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Supplementary material for this article is available [online](#)

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 *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 (Sturm *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.

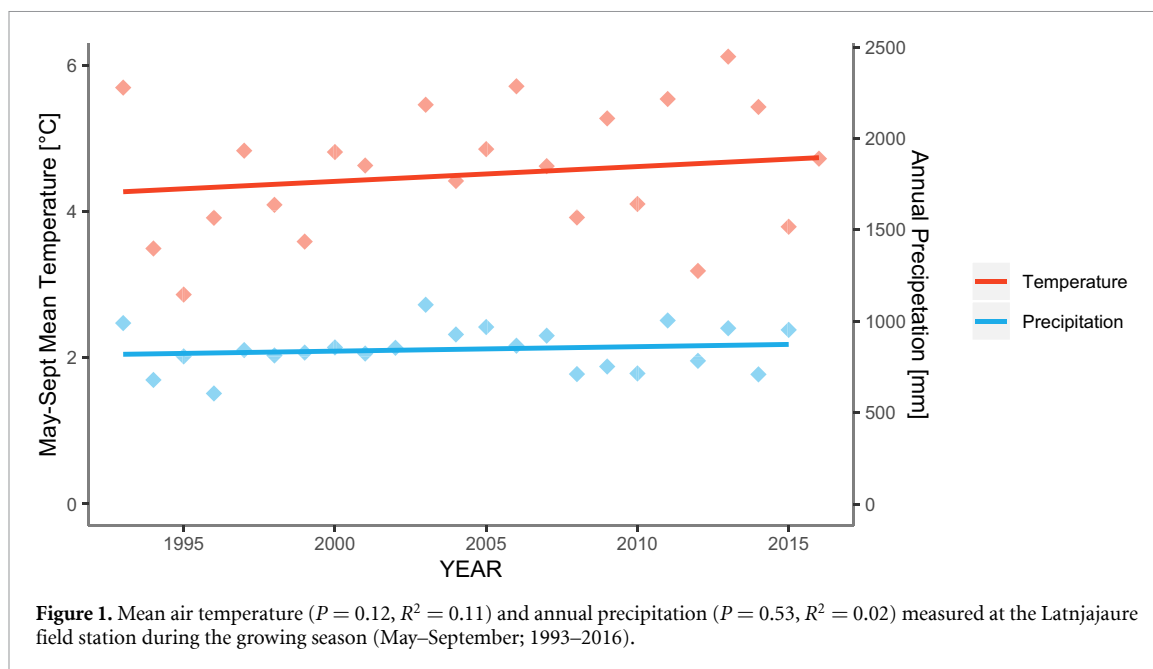
In current studies of functional diversity there is still considerable residual variation, both in the degree that functional traits explain underlying ecosystem functions of interest (Diaz *et al* 2016, Remy *et al* 2019, Van Der Plas *et al* 2020), and in observed variation in functional trait and 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

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
<i>Cassiope tetragona</i>	<i>Eriophorum vaginatum</i>	<i>Dryas octopetala</i>	<i>Dryas octopetala</i>	<i>Carex bigelowii</i>
<i>Betula nana</i>	<i>Phyllodoce caerulea</i>	<i>Vaccinium vitis idaea</i>	<i>Carex bigelowii</i>	<i>Bistorta vivipara</i>
<i>Salix herbacea</i>	<i>Vaccinium vitis idaea</i>	<i>Festuca ovina</i>	<i>Carex vaginata</i>	<i>Carex lachenalii</i>
<i>Vaccinium vitis idaea</i>	<i>Salix herbacea</i>	<i>Carex bigelowii</i>	<i>Bistorta vivipara</i>	<i>Calamagrostis stricta</i>
<i>Empetrum nigrum</i>	<i>Betula nana</i>	<i>Bistorta vivipara</i>	<i>Vaccinium uliginosum</i>	<i>Poa arctica</i>

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 (Kato 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 1×10^{-7} and 1×10^{-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:

$$bc = bl \times 2(d \times o) \quad (1)$$

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 β 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 ($R^2 = 0.24\text{--}0.34$, $P < 0.05$; table 2). We observed a significant increase in dispersion in phylogenetic β diversity over time in warmed mesic ($F_{2,15} = 4.62$, $P = 0.02$) 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).

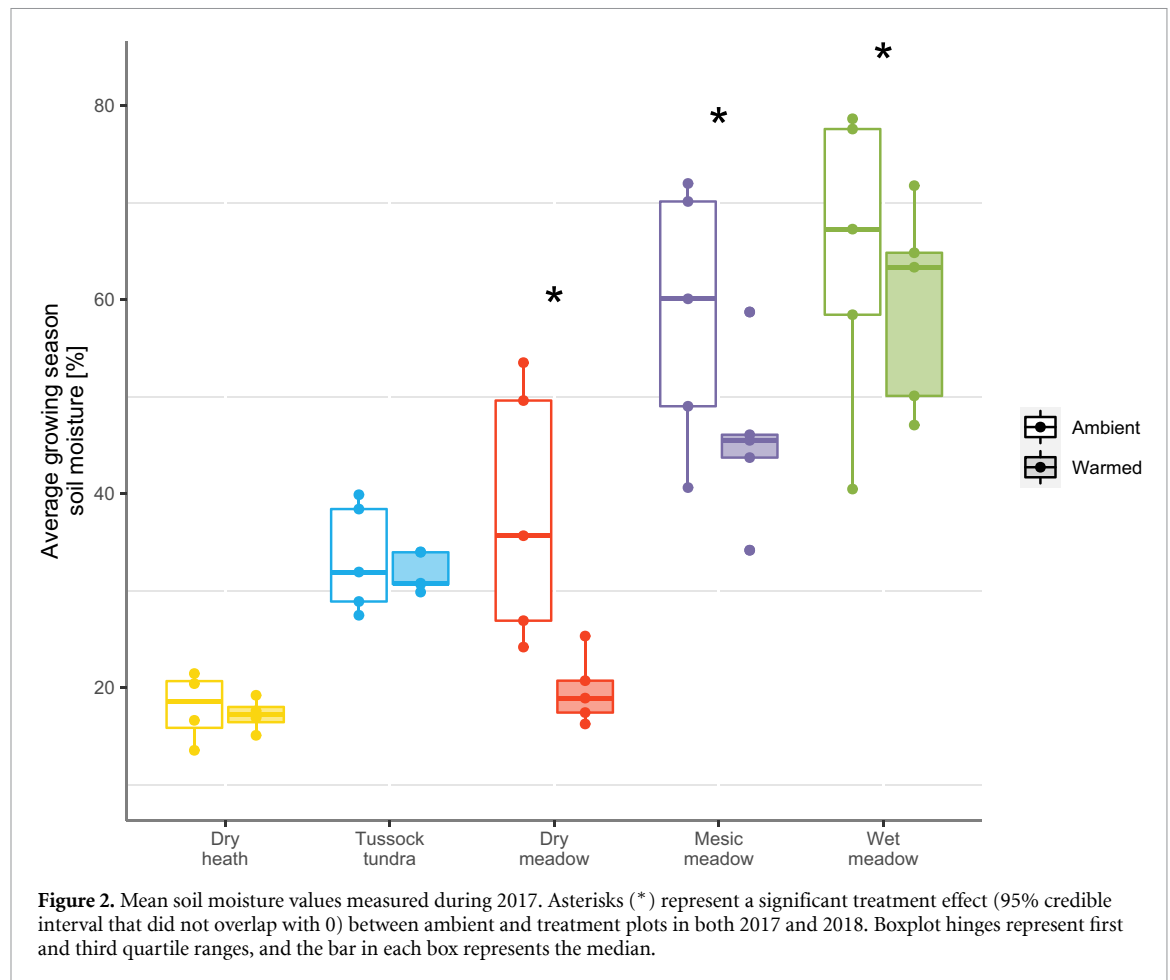


Figure 2. Mean soil moisture values measured during 2017. Asterisks (*) represent a significant treatment effect (95% credible interval that did not overlap with 0) between ambient and treatment plots in both 2017 and 2018. Boxplot hinges represent first and third quartile ranges, and the bar in each box represents the median.

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

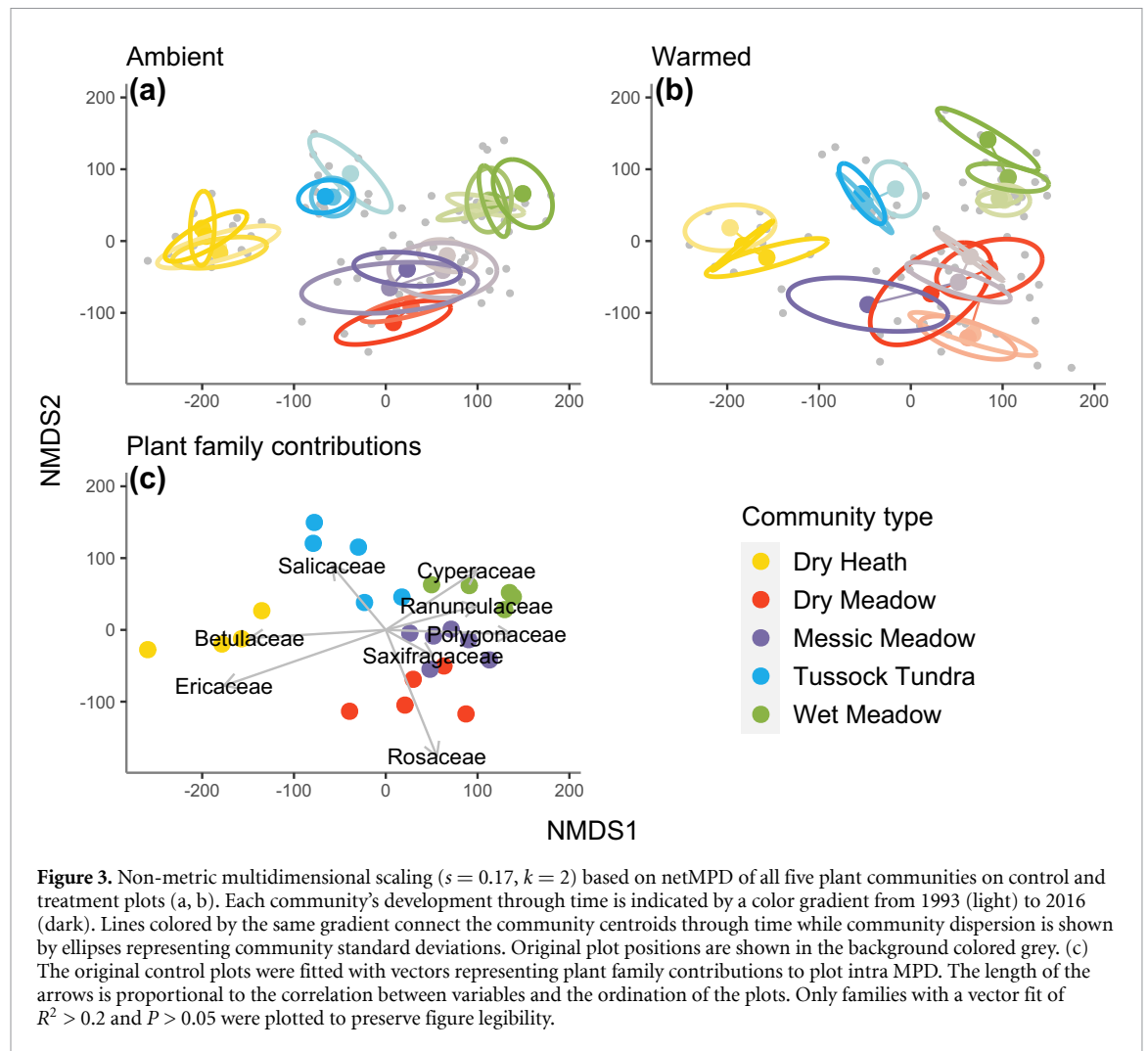


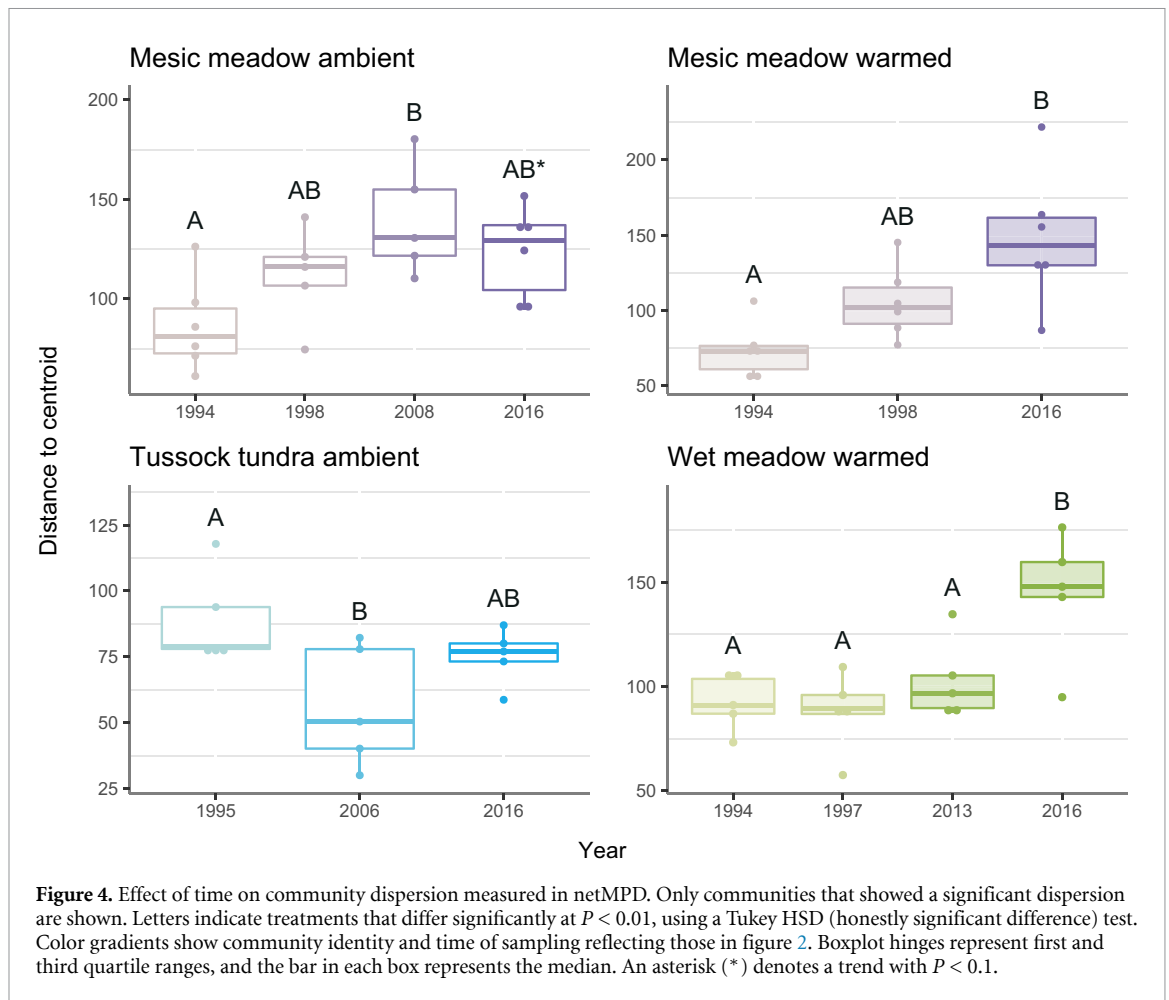
Table 2. Results of PerMANOVA, examining the effect of time in each treatment per community. P values shown are adjusted using Bonferroni correction.

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 phylogenetic β diversity 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



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 snow-melt 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 β 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 β 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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