Comparison of the distribution and phenology of Arctic Mountain plants between the early 20th and 21st centuries

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Century-long changes in the distribution and phenology of arctic mountain plants

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Abstract: Arctic species are well adapted to climatic variability, but their long-term responses to warming remain unclear. Responses may be across-generation, via migration, or within-generation, involving phenological shifts in the timing of growth and reproduction. Using unprecedented century-long (1917-1919 vs 2017-2018) data on migration and phenology for 83 arctic and boreal mountain species in northern Sweden, we show dramatic distributional change associated with warming. 69% of species shifted uphill, averaging 6.1 m per decade, especially boreal woodland taxa whose upward expansion reduced unforested arctic habitat by 30%. Simultaneously, 20% of summit species were displaced downslope especially moisture-associated snowbed flora. Comparing differences in emergence, senescence, and duration of leafing and flowering between the early 1900s and present-day, we detected wide interannual variability in leafing and flowering within the two eras but no detectable shift between them. This was explained by two mechanisms. First, plant emergence mirrored snowmelt, whose timing was influenced by warmer years having greater snowfall – warmer springs did not always result it earlier emergence because snowpacks persisted longer. Second, the onset of reproductive senescence was unchanged even between years when emergence differed by a month – species that started earlier finished earlier, possibly due to intensified summer heat stress or canalized "hard-wiring" where the timing of senescence occurs regardless of summer temperature. Migrations in this system have likely buffered species loss. However, boreal expansion, warming temperatures, altered snow accumulation, and a potential lack of flexibility in timing of senescence may foreshadow challenges for high-latitude flora.

Keywords: arctic flora, climate change, resiliency, migration, phenology, mountain, historical data,

Introduction

The Arctic climate is one of the more rapidly changing on the planet, having warmed by 2-3°C over the last century with projected increases towards 4°C (Nogues-Bravo *et al.*, 2007, Parmesan & Yohe, 2003, Sala *et al.*, 2000). These changes have significant consequences for arctic flora, including on mountains where warming can be especially pronounced (Lenoir *et al.*, 2008, Prevey *et al.*, 2019, Steinbauer *et al.*, 2018), growing seasons short, and the availability of high-elevation refugia finite (Prevey *et al.*, 2019, Steinbauer *et al.*, 2018).

The biological impacts of a changing arctic climate, on mountain plants and more broadly, will be dictated by their ability to maintain growth and reproduction. This occurs by two pathways: migration across generations, progressively moving northward, uphill, or both, and phenological adjustments that better match growth and reproduction to changes including

warmer springs, drier summers, extended periods of autumn warmth, and altered precipitation dynamics including snowfall (e.g., Alexander *et al.*, 2015). However, the capacity for resilience emerging from these mechanisms, historically and going forward, remains unclear. Persistence of high-latitude plants is strongly dictated by distributional range and phenology, given the compressed growing season of the arctic climate (Harsch *et al.*, 2009). There are numerous traits that could well-equip Arctic species for rapid phenological adjustments to warming, such as early emergence, delayed reproduction, or extended leafing senescence. These same traits could also predict species loss, if climatic change exceeds the trait-based limits of adjustment, or if change favors suites of larger- and faster-growing competitively superior southern invaders (Alexander *et al.*, 2015). If high-latitude plants cannot phenologically adjust, then multi-generational upward or northward shifts via migration will be needed to maintain the climatic envelope, escape southern invaders, or both (Alexander *et al.*, 2015).

It has been difficult to empirically determine whether plants are successfully adjusting to a changing Arctic climate, given an absence of long-term data especially prior to recent decades when warming has accelerated (Steinbauer *et al.*, 2018). There is some evidence for both spatial and phenological shifts (Lenoir *et al.*, 2008), but there has also been wide variability in response (Myers-Smith *et al.*, 2015). For example, sometimes shrub- and tree-lines advance in elevation or latitude but many times they do not (Harsch *et al.*, 2009, Myers-Smith *et al.*, 2015, Van Bogaert *et al.*, 2011). The same holds for changes in species richness of cold-adapted plants – there has been reports of increases (Klanderud & Birks, 2003), losses (Engler *et al.*, 2011, Wilson & Nilsson, 2009), and no change (Vanneste *et al.*, 2017). Furthermore, research tends to target the front of the range (expansion), whereas range changes may derive more from the back (contraction) especially if climate impacts are indirectly channeled through altered species interactions (Van Bogaert *et al.*, 2011). In this latter case, phenological changes alone will not buffer warming if "warm-tolerant" species are sweeping in from behind – only northward or upward range expansion by arctic flora would maintain persistence. Phenologically, there has been an understandable emphasis on early flowering given the advancement of growing seasons globally (Alexander *et al.*, 2015), but growing season length and senescence also impact plant fitness and are less investigated in the arctic (Prevey *et al.*, 2019). Even so-called "Arctic greening-up" in high-latitude plant communities, involving extended growing seasons and increased net primary production, has not been universally detected (Myers-Smith *et al.*, 2011, Pauchard *et al.*, 2016). In total, these uncertainties on phenological and migrational responses limit our ability to predict future impacts of a warming Arctic (Niskanen *et al.*, 2019)

Here, we present evidence of century-long distributional and phenological adjustments by 83 arctic and boreal mountain flora in northern Scandinavia. Climate conditions in this region have changed dramatically especially since the 1980s (Fig. S1), while the arctic mountain plants of northern Scandinavia have been modelled to undergo substantial species loss and range contraction (Niskanen *et al.*, 2019). Our work centers on a unique 100-year dataset, identically sampled in 1917-1919 and in 2017-2018 along an elevational gradient straddling both Arctic and Boreal biomes in the Scandes Mountains. Using data on shifts in the onset and senescence of leafing and flowering, changes in elevational occurrence, the timing of snow melt, along with species-specific plant traits and local daily climate data back to 1914, we test the relative importance of migration and phenology on plant persistence. Our distributional analysis includes data on the maximum and minimum range limits of each species, allowing us to determine if change happens more at higher elevation, where direct temperature effects should be most limiting, or towards the mountain base where climate impacts should be channeled through

species interactions especially invasion by southern taxa. We also test differences in the richness and composition of summit vegetation, given that mountain tops can be especially sensitive to climate change as described elsewhere in Europe (e.g., Pauli et al. 2012; Gottfried et al. 2012; Matteodo et al. 2013).

Methods

Work was conducted in two sampling periods on a 900 m ASL long elevation transect on Mount Nuolja (1169 m ASL) in Abisko National Park, Sweden, located 195 km north of the arctic circle (68.3495° N, 18.8312° E). The study area occurs within a rain shadow of the Scandes Mountains, with long-term (1914-2013) precipitation averaging 307 mm per year and mean annual temperatures of -0.5^{o} C. About 50% of annual precipitation falls as snow typically between October-April. Snowbeds can persist well into the summer months, depending on elevation, and in some years there are areas that maintain snowcover for the entire summer. All climate data come from a meteorological station at Abisko Scientific Research Station (founded 1913), near the base of the transect (388 m ASL) – data were measured every three hours from 1914-2004, and then hourly since (Kohler et al. 2006, Callaghan et al. 2010). Long-term trajectories of warming over the 20th and early 21st centuries at the station show increases, but these trends are not linear. The most consistent period of increased warming has been since the 1980s (Fig.S1), with the largest relative changes involving warmer spring and fall seasons. Prior to the 1980s, inter-decadal warming was more variable including extended cold winters during the 1950s-70s.

The Abisko region straddles the boreal and arctic vegetation zones of northern Scandinavia. Boreal areas of Abisko are currently dominated by the subalpine mountain birch (*Betula pubescens*), with some pine (*Pinus sylvestrus*). Unforested tundra alpine areas are most often confined to upper mountainous slopes, including Mt. Nuolja (Fig. S2A), with a high diversity of dwarf shrub and herbaceous plants. The region has been widely grazed by domesticated reindeer for centuries with varying intensities and land use practices since the 1800s (Emanuelsson 1987). Major predators have largely been eliminated. Our study site on Mt. Nuolja lacks melting glacial beds and has some of lowest levels of anthropogenic-based nitrogen deposition in Europe (Dentener, 2006) - both can otherwise accelerate uphill colonization of plants, confounding tests of direct climate responses.

The study transect consists of twenty permanent monitoring plots established from base to summit in 1916 (Fig. S2). All work during 1917-1919 was conducted in 78 subplots within the 20 plots, with data amalgamated to the plot level for analysis (Fries 1925). These subplot data were subsequently lost, thus all historical comparisons in this paper are among-plot. The plots are separated by an average of 18.6 m of elevation depending on the steepness of the mountain face (range 8.9 – 63.06 m). The longest annual duration of sampling during the first survey period was 1918, from May 25th-August 31st. Sampling ended earlier in 1917 (August 7th) and 1919 (June 24th).

Initial sampling from 1917-1919 involved monitoring of plant phenology, including onset and senescence of leafing and flowering, for all species at five-day intervals starting May 25 of each year when most plots tended to be snow covered. The repeated visitation of plots helped accurately identify all species, with sufficient frequency to capture the timing of phenophase transition. The frequency of plot re-visitation, however, demanded logistical trade-offs given the mountainous and often snow-covered terrain with many dozens of species. To that end, all phenological data were assessed at the plot level, thus ignoring the abundance and phenological variation of each species within each plot. For example, the timing of leaf senescence for a

species would be determined by the first observation of senescence by any individual of that species in that plot. If that species was found in ten plots on the transect, then there would be ten datapoints for that species at each sampling period.

In addition to phenological shifts, the percent coverage of snow per plot was also repeatedly measured every five days - this was conducted given the importance for the timing of snowmelt by elevation for arctic plant phenology (e.g., Wookey et al. 2009, Semenchuk et al. 2016). A 50 m measuring chain was sequentially laid, plot by plot, along the entire mountain transect, with % snow cover determined by the distance of the chain contacting snow versus open ground. This procedure was used 1917-1919 and again in 2017, before switching to a Trimble R8 dGPS (2018-present).

The transect plot markers were periodically maintained as recently as the 1960s, enabling relocation of 59 of the 78 subplot poles along the transect in 2016. Areas without poles were easy to identify given the detailed description of distance and bearing between the poles (Fries 1925), and because the piles of rocks used to support the missing poles often remained evident. We were thus able to conduct our contemporary surveys in the exact locations of the 1917-1919 work, with one exception. In 1964 a chairlift was installed that bisected the gradient within the birch woodland at ~650 m ASL; three of the poles were shifted by ~10 meters in the summer of 1964, perpendicular to the axis of the gradient.

During 2017 and 2018, the survey protocols for phenology and snow cover as described for 1917-1919 were followed identically. By using the exact plot locations, we were able to detect the altered plot-level distribution and performance of each species. For migration, we were able to determine changes in mean plot distribution, shifts in the upper maximum plot occurrence, changes in the lower minimum of occurrence, and whether species ranges have expanded or contracted from the top, the bottom, or both. To calculate spatial shifts, we used plant data from 1918 as it had the widest span of observations from May 25th- August 31st. The 2017 and 2018 data included this May 25th - August 31st interval.

For phenological change, we pooled 55,016 observations from 83 vascular plant species deriving from the repeated species-specific plot visitation every five days from the two eras. The data from 1917-1919 contained 156 species (Fries 1925), representing 47% of all species known from Abisko National Park at the time (Fries 1910). We recorded an additional 15 species during our sampling period, while observing all of the previously reported species on the transect or nearby on the mountain. Our 83 species were selected based on being present in both eras and occurring in three of more plots. We eliminated several morphological cryptic taxa as a precautionary measure because of uncertainty about their historical distribution (e.g., *Anthoxanthum odoratum* vs *A. alpinum*, some sedges and willows). Overall, there was a wide range in plot frequency per species (n/20 plots), with occupancy among the 83 species averaging 40%. Three species occurred in a maximum of 15/20 plots, while 1.5% of the species were only found in one plot in one or both sampling periods.

We classified the 83 species into four habitat categories, to test whether species responses unfolded in definable ‘syndromes’ based on established affinities with temperature and soil moisture (Table S1). Boreal flora derive from forested habitats with southerly distribution centers - these taxa tend be expanding rapidly into the warming Arctic (Vuorinen et al. 2017; Bjorkman et al. 2018). Soil moisture classifications centered on taxa with “broad” tolerances including xeric conditions, and cold-affiliated “mesic” species that are typically associated with moist soils derived from seeps and melting snowbeds. We also determined major traits of leaf biomass, leaf surface area, and plant height for each species, testing whether plant morphology

predicted migrational response over time. Data were combined from the TRY and the Tundra Trait Team databases (Kattke et al.2011; Bjorkman et al. 2018).

All phenology stages were defined by Fries (1925). The phenology classification for each species was summarized at the plot level, for six response variables: first observed onset of leafing species^{-1} plot^{-1}, first observation of leaf senescence species^{-1} plot^{-1}, first observed onset of flowering species^{-1} plot^{-1}, first observation of flower senescence species^{-1} plot^{-1}, and the duration of leafing and flowering based on the differences between onset and senescence for each species. Senescence was defined as detectable changes in leaf or flower colour, or the onset of visible wilting. For each of the six responses, we calculated log response ratios derived from differences in means among plots for the two sampling periods.

Changes in elevational occurrence were calculated by comparing differences in plot presence/absence between the two sampling periods. As described, we lacked exact measures of where individual plants occurred within a plot, but we did know the elevations of the plots they occupied. We thus calculated change based on those plot elevations. For example, a species occurring in plots 1-3 in 1918 would have a mean elevation of 437.02 m based on the three starting elevations of the plots (418.2, 436.3 m, and 456.6 m). If that same species was found in plot 8-10 in 2017, then its current mean elevation would be 705.5 m and its change over time would be an increase of 287 m (or 28.7 m per decade). We calculated elevational shifts in the maximum and minimum plots of occurrence, simply by taking the differences of these two measures between the time periods.

We used aerial drone imagery to test relationships among estimated plant productivity (NDVI), elevation, and species distribution, given that standing biomass can represent plant-plant competitive dynamics especially at lower elevations including impacts on ground level temperatures, light, and the timing of snowmelt (i.e., Alexander et al. 2017). Aerial imagery was collected between 23-27 June 2018 using an *eBee* fixed-wing drone (senseFly, Switzerland) in combination with a *Sequoia* multi-spectral sensor (Parrot, France) and a SONY DSC-WX220 RGB camera. NDVI was calculated from the multi-spectral sensor and radiometrically calibrated using Mosaic Mill reflectance targets. The imagery was georeferenced to >10 known DGPS locations of equally distributed poles along the transect visible in the imagery. Pix4dmapper was used for post-processing of the imagery (Pix4D, Switzerland). A 2 m resolution digital elevation model (© Lantmäteriet, Sweden) was used to derive terrain variables in SAGA GIS (*44*). These include slope, wind exposition index, SAGA wetness index and annual potential incoming solar radiation. NDVI and terrain variables were extracted on a per pixel basis along a 10 m wide buffered band along the 20 plots and are summarized in Table S3**.**

Our primary analyses centered on describing the magnitude and direction of elevational and phenological changes among the 83 species, using log proportional change in means (log response-ratios) between the two study periods. We used principle components analysis to examine relationships between major plant traits and the extent of mean, maximum, and minimum elevational change for the four major habitat groupings of plants. We used linear regression to test relationships between elevation and snow melt by year and season; how elevation influenced the timing of the onset, duration, and senescence of leafing and flowering; and to determine associations between species-specific distributional changes at the maximum and minimum elevations of occurrence. We used multiple correspondence analysis (MCA) to test associations between four vegetation classes based on temperature and moisture, and whether species were lost, gained, or remain unchanged. All analyses were conducted on JMP 14.0 (SAS Institute Inc., Cary, NC, 1989-2019).

Results

The most detectable century-long changes were spatial/elevational rather than phenological. Since 1918, 95% of the 83 species had altered mean distributions along the montane gradient (Fig. 1). Most of these shifts have been upward, affecting 69% of all taxa. There has been significant widening of species ranges, averaging 7.5 m per decade and mostly explained by increases in upper range limits. There were four species lost from the transect (Table S1), although each currently resides nearby (within ~1 km) on the mountain (Larson, unpublished data) - we thus found no evidence of local extirpation despite pronounced warming in recent decades (Fig. S1). Conversely, there were fifteen new occurrences since 1917-1919, mostly larger-sized herbaceous species with Boreal affiliations (Figs. 2AB, Table S1).

Although many species had higher average ranges, there was no single shared response by all taxa (Fig. 1). While mean range shifts averaged 6.1 m decade^{-1}, variation among species ranged 10-fold. Some species climbed ~½ km over the last century while others descended to the same extent. Further, higher mean range shifts were associated with two responses: contraction from the bottom or expansion at the top (contraction: $F_{1,82}$= 6.1, $p<0.02$; expansion: $F_{1,82}$= 21.1, $p<0.0001$). Few species demonstrated both responses, such that increases in upper and lower occurrence limits were not consistently related ($F_{1,82}$ = 1.4; P = 0.24). Range contraction from the base of the mountain by arctic-affiliated taxa was presumably related to an inability to persist in expanding woodland and shrub thickets (Fig. 2), especially in areas formerly characterized as open habitat but now with significantly greater standing biomass (Fig. S3C).

At the mountain summit, there were small net changes in overall species richness but high turnover since 1917-1919. There were 17 new summit species, mostly boreal taxa, that coincided with the loss of 20% of species formerly present (Figs. 3 and S4; Table S2). Loss from the summit were mostly mesic arctic species of wetter and cooler vernal conditions (Fig. S4). These taxa were largely displaced to lower elevations (Fig. 1), where snowbeds persist longer (Fig. 4). Interestingly, there was not a dramatic change in the timing of snowmelt at the summit since the early 1900s - the summit has always become snow-free earlier in the season compared to downslope, presumably due to high wind exposure (Figs. 4, S2B).

Downslope, the treeline was higher by 63 m since 1918, subsuming the former zone of shrubs (Fig S2A). That shrub zone, however, expanded even more and is now 123 m higher. Overall, expansion of the forest and shrub zones has decreased the open alpine zone by ~30% since 1918 (Fig. S2). This upward expansion of woody plants into high-elevation open areas appears to be on-going, with juveniles of a number of forest species including birth trees found in all plots above the shrubline including the summit (Fig. 3).

Snowmelt dynamics among the five years examined (1917-1919, 2017-2018) varied strongly by elevation and by year, but not by ‘era’ in the sense that trends in the early 1900s and present-day were similar (Figs. 4A, B). Our data for local long-term winter weather (defined as Nov-Mar each year) and plot-level snow melt clearly illustrate the well-established positive connection between higher winter temperatures and increased precipitation ($F_{1,528}$=19.47; $p<0.0001$). There was variation with in snowbed persistence with elevation, with middle of the transect maintaining snow the longest into the summer (Fig. 4). This trend has not changed over the last century with the lower and warmer forested areas and upper and more exposed summit becoming snow-free weeks or even months earlier (May 25th snowmelt [year, elevation]: - $F_{5,119}$ = 1.63; p = 0.157; Figs. 4, S3).

There was wide interannual variability in phenology, but no overall change in community-level phenological duration (Figs. 5AB). The net effect is a similar pattern of plant emergence

relative to snowmelt between 1918 and 2017-2018, with high interannual variability depending on winter temperatures but no overall difference in snowmelt starting time on May 25th or elevation over the growing season (Fig, 4). For example, winter 2017 was warmer with more precipitation (Fig. S1), extending the spring melt period that, in turn, delayed plant emergence compared to 1918. By contrast, 2018 had a cold and dry winter with little snow (Figs. 4, S1), such that many plots were snow-free in late May – predictably, emergence of leafing and flowering was faster in 2018 than 1918. Phenological duration was also maintained by a tight connection between emergence and senescence – species that started earlier also ended earlier, for both leafing and flowering (Fig. 5). The net effect was that the duration of growing season, defined as emergence to senescence, was largely unchanged between 2017 and 2018 versus 1918 ($F_{2,602} = 2.28$; $p = 0.104$), even though emergence in 2018 was almost 30 days earlier on average per species compared to 2017 (Fig. 5).

Discussion

We tested for changes in the distribution and phenology of arctic mountain plants with an unprecedented century-wide dataset. Given pronounced local warming especially since the 1980s, we predicted a high likelihood of range shifts, species displacement, and the dramatic alteration of leafing and flowering. Overall, we did observe pronounced ranges shifts by most species, accompanied by the invasion of southern-affiliated flora. Phenologically, however, there were no pronounced differences between the timing and duration of emergence and growth between the two survey periods – relationships among snow melt, the onset of leafing and flowering, and the timing of senescence were similar between the two eras. We also observed no evidence of species loss – all taxa seen in the early 1900s were present in the plots or, if displaced, still occurred nearby on the mountain. These data represent a rare opportunity to look back in time, to test for evidence of resilience mechanisms involving migration and phenological timing against significant warming. They reveal that distributional shifts, including range contraction, have likely helped to maintain the persistence, especially against the upward expansion of southern-affiliated plants. However, ongoing invasion by boreal taxa into the remaining open arctic habitat, and a potential lack of flexibility in the timing of senescence among many arctic plants could indicate looming challenges.

One limitation in quantifying past climate responses in the arctic, including resiliency, has been a rarity of spatially precise long-term data. A warmed arctic can be more productive and highly invaded by southern taxa yet variability in these patterns can be widespread for reasons that are not always clear (Myers-Smith et al. 2020). These mixed responses could reflect lags created by long generation times of plants, the possibility that substantial change occurred prior to onset of most studies, or that range impacts are localized thus affecting some portions of the range more than others. We observed evidence suggesting the influence of each of these confounding factors, providing critical insight on the magnitude of change for arctic plants and the underlying causal mechanisms.

Distributionally, we see an average mean range shift at 6.1 m higher in altitude per decade - less than the 11 m estimate of Chen et al. (2011) but identical to Parmesan and Yohe (2003). These higher mean ranges reflect upward migration, lower contraction, but rarely both. Changes in maximum elevation have commonly been used to assess montane range shifts but can be biased if they reflect rare dispersal events - our work shows that mean and maximum range shifts closely align. At the summit, we see limited change in species richness that are contrary to other studies reporting big gains or big losses (citations), yet we also observed substantial turnover especially downward shifts by mesic taxa (Crimmins *et al.*, 2011). Finally, our species-specific

migration data illustrate a complex mixture of expansion, contraction, and retreat, demonstrating the challenges in assessing the drivers of distributional change in arctic flora. For example, the upper range limit of mesic species *Oxyria digyna* dropped by 114 m since 1917-19 but its mean elevation only changed +10 m because of a similarly large contraction from below (204 m higher) - the small change in mean distribution hides a narrowing range width by 318 m.

Despite these notable species-level changes in distribution, we still detected several broad response syndromes - rapidly climbing boreal species invading from lower elevations, a small group of arctic species whose mean distribution shifted downhill (14% of all species), and a group of arctic species with higher mean distributions driven by contraction from below which presumably reflects species interactions. Invading southern species were typical of Boreal Scandinavia with distributional centers below the Arctic circle, including the widespread canopy tree *Betula pubescens* and a suite of woody shrubs especially non-Arctic species of *Salix.* This expansion of woody trees and shrubs into Arctic landscapes is consistent with observations globally (Myers-Smith *et al.*, 2011). There was also a compliment of invading herbaceous flora mostly of the forest understory, which have been reported as expanding to higher latitudes and elevations elsewhere (Pauchard *et al.*, 2016), and are generally taller and faster growing than typically more prostrate arctic flora. Interestingly, many of these southern invaders are palatable to reindeer, with preferential grazing elsewhere acting to stabilize arctic communities against their establishment (Olofsson *et al.*, 2009). Indeed, reindeer herds persist on Mount Nuolja, sometimes in large numbers, but do not occur at the consistently high densities seen elsewhere in the Scandes Mountains, and obviously not in high enough densities to stabilize tree and shrub expansion. In particular, the use of the lower parts of the transect by reindeer have decreased since the 1917-1919 due in part to changes in herding practices (Callaghan *et al.*, 2013) – this may play a contributing role in the upward invasion of plants at our site, that might be resisted elsewhere (Sorensen, 1941).

The second response group was arctic flora of mesic habitats, with generally narrower and lower range occurrences. Long-term studies on climate responses by summit plants have occurred across the Europe, sometimes showing large changes in species richness, by a range of mechanisms (Pauli *et al.*, 2012, Steinbauer *et al.*, 2018). The trends with our summit taxa reveal great change but also complex mechanisms, that characterize the data as a whole - things are not simply warmer and less snowy. On top, no change at all in snowmelt but big turnover nonetheless with the displacement of arctic-affiliated species. The bigger change, however, maybe be the warming of Arctic temperatures, suggesting that even if the timing of snow melt may not differ substantially due to higher snowfall, plants are likely experiencing warmer and possibly drier conditions when they emerge. The net effect for mesic arctic species is a displacement to lower elevations where snowbeds persist longer. The ones establishing are a mix of wind-dispersed species but also ones occurring with broader habitat affiliations including drier sites. Importantly, this reinforces that arctic climate reflects complex temperature and moisture interactions which will variously affect plants – warming responses will differ profoundly depending on moisture levels.

Finally, there was a response group of arctic species associated with areas of open meadow between the treeline and summit. This part of the transect has the longest persisting snowbeds each year, a trend that has not changed over the last century with the lower forested areas and upper summit becoming snow-free weeks or even months earlier. Overall, expansion of the forest and shrub zones has decreased the size of this open alpine zone in our plots by ~30% since 1918, consistent with other systems showing that arctic mountain species can become

increasingly habitat limited as southern species sweep uphill. This suggests competition from below is the biggest driving factor of change. Numerous studies have shown the importance of indirect climate effects channeled through vegetation shifts. Indeed, we observed birch trees even in summit plots, as well as everywhere else. These "invaders" were only seedlings, with the absence of adults indicating upward dispersal but also too extreme for survival at least for the time being. This illustrates a core challenge for arctic mountain plats being squeezed from both sides, that may limit their ability to persist as invaders rush towards the summit.

Distribution shifts are a longer-term response to climate involving new colonization. Given the dramatic interannual and interdecadal swings in climate seen in our study region since 1914, shifts in phenological timing would presumably be a more immediate mechanism of resilience. Indeed, such shifts have been seen widely in arctic flora, including both earlier emergence and contraction of flowering seasons (Prevey *et al.*, 2019). Other studies have shown the importance of warmed autumns, for extending growing seasons and invasion (Fridley), which are less tested in arctic systems compared to early vernal patterns (Gallinat *et al.*, 2015). Here, we possess an unprecedented measure of plant leaf and flowering phenology. In short, we see dramatic interannual variability in phenology that was similar within both eras, but no overall change among them in terms of community-level phenological duration – unexpectedly, the length of time between emergence and sensence in the early 1900s and now were similar.

The reasons for this lack of overall change in duration appear to be two-fold. Foremost is the timing of snow-melt – we found that phenological emergence each year is regulated by snow cover, not warming per se (e.g. Bjorkman *et al.*, 2015), and the average timing of snow melt since 100 years ago has not shifted substantially, by elevation or timing in spring. Our data for local long-term weather and plot-level snow melt clearly illustrate the well-established positive connection between winter (Nov-Mar 1914-2018) temperature and precipitation: our region is warmer overall, and as a result warm winters receive higher snowfall that takes longer to melt in the spring. The net effect is a similar pattern of plant emergence relative to snowmelt between 1918 and 2017-2018, with high interannual variability depending on winter temperatures, but no overall difference in snowmelt starting time on May 25th or elevation over the growing season. For example, winter 2017 was warmer with more precipitation, extending the spring melt period that, in turn, delayed plant emergence compared to 1918. By contrast, 2018 had a cold and dry winter with little snow, such that many plots were snow-free in late May – predictably, emergence of leafing and flowering was faster in 2018 than 1918.

The second factor preserving phenological performance was a tight connection between emergence and senescence – species that started earlier also ended earlier, for both leafing and flowering. The net effect was that the duration of growing season, defined as emergence to senescence, was largely unchanged between 2017 and 2018 versus 1918 even though emergence in 2018 was almost 30 days earlier on average per species compared to 2017. Reports of lack of change in phenological duration have been made elsewhere in the Arctic (Semenchuk *et al.*, 2016). Our work indicates this could be a consistent outcome even at a century scale.

The reasons for tight linkages of emergence and senescence are difficult to determine. One possibility relates to growing conditions in 2018, with a considerably warmer summer potentially triggering early senescence – mean temperatures in May 2018 were six times warmer than the previous year, and never went below zero. July 2018 was 3 times warmer than July 2017, with highs of 23° C. These spring and summer temperatures for 2018 are well above both century-long and 30-year averages for our region. An alternative explanation is the presence of some level of adaptive canalization in arctic plants, where the duration of phenological periods are

fixed relative to emergence even though growing conditions into the summer could remain favorable (Semenchuk *et al.*, 2016). Several arctic studies have alluded to this possibly of phenological "hard-wiring" (Sorensen, 1941, Starr *et al.*, 2000, Wookey *et al.*, 2009). The reasons for canalization could relate to evolved physiological time constraints on reproductive completion, to mitigate the risk of late-summer cold or drought sometimes characteristic of Arctic summers. They may also be adaptive connections that maintain synchrony with pollinators, which also emerge at snowmelt and can have short foraging seasons at high latitudes (Semenchuk *et al.*, 2016). Regardless, the net effect is no detectable net change in duration despite significant climate changes. It is critical to note that this does not necessarily mean there are no adaptations to arctic warming. However, if they have occurred, they are difficult to detect in the field because inter-annual changes are so vast as to mask any adaptive changes during the last 100 years. As well, almost all of the 83 species were examined are longer-lived perennials especially arctic plants, such that 100 years of warming may still only cover one of several generations.

There are several prognoses for the future of our high-latitude mountain plant community. One, ongoing upward expansion from southern species threatens to increasingly restrict the extent of non-forested habitat, as has been observed repeatedly elsewhere (e.g., Arft *et al.*, 1999, Van Bogaert *et al.*, 2011). Indeed, we recorded the presence of one or more juveniles of Boreal species in every plot above the shrub line, with *Betula pubescens* seedlings even recruiting on the summit. These individuals may not survive, but demonstrate persistent establishment at higher elevations with ever-warming conditions presumably increasing survival odds (Kullman, 2002) and a very real risk of treeless alpine disappearing altogether (Moen *et al.*, 2004).

Secondly, we detected migration shifts by most species since 1918, which we interpret primarily as direct or indirect responses to warming. Clearly arctic montane plants face challenges in time and space. Temporally, the easiest responses are immediate within-season adjustment in phenology to snowmelt and summer temperatures, which we noted for most species (Fig. 4). Given the wide range in timing of emergence in 2017 (late) vs 2018 (early), most arctic species appear capable of making these adjustments. Spatially, however, the risk of not moving is to be over-run by boreal species sweeping uphill (Figs. 5, S2). Temporal responses may be necessary to withstand the immediate effects of warming, but insufficient longer-term.

Thirdly, the pronounced and largely concordant trends in leafing and flowering phenology (Fig. 4B) indicate capabilities of both phenophases to rapidly adjust to interannual variation in conditions but also suggests they may be tightly coupled (e.g., Kochmer & Handel, 1986). For example, the delayed emergence of leafing with late snow melt in 2017 was largely mirrored in the timing of flower emergence later in the growing season. Similarly, the early spring of 2018 produced closely matched trends for leafing and flowering, including early emergence and faster senescence at lower elevations possibly in response to forest canopy closure. Any form of tight coupling where flowering is dependent on vegetative development may be expected on arctic mountains, given their narrow and sometimes harsh and unpredictable growing seasons. On the other hand, the tight coupling of phenophases, especially limited flexibility in flower time, could become problematic with more novel and extreme arctic climates such as summer drought. The strength of phenological coupling in arctic flora requires further testing.

There are several caveats to our results. The first is the clear difficulty in accurately quantifying trends in early emergence, given that the key driver of emergence – snow melt – can fluctuate interannually by weeks or even months. Indeed, 2018 had the fastest spring snow melt on the mountain and 2017 the slowest, for the six years of data including 1917-1919. Emergence

times between these two years varied accordingly. Relatedly, the same quantification challenges exist with the influence of elevation– interannual fluctuations in phenological performance including emergence and senescence interacted strongly with elevation. Many of our species are distributed across at least two of the three broad vegetation zones (e.g., forest, open alpine, summit), such that "early emergence" will likely unfold differently for species by location. Finally, even our long-term historical comparisons present potential challenges, in that the year of comparison with contemporary trends profoundly shapes analytical outcome. Climatic conditions in 1918 happened to be representative of 30-year averages of that era. However, the overall trends in climate in the 20th century were non-linear. For example, we would have observed significantly different comparative outcomes in phenology if our historical data derived from the 1960s, when conditions were the coldest in the last 110 years.

There are numerous reports of large and rapid transformation of the diversity and distribution of the high-latitude montane flora, with suggestions that this system may be a bell-weather for widespread species loss in ecosystems globally. These projections have been modelled (Niskanen *et al.*, 2019) or based on data that are often lacking in spatial or temporal precision because historical limitations (Myers-Smith *et al.*, 2015). Here, we have full data for dozens of species, pulling back the curtain on plant responses over a century. Species have adjusted their distributions profoundly, providing possible temporary resiliency especially against invading southern plant communities. However, with potential limits on phenological duration, the downwards contraction of some arctic flora towards areas with the most persistent snowbeds, and with recruiting invaders at every point along the gradient, our work powerfully demonstrates the complexity of constraints faced by Arctic mountain species that appear increasingly squeezed from all sides.

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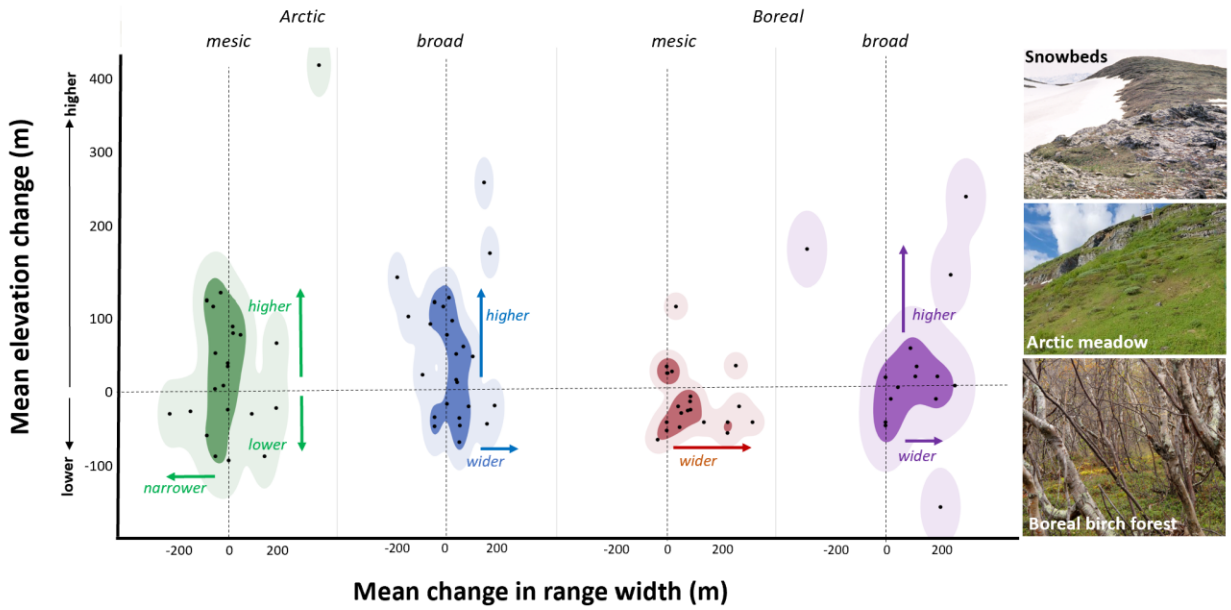
Figures

Figure 1. Distributional changes in mean elevation and range width for 83 species along a 900 m elevational gradient on Mt. Nuolja Sweden - 1918 versus 2017. Species are grouped based on habitat affiliations of temperature (arctic, boreal) and moisture (broad tolerance, mesic obligate) following the maps of Mossberg et al. (Mossberg *et al.*, 1992), and the altitudinal limits of the alpine species given by Heintze (Heintze, 2013), Kilander (Kilander, 1955), and Mossberg & Stenberg (Mossberg & Stenberg, 2018). Arctic species of moister soils (green) are commonly associated with melting snowbeds at our site. The black dots are the mean range and elevation changes of each species, surrounded by 2-dimensional density contours (bivariate nonparametric density) for visualization purposes. Arrows indicate predominant qualitative responses within each of the habitat groups.



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