiple dimensions of bacterial diversity on functioning, stability and multifunctionality Ecology 97 2716–28

Sanderson M J 2002 Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach Mol. Biol. Evol. 19 101–9

Sanderson M J 2003 r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock Bioinformatics 19 301–2

Sayers E W, Cavanaugh M, Clark K, Ostell J, Pruitt K D and Karsch-Mizrachi I 2020 GenBank Nucleic Acids Res. 48 D84–6

Smith S A and O’Meara B C 2012 treePL: divergence time estimation using penalized likelihood for large phylogenies Bioinformatics 28 2689–90

Stamatakis A 2014 RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies Bioinformatics 30 1312–3

Stocker T F et al 2013 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: Cambridge University Press) pp 33–115

Sturm M, Holmgren J, McFadden J P, Liston G E, Chapin III F S and Racine C H 2001 Snow–shrub interactions in Arctic tundra: a hypothesis with climatic implications J. Clim. 14 336–44

Su Y-S and Yajima M 2015 R2jags (available at: www.rdocumentation.org/packages/R2jags)

Sundqvist M K, Giesler R, Graae B J, Wallander H, Fogelberg E and Wardle D A 2011 Interactive effects of vegetation type and elevation on aboveground and belowground properties in a subarctic tundra Oikos 120 128–42

Tape K, Sturm M and Racine C 2006 The evidence for shrub expansion in Northern Alaska and the Pan-Arctic Glob. Change Biol. 12 686–702

Thomas H J et al 2019 Traditional plant functional groups explain variation in economic but not size-related traits across the tundra biome Glob. Ecol. Biogeogr. 28 78–95

Tucker C M, Davies T J, Cadotte M W and Pearse W D 2018 On the relationship between phylogenetic diversity and trait diversity Ecology 99 1473–9

Van Der Plas F, Schröder-Georgi T and Weigelt A et al 2020 Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning Nat. Ecol. Evol. 4 1602–11

Vilma T et al 2016 The atmospheric role in the Arctic water cycle: a review on processes, past and future changes, and their impacts J. Geophys. Res. Biogeosci. 121 586–620

Vowles T and Björk R G 2019 Implications of evergreen shrub expansion in the Arctic J. Ecol. 107 650–5

Vowles T, Gunnarsson B, Molau U, Hickler T, Klemmedtsson L and Björk R G 2017 Expansion of deciduous tall shrubs but not evergreen dwarf shrubs inhibited by reindeer in Scandes mountain range J. Ecol. 105 1547–61

Wahren C-H, Camac J, Jarrad F C, Williams R, Papst W and Hoffmann A 2013 Experimental warming and long-term vegetation dynamics in an alpine heathland Aust. J. Bot. 61 36–51

Walker M D et al 2006 Plant community responses to experimental warming across the tundra biome Proc. Natl Acad. Sci. 103 1342–6

Webb C O, Ackerly D D and Kembel S W 2008 Phylocom: software for the analysis of phylogenetic community structure and trait evolution Bioinformatics 24 2998–3000

Webb C O, Ackerly D D, McPeek M A and Donoghue M J 2002 Phylogenies and community ecology Annu. Rev. Ecol. Syst. 33 475–505

Winkler D E, Amagai Y, Huxman T E, Kaneko M and Kudo G 2016 Seasonal dry-down rates and high stress tolerance promote bamboo invasion above and below treeline Plant Ecol. 217 1219–34