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# Tracing phenology of subarctic plants over the last century

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**Abstract**: Climate change has been affecting plants over the last century and caused changes in life history features such as the flowering time. Herbarium specimens provide a snapshot of the past environmental conditions during their collection. The collection date in a herbarium specimen is a good proxy to determine the flowering period (phenology). In this study, phenological data from subarctic plant specimens collected over 100 years were gathered by using one of the largest herbarium databases in the World. The collection dates of 7146 herbarium specimens were analyzed and significant shifts in the phenology of subarctic plants were detected. In this study, most of the analyzed 142 species in a subarctic biogeographic region tended to flower earlier in the 1950–2018 period compared to the 1900–1949 as a possible result of the climate change. Flowering time shifted from 8 to 26 days in some species. Changes in flowering time may alter species interactions, community composition, and species distribution in a region. Therefore, results of this study may shed light on the possible shifts in phenology and plant responses under the climate change.

Key words: Subarctic, flowering time, herbarium specimens, climate change.

## Introduction

Climate change has several impacts on ecosystems and it may cause changes in plant phenology including flowering time (Walther *et al*. 2002; Parmesan 2007; Richardson *et al*. 2013; Gugger *et al*. 2015), species richness and interactions (Menendez *et al*. 2006; Cahill *et al*. 2012; Elmendorf *et al*. 2012), ecosystem processes and functioning (Clavel *et al*. 2011; Chapin *et al*. 2014; Maestre *et al*. 2016; Zhu *et al*. 2017). For example, climate change may cause altitudinal shifts of plant species in alpine biomes. Therefore, alpine communities may be homogenized in terms of species diversity (Jurasinski and Kreyling 2007). Likewise, latitudinal shifts in vegetation and changes in species composition can be observed due to the climate change as in the case of Arctic Alaska during the past 50 years (Sturm *et al*. 2001).

Greenhouse gases produced by human activities are major sources of climate change and they have been affecting the Earth's temperature and causing global warming (IPCC 2013). In 1900, the mean $CO_2$ atmospheric dry molar fraction was 295.7 parts per million by volume (ppmv) and became 311.3 ppmv in 1950. Since then, it elevated up to 406.7 ppmv in 2017. The $CO_2$ level is expected to be around 443.7 by 2049 (Nazarenko *et al*. 2015). Another greenhouse gas, methane ($CH_4$) that is estimated to have between 20× and 80× the warming effect of the same amount of $CO_2$, has increased over the last century. In 1900, the mean $CH_4$ was 0.88 ppmv and escalated to 1.15 and 1.84 ppmv in 1950 and 2016, respectively (Bacastow *et al*. 1985; Keeling *et al*. 2005). To sum up, greenhouse gases have probably caused 0.5 to 1.3°C temperature increase from 1951 to 2010 during ongoing climate change (IPCC 2013).

The average global temperature has recently increased and ice sheet has been reduced in the Polar Regions (IPCC 2013). Terrestrial permafrost cover has been diminishing and additional $CO_2$ has been released to the atmosphere due to permafrost thawing (Schaefer *et al*. 2011; Walter Anthony *et al*. 2012). Moreover, snow cover has been declining (Lemke *et al*. 2007). The ability of the polar region to reflect heat back into the atmosphere (surface albedo) diminishes when snow and ice melt and this situation further advances the global warming. Furthermore, Arctic $CH_4$ emissions have been escalated in recent years (Dlugokencky *et al*. 2011). Vegetation in Arctic region has been quickly changing due to increased temperature and decreased sea ice according to satellite data (Bhatt *et al*. 2010). Therefore, the effects of climate change (especially warming) on the Polar regions are particularly important.

Long-term effects of climate change on vegetation, such as the phenology, can be detected using historical herbarium specimens (Primack *et al*. 2004; Miller-Rushing *et al*. 2006; Lavoie 2013; Willis *et al*. 2017). Approximately 350 million plant specimens have been collected and stored in 3000 herbaria worldwide since the 16$^{th}$ century (http://sweetgum.nybg.org/science/ih) and the digitization of herbarium specimens is underway in an increasing number of countries. Data obtained from herbarium records can allow us to track changes in plant morphology, distribution, flowering time (phenology), and species richness over long periods. Herbarium specimens can be considered as a reliable source to test the phenology and therefore, the number of studies using herbarium specimens has been recently increasing (Davis *et al*. 2015).

Numerous studies examined phenological responses of plants using herbarium specimens from several biomes: temperate (Rumpff *et al*. 2010; Park and Schwartz 2015), tropical (Boulter *et al*. 2006; Zalamea *et al*. 2011), desert (Bowers 2007; Neil *et al*. 2010), alpine (Gallagher *et al*. 2009; Mohandass *et al*. 2015), and Arctic (Panchen and Gorelick 2017). However, there are no herbarium studies in the subarctic biome (*e.g.*, Alaska) where is predicted to be one of the most affected areas under global climate change (IPCC 2013; Chapin *et al.* 2014; Baruah *et al.* 2017). For example, throughout the last century, there was 1.4°C increase in temperature of Alaska, USA, whereas this increase was 0.8°C in the rest of the World (Wendler and Shulski 2009). Although abovementioned studies already detected phenology shifts in plants from different biomes, subarctic plants have been under-examined and there is a knowledge gap regarding the phenology of subarctic plants.

In this study, phenological data concerning subarctic plant specimens were collected by using a herbarium database including one of the largest botanical collections worldwide (https://collections.nmnh.si.edu). The collection dates of 7146 herbarium specimens from subarctic America (from 1900 to 2018) were examined to analyze possible shifts in the phenology of subarctic plants (at the species, genus, and family levels) over the last century.

## Methods

Phenological data from herbarium specimens were gathered from the National Herbarium at the National Museum of Natural History, Smithsonian Institution in the US (https://collections.nmnh.si.edu) by selecting 'Catalog': Flowering Plants and Ferns, 'Biogeographical Region': Subarctic America, 'Collection Date': 1900-01-01 to 1949-12-31 and 1950-01-01 to 2018-01-01. Data were collected on 08 January 2018 when there were 2,576,508 total records in the database.

After a preliminary examination, three largest families were selected: Asteraceae, Cyperaceae, and Fabaceae. Criteria to be included in the analysis: a) specimens with an exact collection date including the day; b) specimens identified until species level; c) each species has at least 5 herbarium records in both periods (years: 1900–1949 versus 1950–2018). In total, 7146 herbarium records which met the selection criteria were chosen from 29 genera and 142 species and included in the analysis. Later, collection date formats were manually edited to calculate day of the year (*e.g.*, 25-07-1987 is the 206$^{th}$ day of the year). Some specimens contained a collection period (*e.g.*, from 20 to 23 July) instead of a single day. Only the first day of the collection was included in this analysis.

One-way analysis of variance (ANOVA) tests were carried out to determine statistical differences at the family, genus and species level across years. All statistical analyses were performed using JMP software v.13.2 (SAS Institute Inc., NC, USA) and graphs were prepared using SigmaPlot software v.12.5 (Systat Software Inc., CA, USA). Moreover, possible effects of sample overrepresentation on the overall result were tested with one-way ANOVA.

## Results

The overall result detected a significant difference between two periods (1900–1949 versus 1950–2018) ($p < 0.0001$). On average, collection dates of herbarium specimens have become approximately 4 days earlier (Table 1 and Fig. 1 for the complete dataset please see Appendix A, http://www.czasopisma.pan.pl/dlibra).

Table 1

Mean values for the collection day of the year versus years (1900–1949 versus 1950–2018). SE stands for the standard error.

| Period (years) | N | Collection day of the year | |
|---|---|---|---|
| | | Mean | SE |
| 1900–1949 | 4109 | 204.15 | 0.36 |
| 1950–2018 | 3037 | 200.58 | 0.42 |

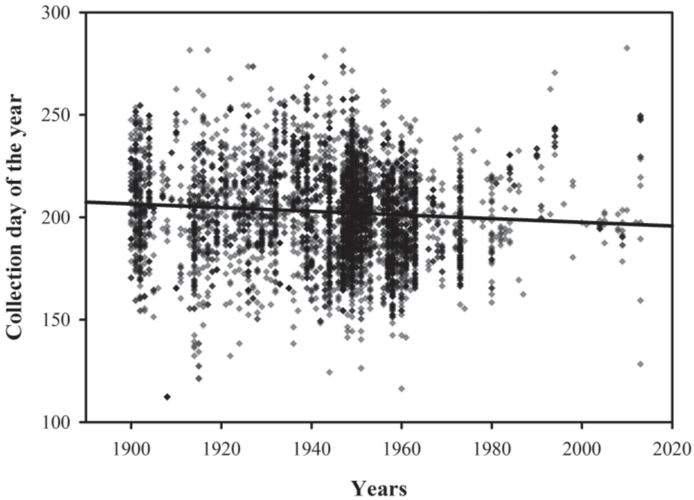


Fig. 1. Collection day of the year in subarctic plant specimens across years.

At the family level, Asteraceae and Cyperaceae indicated significant differences across periods, whereas in Fabaceae the difference was not significant according to one-way ANOVA tests (Fig. 2 and see Appendix B for ANOVA test results of three families, http://www.czasopisma.pan.pl/dlibra).

At the genus level, four out of 29 genera indicated statistically significant differences in flowering days according to one-way ANOVA tests (Table 2 and see Appendix C for ANOVA test results of all 29 genera, http://www.czasopisma.pan.pl/dlibra). In *Carex* genus that has the largest collected specimens, the difference

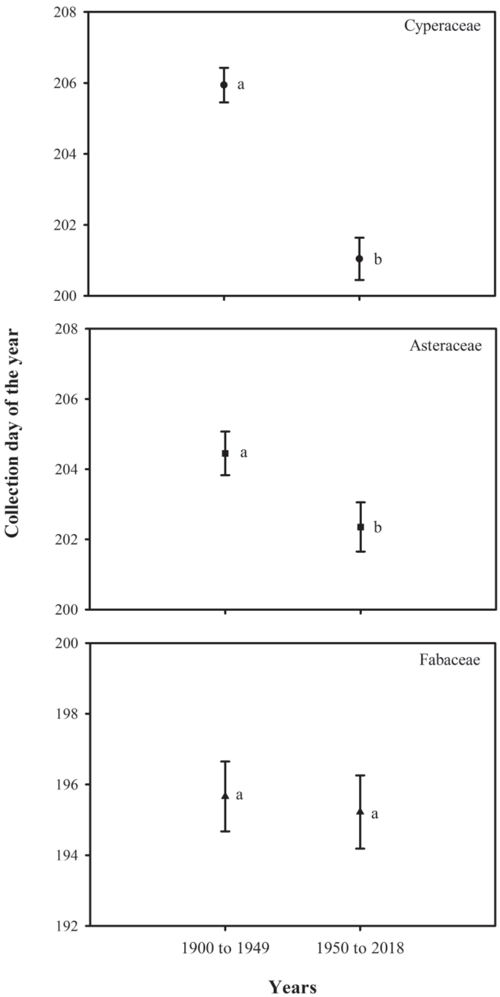


Fig. 2. Mean collection day of the year versus years (1900–1949 versus 1950–2018). Different letters indicate significant differences between groups ($p$<0.05).

between mean collection day of the year was 5.6 days and in other genera, the difference ranged from 12 to 25 days (Table 2).

At the species level, 21 out of 142 species indicated significant differences according to one-way ANOVA tests ($p \leq 0.05$) (Table 3 and see Appendix D for ANOVA test results of all 142 species, http://www.czasopisma.pan.pl/dlibra). *Carex aquatilis* that has the largest collected specimens, the difference between mean collection day of the year was 5.8 days and in other genera, the difference ranged from 9 to 26 days (Table 3). However, in five species, collection day of the year was delayed (8 to 19 days).

Table 2

Collection day of the year across years in all genera used in this analysis. *p*-values indicate one-way ANOVA test results. SE stands for the standard error.

| family | genus | 1900–1949 | | | 1950–2018 | | | Difference between means | *p*-value |
|---|---|---|---|---|---|---|---|---|---|
| | | N | Mean | SE | N | Mean | SE | | |
| Asteraceae | *Achillea* | 74 | 209.2 | 2.8 | 68 | 204.4 | 2.4 | 4.8 | 0.20 |
| Asteraceae | *Anaphalis* | 16 | 236.1 | 5.8 | 7 | 210.9 | 7.4 | 25.3 | **0.02** |
| Asteraceae | *Antennaria* | 34 | 192.5 | 4.2 | 12 | 188.4 | 4.1 | 4.1 | 0.59 |
| Asteraceae | *Arnica* | 190 | 199.0 | 2.0 | 106 | 200.1 | 1.7 | -1.2 | 0.70 |
| Asteraceae | *Artemisia* | 181 | 210.8 | 1.6 | 157 | 208.6 | 1.4 | 2.2 | 0.31 |
| Asteraceae | *Crepis* | 11 | 193.4 | 12.9 | 22 | 197.6 | 4.3 | -4.3 | 0.70 |
| Asteraceae | *Dendranthema* | 60 | 205.3 | 3.7 | 34 | 197.1 | 4.1 | 8.3 | 0.16 |
| Asteraceae | *Erigeron* | 178 | 205.0 | 1.7 | 118 | 200.9 | 1.7 | 4.1 | 0.11 |
| Asteraceae | *Eurybia* | 76 | 203.6 | 2.9 | 53 | 205.9 | 2.1 | -2.3 | 0.56 |
| Asteraceae | *Hieracium* | 18 | 224.2 | 4.5 | 8 | 211.9 | 5.4 | 12.3 | 0.12 |
| Asteraceae | *Matricaria* | 22 | 215.6 | 4.5 | 14 | 213.6 | 4.0 | 2.0 | 0.76 |
| Asteraceae | *Packera* | 37 | 196.3 | 3.0 | 39 | 198.6 | 3.5 | -2.3 | 0.62 |
| Asteraceae | *Petasites* | 69 | 192.1 | 3.0 | 77 | 190.8 | 2.5 | 1.3 | 0.74 |
| Asteraceae | *Saussurea* | 34 | 204.0 | 5.2 | 50 | 204.0 | 2.0 | 0.0 | 1.00 |
| Asteraceae | *Senecio* | 177 | 202.7 | 1.7 | 172 | 202.8 | 1.5 | -0.1 | 0.95 |
| Asteraceae | *Solidago* | 122 | 205.3 | 2.0 | 67 | 205.6 | 2.2 | -0.3 | 0.92 |
| Asteraceae | *Taraxacum* | 23 | 208.6 | 5.4 | 31 | 199.2 | 3.5 | 9.4 | 0.13 |
| Asteraceae | *Tripleurospermum* | 12 | 217.7 | 4.3 | 9 | 203.1 | 3.8 | 14.6 | **0.03** |
| Cyperaceae | *Carex* | 1809 | 206.6 | 0.6 | 1166 | 201.0 | 0.6 | 5.6 | **<.0001** |
| Cyperaceae | *Eleocharis* | 22 | 204.2 | 4.5 | 24 | 204.9 | 3.9 | -0.7 | 0.91 |
| Cyperaceae | *Eriophorum* | 328 | 201.9 | 1.6 | 272 | 201.0 | 1.4 | 0.9 | 0.69 |
| Cyperaceae | *Kobresia* | 31 | 219.7 | 3.4 | 19 | 207.5 | 5.1 | 12.2 | **0.04** |
| Cyperaceae | *Trichophorum* | 64 | 202.3 | 3.5 | 37 | 196.9 | 2.9 | 5.4 | 0.30 |
| Fabaceae | *Astragalus* | 119 | 196.7 | 2.2 | 177 | 193.5 | 1.7 | 3.1 | 0.26 |
| Fabaceae | *Hedysarum* | 96 | 196.5 | 2.3 | 91 | 201.3 | 2.1 | -4.9 | 0.12 |
| Fabaceae | *Lathyrus* | 76 | 200.9 | 2.9 | 36 | 194.0 | 2.9 | 6.9 | 0.14 |
| Fabaceae | *Lupinus* | 78 | 186.7 | 2.9 | 52 | 192.3 | 2.9 | -5.5 | 0.20 |
| Fabaceae | *Oxytropis* | 143 | 196.8 | 1.9 | 113 | 195.0 | 1.8 | 1.8 | 0.50 |
| Fabaceae | *Trifolium* | 9 | 189.0 | 8.4 | 6 | 188.8 | 4.2 | 0.2 | 0.99 |

Table 3

Collection day of the year across years in species indicated significant differences in their phenology ($p \leq 0.05$). SE stands for the standard error.

| family | species | 1900–1949 | | | 1950–2018 | | | Difference between means |
|---|---|---|---|---|---|---|---|---|
| | | N | Mean | SE | N | Mean | SE | |
| Asteraceae | *Anaphalis margaritacea* | 16 | 236.1 | 5.8 | 7 | 210.9 | 7.4 | 25.3 |
| Asteraceae | *Arnica angustifolia* | 16 | 181.1 | 3.1 | 9 | 196.0 | 4.7 | -14.9 |
| Asteraceae | *Arnica griscomii* | 44 | 190.9 | 2.8 | 29 | 199.4 | 3.3 | -8.5 |
| Asteraceae | *Arnica unalashcensis* | 15 | 233.1 | 7.1 | 7 | 206.9 | 9.0 | 26.3 |
| Asteraceae | *Erigeron peregrinus* | 47 | 213.1 | 3.4 | 17 | 198.6 | 3.4 | 14.5 |
| Asteraceae | *Senecio yukonensis* | 12 | 198.2 | 2.8 | 9 | 189.0 | 3.6 | 9.2 |
| Asteraceae | *Tripleurospermum maritimum* | 12 | 217.7 | 4.3 | 9 | 203.1 | 3.8 | 14.6 |
| Cyperaceae | *Carex aquatilis* | 134 | 209.9 | 2.1 | 112 | 204.1 | 2.0 | 5.8 |
| Cyperaceae | *Carex atrofusca* | 40 | 210.6 | 2.8 | 23 | 199.0 | 4.2 | 11.5 |
| Cyperaceae | *Carex bigelowii* | 55 | 212.4 | 2.2 | 80 | 196.4 | 2.1 | 16.1 |
| Cyperaceae | *Carex bipartita* | 57 | 218.7 | 2.2 | 8 | 201.8 | 5.6 | 17.0 |
| Cyperaceae | *Carex media* | 25 | 180.0 | 3.7 | 13 | 199.2 | 4.0 | -19.3 |
| Cyperaceae | *Carex nigricans* | 16 | 235.1 | 5.0 | 7 | 215.0 | 5.9 | 20.1 |
| Cyperaceae | *Carex paupercula* | 13 | 197.6 | 3.8 | 8 | 210.6 | 4.5 | -13.0 |
| Cyperaceae | *Carex podocarpa* | 42 | 212.6 | 3.2 | 43 | 196.6 | 2.6 | 16.0 |
| Cyperaceae | *Carex rariflora* | 34 | 216.4 | 3.9 | 20 | 199.9 | 3.4 | 16.5 |
| Cyperaceae | *Carex subspathacea* | 22 | 210.7 | 3.3 | 6 | 194.0 | 10.3 | 16.7 |
| Cyperaceae | *Carex williamsii* | 10 | 221.5 | 4.2 | 11 | 195.0 | 3.9 | 26.5 |
| Cyperaceae | *Kobresia simpliciuscula* | 31 | 219.7 | 3.4 | 19 | 207.5 | 5.1 | 12.2 |
| Fabaceae | *Lathyrus palustris* | 26 | 210.8 | 3.8 | 14 | 190.6 | 5.0 | 20.2 |
| Fabaceae | *Lupinus polyphyllus* | 42 | 181.9 | 3.8 | 35 | 194.1 | 3.4 | -12.2 |

In this analysis, *Carex* genus has a high number of records. Therefore, all *Carex* species were excluded and one-way ANOVA tests were rerun to check if overrepresentation of a genus affected the overall results. It was found that the exclusion of *Carex* species did not change the results and there were still significant phenological differences between the periods of 1900–1949 and 1950–2018.

## Discussion

The main finding of this study indicated that there are apparent shifts in the phenology of subarctic plants over the last century (Figs. 1 and 2). The flowering time significantly shifted from 8 to 26 days in some species (Table 3) and most of the subarctic plants flowered earlier in 1950–2018 period compared to 1900–1949, probably due to the climate change. Most subarctic plants have probably been taking the advantage of warmer climatic conditions and started flowering earlier due to advanced spring and summer phases. Snowmelt timing can greatly affect the flowering timing (Delnevo *et al*. 2018). For example, earlier snowmelt in spring allows an earlier flowering in Alaska (Wendler and Shulski 2009). Satellite observations of Arctic Russia also confirm significant shifts in vegetation phenology due to the climate change (Zeng *et al*. 2013). Similarly, increased temperatures in subarctic regions have been causing an earlier flowering (Park 2016).

A long-term experimental warming study in tundra found that the values of plant traits (*i.e*., biomass, height, and leaf traits) were increased due to increased temperature (Baruah *et al*. 2017). In Arctic Alaska, the total aboveground phytomass is expected to increase under increasing temperature (Walker *et al*. 2003). These findings suggest that there will be changes in species interactions due to the increased competitive ability of some species. Moreover, plant productive response to experimental warming is higher in tundra compared to grassland and forest ecosystems (Rustad *et al*. 2001). Similarly, Arctic plants generally respond to global warming by flowering earlier (Hollister *et al*. 2005; Barrett *et al*. 2016).

Responses of plants to changing climate are species-specific as each species has a different evolutionary history (Menzel *et al*. 2006; Gray and Brady 2016). In this analysis, some subarctic plants (*i.e*., *Arnica angustifolia*, *Arnica griscomii*, *Carex media*, *Carex paupercula*, *Lupinus polyphyllus*) delayed flowering in 1950–2018 period compared to 1900–1949 (Table 3). Climate change has probably prolonged the growing season because of warming and earlier snowmelt in subarctic America (IPCC 2013; Chapin *et al*. 2014). For example, there is 45% increase in growing season length in Alaska (Wendler and Shulski 2009). The number of snow-free days has been increasing 5–6 days per decade in the Northern Hemisphere (Dye 2002). Consequently, some species may take advantage of this prolonged season in the Polar Regions to grow larger and produce more seeds in the long term by delaying flowering as suggested by the plant strategy theory (Grime 1979; Campbell and Grime 1992).

Herbarium specimens may have a potential limitation such as flowering stage of collected plants (*i.e*., early or late flowering stage). However, herbarium specimens usually reflect field observations of the first flowering period (Davis *et al*. 2015). Therefore, the collection day of herbarium specimens is a good proxy for the flowering time because plant individuals are usually collected by botanists when they blossom. Moreover, herbarium specimens are widely used in the literature to track phenological changes (Primack *et al*. 2004; Lavoie 2013). In future, more data will be available from herbarium specimens to examine the past environmental conditions as the digitization of herbarium specimens accelerates (Willis *et al*. 2017). In this study, a large number of analyzed specimens and species (N=7146 and 142 in total; respectively) prevents a potential bias in phenological data. The results of this study are statistically significant and therefore reliable.

The ability to respond to climatic changes is crucial especially for plant species as they are sessile. Changes in performance, reproductive and functional traits of plants can determine plant adaptations and their existence (Gugger *et al*. 2015; Nazarenko *et al*. 2015; Gray and Brady 2016). It is difficult to isolate direct connections (*e.g*., a cause and effect relationship) between the climate change and plant phenology, but apparent changes in phenology of several subarctic plants were detected in this study. Understanding of plant responses is important for conservation management, ecotourism activities, agricultural practices, ecosystem services, and urban ecology applications. Analysis of herbarium specimens as archives indicating the relationships between plants and their past environmental conditions can provide invaluable information and better insight into future responses of plants, especially under ongoing climate change.

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## References

BACASTOW R.B., KEELING C.D. and WHORF T.P. 1985. Seasonal amplitude increase in atmospheric $CO_2$ concentration at Mauna Loa, Hawaii, 1959–1982. *Journal of Geophysical Research* 90: 10529–10540.

BARRETT R.T. and HOLLISTER R.D. 2016. Arctic plants are capable of sustained responses to long-term warming. *Polar Research* 35: 25405.

BARUAH G., MOLAU U., BAI Y. and ALATALO J.M. 2017. Community and species-specific responses of plant traits to 23 years of experimental warming across subarctic tundra plant communities. *Scientific Reports* 7: 2571.

BHATT U.S., WALKER D.A., RAYNOLDS M.K., COMISO J.C., EPSTEIN H.E., GENSUO J.G., GENS R., PINZON J.E., TUCKER C.J., TWEEDIE C.E. and WEBBER P.J. 2010. Circumpolar arctic tundra vegetation change is linked to sea ice decline. *Earth Interactions* 14: 1–20.

BOULTER S.L., KITCHING R.L. and HOWLETT B.G. 2006. Family, visitors and the weather: patterns of flowering in tropical rain forests of northern Australia. *Journal of Ecology* 94: 369–382.

BOWERS J.E. 2007. Has climatic warming altered spring flowering date of Sonoran desert shrubs? *Southwestern Naturalist* 52: 347–355.

CAHILL A.E., AIELLO-LAMMENS M.E., FISHER-REID M.C., HUA X., KARANEWSKY C.J., RYU H.Y., SBEGLIA G.C., SPAGNOLO F., WALDRON J.B. and WARSI O. *et al*. 2012. How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences* 280: 20121890.

CAMPBELL B.D. and GRIME J. 1992. An experimental test of plant strategy theory. *Ecology* 73: 15–29.

CHAPIN F.S.III., TRAINOR S.F., COCHRAN P., HUNTINGTON H., MARKON C., MCCAMMON M., MCGUIRE A.D. and SERREZE M. 2014. *Ch. 22: Alaska*. *Climate Change Impacts in the United States: The Third National Climate Assessment*. *In*: J.M. Melillo, Terese T.C. Richmond, and G.W. Yohe (eds), U.S. Global Change Research Program, 514–536.

CLAVEL J., JULLIARD R. and DEVICTOR V. 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and Environment* 9: 222–228.

DAVIS C.C., WILLIS C.G., CONNOLLY B., KELLY C. and ELLISON A.M. 2015. Herbarium records are reliable sources of phenological change driven by climate and provide novel insights into species' phenological cueing mechanisms. *American Journal of Botany* 102: 1599–1609.

DELNEVO N., PETRAGLIA A., CARBOGNANI M., VANDVIK V. and HALBRITTER A.H. 2018. Plastic and genetic responses to shifts in snowmelt time affects the reproductive phenology and growth of *Ranunculus acris*. *Perspectives in Plant Ecology, Evolution and Systematics* 30: 62–70.

DLUGOKENCKY E., NISBET E., FISHER R. and LOWRY D. 2011. Global atmospheric methane: Budget, changes and dangers. *Philosophical transactions-Royal Society. Biological Sciences* 369: 2058–2072.

DYE D.G. 2002. Variability and trends in the annual snow-cover cycle in Northern Hemisphere land areas, 1972–2000. *Hydrological Processes* 16: 3065–3077.

ELMENDORF S.C., HENRY G.H., HOLLISTER R.D., BJÖRK R.G., BJORKMAN A.D., CALLAGHAN T.V., COLLIER L.S., COOPER E.J., CORNELISSEN J.H. and DAY T.A. *et al*. 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters* 15: 164–175.

GALLAGHER R.V., HUGHES L. and LEISHMAN M.R. 2009. Phenological trends among Australian alpine species: using herbarium records to identify climate-change indicators. *Australian Journal of Botany* 57: 1–9.

GRAY S.B. and BRADY S.M. 2016. Plant developmental responses to climate change. *Developmental Biology* 419: 64–77.

GRIME J.P. 1979. *Plant Strategies and Vegetation Processes*. John Wiley & Sons, Chichester, 222 pp.

GUGGER S., KESSELRING H., STOECKLIN J. and HAMANN E. 2015. Lower plasticity exhibited by high- versus mid-elevation species in their phenological responses to manipulated temperature and drought. *Annals of Botany* 116: 953–962.

HOLLISTER R.D., WEBBER P.J. and TWEEDIE C.E. 2005. The response of Alaskan Arctic tundra to experimental warming: differences between short- and long-term responses. *Global Change Biology* 11: 525–536.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, United Kingdom and NY, USA, 1535 pp.

JURASINSKI G. and KREYLING J. 2007. Upward shift of alpine plants increases floristic similarity of mountain summits. *Journal of Vegetation Science* 18: 711–718.

KEELING C.D., PIPER S.C., BACASTOW R.B., WAHLEN M., WHORF T.P., HEIMANN M. and MEIJER H.A. 2005. Atmospheric $CO_2$ and $^{13}CO_2$ exchange with the terrestrial biosphere and oceans from 1978 to 2000: observations and carbon cycle implications. *In*: J.R. Ehleringer, T.E. Cerling, and M.D. Dearing (eds) *A History of Atmospheric $CO_2$ and its effects on Plants, Animals, and Ecosystems*. Springer Verlag, New York, USA: 83–113.

LAVOIE C. 2013. Biological collections in an ever changing world: Herbaria as tools for biogeographical and environmental studies. *Perspectives in Plant Ecology, Evolution and Systematics* 15: 68–76.

LEMKE P., REN J., ALLEY R.B., ALLISON I., CARRASCO J., FLATO G., FUJII Y., KASER G., MOTE P., THOMAS R.H. and ZHANG T. 2007. Observations: Changes in Snow, Ice and Frozen Ground. *In*: S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds) *Climate Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA: 1–48.

MAESTRE F.T., ELDRIDGE D.J., SOLIVERES S., KEFI S., DELGADO-BAQUERIZO M., BOWKER M.A., GARCIA-PALACIOS P., GAITAN J., GALLARDO A. and LAZARO R. *et al*. 2016. Structure and functioning of dryland ecosystems in a changing world. *Annual Review of Ecology, Evolution, and Systematics* 47: 215–237.

MENENDEZ R., MEGIAS A.G., HILL JK., BRASCHLER B., WILLIS S.G., COLLINGHAM Y., FOX R., ROY D.B. and THOMAS C.D. 2006. Species richness changes lag behind climate change. *Proceedings of the Royal Society B: Biological Sciences* 273: 1465–1470.

MENZEL A., SPARKS TH., ESTRELLA N., KOCH E., AASA A., AHAS R., ALM-KÜBLER K., BISSOLLI P., BRASLAVSKA O. and BRIEDE A. *et al*. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12: 1969–1976.

MILLER-RUSHING AJ., PRIMACK R.B., PRIMACK D. and MUKUNDA S. 2006. Photographs and herbarium specimens as tools to document phenological changes in response to global warming. *American Journal of Botany* 93: 1667–1674.

MOHANDASS D., ZHAO J.L., XIA Y.M., CAMPBELL M.J. and LI Q.J. 2015. Increasing temperature causes flowering onset time changes of alpine ginger Roscoea in the Central Himalayas. *Journal of Asia-Pacific Biodiversity* 8: 191–198.

NAZARENKO L., SCHMIDT G.A., MILLER R.L., TAUSNEV N., KELLEY M., RUEDY R., RUSSELL G.L., ALEINOV I., BAUER M., BAUER S. and BLECK R. *et al*. 2015. Future climate change under RCP emission scenarios with GISS ModelE2. *Journal of Advances in Modeling Earth Systems* 7: 244–267.

NEIL K.L., LANDRUM L. and WU JG. 2010. Effects of urbanization on flowering phenology in the metropolitan phoenix region of USA: findings from herbarium records. *Journal of Arid Environments* 74: 440–444.

PANCHEN Z.A. and GORELICK R. 2017. Prediction of Arctic plant phenological sensitivity to climate change from historical records. *Ecology and Evolution* 7: 1325–1338.

PARK I.W. and SCHWARTZ M.D. 2015. Long-term herbarium records reveal temperature-dependent changes in flowering phenology in the southeastern USA. *International Journal of Biometeorology* 59: 347–355.

PARK I.W. 2016. Timing the bloom season: a novel approach to evaluating reproductive phenology across distinct regional flora. *Landscape Ecology* 31: 1567–1579.

PARMESAN C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* 13: 1860–1872.

PRIMACK D., IMBRES C., PRIMACK R.B., MILLER-RUSHING A.J. and TREDIC P.D. 2004. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany* 91: 1260–1264.

RICHARDSON A.D., KEENAN T.F., MIGLIAVACCA M., RYU Y., SONNENTAG O. and TOOMEY M. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169: 156–173.

RUMPFF L., COATES F. and MORGAN J.W. 2010. Biological indicators of climate change: evidence from long-term flowering records of plants along the Victorian coast, Australia. *Australian Journal of Botany* 58: 428–439.

RUSTAD L.E., CAMPBELL J.L., MARION G.M., NORBY R.J., MITCHELL M.J., HARTLEY A.E., CORNELISSEN J.H.C. and GUREVITCH J. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126: 543–562.

SCHAEFER K., ZHANG T., BRUHWILER L. and BARRETT A. 2011. Amount and timing of permafrost carbon release in response to climate warming. *Tellus B* 63: 165–180.

STURM M., RACINE C. and TAPE K. 2001. Climate change – increasing shrub abundance in the Arctic. *Nature* 411: 546–547.

THIERS B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. (http://sweetgum.nybg.org/science/ih) (accessed: January 2018).

WALKER D.A., EPSTEIN H.E., JIA G.J., BALSER A., COPASS C., EDWARDS E.J., GOULD W.A., HOLLINGSWORTH J., KNUDSON J., MAIER H.A., MOODY A. and RAYNOLDS M.K. 2003. Phytomass, LAI, and NDVI in northern Alaska: Relationships to summer warmth, soil pH, plant functional types, and extrapolation to the circumpolar Arctic. *Journal of Geophysical Research* 108: 8169.

WALTER ANTHONY K.M., ANTHONY P., GROSSE G. and CHANTON J. 2012. Geologic methane seeps along boundaries of Arctic permafrost thaw and melting glaciers. *Nature Geoscience* 5: 419–426.

WALTHER G.R., POST E., CONVEY P., MENZEL A., PARMESAN C., BEEBEE T.J., FROMENTIN J.M., HOEGH-GULDBERG O. and BAIRLEIN F. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.

WENDLER G. and SHULSKI M. 2009. A Century of Climate Change for Fairbanks, Alaska. *Arctic* 62: 295–300.

WILLIS C.G., ELLWOOD E.R., PRIMACK R.B., DAVIS C.C., PEARSON K.D., GALLINAT A.S., YOST J.M., NELSON G., MAZER S.J., ROSSINGTON N.L., SPARKS T.H. and SOLTIS P.S. 2017. Old Plants, New Tricks: Phenological Research Using Herbarium Specimens. *Trends in Ecology & Evolution* 32: 531–546.

ZALAMEA P.C., MUNOZ F., STEVENSON P.R., PAINE C.E.T., SARMIENTO C., SABATIER D. and HEURET P. 2011. Continental-scale patterns of *Cecropia* reproductive phenology: evidence from herbarium specimens. *Proceedings of the Royal Society B Biological Sciences* 278: 2437–2445.

ZENG H., JIA G. and FORBES B.C. 2013. Shifts in Arctic phenology in response to climate and anthropogenic factors as detected from multiple satellite time series. *Environmental Research Letters* 8: 035036.

ZHU J., ZHANG Y. and JIANG L. 2017. Experimental warming drives a seasonal shift of ecosystem carbon exchange in Tibetan alpine meadow. *Agricultural and Forest Meteorology* 233: 242–249.

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