

Vegetation responses to 26 years of warming at Latnjajaure Field Station, northern Sweden.

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Abstract

Climate change is rapidly warming high latitude and high elevation regions influencing plant community composition. Changes in vegetation composition have motivated the coordination of ecological monitoring networks across the Arctic, including the International Tundra Experiment (ITEX). We have established a long-term passive warming experiment using open-top chambers, which includes five distinct plant communities (Dry Heath; Tussock Tundra; and Dry, Mesic, and Wet Meadow). We have measured changes in plant community composition based on relative abundance differences over 26 years. In addition, relative abundance changes in response to fertilization and warming treatments were analysed based on a 7-year Community-Level Interaction Program (CLIP) experiment. The communities had distinct soil moisture conditions, leading to community specific responses of the plant growth forms (deciduous shrubs, evergreen shrubs, forbs and graminoids). Warming significantly affected growth forms, but the direction of the response was not consistent across the communities. Evidence of shrub expansion was found in nearly all communities, with soil moisture determining whether it was driven by deciduous or evergreen shrubs. Graminoids increased in relative abundance in the Dry Meadow due to warming. Growth form responses to warming are likely mediated by edaphic characteristics of the communities and their interactions with climate.

Keywords:

International Tundra Experiment (ITEX), Climate Warming, Arctic, Vegetation, Latnjajaure

Introduction

Climate change is causing drastic changes to the world's biomes, typically associated with rising global air temperatures. This is especially pronounced in the Arctic and high altitude environments where the temperature has been rising at approximately twice the rate of the global average (Meredith et al. 2019). One of the most noticeable effects is the alteration of plant community composition (Pearson et al. 2013). Changes in tundra plant abundance and diversity can have a variety of consequences at both local and global scales. Among other things, the identity and

abundance of the local plant species determine litter decomposability and palatability, which can affect nutrient cycles and local food webs (Christiansen et al. 2018; Sarneel et al. 2020). At a global scale, the increase towards taller, more productive vegetation in the tundra can affect climate through its effect on carbon storage and surface albedo (Myers-Smith et al. 2011; Post et al. 2019). Investigating the effects of warming due to climate change on this particularly sensitive biome was one of the primary motivations for the founding of the International Tundra Experiment (ITEX).

By utilizing a set of standardized methods and protocols (Henry and Molau 1997), the data from all of the participating ITEX field sites have been directly comparable which has led to multiple circumpolar synthesis studies (Walker et al. 2006; Elmendorf et al. 2012a, 2012b, 2015). These studies revealed biome wide responses such as increases in plant height and the abundance of taller growth forms, such as shrubs, at the cost of prostrate growth forms such as lichen and bryophytes. The results highlight that long-term ecological studies are necessary to demonstrate the impacts of both ambient and experimental warming and to separate treatment impacts from annual variability. Such syntheses perform better when investigating complex processes over timescales that are relevant to climate issues and predicting future changes (Lindenmayer et al. 2012). However, the results of the syntheses have also demonstrated large variations in the responses of individual study sites to the passive warming treatment. Comprehensive analysis of individual site responses should provide a more detailed understanding of how warming affects vegetation (Bjorkman et al. 2020). Local-scale warming studies are commonly used for climate change research; however, ITEX sites have a unique value in that they have been applying the same warming treatment for over 20 years, which promotes better understanding of long-term responses. Analysis of the long-term ITEX datasets at the local scale allows for a more complete understanding of specific vegetation community responses to climate warming.

The Latnjajaure Field Station (LFS) has been included in several circumpolar syntheses (e.g., Welker et al. 1997; Walker et al. 2006; Elmendorf et al. 2012a, 2012b, 2015); however, the full set of abundance data has not been analyzed at the local scale. In this paper, we address the effects of passive warming on local patterns in plant community structure over a 26-year period. In addition, we also determine the impact of nutrient addition along with passive warming on these communities through a reanalysis of data collected from 1995-2001 during the Community Level Interaction Program (CLIP) (Molau and Alatalo, 1998; Alatalo *et al.*, 2014, 2015; Little *et al.*,

2015; Alatalo *et al.*, 2015). The reanalysis allowed us to directly compare both of the long-term warming studies within the Latnjavagge basin by putting them into the same categorical framework. Lastly, we utilized remote sensing data to model the extent of the plant communities to visualize their abundance in a wider regional context.

Methods

General site description

History

In Saami, the word Latnja means a room or a widening, which certainly applies to the valley of Latnjajaure. LFS was established 1965 as a project from the Department of Limnology at Uppsala University. It was headed by Arnold Nauwerck, whose general idea was to investigate the lake in all aspects (physics, chemistry, biology; see Nauwerck, 1967), and later, in phase 2 of the project, introduce fish (arctic char) in the hitherto fish-empty lake. Phase 2, however, never happened, as the PI left for Austria to be the head of the Mondsee Limnology Institute. Subsequently, LFS was virtually mothballed for many years, with basic management from the Abisko Research Station (ANS). Some scientific efforts were made during these years, notably the ^{14}C dating of lake bottom sediments, which provided the first records of biological life in the valley, dating back to 8200 BP (Jonasson 1991).

In August 1989, Ulf Molau visited LFS for the first time, supported by the former director of ANS, Mats Sonesson. Molau found it to be an appropriate site for his studies in the reproductive ecology of alpine plants. He also initiated the ITEX monitoring at the site, as well as several other international projects, e.g., GLORIA.

Landscape

Latnjavagge is a periglacial drainage basin representative of mountainous tundra environments in northernmost Swedish Lapland (68.35 °N, 18.49 °E). The full basin is approximately 9 km², with the valley floor at approximately 950 m a.s.l and peaks as high as 1440 m. The bedrock is primarily composed of Cambro–Silurian mica-garnet schists with inclusions of marble and outcrops of

dolomite (Kulling 1964). Intrusions of acidic granites do occur but are restricted to the plateau in the northern part of the valley. The slope to the east of the valley is predominantly limestone, whereas the slope to the west is a glacial end moraine of acidic material. The regolith thickness rarely exceeds two meters, but increases towards the basin outlet into a larger valley system (Kårsavagge). Deglaciation occurred approximately 8000–10,000 yr BP (André 1995), with little postglacial modification due to the stable vegetation and moderate topography (Beylich and Laute 2018).

Climate

Since 1992, climate variables have been recorded year-round at LFS, including air and soil temperatures, precipitation, relative humidity, global radiation, wind speed and direction, etc., according to the ITEX Manual (Molau and Mølgaard 1996). To investigate temperature and precipitation trends in Latnjajaure, we analyzed the data for LFS (1992-2019) using a Bayesian approach (Supplementary Fig. S1). Due to the sometimes harsh conditions at LFS and issues with maintaining continuous measurements at remote locations, missing periods in the data record have been filled in with modeled data, by first establishing monthly lapse rates between existing data at LFS and the monitoring data at Abisko Scientific Research Station (Callaghan *et al.*, 2010, *data available from the Swedish Polar Research Secretariat*). Missing data at LFS were then gap filled using the given lapse rates on the Abisko data series. For precipitation analysis, we used data from the Katterjåkk meteorological station (*available at www.smhi.se*), where we have found a good correlation between daily manual measurements at LFS and Katterjåkk.

The long-term Mean Annual Air Temperature (MAAT) for LFS is -1.7°C , with February as the coldest month (average -9.7°C) and July as the warmest (average 8.6°C) months, with a low but significant increase of 0.3°C per decade (Fig. S1). Due to some colder years in 2011 and 2012, this trend is lower than the earlier estimate by Björk *et al.*, (2007). Warm periods have also been shown in a century long air temperature record from Abisko, with an earlier period during the 1930's and 1940's that was followed by a colder period until the 1970's (Callaghan *et al.* 2010). Since the mid 1970's the mean annual temperatures have exceeded the earlier warm ing period. The LFS mean growing season (May-August) and non-growing season (September-April) temperatures also show increasing trends, both with a mean increase of 0.2°C per decade, but these trends are not

statistically significant. Annual precipitation ranges from 600 to 1100 mm, with an average of 855 mm, with no discernible trends over the investigated period, and thus higher than what is recorded in Abisko which is situated in the rain shadow during westerly air flows (Callaghan et al. 2010).

Soils

The soil at LFS is pergelic cryorthent (regosolic turbic cryosol) developed from a mica-garnet schist parent material (see Marion *et al.*, 1997 for a summary of the soil from 2.5-72.5 cm depth). This single categorization may not represent the whole basin or its current conditions as the different plant communities influence soil formation, and the permafrost has disappeared from this area in the last twenty years (Beylich et al. 2003, 2004). More in-depth soil profiles should be undertaken at the different communities to develop a clearer picture of the spatial heterogeneity.

The dominant communities are differentiated based on soil characteristics, predominantly pH and moisture. Extensive chemical analyses, emphasizing nitrogen processes, have been conducted on both organic and mineral soils in the dominant plant communities and two snowbed communities (Björk et al. 2007a). Net N mineralization and C/N ratio distinguish the meadow and heath communities, where mineralization was higher in the meadow than in the heath. N mineralization rates were negatively correlated with organic soil C/N ratio, while positively correlated with organic soil pH.

Plant communities

At LFS, we have included five plant community types for ITEX monitoring: Dry Heath (HD), Dry Meadow (MD), Mesic Meadow (MM), Wet Meadow (MW), and Tussock Tundra (TT; See Fig. S2, for a visual representation of all communities). These communities are differentiated mainly based on dominant plant species, soil pH and moisture content, as summarized in Table S1 and S2.

The three meadow communities, Dry, Mesic, and Wet, are differentiated from each other based on their growing season soil moisture content, resulting from variation in the thickness of winter snow cover and influence of surface melt-water percolation. All the meadow communities have relatively basic and nutrient-rich soil, owing to the calcareous bedrock found below (Molau and Alatao 1998). In the MW site, the vegetation has a high ground cover and increased dominance of forbs and grasses relative to the drier conditions of the MD site. Across the three communities,

graminoids (mainly sedges) become more dominant with increasing soil moisture. In contrast, evergreen prostrate dwarf shrubs such as *Dryas octopetala* and *Empetrum nigrum* are more prevalent in the lower moisture range.

The HD site is found on acidic (siliceous) glacial moraine ridges and flats. The vegetation cover is sparse and characterized by species adapted to nutrient poor dry soils such as *E. nigrum*, *Diapensia lapponica*, *Cassiope tetragona* and *Kalmia procumbens*.

Like the HD site, the TT site has a more siliceous bedrock, making the soil slightly acidic. Stands of the TT community occur on water-soaked mineral soil (Molau 2010). TT communities are also usually associated with permafrost; however, the permafrost near Latnjajaure disappeared during the first decade of the study (Beylich et al. 2003, 2004; Molau 2010). Over the 26-year duration of the experiments, a substantial increase (79-92%) in biomass has been observed, mainly due to the expansion of evergreen shrubs (*E. nigrum*, *Vaccinium vitis-idaea* & *Phyllodoce caerulea*) (Molau 2010). The dominant species *Eriophorum vaginatum* has declined in cover by 6-15%, leading to increased local species diversity (Molau 2010). This observation is consistent with the pattern of increased shrub expansion found in the low arctic (Myers-Smith et al. 2011; Elmendorf et al. 2012a, 2012b) and was likely driven by the disappearance of underlying permafrost, as suggested by the similarity in responses between warmed and control plots for this plant community (Molau 2010).

We also conducted a separate analysis of local plant community changes in the long-term CLIP experiment that also applied nutrients in addition to passive warming. The CLIP experiment utilized two additional locations, separate from the ITEX plots, within the Latnjavagge basin that also have been included in pan-Arctic syntheses (e.g., Elmendorf et al. 2012a, 2012b). These experiments were focused on the HD and MM plant communities. Various names have been used for both the CLIP and the ITEX communities throughout time (see summary in Sarneel et al. 2020), and the CLIP communities will here (and recommended for future work) be referred to as “Poor Heath (HP)” and “Rich Meadow (MR)” to avoid confusion.

Mapping

Vegetation maps are essential for monitoring plant diversity over time and larger areas. Maps with varying spatial resolution and thematic classes exist for Latnjajaure. The most relevant maps are a) Lindblad et al. (2006); b) the Mountain Vegetation Map (Rafstedt et al. 1985); c) the National Landcover Data (NMD; Naturvårdsverket 2019); and d) the Swedish Landcover Data (SMD; Naturvårdsverket 2014). To date, Lindblad et al.'s (2006) map is the most comprehensive representation of the area with 14 thematic classes, and utilizes both color-infrared aerial photographs and field-inventoried data. The Mountain Vegetation Map, however, uses 10 thematic classes and provides a picture of the more recent history of the vegetation in the area giving insight into how the valley has changed in the last several decades. It also covers the full Scandic Mountain Range; it was created by manual photo-interpretation of stereo aerial photographs, as was Lindblad et al.'s (2006) map. The National and Swedish Landcover Data maps reduce the area into four basic thematic classes (Forest, Open Land, Water, and Rock), which are not detailed enough to be used in an ecological context.

Thematically detailed maps from satellite data can be achieved when field inventory data and advanced image processing techniques are used. For this paper, we created a new satellite-based vegetation map over Latnjajaure and its surroundings (Fig. 1; Table S3) using five multi-temporal Sentinel-2 satellite images (Copernicus Sentinel data, 2018, 2019, 2020) from early July to early August of 2018 to 2020, a digital elevation model (2 m grid cell size, Lantmäteriet, 2015), a color-infrared orthophoto from 2018 (0.5 m grid cell size, Lantmäteriet, 2018) (Fig. S3) and field inventory data in a machine learning Random Forest classification. Manual identification of Tussock tundra and Wet patterned heath classes could be done from the orthophotos, but not by automated classification. For all other classes, a supervised Random Forest classification (Breiman, 2001) was applied, using the randomForest Package (Liaw and Wiener, 2002) in R software (R Core Team, 2019). The resulting map has 17 thematic classes which follow the definitions in Lindblad et al. (2006), Rafstedt et al. (1985), and Reese et al. (2014), with plant community abbreviations taken from the present study as well as Lindblad et al. (2006) in parentheses. Grass Heath (HG), Fellfields (FF), Extremely Dry Heath (included here in HD), Dry Heath (HD), Mesic Heath (HM), Mesic Meadow (MM), Tall Mesic Meadow (RP in Lindblad et al. 2006), Wet Meadow/Fen (MW/Fen), Tussock Tundra (TT), Wet Patterned Heath (HWP),

Willow, Wetland, Snowbed (HSS), Intermittent Snow, Persistent Snow, Rock/Stone (HB and R/S), and Water.

Experimental design

Open-top chambers were established at the five ITEX monitoring plant communities at LFS between 1993 and 1994. These open-top chambers have been reported to warm the soil surface and surrounding air temperature (up to a height of 15 cm) by 0.6 and 1.6 °C (respectively) compared to ambient conditions (Molau and Mølgaard 1996; Marion et al. 1997). The warming setup has five replicates within each of the five ITEX communities ($N = 50$, $n_{\text{warming}} = 25$, $n_{\text{control}} = 25$).

A similar setup was used for the CLIP experiment run between 1995-2001. The full methods are described in Molau and Alatalo (1998). Briefly, in addition to the warming, a fertilization treatment and a combination of the two was applied. For the fertilization, 5 g N (as NH_4NO_3) and 5 g P (as P_2O_5) m^{-2} were dissolved in 10 L water and applied annually. Within each plant community there were four plots per treatment and eight control plots ($N = 40$, $n_{\text{warming}} = 8$, $n_{\text{fertilization}} = 8$, $n_{\text{warming} + \text{fertilization}} = 8$, $n_{\text{control}} = 16$). In addition to vascular plant monitoring, the CLIP experiment also included species-level data on lichen and bryophyte abundance (Molau and Alatalo 1998; Jägerbrand et al. 2003, 2006, 2009, 2012; Alatalo et al. 2017).

Data collection

A standardized 1 m^2 point-frame method was used to monitor species-level abundance, according to Molau and Mølgaard (1996), with three to five measurements between 1994 and 2016 varying between communities (Table S5, github link to data repository to be added). The first plant abundance measurements were taken 1 year after the establishment of the OTCs.

Statistical analysis

We conducted all analyses using the R programming language (version 4.0.0 Arbor Day, R Core Team 2020). Packages used during analyses included, *tidyr* (v1.1.0; Wickham and Henry 2020), *ggplot2* (v3.3.2; Wickham 2016), *ggordiplots* (v0.3.0; Quensen 2018), *ggnewscale* (v0.4.1; Campitelli 2020), *vegan* (v2.5-6; Oksanen et al. 2019), *rjags* (v4-10; Plummer 2016), and *R2jags*

(v0.6-1; Su and Yajima 2015). The full reproducible codes are available in Supplementary Materials.

To evaluate local changes for all communities, we assessed the effect of time and warming over the 26-year duration of the experiments using the relative abundance of the growth forms (Molau 2010; Elmendorf et al. 2012a, 2012b; Graminoid, Forb, Evergreen Shrub, Deciduous Shrub in the canopy layer and Bryophyte and Lichen in the bottom layer).

To estimate the temporal response of each growth form within each community to treatment, we used a generalizable Bayesian modelling approach. The temporal response model included relative growth form abundance as a dependent variable and Community, Treatment, Growth Form, Year (Continuous) and their interactions as fixed effects.

Community-level slopes were used to fit an average trend of the plant functional relative abundance values over time, with Y representing calendar year as a linear predictor.

$$\begin{aligned}
 RA_{discrete} &\sim \text{bernoulli}(\mu_{c,t,g,y} + \alpha_p) \\
 RA_{continuous} &\sim \text{beta}(\mu_{c,t,g,y} + \alpha_p\phi, 1 - \mu_{c,t,g,y} + \alpha_p\phi) \\
 \mu_{c,t,g,y} &\sim \text{normal}(\alpha_{c,t,g} + \beta_{c,t,g}Y_y, \sigma_0)
 \end{aligned}$$

Where $RA_{discrete}$ = relative abundance of the discrete portion of the dataset, $RA_{continuous}$ = relative abundance of the continuous portion of the dataset, $\mu_{c,t,g,y}$ = mean value for each community, treatment, growth form and year, $\alpha_{c,t,g}$ = intercept value for a specific community, treatment and growth form, $\beta_{c,t,g}$ = slope value for a specific community, treatment, and growth form, α_p = plot level random effect, ϕ = variance parameter of beta distribution, and σ = variance parameter of normal distribution. This will be referred to as model 1 in the below results.

To determine the effect of passive warming itself on the communities we also estimated the yearly treatment effect of OTC's on each growth form across all communities using a factorial Bayesian model. The factorial model included the same variables as the temporal response model, except that Year was a factor. The factorial model differed from the model 1 equation in that:

$$\mu_{c,t,g,y} \sim \text{normal}(\alpha_{c,t,g,y}, \sigma_0)$$

This will be referred to as model 2 in the below results.

All Bayesian models utilized MCMC with two chains each consisting of 30,000 iterations of which the first 20,000 were discarded as burn-in. We define a “significant” treatment response as a slope difference between control and treated plots that do not overlap with 0 in its 95% credible interval. A difference in yearly treatment effect is significant when the 95% credible interval of the difference in community means does not overlap with 0. We define a “significant” temporal response as a slope coefficient that does not overlap with 0 in its 95% credible interval. As relative abundance is proportional data (bounded by 0 and 1), we used beta-Bernoulli mixed models with mixing occurring at the Community x Growth Form effect. We first estimated the effect of the Community x Treatment x Growth form interaction by year to account for the non-independence of observations within the same year. The models also included Plot as a random effect to account for non-independence of plants measured within the same plot, and the same plot measured over time. We used non-informative priors for all coefficients and checked for convergence of chains for all parameters using the Gelman–Rubin convergence statistic (Gelman et al. 1992).

Results

ITEX warming

In the ITEX experiment, we investigated the effect of passive warming on plant relative abundance through time in the five plant communities. In general, results from analyses of the growth form response over time evaluated by model 1 (Fig. 2-3) matched those of the yearly treatment effect evaluated by model 2 (Fig. S4). In both analyses, there was a significant effect of warming on individual plant growth forms in several communities; however, no growth forms responded consistently across community types (Fig. 2; Fig. S4). In the MD site, graminoid relative abundance increased together with evergreen shrubs showing an increasing trend. Both forbs and deciduous shrubs decreased. Within the HD site, deciduous shrubs had a decreasing trend, while evergreen shrubs had an increasing trend. Graminoids showed a high level of variability, while forbs could not be modeled due to low abundance. In the MW site, deciduous shrubs increased while graminoids and forbs showed a decreasing trend. Evergreen shrubs were unable to be

modeled due to low abundance. In contrast, there was no warming effect in the MM or TT site; however, there was a time effect where graminoids decreased, and evergreen shrubs increased, while deciduous shrubs had an increasing trend.

In two cases, the treatment response (model 1) and yearly treatment effects (model 2) did not agree due to the die-off of one growth form in one of the plot types (OTC or control). In both cases, the absence led to convergence issues in the linear models. In the HD site, forbs were lost from the OTCs, and in the MW site the evergreen shrubs were absent from the control plots resulting in a significant yearly treatment effect in both cases. In the MD site, forbs responded significantly to the treatment as shown by the inverse slopes of the OTC and control plots, but did not have significantly different yearly effects (Fig. 4).

To evaluate ambient changes over time, we considered the control and warming treatments separately (Fig. 3). Interestingly, the control rather than the warmed plots drove the response in the HD site, where evergreen shrubs increased while deciduous shrubs decreased over time.

CLIP warming and fertilization

In the CLIP experiment, we were interested in the effects of warming, fertilization and their interaction on relative plant abundance over seven years. There was no significant time effect in the controls (Fig. S5); therefore, we only present the treatment effect on plant growth form response (model 1)(Fig. 5). Consistent with our ITEX warming experiment results, there was no community-level response to warming within the seven years. Responses to fertilizer and fertilizer + warming treatment were consistent with one another, indicating that the fertilization treatment drove the main responses. Responses within the MR and HP sites tended to be similar in direction but varied in magnitude resulting in most growth forms failing to pass the set significance threshold in both communities. The overall pattern showed that fertilization resulted in an increased graminoid relative abundance, while deciduous and evergreen shrubs decreased in the canopy layer. The response of deciduous shrubs was strongest in the HP site. Though the responses of evergreen shrubs were non-significant, the direction of the response was consistently negative in both fertilization treatments. There was no discernible pattern in the forbs' response. The abundance of

bryophytes was significantly reduced in both communities in the bottom layer, while lichens declined only in the HP site.

Satellite mapping

The Latnjajaure catchment is approximately 13.1 km² and includes 17 plant communities with the areal coverage for all plant communities given in Table S3. For our ITEX communities, MD and MM were challenging to distinguish in spectral data, and therefore both communities were classified as Mesic Meadow in the vegetation map. The HD and MW communities all separated into distinct categories in the spectral data, while TT was delineated from color-infrared orthophotographs.

The satellite-generated map (Fig. 1; Fig. S3) correctly mapped the plant communities of the ITEX plots in TT, HD and MD (Table 1; Table S4; Fig. S3). However, four ITEX plots within the MM were identified in the satellite-generated map as Wet Meadow and four ITEX plots within the MW were identified in the satellite-generated map as Dry Heath (Table S4; Fig. S3). In these cases, the errors in the satellite map are likely due to scale differences, as the satellite data uses grid cells of 10 – 20 m. The four MW plots mistakenly identified in the satellite map as Dry Heath are located on a narrow strip close to the LFS cabins (red circle in Fig. S3). The four MM plots (blue circles in Fig. S3) that were mistakenly classified as Wet Meadow in the satellite map were located near a plant community transition area, but only two meters from a Mesic Meadow pixel.

Discussion

The long-term warming at the ITEX plots shows that shrub expansion occurs in all communities except for the Dry Meadow; however, the drivers of expansion varied between communities, whether it was time or passive warming. In these communities, the shrubs are likely outcompeting local forbs and graminoids. Furthermore, there is a distinction between the dry (HD, MD), mesic (MM, TT) and wet (WM) communities. In the dry communities, the evergreen species dominate the shrub expansion, while deciduous species primarily drive the wet community's response. The mesic communities show an increased abundance in both groups, suggesting that soil water content regulates the shrub expansion. Evergreen shrubs are particularly sensitive to frost drought, a process where the freezing of moisture in the soil contributes to drought conditions (Kullman

1989). In an arctic landscape, frost drought commonly occurs during spring on wind-blown ridges with a shallow snow cover (such as our HD and MM). Once the protective snow has thawed, intensive solar radiation and great temperature contrasts between day and night, or between days, triggers frost drought events. However, in our warming experiment in the HD and MM sites, the OTCs collect more snow than ambient, which also mimics future mid-winter predictions for northern Scandinavia (Danco et al. 2016). These changes in snow patterns, in association with warming, can result in substantial alterations in plant communities (Leffler et al. 2016). The warming plots may experience less frost drought during spring compared to ambient plots, which could facilitate the expansion of evergreen shrubs in these communities.

Previous syntheses have also found evidence for shrub expansion in subarctic communities, but the dominant drivers differ (Walker et al. 2006; Myers-Smith et al. 2011; Elmendorf et al. 2012a, 2012b). For example, Elmendorf et al. (2012a) found the increase in shrub abundance compared to graminoids to be primarily tied to the ambient summer temperature of a site. At a local scale, we found that shrubs and graminoids respond differently depending on the community, despite experiencing the same ambient temperature. Therefore, it is possible that the differences in plant growth form responses are linked to the soil characteristics in each community, such as soil moisture and nutrient dynamics.

Moisture can be a key factor modulating the response of both evergreen and deciduous shrubs in subarctic communities (Elmendorf et al. 2012a). Our results reflect this pattern as the magnitude and direction of response of deciduous or evergreen shrubs changes between community types that primarily differ by moisture. There is a strong positive response in the MW site for deciduous shrubs, which transitions to a negative response in the MD and HD sites. The opposite trend occurred in the evergreen shrubs; the inability to model their response in the MW due to low abundance suggests that they are not well adapted to that community's conditions. Deciduous shrubs typically have a stronger response to this gradient. There was a significant positive response in the MW site and a negative response in the MD site, while for evergreen shrubs, we only found a significant response in the HD site. The effect of warming on plant growth traits (leaf length, width, and plant height) was less pronounced in both shrub types compared to the abundance data (Baruah et al. 2017). With the exception of the MD, at least one species of each shrub type increased in one plant growth trait when present in a community (Baruah et al. 2017). Positive

growth response due to passive warming does not necessarily contradict any negative abundance changes in the plots over time; however, more in-depth analysis of plant trait data at the ITEX sites over the 26-year warming period, along with consideration of plant abundance and trait metrics together, are needed to determine the complex connections between communities and plant growth forms.

Contrary to our findings, Elmendorf et al. (2012a) identified a larger increase in evergreen shrubs in wet communities than dry. The disparity between our results may be due to the broader range of moisture variation between the circumpolar sites as well as generally much shallower snowpack compared to Latnjavagge (Virtanen et al. 2016); however, the reversing of the trend may indicate an important distinction between local and biome levels in how growth forms respond. Regardless, changes in moisture regime will have a profound effect on the shrub community, influencing the balance of deciduous and evergreen shrubs in the subarctic. These two shrub growth forms have opposing implications for future feedback on the changing climate (Vowles and Björk 2019). In particular, increases in evergreen shrubs are expected to increase soil carbon storage due to the recalcitrance of their litter and associated mycorrhizae (Langley and Hungate 2003; Aerts 2006; Vowles and Björk 2019). Determining the mechanisms driving the shrub response to moisture changes at the local and biome levels is important to understand how tundra communities will be impacted by future changes in precipitation, temperature, permafrost degradation and local hydrological conditions.

Ambient changes over time significantly impacted many of the growth forms across communities, regardless of warming. These changes are especially important for the HD community as the relative abundance of shrub growth forms changed significantly in the ambient but not the warmed plots. The changes in abundance may not have resulted from warming mediating the shrub response directly in this community; rather, the OTCs themselves may have confounding effects on the microclimate of a plot, including altering moisture, herbivory, and wind regimes (Marion et al. 1997; Richardson et al. 2000). However, the disparity between the ambient and warmed plots highlights the drastic changes due to climate change over the 26-year study period. The only community that did not have a significant change in relative abundance of at least one growth form in the ambient plots was the MD, though it did change with the passive warming. Elmendorf et al. (2012b) also found an increase in abundance of evergreen, low and tall shrubs due to ambient

changes in temperature across ITEX sites. However, the increase in evergreen shrubs was not tied directly to summer climate warming, and the different responses of shrub types were dependent on plot moisture. Ambient changes within long-term ecological experiments result in substantial changes in the communities and need to be considered when comparing with passive warming over time.

The passive warming treatments in the CLIP plots did not result in any significant effect in any of the plant growth forms; however, the fertilization and fertilization + warming treatments did have significant effects (Fig. 5). Abiotic environmental variables, especially edaphic properties, can have a substantial impact on plant communities over time (Schimel et al. 2004; Sundqvist et al. 2011). Nutrient addition was the only significant driver of growth form response in the two communities, regardless of warming. The lack of general responses in some growth forms may be due to highly individualistic responses of plant species within each growth form (Hautier et al. 2015; Little et al. 2015; Thomas et al. 2019). Observed responses however tended to be monotonic. There were no clear differences between short- and mid- to long-term responses; instead, the slower responses did not become statistically detectable until later in the study. These results highlight the importance of long-term evaluations of the treatment effects in determining the true trajectory of relationships (Alatalo and Little 2014). The conclusions drawn from the short-term responses did not always match the long-term trends.

ITEX-CLIP comparison

The ITEX and CLIP experiments included the HD and MM community types and studied effects of passive warming on plant community composition with the same type of OTCs. The ITEX experiment ran 19 years longer, thereby giving a more reliable view of long-term ambient and passive warming scenarios. In contrast, the CLIP experiment included fertilization and the bottom layer species (lichens and bryophytes). Comparison and interpretation of the experiments' results provide a more cohesive understanding of relevant environmental changes on community characteristics. Namely, the variation in response of a community type to the treatment, the length of time necessary to observe a response to the treatment across community types, and how the type and number of plant growth forms affect the interpretation of the results.

The HD and MM communities did not respond significantly to the warming treatment in either the ITEX or CLIP experiments. The MW and MD communities did have a significant response, indicating that soil moisture differences may influence the response to the warming treatment. Regardless, none of the ITEX communities responded significantly to passive warming within seven years of treatment. Our results support previous conclusions that long-term monitoring is required to capture community responses to ambient and experimental warming (Lindenmayer et al. 2012; Elmendorf et al. 2015). The CLIP experiment included bryophytes and lichens as bottom layer species in their analyses, which is lacking in ITEX. These non-vascular growth forms did not respond to the warming treatment in the CLIP data presented here. However, longer-term study of the responses of lichens to warming treatments have identified a shift in their relative abundance and species richness (Alatalo et al. 2017). Given the prevalence of bryophytes and lichens in the subarctic tundra and their contributions to soil characteristics and ecosystem processes (Olofsson et al. 2004; Campioli et al. 2009; Stoy et al. 2012; Bueno et al. 2016), future assessments of community dynamics at LFS should include these growth forms.

The communities included in the CLIP experiment had strong responses to the fertilization treatment over the study period. By comparing these results to the ITEX ambient plots, we can infer whether the effects of ambient nutrient deposition can be observed in the long-term community response. Interestingly, graminoid abundance consistently declined in the ITEX communities, whereas the dominant response under fertilization was the opposite. Moreover, the increases in deciduous shrubs in the ITEX MM and HD were also contrary to their CLIP counterparts. Lastly, the evergreen shrubs, which did not change significantly under fertilization, did show an increase and decrease in their ITEX MM and HD counterparts, respectively. The community responses to ambient conditions over the 26 years did not match the suggested outcomes from the fertilization experiment, likely because of the difference in the amount of fertilizer added compared to the expected increase in atmospheric nitrogen deposition due to climate change. We have not measured the natural nitrogen deposition rate for the valley, but it is estimated to be 70 - 120 mg N m⁻² yr⁻¹ for the Arctic as a whole (Hole et al. 2009). Thus, the nitrogen applied was between 41.7 and 71.4 times the natural rate of nitrogen deposition. Potential conclusions are therefore limited in scope due to the excess of nutrients added above predicted

ambient conditions. The CLIP experiment strongly indicates that these communities are nutrient-limited; however, it does not necessarily reflect the most realistic future scenario.

Implications at the catchment level

Overall, the difference in responses suggests that some communities are more sensitive to climate warming than others, which may be related to moisture and nutrient conditions. Variability in these conditions would result in a mosaic pattern based on each community's sensitivity to climate changes at a regional scale. Moisture and nutrient conditions might be especially relevant in alpine regions, which are heterogeneous due to variation in topographic and environmental conditions within a small geographic area (Spasojevic et al. 2013). Because of this heterogeneity in environment and community responses, it would be difficult to determine the vegetative response to climate change across the Arctic without a better understanding of local-scale processes. With the new satellite-based vegetation map of LFS and the greater Latnjavagge, we were able to capture the heterogeneity of the landscape. The map not only illustrates the importance of our focal plant communities within the region but can also be used to disseminate the plot-scale experiment at the catchment level. Dry heaths are among the most dominant plant communities in the catchment and are currently decreasing in relative evergreen shrub abundance while remaining stable in warmed conditions. If similar responses are expected in comparable communities (Extreme Dry Heaths, Grass Heaths, Fellfields and Mesic Heaths), we may have an even stronger impact of the evergreen shrub expansion across the landscape. These heath-like communities, constituting more than $\frac{1}{3}$ of the catchment area, may contribute to increased evergreen shrub abundance on the landscape via their stable growth form composition under warmed conditions. With increasing evergreen shrub abundance in the TT and MM communities, this may indicate an expansion of the heath-like communities in the area, although the TT has a low areal representation. Concurrently, the MW communities are increasing in deciduous shrub abundance, which contributes to shrub expansion in the catchment. This maps level of detail will allow us to monitor future changes in plant community responses and patterns in a meaningful ecological context. Bearing in mind that the Arctic ITEX sites experimentally increase annual mean air temperature with 0.5-2 °C (Bokhorst et al. 2013), these future predictions are in the lower end of future scenarios, RCP 2.6 (Meredith et al. 2019). Thus, we cannot rule out the potential for larger vegetation shifts than observed in our study.

Conclusions

Plant growth forms' response to passive warming is regulated by the local environmental conditions, including soil moisture and nutrients. The investigated communities are primarily distinguished by their edaphic characteristics, suggesting a potential interaction between these characteristics and climate. Moisture, in particular, seems to be an important driver of the shrub response; however, the trend may be affected by the scale at which it is investigated.

Climate highly regulates plant performance, and the variation in the Arctic tundra climate, including relatively regular extreme climatic events, makes determining long-term responses/trends extremely challenging. Longer-term studies are critical for assessing plant community changes as the relationships, both abiotic and biotic, driving the changes are complex and may have associated time lags necessitating a long temporal window for them to be understood.

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Tables

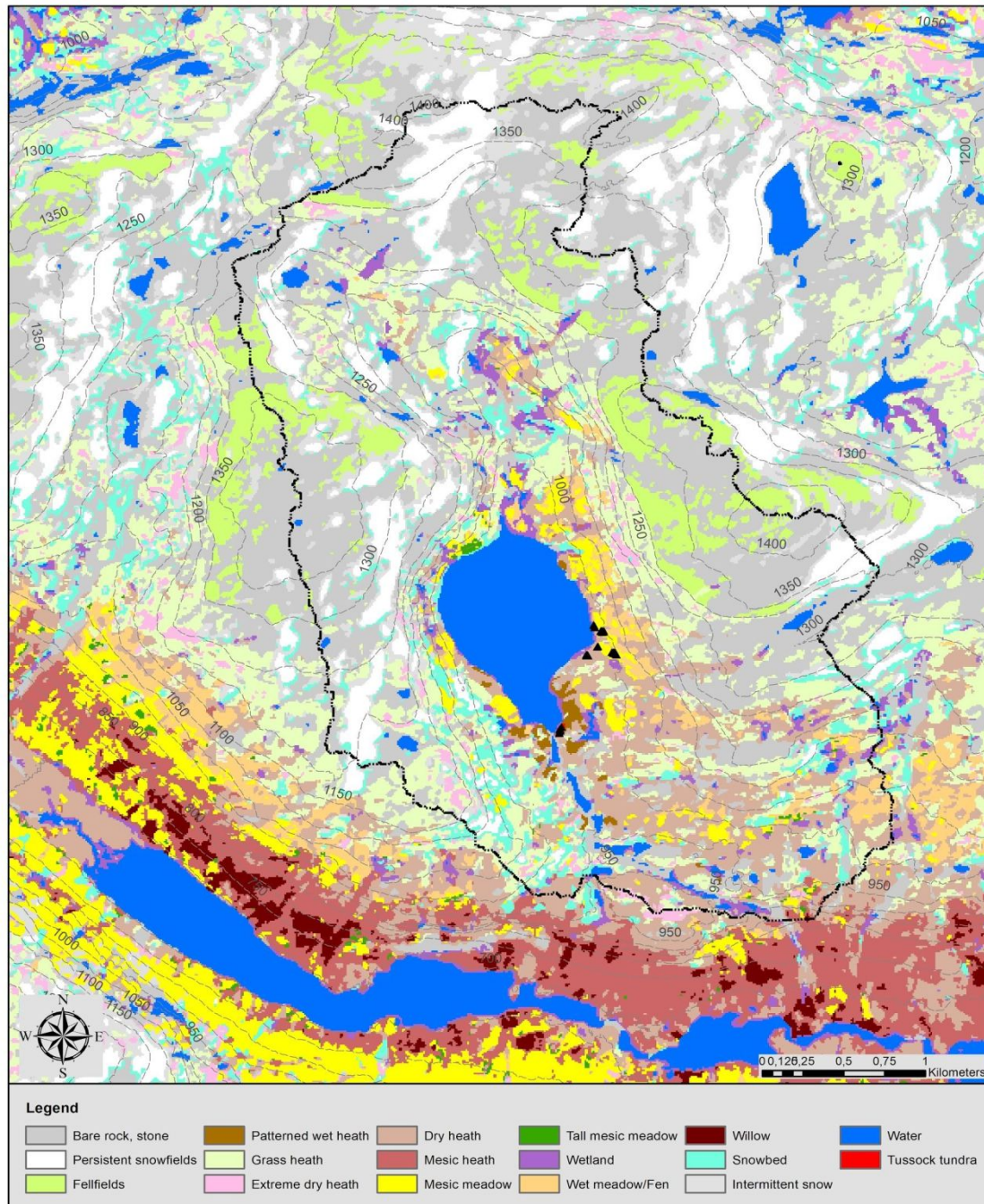
Table 1. Site type association as a percent of the 50 ITEX plots according to their ITEX plant community association, the satellite-generated map, as well as the percent of each class within the 13.1 km² catchment area from satellite-generated map.

Identification method	Dry Meadow	Mesic Meadow	Wet Meadow	Dry Heath	Tussock Tundra
Original ITEX identity	20.0%	20.0%	20.0%	20.0%	20.0%
Satellite-generated map	0.0%*	32.0%*	20.0%	28.0%	20.0%
Percentage within the catchment area	0.0%*	2.4%*	2.8%	11.5%	<0.1%

*There is not a Dry Meadow class in the satellite-generated map. The class Mesic Meadow in the satellite-generated map contains both Dry and Mesic Meadow.

Figures

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Vegetation classification derived from five dates of Sentinel-2 satellite images (Copernicus Sentinel data, 2018, 2019, 2020), a color-infrared orthophoto (Lantmäteriet, 2018), a ground elevation model at 2 m grid cell size (Lantmäteriet, 2015), and field data. The black dashed line indicates the Latnjajaure catchment, gray dashed lines show elevation contours at 50 m intervals (derived from the ground elevation model © Lantmäteriet, 2015), and black triangles show ITEX

experimental sites. Map and catchment layer created by Heather Reese using ESRI ArcMap (<https://desktop.arcgis.com/en/arcmap/>) Version 10.6.0.

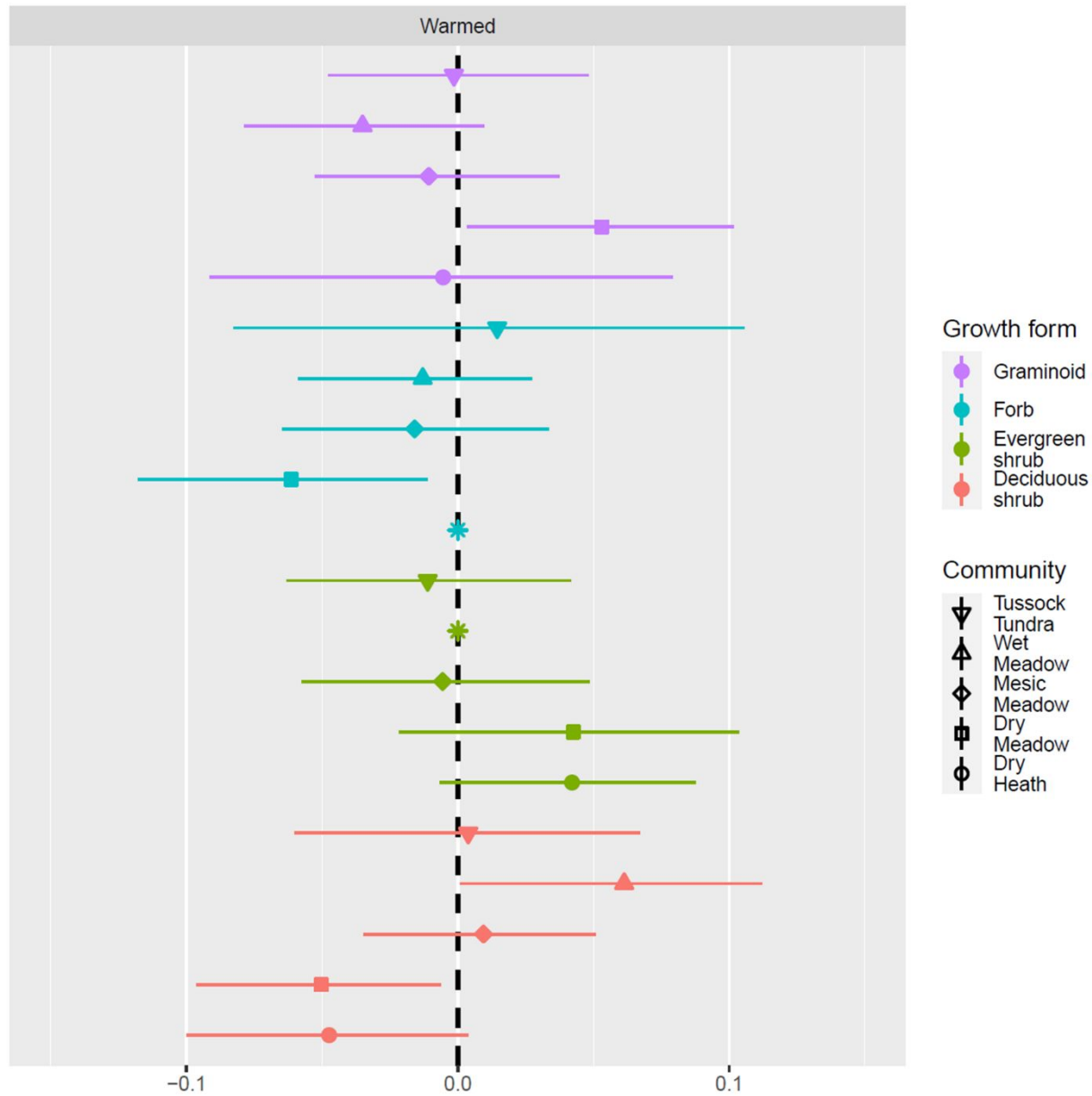


Figure 2. Difference in growth form time sensitivity (slopes) between the control and experimentally warmed treatments within five plant communities evaluated by model 1. Negative values indicate a negative trend relative to the control while positive values indicate the opposite. Growth Form \times Community interactions that did not converge due to zero inflation are marked with *. Coloured points represent the estimated difference time sensitivity (slope) for each Growth Form \times Community interaction, and vertical lines span the 95% credible intervals for each estimate.

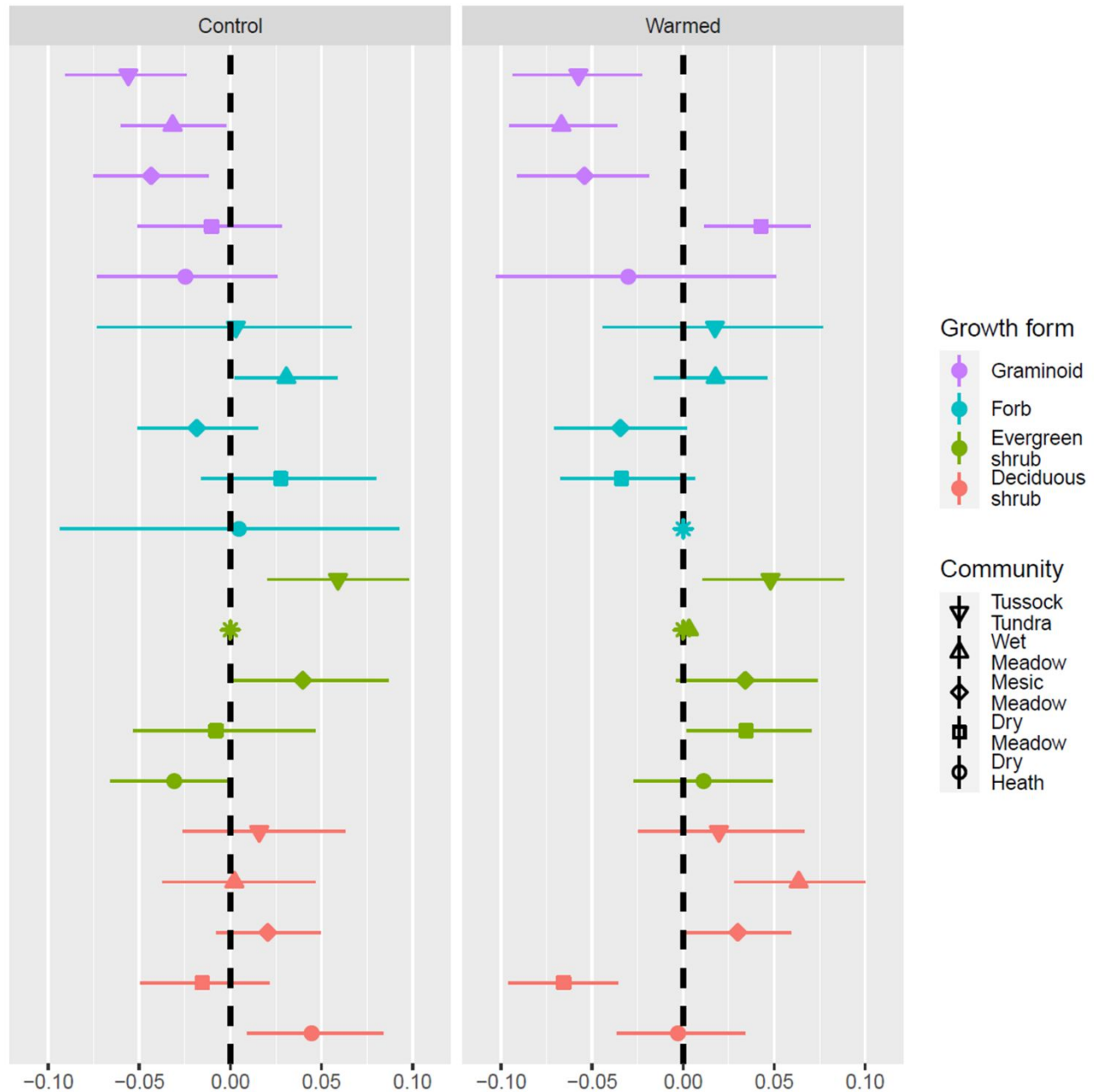


Figure 3. Time sensitivity of plant growth forms between control and warming treatment within five plant communities at Latnjajaure evaluated by model 1. Growth Form × Community interactions that did not converge due to zero inflation are marked with *. Coloured points represent the estimated time sensitivity (slope) for each Growth Form × Community interaction, and vertical lines span the 95% credible intervals for each estimate.

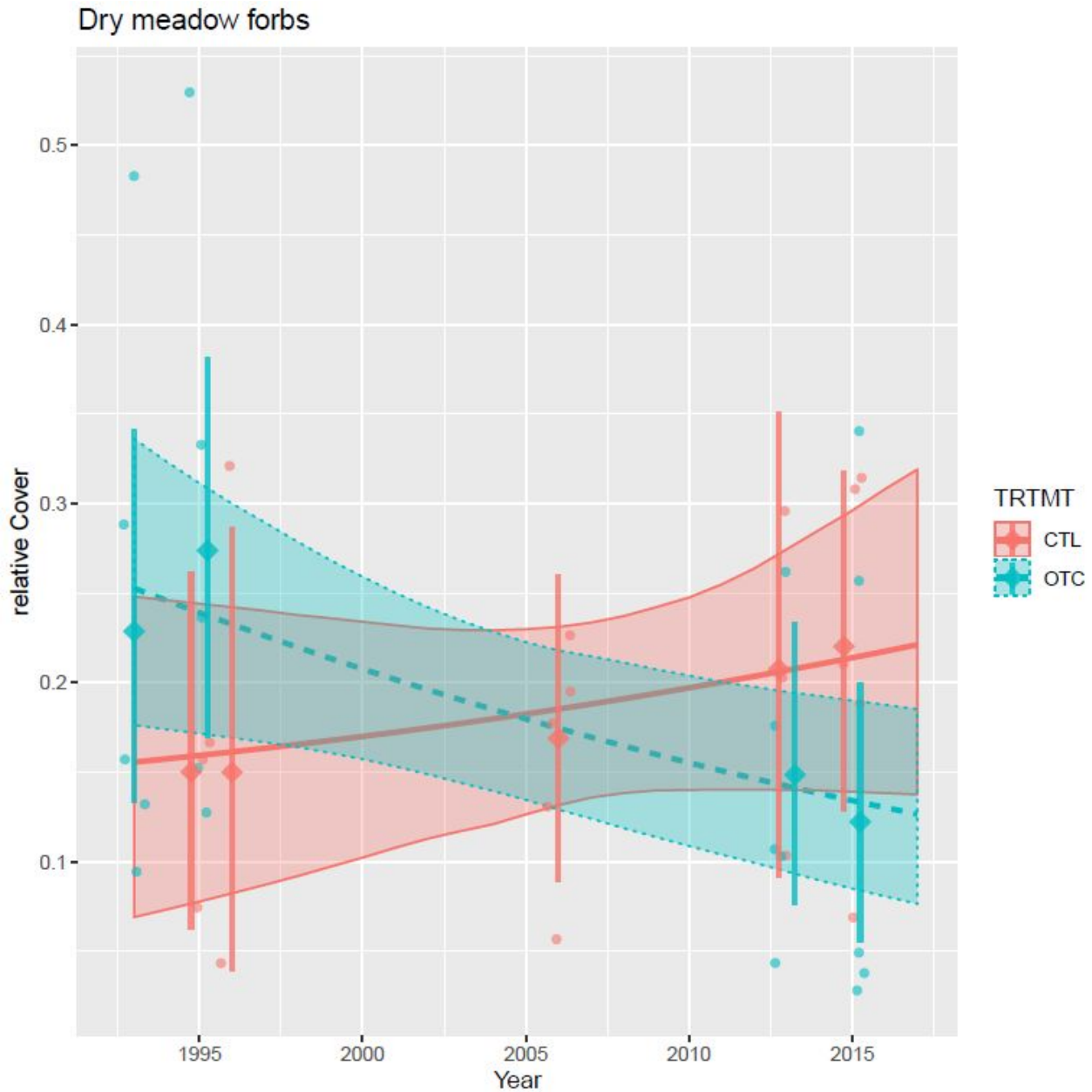


Figure 4. Continuous and factorial model results of relative abundance of forbs in the dry meadow treatment and control plots over the 26 years of study duration. Results of the factorial model in the years of sampling are represented by points with surrounding 95% credible interval, while the lines represent the results of the continuous model. Vertical lines and shaded areas span the 95% credible intervals for the factorial and continuous model, respectively. The points represent the raw values observed in each plot.

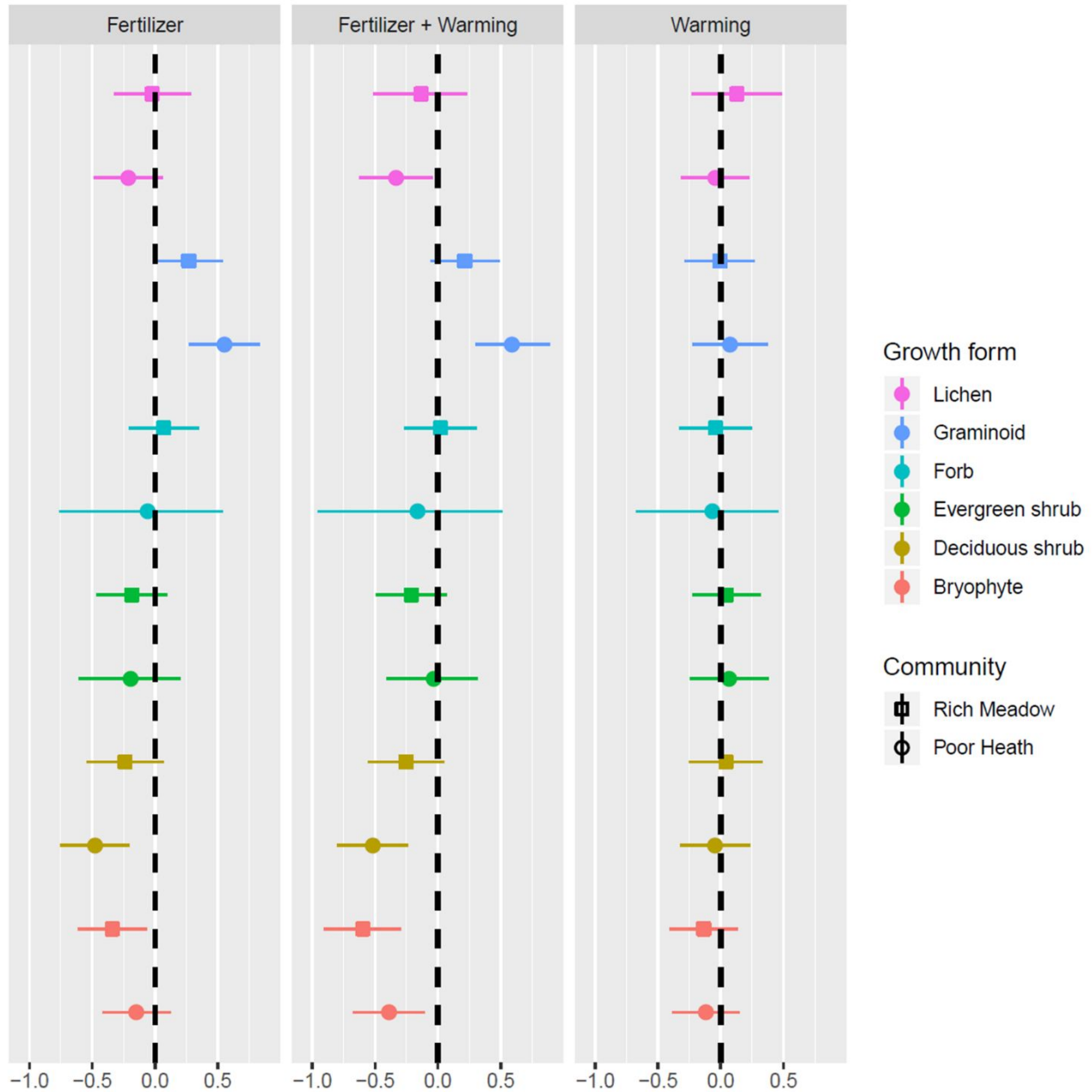
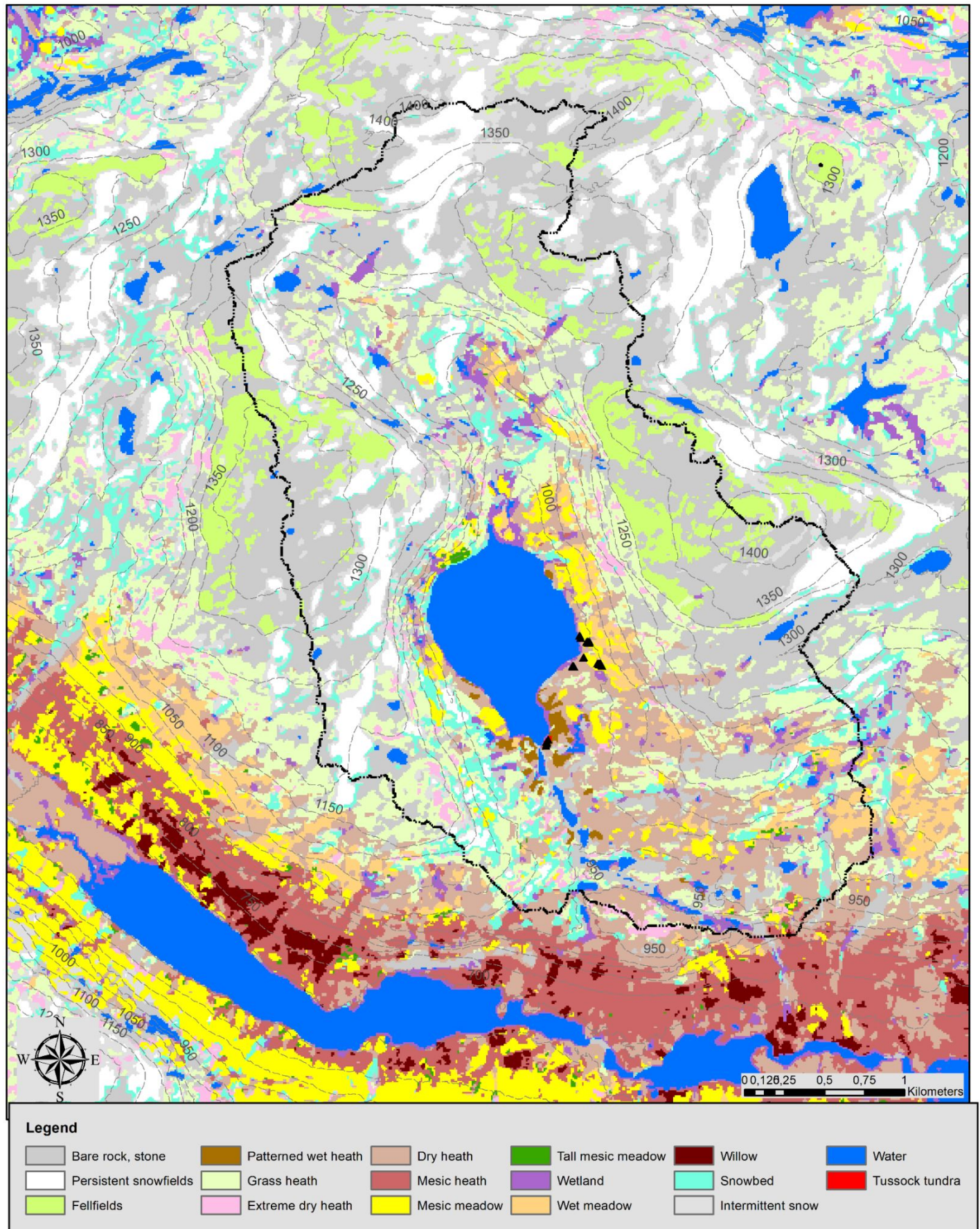


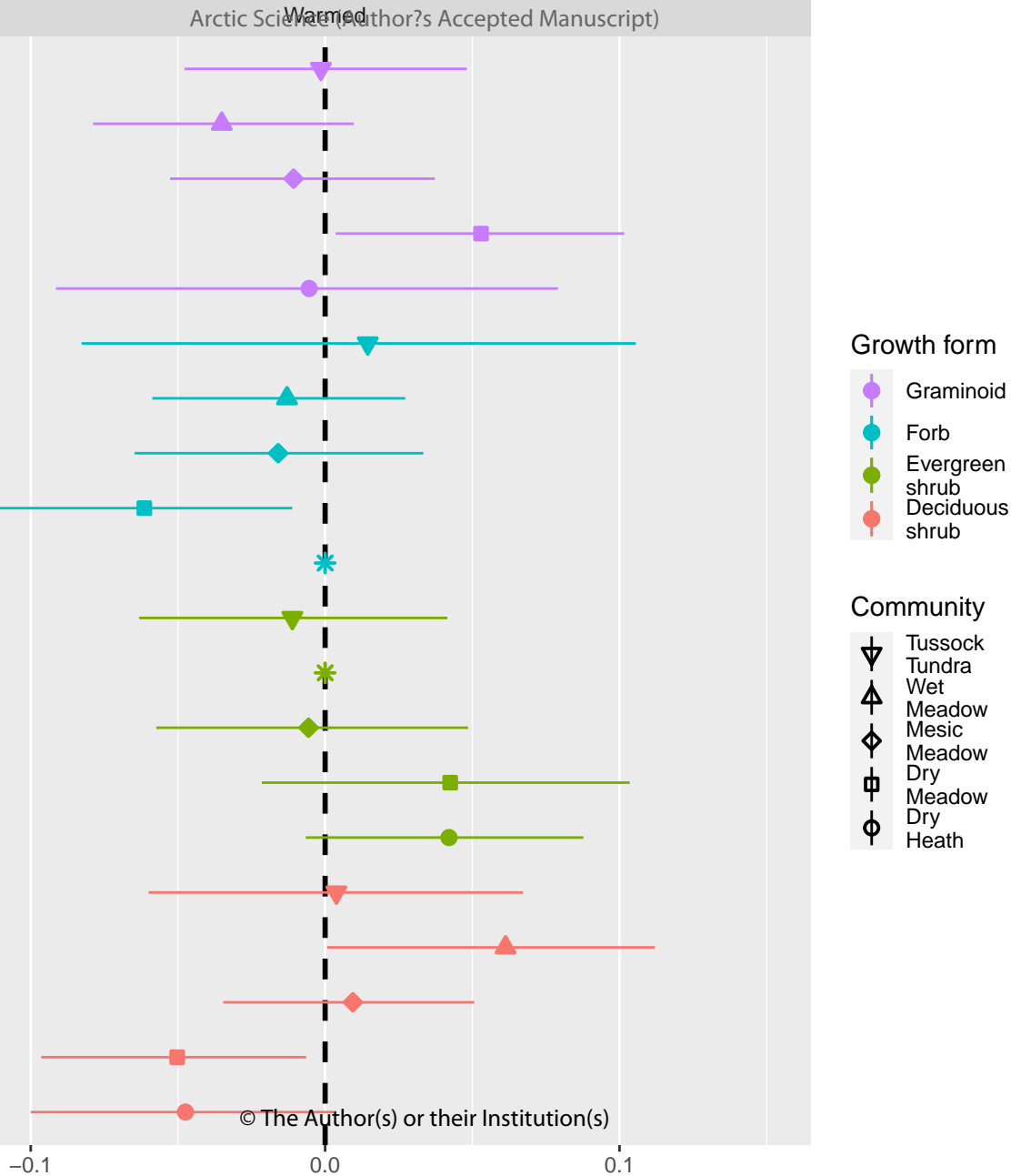
Figure 5. Difference in growth form time sensitivity (slopes) between the control and treatment (Warming, Fertilization, Warming + Fertilization) within five plant communities evaluated by model 1. Negative values indicate a negative trend relative to the control while positive values indicate the opposite. Growth Form \times Community interactions that did not converge due to zero inflation are marked with *. Coloured points represent the estimated difference time sensitivity (slope) for each Growth Form \times Community interaction, and vertical lines span the 95% credible intervals for each estimate.

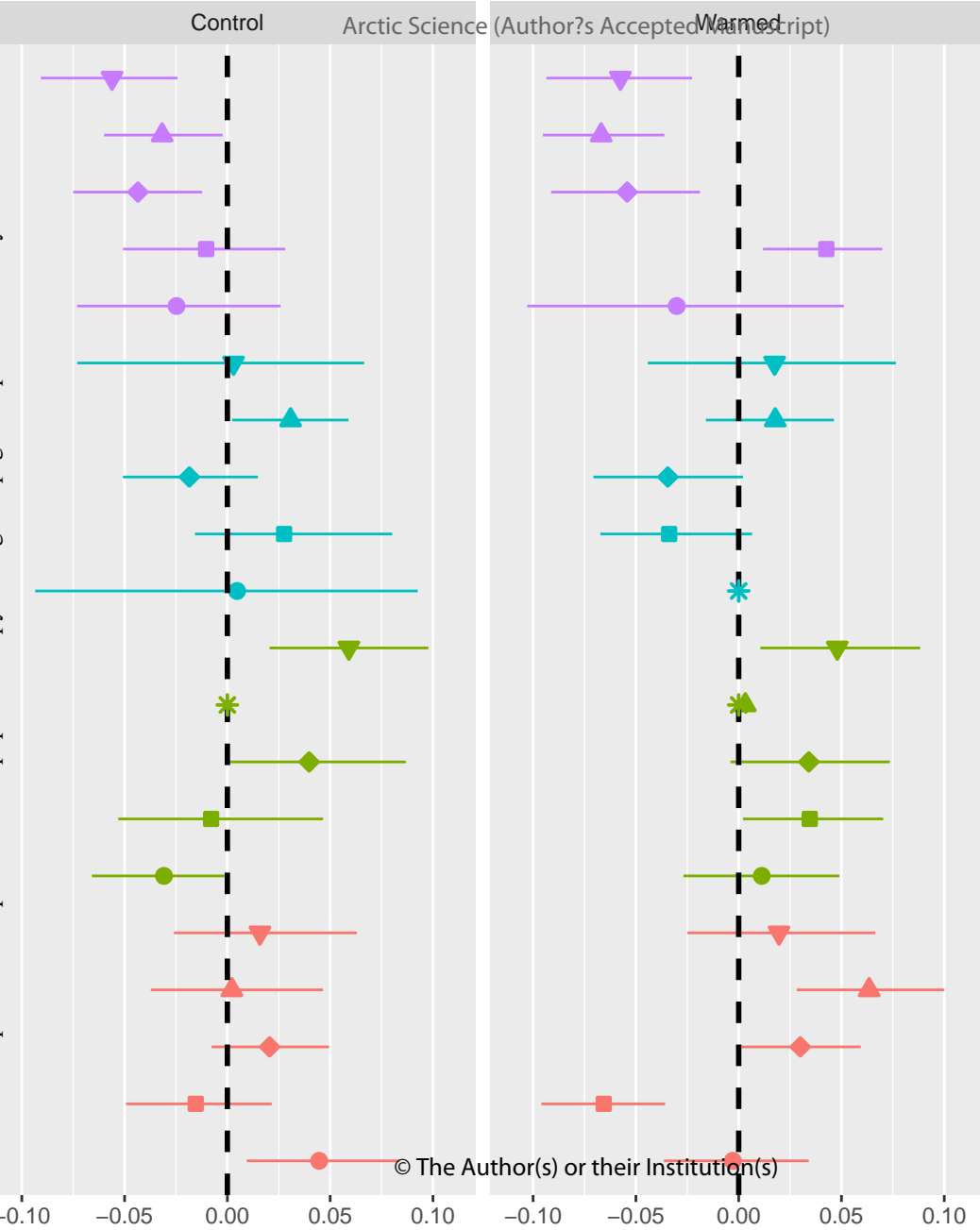
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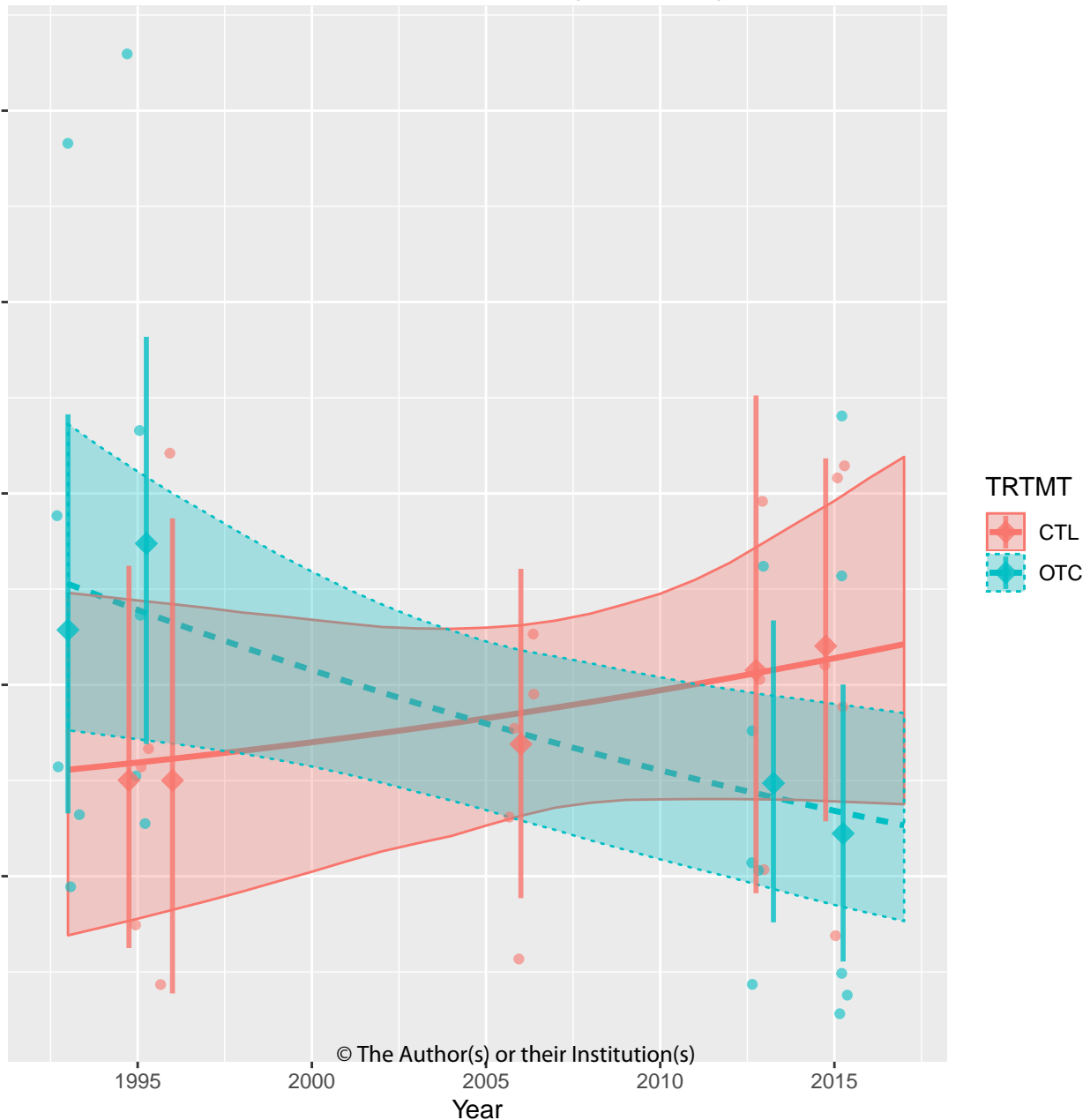


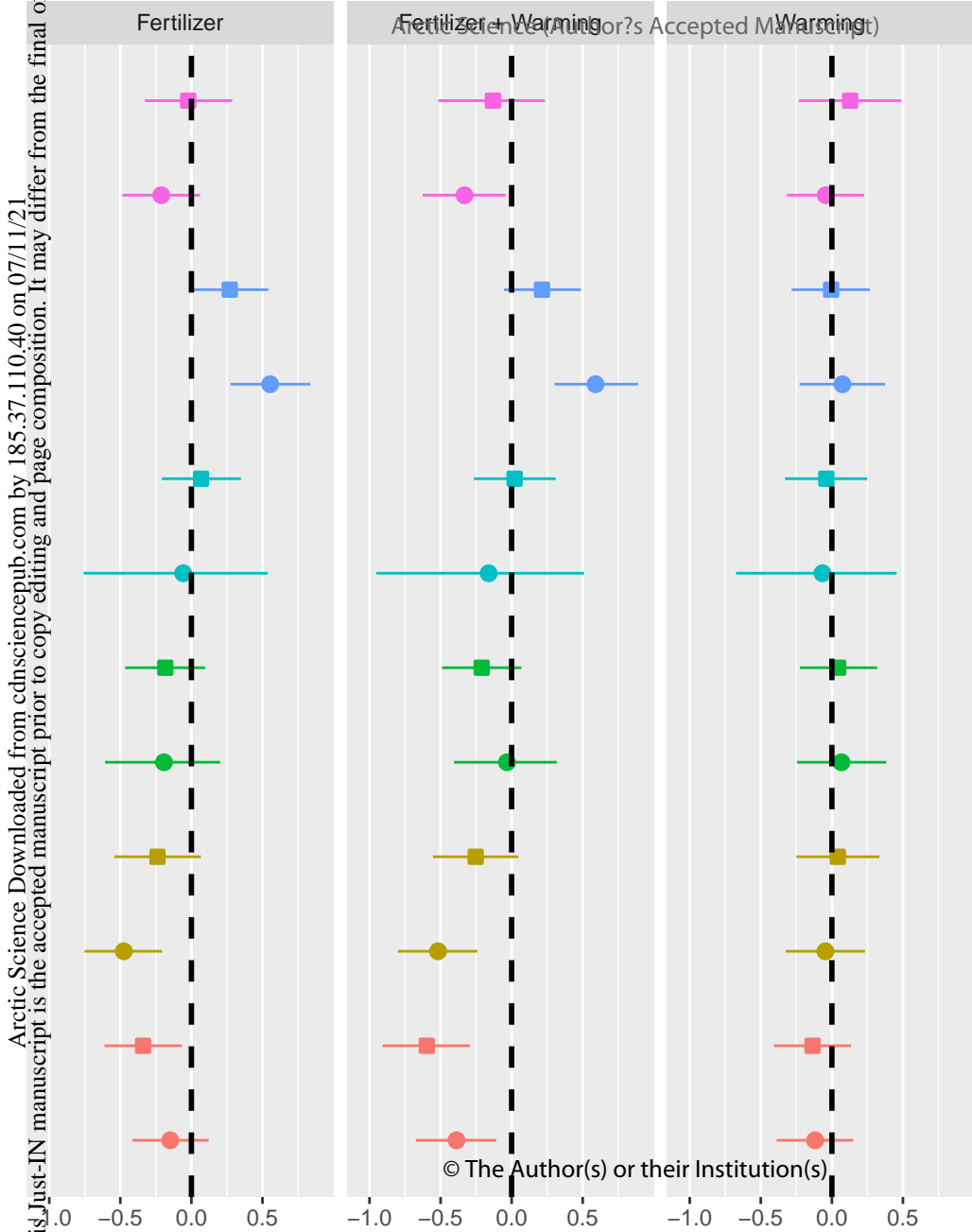
Growth form

- Graminoid
- Forb
- Evergreen shrub
- Deciduous shrub

Community

- ▼ Tussock
- ▲ Tundra
- ▲ Wet
- ◆ Meadow
- ◆ Mesic
- ◻ Meadow
- ◻ Dry
- ◻ Meadow
- ◻ Dry
- ◻ Heath





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