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Citation for published version:

Bjorkman, AD, García Criado, M, Myers-smith, IH, Ravolainen, V, Jónsdóttir, IS, Westergaard, KB, Lawler, JP, Aronsson, M, Bennett, B, Gardfjell, H, Heiðmarsson, S, Stewart, L & Normand, S 2019, 'Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring', *AMBIO*.
<https://doi.org/10.1007/s13280-019-01161-6>

Digital Object Identifier (DOI):

[10.1007/s13280-019-01161-6](https://doi.org/10.1007/s13280-019-01161-6)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

AMBIO

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Status and trends in Arctic vegetation: evidence from experimental warming and long-term monitoring

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Acknowledgements

ADB was supported by The Danish Council for Independent Research - Natural Sciences (DFR 4181-00565 to SN). MGC was funded by the University of Edinburgh, IHMS by the UK Natural Environment Research Council (ShrubTundra Project NE/M016323/1) and SN by the Villum Foundation's Young Investigator Programme (VKR023456).

Author biographies

Anne D. Bjorkman is a postdoctoral scholar at the Senckenberg Biodiversity and Climate Research Centre. Her research interests include biogeography, functional ecology, and community ecology, with a particular focus on the ecological consequences of climate change in tundra ecosystems.

Mariana García Criado is a PhD candidate at The University of Edinburgh (Scotland). She is a conservation scientist specialized in macroecology and biogeography, and is currently working to quantify vegetation shifts under climate change in extreme biomes such as the tundra and the savannah.

Isla H. Myers-Smith is a Chancellor's Fellow and Senior Lecturer at the University of Edinburgh. Her research quantifies how global change alters plant communities and ecosystem processes, with a focus on the tundra biome.

Signe Normand is an Associate Professor at Aarhus University. She is a macro- and vegetation ecologist dedicated to understanding patterns of species' occurrence and biodiversity. The main goal of her research is to find answers to fundamental questions in ecology, but also to inform nature conservation about the impact of global change on biodiversity. Her current research is focused on understanding global change effects on Arctic ecosystems by dendroecological and drone-based investigations.

1 **Status and trends in Arctic vegetation: evidence from experimental warming and long-term**
2 **monitoring**

3
4 **Abstract**

5
6 Changes in Arctic vegetation can have important implications for trophic interactions and ecosystem
7 functioning leading to climate feedbacks. Plot-based vegetation surveys provide detailed insight into
8 vegetation changes at sites around the Arctic and improve our ability to predict the impacts of
9 environmental change on tundra ecosystems. Both long-term monitoring and experimental
10 manipulation of environmental drivers (e.g. temperature) have shown impacts of environmental
11 change, particularly climate warming, on tundra vegetation. Here, we review 30 studies of vegetation
12 change and 12 studies of phenological change from both long-term monitoring and warming
13 experiments in Arctic environments, including vegetation attributes identified in international
14 assessments as monitoring priorities. General responses to natural or experimental warming include
15 an increase in overall plant cover, particularly in the abundance of shrubs and grasses, and a decrease
16 in lichens and mosses, but the most common abundance response was one of no change. Plant
17 phenology often advanced in response to experimental warming, but trends over time varied by site,
18 species, and phenostage. This synthesis demonstrates that Arctic plant communities and species are
19 generally sensitive to warming, but trends over time are heterogeneous and complex and do not
20 always mirror expectations based on responses to experimental manipulations. Our findings highlight
21 the need for more geographically widespread, integrated and comprehensive monitoring efforts that
22 can better resolve the interacting effects of warming and other local and regional ecological factors.

23
24 **Keywords**

25
26 vegetation change, phenology, Arctic, experimental warming, long-term monitoring

27
28 **Introduction**

29
30 A major goal of global change ecology is to document and predict the impacts of environmental
31 change on species, communities and ecosystems worldwide. In the Arctic, exceptionally rapid
32 warming (IPCC 2013) has the potential to lead to dramatic changes in vegetation through longer
33 growing seasons, increased thaw depth, and altered snow regimes. High latitudes contain up to 50%
34 of the world's soil carbon stored in permafrost soils; this carbon is vulnerable to loss with warming
35 (Schuur et al. 2015; Crowther et al. 2016; van Gestel et al. 2018). Thus, change in vegetation carbon
36 and nutrient inputs to tundra soils could have potentially global impacts. For example, shifts in
37 species composition could lead to changes in aboveground carbon storage, nutrient cycling,

38 decomposition rates, and albedo (Callaghan et al. 2004), potentially leading to global climate
39 feedbacks (Chapin et al. 2005; Pearson et al. 2013). Changing vegetation could also alter trophic
40 interactions (Post et al. 2009; Gauthier et al. 2013) and thus influence Arctic wildlife populations and
41 the human communities that rely on them for resource provision or cultural purposes (Weller et al.
42 2004; Henry et al. 2012; Stern and Gaden 2015).

43

44 A key source of information about the consequences of climate warming for Arctic vegetation comes
45 from plot-based research at sites across the Arctic (Henry and Molau 1997). This includes both long-
46 term monitoring of species composition, diversity, and phenology over time (up to four decades), as
47 well as experimental manipulation of key abiotic and biotic drivers (e.g., temperature, snow, nutrients,
48 grazing). Community composition, diversity, and phenology have all been identified as “Focal
49 Ecosystem Components” (FECs) by the international Circumpolar Biodiversity Monitoring Program
50 (Christensen et al. 2013), as monitoring of these attributes facilitates a more rapid detection,
51 communication, and response to significant biodiversity-related trends and pressures affecting the
52 circumpolar world. In addition, comparing the results of observed trends over time with experimental
53 studies can help to elucidate the drivers of observed trends and inform predictions of future change
54 (Elmendorf et al. 2015).

55

56 Here, we synthesize what is currently known about plot-based changes in vegetation composition
57 (abundance), phenology, diversity, and functional traits. We compiled information from single-site
58 studies of composition and phenological change to document 1) the direction and significance of
59 change over time, and 2) the direction and significance of responses to experimental warming. We
60 compare these results to published syntheses of long-term monitoring and experimental warming. We
61 additionally review studies of plot-based changes in plant functional traits and diversity, for which
62 published observations are relatively scarce. Finally, we discuss the broader implications of observed
63 and predicted Arctic vegetation change and recommend priorities for future monitoring efforts.

64

65 **Materials and Methods**

66

67 *Literature review of vegetation trends*

68

69 We conducted a literature review to identify single-site studies of changes in plant community
70 composition (abundance) and phenology both over time and in response to experimental warming.
71 Our search included combinations of the terms “tundra”, “arctic”, “vegetation”, “plot”, “change”,
72 “ITEX”, “cover”, “abundance”, “phenology”, “diversity”, “functional trait”, “warming”, and
73 “experiment”. These terms encompasses two Focal Ecosystem Components included in the
74 Circumpolar Biodiversity Monitoring Program terrestrial monitoring plan: i) diversity, composition

75 and abundance and ii) phenology. We do not include the attributes “diversity and spatial structure”,
76 “productivity”, “Rare species, species of concern”, or “food species” in this review due to a paucity of
77 published plot-based monitoring and/or experimental studies on these topics. The attribute “non-
78 native species” is addressed in a separate article in this issue [WASOWICZ ET AL., THIS ISSUE].
79

80 We included only studies at sites above 63 °N and identified as “Arctic” or “tundra” by the authors.
81 This latitudinal cut-off includes some sub-Arctic sites but is roughly comparable to areas included in
82 the Arctic Biodiversity Assessment (CAFF 2013 2013). For community composition/abundance, we
83 included measured responses in any variable called abundance, biomass, or percent cover. We
84 included studies that analyzed changes in abundance at both the species and functional group level.
85 For studies where abundance trends were identified at the species level, we included all species but
86 grouped them by functional group for visualization purposes. All phenological responses were
87 provided at the species level.
88

89 For phenological studies, we recorded all phenostages provided by the authors, but here we report
90 only the most commonly observed phenostages: leaf emergence, flowering, and leaf senescence. Leaf
91 emergence is the day at which leaf bud-break first occurs or the first day on which overwintered
92 leaves re-green. Flowering encompasses several phases related to the timing of flowering, including
93 inflorescence elongation, first open flower, onset of pollen release, and peak flowering. Leaf
94 senescence is the date on which leaves change color or die, indicating the end of the growing season
95 for most plants. Studies reporting responses of diversity and/or functional traits were scarce; thus, we
96 review the available information but do not attempt to categorize and quantify these responses.
97

98 For all studies we recorded the direction (increase/stable/decrease for abundance change, or
99 earlier/stable/later for phenological change) and significance (yes/no) of responses for all species and
100 functional groups identified. A response could be recorded as directional (increase/decrease or
101 earlier/later) and non-significant if the authors identified it as such, or if the p-value provided was
102 between 0.05 and 0.1. We adopted this approach in order to standardize alpha levels across all studies
103 (e.g. if some studies used an alpha level cut-off of 0.05 to assess significance while others used an
104 alpha level of 0.1). If a response was identified by the authors as directional but no indication of
105 significance was given (either in the text or in a figure/table), the response was categorized as non-
106 significant. The difference between significant and non-significant directional changes is shown in the
107 figures and provided in the supplementary data table. We used this “vote-counting” approach, rather
108 than a traditional meta-analysis, in order to include the many studies that do not provide response
109 effect sizes or estimates of error. In addition, this approach allows us to visualize the full distribution
110 of vegetation responses to ambient and experimental warming, as a meta-analysis finding of “no-

111 change” could in fact be made up of multiple significant changes in different directions (e.g. context
112 dependency).

113

114 Experimental warming was generally conducted through the use of clear-sided, open-top chambers
115 that passively warm air temperatures by ~1.5-3 °C, with most of the studies following International
116 Tundra Experiment (ITEX) protocols (Molau and Mølgaard 1996; Marion et al. 1997), though some
117 experiments used greenhouses or other warming methods (Chapin and Shaver 1996; Wang et al.
118 2017). The seasonal duration of warming also varies by study; some warming chambers were in place
119 only during the summer, while others were present year-round. Both warming chambers and
120 greenhouses can influence environmental factors other than temperature (e.g. soil moisture, wind,
121 snow accumulation), though the magnitude and significance of these effects are variable among sites
122 (Marion et al. 1997).

123

124 *Comparison to tundra-wide syntheses*

125

126 In order to evaluate the consistency of patterns revealed by the literature review, we compared the
127 results of our review with tundra-wide syntheses of community composition and phenological change
128 (Arft et al. 1999; Walker et al. 2006; Elmendorf et al. 2012a; Elmendorf et al. 2012b; Oberbauer et al.
129 2013), both over time and in response to experimental warming. These syntheses used primary data
130 and were not based on published studies, though some data included in the syntheses may be from the
131 same sites as the single-site studies included in our literature review. However, the synthesis and
132 single-site studies likely include different combinations of sites and years, and use different statistical
133 methods to analyze responses. In addition, many of the synthesis studies included both Arctic and
134 alpine tundra sites, while here we focused exclusively on Arctic and sub-Arctic locations. Thus,
135 evidence that synthesis studies found trends consistent with those documented in this literature review
136 can help evaluate the robustness of observed patterns in Arctic vegetation change.

137

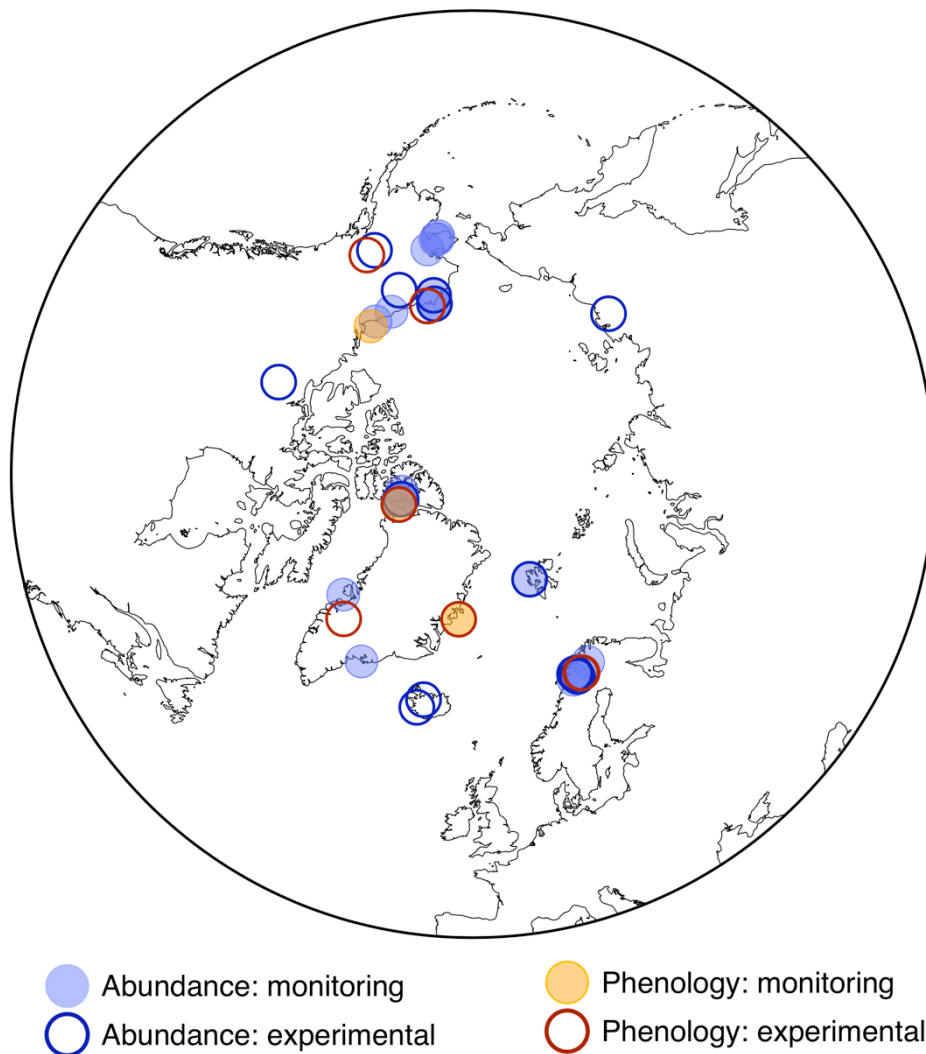
138 **Results**

139

140 We identified a total of 560 vegetation composition/abundance observations (species or functional
141 group) from 19 studies of long-term monitoring and 209 observations from 14 studies of responses to
142 experimental warming (Figure 1, Table 1). The duration of monitoring studies ranged from five to 43
143 years, with a median duration of 19 years. We additionally identified long-term monitoring of
144 phenology for 17 species in three studies and responses to experimental warming of 52 species from
145 nine studies (Figure 1, Table 1). Phenological monitoring studies ranged from nine to 21 years in
146 duration, with a median duration of 16 years.

147

148 Our literature review reveals geographical gaps in both long-term monitoring and experimental
 149 warming studies. The FEC (Christensen et al. 2013) encompassing composition and abundance is
 150 better represented than that encompassing phenology, but both lack published records of change from
 151 Siberia and wide swaths of the Canadian Arctic. Intensive, multivariate monitoring is concentrated
 152 primarily in Alaska and Scandinavia, with the exception of one site in high-Arctic Canada (Muc et al.
 153 1989; Freedman and Svoboda 1994; Hudson and Henry 2009; Hill and Henry 2011; Bjorkman et al.
 154 2015).



156
 157 *Figure 1. Map of plot-based vegetation change studies identified in a review of the literature. Blue points*
 158 *designate studies of community composition (abundance) change, while orange points designate studies of*
 159 *phenological change. Filled circles denote long-term monitoring studies (change over time) while open circles*
 160 *indicate experimental studies (responses to experimental warming).*

161
 162 *Vegetation composition change*

163 In all cases, the most common response documented by long-term monitoring of compositional
 164 change was one of no trend (52-84% of trends did not differ from zero, depending on the significance

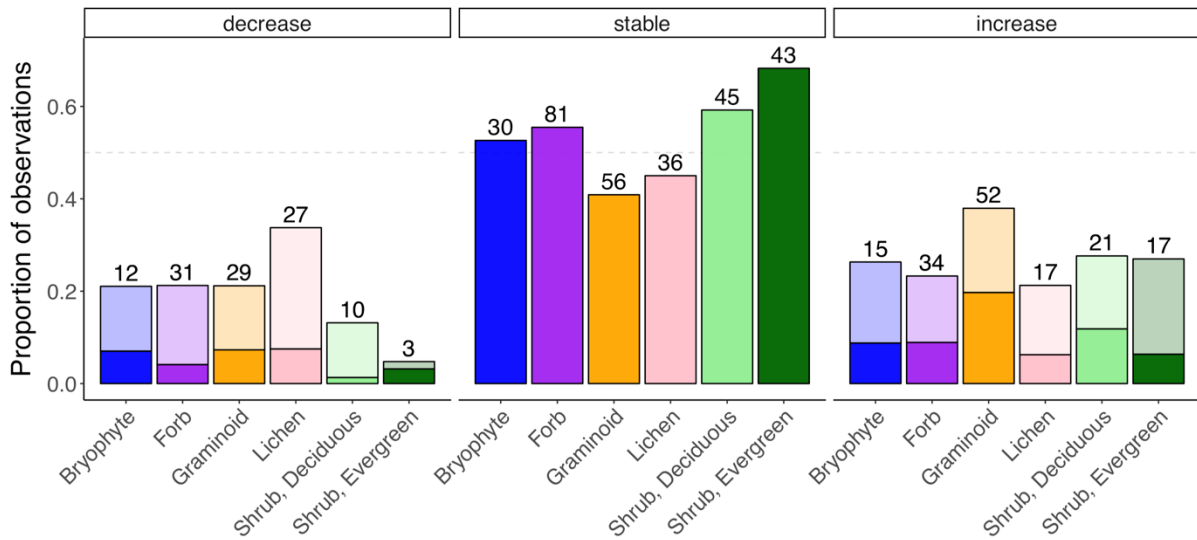
165 cutoff used; Figure 2). This is likely an underestimate of the proportion of no-change responses, as
166 some studies reported results only for species that changed significantly over time (Tømmervik et al.
167 2004). Forbs, graminoids and both evergreen and deciduous shrubs were slightly more likely to
168 increase in abundance over time than decrease, but were most likely to remain stable. Experimental
169 warming led to more dramatic responses, particularly in lichens, which were far more likely to
170 decrease in abundance in response to experimental warming (46-63%) than to increase (0%) or
171 remain stable (37%). Bryophytes also had a tendency to respond negatively to experimental warming,
172 while evergreen and deciduous shrubs were more likely to respond positively.

173

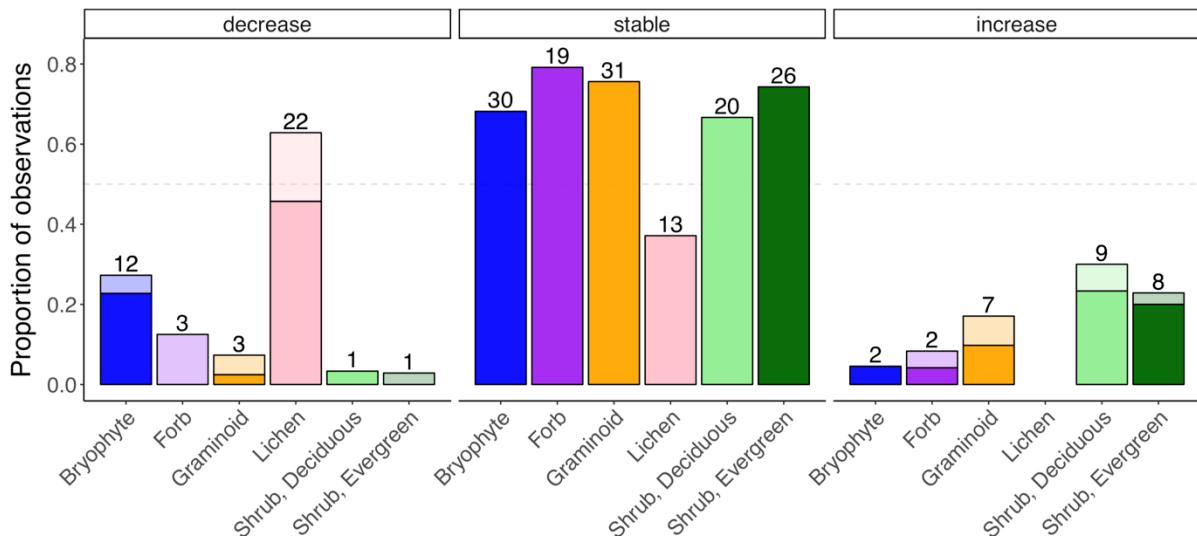
174 Few studies included both above- and below-ground measurements; of those that did, above- and
175 below-ground responses were not always consistent. Above-ground responses to experimental
176 warming in northern Alaska were greater than below-ground responses (Chapin and Shaver 1996), but
177 below-ground biomass increased more than above-ground biomass over 30 years of monitoring at
178 Alexandra Fiord, Ellesmere Island (Hill and Henry 2011). At Daring Lake, Canada, experimental
179 warming enhanced both above- and below-ground biomass in evergreen shrubs, but only above-
180 ground biomass in deciduous shrubs (Zamin et al. 2014).

181

a) Direction of abundance change over time



b) Abundance response to experimental warming



182

183 *Figure 2. Summary of studies investigating abundance change over time (a) and abundance change in response*
 184 *to experimental warming (b) by species or functional group. Panels represent, from left to right, the proportion*
 185 *of observations decreasing in abundance, stable, or increasing in abundance over time (median 20.5 years) or in*
 186 *response to experimental warming. Species-specific trends were grouped into the relevant functional group*
 187 *category. The darker portions of each bar represent “significant” ($p < 0.05$) change (decrease or increase) or*
 188 *insignificant (stable; $p > 0.1$) results, while lighter colors represent borderline or marginally significant change*
 189 *(e.g., p -values between 0.05 and 0.1). The numbers above each bar represent a count of the number of*
 190 *observations included in that group. The proportion of “stable” species is underrepresented in this figure, as*
 191 *some studies only reported results for species that changed in abundance.*

192

193

194

195

196

197

These responses are largely in line with those revealed in tundra-wide syntheses of vegetation change at the functional group level. In a recent thirty-year study of vegetation change across 46 Arctic, alpine and Antarctic tundra locations (Elmendorf et al. 2012b), only evergreen shrubs (but not deciduous) increased significantly over time. Bryophytes were more likely to decrease than increase, but the response was not significant. Similar to results from our literature review, responses to experimental warming were more dramatic. Deciduous but not evergreen shrubs increased

198 significantly in abundance in response to experimental warming, while both lichens and bryophytes
199 decreased significantly (Elmendorf et al. 2012a). In both monitoring and experimental synthesis
200 studies, the quantity of dead material (litter and attached dead) increased over time or with warming
201 (Elmendorf et al. 2012a; Elmendorf et al. 2012b).

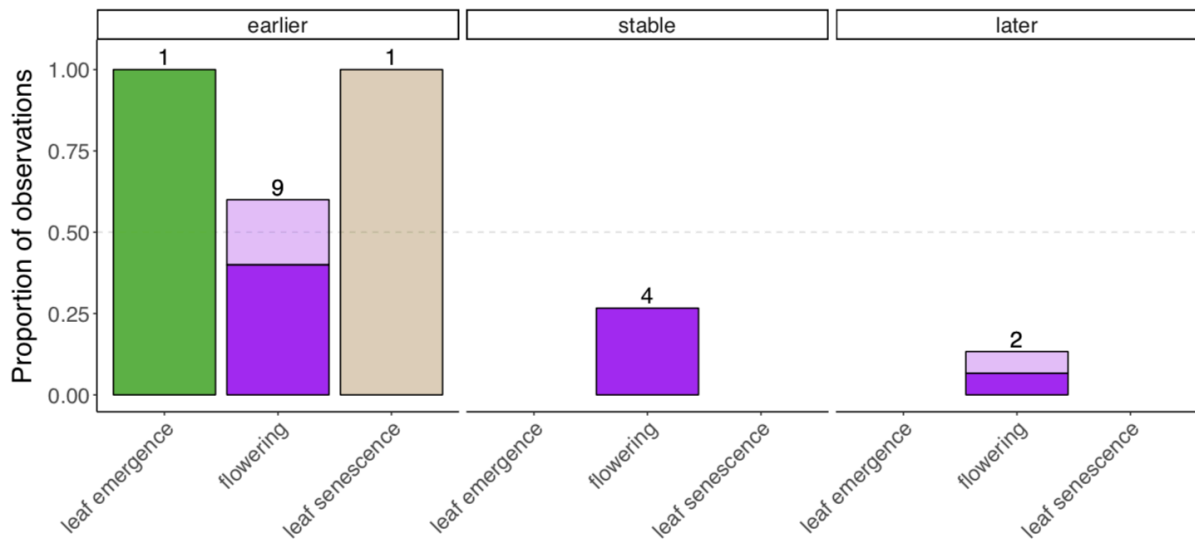
202

203 *Phenological change*

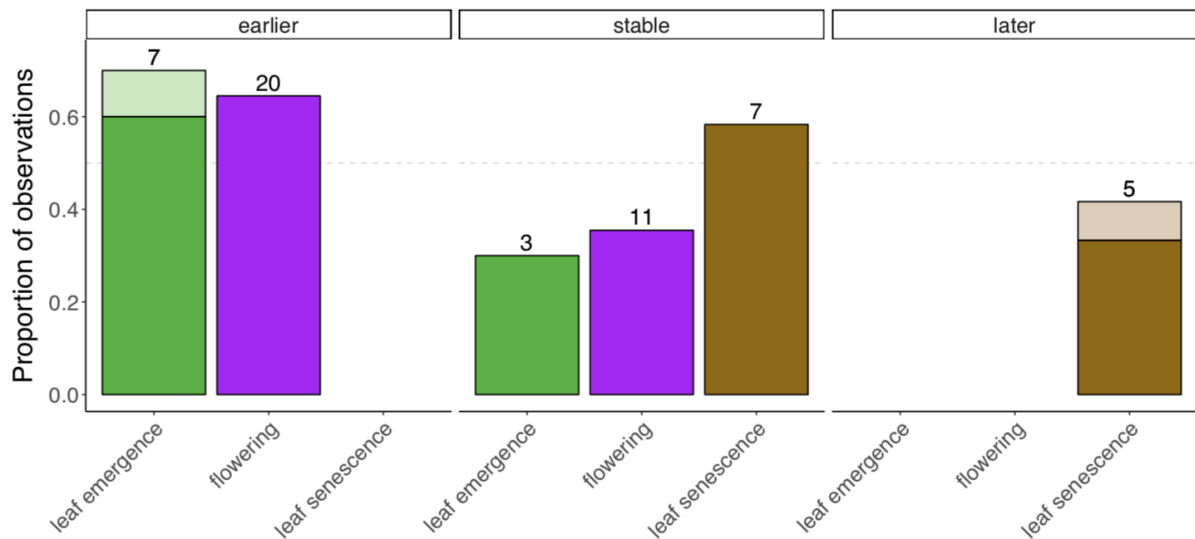
204 In general, the timing of leaf emergence and flowering advanced both over time and with
205 experimental warming, though a minority of species experienced stable or even delayed flowering
206 over time (Figure 3). Interestingly, experimental warming led to later leaf senescence in all cases,
207 while the one study that documents long-term trends in leaf senescence (Myers-Smith et al. 2018)
208 found a non-significant trend toward earlier leaf senescence over 16 years of monitoring.

209

a) Direction of phenological change over time



b) Phenological response to experimental warming



210

211 *Figure 3. Summary of studies investigating phenological change over time (a) and in response to experimental*
 212 *warming (b). Panels represent, from left to right, the proportion of observations that advanced (“earlier”)*
 213 *in a given phenological stage, remained stable, or were delayed (“later”) over time or in response to experimental*
 214 *warming. All observations represent species-specific responses. The darker portions of each bar represent*
 215 *“significant” ($p < 0.05$) change (decrease or increase) or insignificant (stable; $p > 0.1$) results, while lighter*
 216 *colors represent borderline or marginally significant change (e.g., p -values between 0.05 and 0.1). The numbers*
 217 *above each bar represent a count of the number of observations included in that group.*

218

219 In a 17-year synthesis of phenological trends at 12 tundra sites (including two alpine locations), there
 220 was no significant change in the timing of flowering or leaf senescence, though both events tended to
 221 advance over time (Oberbauer et al. 2013), as we also found in the literature review. Surprisingly, this
 222 same synthesis study found that leaf emergence was significantly delayed over time despite increasing
 223 temperatures over the same period. In a separate synthesis of responses to experimental warming at 10
 Arctic sites, leaf emergence and flowering both occurred significantly earlier when warmed, but

224 senescence was not affected (Arft et al. 1999). This is also in agreement with our literature review,
225 where most sites reported no difference in leaf senescence or a slight delay.

226

227 **Discussion**

228

229 Studies of plot-based vegetation change reveal that while some sites and species or functional groups
230 have experienced substantial shifts in vegetation and phenology in response to ambient or
231 experimental warming, the most common response overall is one of no change. Furthermore,
232 vegetation changes over time did not always match responses to experimental warming. One pattern
233 emerges: both long-term monitoring and experimental studies suggest that the graminoid and shrub
234 functional groups respond positively to warming and are slightly more likely to increase in abundance
235 over time. This is in line with studies of shrub infilling and expansion across much of the tundra
236 (Sturm et al. 2001; Myers-Smith et al. 2011a; Martin et al. 2017). Even so, the majority of graminoid
237 and shrub abundance responses in our literature review were that of no significant trend over time and
238 no significant response to experimental warming. Further exploration of these trends reveals that
239 increasing shrub abundance primarily occurs in relatively warm tundra regions with mesic or wet
240 soils, while colder and dry tundra sites have not experienced increasing shrub abundance (Elmendorf
241 et al. 2012b) consistent with patterns in the climate sensitivity of shrub growth (Myers-Smith et al.
242 2015). Grazing may also influence shrub responses to summer temperature change (Bråthen et al.
243 2017). The lack of strong trends over time in many sites and for many species suggests that tundra
244 plant communities are remarkably resilient to moderate warming, at least over decadal time spans,
245 and that site-specific factors such as moisture availability and grazing may limit vegetation responses
246 to warming (Elmendorf et al. 2012b; Myers-Smith et al. 2015; Ackerman et al. 2017).

247

248 Differing responses to experimental and ambient (natural) warming highlight both the benefits and the
249 challenges of using experimental approaches to understand tundra vegetation responses to climate
250 change. When experimental and monitoring results agree, experimental studies enable us to pinpoint
251 the likely drivers of change over time (Elmendorf et al. 2015), and improve our confidence in
252 predictions of the impacts of warming on vegetation (e.g., increasing shrub abundance). Diverging
253 responses can challenge our understanding of tundra vegetation change. For example, while
254 experimental warming led to fairly dramatic declines in lichen abundance (Walker et al. 2006;
255 Elmendorf et al. 2012a and this study), lichen abundance did not decline over time in long-term
256 monitoring studies (Elmendorf et al. 2012b and this study). Similarly, while experimental warming
257 generally led to later leaf senescence (Arft et al. 1999 and this study), monitoring studies indicate that
258 senescence is in fact advancing over time, though not significantly (Oberbauer et al. 2013 and this
259 study). Trends in the timing of flowering and leaf emergence are also varied despite a relatively
260 consistent advance in these variables in response to experimental warming.

261

262 The reasons underlying these heterogeneous and contrasting trends are not entirely clear, but may
263 have to do with interactions among environmental drivers that are not captured by experimental
264 isolation of a single driver. For example, lichens are sensitive to soil moisture, and may be responding
265 to changes in precipitation, hydrology, or snow regimes over time rather than temperature trends
266 alone (Björk and Molau 2007). Similarly, phenological advance with warming temperatures (Høye et
267 al. 2007) may be limited by concurrent changes in winter snowfall (Bjorkman et al. 2015) and
268 snowmelt date (Cooper et al. 2011). In addition, growing season phenology might be controlled by
269 deterministic leaf age (Starr et al. 2000) or adaptation to photoperiod (Kummerow 1992; Bjorkman et
270 al. 2017) in many Arctic species, thus limiting the impact of temperature change alone. Phenological
271 responses to different drivers may interact or be non-linear, leading to more complex responses than
272 can be easily detected from simple experiments or ecological monitoring studies (Iler et al. 2013).
273 Finally, experimental warming chambers can alter conditions other than temperature alone (Marion et
274 al. 1997), and vegetation could be responding to these unwanted environmental side-effects.

275

276 Improved monitoring of multiple environmental drivers and experimental studies that manipulate
277 several variables simultaneously (e.g. snow depth, moisture availability) could help to elucidate the
278 importance of these interactions. Multi-site syntheses can also help to clarify the context dependency
279 of trends over time. For example, additional syntheses of tundra plant phenology have shown that a
280 plant's sensitivity to temperature varies by the temperature of the site (greater sensitivity at colder
281 sites; Prevéy et al. 2017) as well as the phenological niche of the species (greater sensitivity in late-
282 flowering species; Prevéy et al. 2018).

283

284 *Other vegetation trends: functional traits and diversity*

285

286 While trends in composition and phenology are perhaps the most studied plot-based responses to
287 global change, a handful of studies document changes in other vegetation parameters. Of these,
288 increasing height is likely the most well-documented. Increases in community height have been
289 documented by synthesis studies of responses to experimental warming (Elmendorf et al. 2012a) and
290 over time (Bjorkman et al. 2018), a change driven primarily by the influx of taller species into the
291 monitoring plots (Bjorkman et al. 2018). Some single-site studies have also documented increasing
292 height over time (Hollister et al. 2015) and in response to experimental warming (Hudson et al. 2011;
293 Hollister et al. 2015; Baruah et al. 2017). Changes in other plant traits have also been documented.
294 Experimental warming at Alexandra Fiord in high Arctic Canada resulted in greater leaf size, lower
295 specific leaf area (the ratio of leaf area to leaf dry mass), and decreased leaf carbon content for at least
296 some species-site combinations (Hudson et al. 2011) but did not affect leaf nitrogen (N) content, leaf
297 dry matter content, or nitrogen isotope signatures. Other studies have documented mixed responses of

298 leaf size to experimental warming in the Swedish subarctic tundra (Graglia et al. 1997; Baruah et al.
299 2017) and one study found trends toward reduced leaf size over time (Barrett et al. 2015). Additional
300 studies of leaf N content responses to experimental warming are also mixed; leaf N content increased
301 in response to winter but not summer warming across six species at Eight Mile Lake, Alaska (Natali
302 et al. 2012) but was either unaffected by temperature or declined in response to warming at Toolik
303 Lake, Alaska (Chapin and Shaver 1996) and Alexandra Fiord, Canada (Tolvanen and Henry 2011). A
304 synthesis of community-weighted mean functional trait change across the tundra biome (including
305 alpine sites) over 27 years found no significant change in leaf area, leaf N content, leaf dry matter
306 content, or specific leaf area (Bjorkman et al. 2018). Overall, species composition has shifted toward
307 more thermophilic (warm-loving) species both over time and in response to experimental warming
308 (Elmendorf et al. 2015).

309

310 Over the long term, climate warming may lead to increased diversity in the Arctic as southern,
311 species-rich floras move northward (Parmesan 2006). However, short-term responses to warming
312 might differ substantially from long-term trends, as immigration is likely to be slow relative to local
313 assembly processes (e.g. competition; Walker et al. 2006). Thus far, evidence of plot-scale diversity
314 change in Arctic ecosystems is mixed. A multi-site synthesis found a significant decline in both
315 Shannon diversity and species richness after three to six years of experimental warming (Walker et al.
316 2006), but a more recent, longer-term synthesis found no response (Elmendorf et al. 2012a). Lichen
317 diversity was found to decline significantly in response to long-term experimental warming at three
318 sites in northern Sweden and Alaska (Lang et al. 2012). Among monitoring studies, a recent synthesis
319 found no change in vascular plant diversity over three decades of monitoring across dozens of tundra
320 sites (Elmendorf et al. 2012b). This is in stark contrast to ongoing changes in European mountaintop
321 plant communities, which have experienced rapid and accelerating increases in richness over the past
322 century (Steinbauer et al. 2018). This difference could indicate that diversity change in non-alpine
323 tundra communities is limited by dispersal rates of southerly, warm-adapted species, or that strong
324 gradients in environmental variables other than temperature (e.g. photoperiod) across latitudes limit
325 the establishment success of warm-adapted species from farther south (Bjorkman et al. 2017).

326

327 *Consequences of Arctic vegetation change*

328

329 Changes in tundra vegetation could have far-reaching impacts across trophic levels and to human
330 societies (Weller et al. 2004). Shifts in plant phenology and reproductive success influence individual-
331 and population-level fitness (Berteaux et al. 2004; Cleland et al. 2012) and could lead to trophic
332 mismatches of resources for pollinators (Høye et al. 2013; Wheeler et al. 2015; Prev y et al. 2018),
333 breeding birds (McKinnon et al. 2012; Gauthier et al. 2013; Boelman et al. 2015) and mammals
334 (Hertel et al. 2017). For example, one long-term study at Zackenberg, Greenland documented a

335 shortening of the flowering season with climate warming over time and a concurrent decline in the
336 abundance of insect visits to flowers (Høye et al. 2013). Berry-producing (Hertel et al. 2017) and
337 other tundra plants provide forage for hunted or domestic wildlife (Post and Stenseth 1999; Kerby and
338 Post 2013) and represent culturally important resources for Arctic peoples (Henry et al. 2012).

339

340 The nearly ubiquitous shifts in phenology in response to experimental warming (Arft et al. 1999 and
341 this study) suggest that many Arctic plant species are inherently sensitive to interannual variations in
342 temperature, though concurrent changes in other environmental variables (e.g. precipitation,
343 cloudiness) might limit the degree of advance over time with warming. A meta-analysis of
344 phenological responses to experimental warming in temperate and alpine regions found that the
345 temperature sensitivity of a species' phenology correlates with better growth and/or reproductive
346 performance (Cleland et al. 2012), but it is not known if this pattern holds true in the Arctic. A
347 synthesis of responses to four years of experimental warming at 10 Arctic sites revealed increased
348 reproductive effort (e.g. number of flowers produced) and success (e.g. number of seeds/fruits
349 produced or seed mass) in experimentally warmed plots, though responses were generally not
350 significant (Arft et al. 1999). Single-site studies have also found evidence of increased reproductive
351 effort in experimentally warmed plots (Welker et al. 1997; Klady et al. 2011). Contrasting responses
352 have been documented for seed germination rates, which increased with experimental warming at
353 Alexandra Fiord, Canada (Klady et al. 2011) but not at Toolik Lake, Alaska (Welker et al. 1997).

354

355 Due to the large amount of carbon stored in tundra permafrost soils (Koven et al. 2011; Schuur et al.
356 2015; Crowther et al. 2016) and well-established links between vegetation and carbon storage,
357 vegetation change in the Arctic can influence regional carbon cycling and feedbacks to the global
358 climate (Callaghan et al. 2004; Sturm and Douglas 2005; Petrenko et al. 2016). For example,
359 increasing shrub abundance and/or plant height can lead to increased winter snow trapping, greater
360 insulation of underlying soils, warmer winter soil temperatures (Myers-Smith and Hik 2013), and
361 potentially increased active layer depth and decomposition (Blok et al. 2016). Taller shrubs may also
362 extend above the snowpack, decreasing winter albedo and increasing absorbed solar radiation (Sturm
363 and Douglas 2005). Bryophytes have also been shown to play an important role in soil insulation and
364 energy fluxes; experimental removal of bryophytes leads to increased evapotranspiration and ground
365 heat flux (Blok et al. 2011). Thus, future declines in bryophytes – observed in warming experiments
366 but not yet in monitoring studies – could also lead to deeper summer permafrost thaw and soil carbon
367 release, representing another positive feedback to climate warming.

368

369 Changing vegetation can also impact carbon cycling through changes in the quantity and
370 decomposability of litter (Callaghan et al. 2004), as litter decomposition contributes nearly 70% of
371 global CO₂ fluxes from soils (Raich and Potter 1995). A long-term increase in shrubs, which have

372 relatively recalcitrant litter, could lead to reduced litter decomposability and a negative feedback to
373 climate warming (Cornelissen et al. 2007). A change in litter composition can also indirectly
374 influence soil carbon storage by driving changes in soil microbial communities (Christiansen et al.
375 2018) or altering tundra fuel loads. For example, increased woody litter inputs from shrub expansion
376 might also increase flammability, which could lead to positive feedbacks through fire-induced soil
377 carbon loss (Cornelissen et al. 2007; van Altena et al. 2012).

378

379 **Conclusions**

380

381 Rapid warming in the Arctic has the potential to cause substantial shifts in vegetation, potentially
382 driving widespread changes across trophic levels and altering tundra ecosystem functions. While our
383 review identifies significant shifts at some sites and in some species, the large variation in the
384 magnitude and even direction of responses illustrates the high degree of context dependency in tundra
385 vegetation change. This context dependency highlights the importance of maintaining multiple
386 monitoring sites in many different habitat types across the entire Arctic, as well as increasing
387 monitoring of local ecological and environmental conditions that would improve our understanding of
388 how factors other than temperature influence Arctic vegetation change. Thus, we recommend that
389 international bodies such as the Circumpolar Biodiversity Monitoring Program (Christensen et al.
390 2013) prioritize monitoring efforts that i) fill current geographical gaps, particularly in Canada and
391 Siberia, and ii) enable us to better disentangle the relative importance of climate warming and other
392 environmental factors on the diverging responses reported here.

393

Study	Site name	Lat	Lon	Duration (years)	Abundance		Phenology	
					monitoring	experiment	monitoring	experiment
(Alatalo and Totland 1997)	Latnajaure, Lapland, Sweden	68.21	18.3	1				x
(Bjorkman et al. 2015)	Alexandra Fiord, Ellesmere Island, Canada	78.53	-75.55	21			x	x
(Boulanger-Lapointe et al. 2014)	Alexandra Fiord, Ellesmere Island, Nunavut	78.86	-75.9	13-15	x			
(Boulanger-Lapointe et al. 2014)	Sverdrup Pass, Ellesmere Island, Nunavut	79.13	-79.73	5-23	x			
(Callaghan et al. 2011)	Disko Island, Greenland	69.15	-53.34	43	x			
(Chapin and Shaver 1996)	Toolik Lake, Alaska	68.38	-149.34	4			x	
(Chapin et al. 1995)	Toolik Lake, Alaska	68.38	-149.34	9			x	
(Daniëls and de Molenaar 2011)	Tasiilaq, Southeast Greenland	65.62	-37.67	41	x			
(Graglia et al. 2001)	Abisko, Sweden	68.35	18.82	10			x	
(Hill and Henry 2011)	Alexandra Fiord, Ellesmere Island, Canada	78.53	-75.55	25	x			
(Hobbie and Chapin 1998)	Toolik Lake, Alaska	68.38	-149.34	3			x	
(Hollister and Webber 2000)	Barrow, Alaska, USA	71.18	-156.4	1				x
(Hollister et al. 2015)	Atqasuk, Alaska	70.45	-157.41	16	x		x	
(Hollister et al. 2015)	Barrow, Alaska	71.29	-156.64	17	x		x	
(Høye et al. 2007)	Zackenbergl, Greenland	74.28	-20.34	9				x
(Hudson and Henry 2009)	Alexandra Fiord, Ellesmere Island, Nunavut	78.88	-75.92	28	x			
(Hudson and Henry 2010)	Alexandra Fiord, Ellesmere Island, Nunavut	78.88	-75.92	16			x	
(Jägerbrand et al. 2009)	Latnajaure, Lapland, Sweden	68.35	18.5	5			x	
(Jandt et al. 2008)	Northwestern Alaska	65.1	-163.4	10-15	x			
(Joly et al. 2007)	Seward Peninsula, Alaska	64.85	-163.7	25	x			
(Jonasson et al. 1999)	Abisko, Sweden	68.35	18.82	5			x	

<i>(Jones et al. 1997)</i>	Alexandra Fiord, Ellesmere Island, Canada	78.53	-75.55	1			x
<i>(Jones et al. 1997)</i>	Barrow, Alaska, USA	71.19	-156.37	1			x
<i>(Jones et al. 1997)</i>	Latnjajaure, Lapland, Sweden	68.21	18.3	1			x
<i>(Jónsdóttir et al. 2005)</i>	Audkuluheidi, Iceland	65.27	-20.25	5		x	
<i>(Jónsdóttir et al. 2005)</i>	Thingvellir, Iceland	64.28	-21.08	5		x	
<i>(Jorgenson et al. 2015)</i>	Arctic National Wildlife Refuge, Alaska	69.8	-144.25	26	x		
<i>(Marchand et al. 2004)</i>	Zackenbergl, Greenland	74.28	-20.34	1			x
<i>(Molau 2010)</i>	Latnjajaure, Lapland, Sweden	68.35	18.5	12	x		
<i>(Myers-Smith et al. 2011b)</i>	Qikiqtaruk-Herschel Island, Yukon	69.57	-138.91	11	x		
<i>(Myers-Smith et al. 2018)</i>	Qikiqtaruk-Herschel Island, Yukon, Canada	69.57	-138.91	16-19	x		x
<i>(Natali et al. 2012)</i>	Eight Mile Lake, Alaska, USA	63.52	-149.13	2		x	x
<i>(Pattison et al. 2015)</i>	Arctic National Wildlife Refuge, Alaska	69.8	-144.25	26	x		
<i>(Post and Pedersen 2008)</i>	Kangerlussuaq, Greenland	67.6	-50.2	2			x
<i>(Richardson et al. 2002)</i>	Abisko Valley, Sweden	68	19	9		x	
<i>(Robinson et al. 1998)</i>	Ny Alesund, Svalbard	78.93	11.83	5	x	x	
<i>(Rundqvist et al. 2011)</i>	Abisko Valley, Sweden	68.35	18.82	35	x		
<i>(Stenström and Jónsdóttir 1997)</i>	Latnjajaure, Lapland, Sweden	68.22	18.13	1			x
<i>(Tømmervik et al. 2004)</i>	Kautokeino, Norway	69	23.1	38	x		
<i>(Villarreal et al. 2012)</i>	Barrow, Alaska	71.3	-156.67	39	x		
<i>(Vowles et al. 2017)</i>	Ritsem, Sweden	67.82 4	17.715	18	x		
<i>(Wang et al. 2017)</i>	Kytalyk, Siberia	70.82	147.48	4		x	
<i>(Wilson and Nilsson 2009)</i>	Cievrratjäkka, Sweden	68.01	18.81	21	x		
<i>(Wookey et al. 1993)</i>	Abisko, Sweden	68.21	18.49	1			x
<i>(Zamin et al. 2014)</i>	Daring Lake, NWT	64.87	-111.57	8		x	

396 **References**

- 397 Ackerman, D., D. Griffin, S. E. Hobbie, and J. C. Finlay. 2017. Arctic shrub growth trajectories differ
398 across soil moisture levels. *Global Change Biology* 23: 4294–4302. doi:10.1111/gcb.13677.
- 399 Alatalo, J. M., and Ø. Totland. 1997. Response to simulated climatic change in an alpine and
400 subarctic pollen-risk strategist, *Silene acaulis*. *Global Change Biology* 3: 74–79.
401 doi:10.1111/j.1365-2486.1997.gcb133.x.
- 402 Arft, A. M., M. D. Walker, J. E. A. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer,
403 F. Gugerli, et al. 1999. Responses of tundra plants to experimental warming: meta-analysis of the
404 international tundra experiment. *Ecological Monographs* 69. Eco Soc America: 491–511.
- 405 Barrett, R. T. S., R. D. Hollister, S. F. Oberbauer, and C. E. Tweedie. 2015. Arctic plant responses to
406 changing abiotic factors in northern Alaska. *American Journal of Botany* 102. Wiley-Blackwell:
407 2020–2031. doi:10.3732/ajb.1400535.
- 408 Baruah, G., U. Molau, Y. Bai, and J. M. Alatalo. 2017. Community and species-specific responses of
409 plant traits to 23 years of experimental warming across subarctic tundra plant communities.
410 *Scientific Reports* 7. Nature Publishing Group: 2571. doi:10.1038/s41598-017-02595-2.
- 411 Berteaux, D., D. Reale, A. G. McAdam, and S. Boutin. 2004. Keeping pace with fast climate change:
412 can arctic life count on evolution? *Integrative and Comparative Biology* 44: 140–151.
- 413 Bjorkman, A. D., I. H. Myers-Smith, S. C. Elmendorf, S. Normand, N. Røger, P. S. A. Beck, A.
414 Blach-Overgaaard, D. Blok, et al. 2018. Plant functional trait change across a warming tundra
415 biome. *Nature* 562. Springer US: 57–62. doi:10.1038/s41586-018-0563-7.
- 416 Bjorkman, A. D., M. Vellend, E. R. Frei, and G. H. R. Henry. 2017. Climate adaptation is not enough:
417 warming does not facilitate success of southern tundra plant populations in the high Arctic.
418 *Global Change Biology* 23: 1540–1551. doi:10.1111/gcb.13417.
- 419 Bjorkman, A. D., S. C. Elmendorf, A. L. Beamish, M. Vellend, and G. H. R. Henry. 2015.
420 Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the
421 past two decades. *Global Change Biology* 21: 4651–4661. doi:10.1111/gcb.13051.
- 422 Björk, R. G., and U. Molau. 2007. Ecology of Alpine Snowbeds and the Impact of Global Change.
423 *Arctic, Antarctic, and Alpine Research* 39. The Institute of Arctic and Alpine Research UCB
424 450, University of Colorado, Boulder, Colorado 80309-0450, U.S.A: 34–43.
- 425 Blok, D., B. Elberling, and A. Michelsen. 2016. Initial stages of tundra shrub litter decomposition
426 may be accelerated by deeper winter snow but slowed down by spring warming. *Ecosystems* 19.
427 Springer US: 155–169. doi:10.1007/s10021-015-9924-3.
- 428 Blok, D., M. M. P. D. Heijmans, G. Schaepman-Strub, J. van Ruijven, F. J. W. Parmentier, T. C.
429 Maximov, and F. Berendse. 2011. The Cooling Capacity of Mosses: Controls on Water and
430 Energy Fluxes in a Siberian Tundra Site. *Ecosystems* 14. Springer-Verlag: 1055–1065.
431 doi:10.1007/s10021-011-9463-5.
- 432 Boelman, N. T., L. Gough, J. Wingfield, S. Goetz, A. Asmus, H. E. Chmura, J. S. Krause, J. H. Perez,
433 et al. 2015. Greater shrub dominance alters breeding habitat and food resources for migratory
434 songbirds in Alaskan arctic tundra. *Global Change Biology* 21. Wiley/Blackwell (10.1111):
435 1508–1520. doi:10.1111/gcb.12761.
- 436 Boulanger-Lapointe, N., E. Lévesque, S. Boudreau, G. H. R. Henry, and N. M. Schmidt. 2014.
437 Population structure and dynamics of Arctic willow (*Salix arctica*) in the High Arctic. Edited by
438 Miles Silman. *Journal of Biogeography* 41: 1967–1978. doi:10.1111/jbi.12350.
- 439 Bråthen, K. A., V. T. Ravolainen, A. Stien, T. Tveraa, and R. A. Ims. 2017. Rangifer management
440 controls a climate-sensitive tundra state transition. *Ecological Applications* 27: 2416–2427.
441 doi:10.1002/eap.1618.
- 442 CAFF 2013. 2013. *Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity*. Edited by
443 Hans Meltofte. *Conservation of Arctic Flora and Fauna*. Akureyri.
- 444 Callaghan, T. V., C. E. Tweedie, J. Akerman, C. Andrews, J. Bergstedt, M. G. Butler, T. R.
445 Christensen, D. Cooley, et al. 2011. Multi-decadal changes in tundra environments and
446 ecosystems: synthesis of the International Polar Year-Back to the Future project (IPY-BTF).
447 *Ambio* 40: 705–716.

448 Callaghan, T. V., L. O. Björn, Y. Chernov, F. S. Chapin III, T. R. Christensen, B. Huntley, R. A. Ims,
449 M. Johansson, et al. 2004. Effects on the Function of Arctic Ecosystems in the Short- and Long-
450 Term Perspectives. *Ambio* 33: 448–458.

451 Chapin, F. S., III, and G. R. Shaver. 1996. Physiological and growth responses of Arctic plants to a
452 field experiment simulating climatic change. *Ecology* 77: 822–840. doi:10.2307/2265504.

453 Chapin, F. S., III, G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Responses
454 of arctic tundra to experimental and observed changes in climate. *Ecology* 76. Eco Soc America:
455 694–711.

456 Chapin, F. S., III, M. Sturm, M. C. Serreze, J. P. McFadden, J. R. Key, A. H. Lloyd, A. D. McGuire,
457 T. S. Rupp, et al. 2005. Role of land-surface changes in Arctic summer warming. *Science* 310:
458 657–660. doi:10.1126/science.1117368.

459 Christensen, T., J. Payne, M. Doyle, G. Ibarguchi, J. Taylor, N. M. Schmidt, M. Gill, M. Svoboda, et
460 al. 2013. *The Arctic Terrestrial Biodiversity Monitoring Plan. CAFF Monitoring Series Report*
461 *No. 7*. Akureyri, Iceland: CAFF International Secretariat. doi:10.9752/ts056.10-24-2013.

462 Christiansen, C. T., M. C. Mack, J. DeMarco, and P. Grogan. 2018. Decomposition of Senesced Leaf
463 Litter is Faster in Tall Compared to Low Birch Shrub Tundra. *Ecosystems*. Springer US: 1–16.
464 doi:https://doi.org/10.1007/s10021-018-0240-6.

465 Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E.
466 M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate change.
467 *Ecology* 93. Ecological Society of America : 1765–1771. doi:10.1890/11-1912.1.

468 Cooper, E. J., S. Dullinger, and P. Semenchuk. 2011. Late snowmelt delays plant development and
469 results in lower reproductive success in the High Arctic. *Plant Science* 180. Elsevier Ireland Ltd:
470 157–167. doi:10.1016/j.plantsci.2010.09.005.

471 Cornelissen, J. H. C., P. M. van Bodegom, R. Aerts, T. V. Callaghan, R. S. P. van Logtestijn, J. M.
472 Alatalo, F. S. Chapin III, R. Gerdol, et al. 2007. Global negative vegetation feedback to climate
473 warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters* 10: 619–
474 627. doi:10.1111/j.1461-0248.2007.01051.x.

475 Crowther, T. W., K. E. O. Todd-Brown, C. W. Rowe, W. R. Wieder, J. C. Carey, M. B. Machmuller,
476 B. L. Snoek, S. Fang, et al. 2016. Quantifying global soil carbon losses in response to warming.
477 *Nature* 540: 104–108. doi:10.1038/nature20150.

478 Daniëls, F. J. A., and J. G. de Molenaar. 2011. Flora and Vegetation of Tasiilaq, Formerly
479 Angmagssalik, Southeast Greenland: A Comparison of Data Between Around 1900 and 2007.
480 *Ambio* 40: 650–659. doi:10.1007/s13280-011-0171-3.

481 Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, A. M. Fosaa, W. A. Gould, L. Hermanutz, A.
482 Hofgaard, I. I. Jónsdóttir, et al. 2015. Experiment, monitoring, and gradient methods used to infer
483 climate change effects on plant communities yield consistent patterns. *Proceedings of the*
484 *National Academy of Sciences of the United States of America* 112: 448–452.
485 doi:10.1073/pnas.1410088112.

486 Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, A. D. Bjorkman, T. V. Callaghan, L.
487 S. Collier, E. J. Cooper, et al. 2012a. Global assessment of experimental climate warming on
488 tundra vegetation: heterogeneity over space and time. *Ecology Letters* 15: 164–175.
489 doi:10.1111/j.1461-0248.2011.01716.x.

490 Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, N. Boulanger-Lapointe, E. J. Cooper,
491 J. H. C. Cornelissen, T. A. Day, et al. 2012b. Plot-scale evidence of tundra vegetation change and
492 links to recent summer warming. *Nature Climate Change* 2: 453–457. doi:10.1038/nclimate1465.

493 Freedman, B., and J. Svoboda. 1994. Alexandra Fiord - An ecological oasis in the polar desert. In
494 *Ecology of a Polar Oasis*, eds. J. Svoboda and B. Freedman. Toronto: Captus University
495 Publications.

496 Gauthier, G., J. Bêty, M.-C. Cadieux, P. Legagneux, M. Doiron, C. Chevallier, S. Lai, A. Tarroux, et
497 al. 2013. Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to
498 climate change in the Canadian Arctic tundra. *Philosophical transactions of the Royal Society of*
499 *London. Series B, Biological sciences* 368. The Royal Society: 20120482.
500 doi:10.1098/rstb.2012.0482.

501 Graglia, E., S. Jonasson, A. Michelsen, and I. K. Schmidt. 1997. Effects of shading, nutrient
502 application and warming on leaf growth and shoot densities of dwarf shrubs in two arctic-alpine

503 plant communities. *Écoscience* 4. Taylor & Francis: 191–198.
504 doi:10.1080/11956860.1997.11682395.

505 Graglia, E., S. Jonasson, A. Michelsen, I. K. Schmidt, M. Havström, and L. Gustavsson. 2001. Effects
506 of environmental perturbations on abundance of subarctic plants after three, seven and ten years
507 of treatments. *Ecography* 24. John Wiley & Sons, Ltd (10.1111): 5–12. doi:10.1034/j.1600-
508 0587.2001.240102.x.

509 Henry, G. H. R., and U. Molau. 1997. Tundra plants and climate change: the International Tundra
510 Experiment (ITEX). *Global Change Biology* 3: 1–9.

511 Henry, G. H. R., K. A. Harper, W. Chen, J. R. Deslippe, R. F. Grant, P. M. Lafleur, E. Lévesque, S.
512 D. Siciliano, et al. 2012. Effects of observed and experimental climate change on terrestrial
513 ecosystems in northern Canada: results from the Canadian IPY program. *Climatic Change* 115.
514 Springer Netherlands: 207–234. doi:10.1007/s10584-012-0587-1.

515 Hertel, A. G., R. Bischof, O. Langval, A. Myrsterud, J. Kindberg, J. E. Swenson, and A. Zedrosser.
516 2017. Berry production drives bottom-up effects on body mass and reproductive success in an
517 omnivore. *Oikos* 127. Wiley/Blackwell (10.1111): 197–207. doi:10.1111/oik.04515.

518 Hill, G. B., and G. H. R. Henry. 2011. Responses of High Arctic wet sedge tundra to climate warming
519 since 1980. *Global Change Biology* 17: 276–287. doi:10.1111/j.1365-2486.2010.02244.x.

520 Hobbie, S. E., and F. S. Chapin III. 1998. The response of tundra plant biomass, aboveground
521 production, nitrogen, and CO₂ flux to experimental warming. *Ecology* 79. John Wiley & Sons,
522 Ltd: 1526–1544. doi:10.1890/0012-9658(1998)079[1526:TROTPB]2.0.CO;2.

523 Hollister, R. D., and P. J. Webber. 2000. Biotic validation of small open-top chambers in a tundra
524 ecosystem. *Global Change Biology* 6: 835–842.

525 Hollister, R. D., J. L. May, K. S. Kremers, C. E. Tweedie, S. F. Oberbauer, J. A. Liebig, T. F. Botting,
526 R. T. Barrett, et al. 2015. Warming experiments elucidate the drivers of observed directional
527 changes in tundra vegetation. *Ecology and Evolution* 5. Wiley-Blackwell: 1881–1895.
528 doi:10.1002/ece3.1499.

529 Hudson, J. M. G., and G. H. R. Henry. 2009. Increased plant biomass in a High Arctic heath
530 community from 1981 to 2008. *Ecology* 90: 2657–2663.

531 Hudson, J. M. G., and G. H. R. Henry. 2010. High Arctic plant community resists 15 years of
532 experimental warming. *Journal of Ecology* 98: 1035–1041. doi:10.1111/j.1365-
533 2745.2010.01690.x.

534 Hudson, J. M. G., G. H. R. Henry, and W. K. Cornwell. 2011. Taller and larger: shifts in Arctic tundra
535 leaf traits after 16 years of experimental warming. *Global Change Biology* 17: 1013–1021.
536 doi:10.1111/j.1365-2486.2010.02294.x.

537 Høye, T. T., E. Post, N. M. Schmidt, K. Trøjelsgaard, and M. C. Forchhammer. 2013. Shorter
538 flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate*
539 *Change* 3. Nature Publishing Group: 759–763. doi:doi:10.1038/nclimate1909.

540 Høye, T. T., E. S. Post, H. Meltofte, N. M. Schmidt, and M. C. Forchhammer. 2007. Rapid
541 advancement of spring in the High Arctic. *Current Biology* 17: R449–R451.
542 doi:10.1016/j.cub.2007.04.047.

543 Iler, A. M., T. T. Høye, D. W. Inouye, and N. M. Schmidt. 2013. Nonlinear flowering responses to
544 climate: are species approaching their limits of phenological change? *Philosophical Transactions*
545 *of the Royal Society B: Biological Sciences* 368: 20120489–20120489. doi:10.1890/06-2138.1.

546 IPCC. 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to*
547 *the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Edited by T F
548 Stocker, D Quin, G-K Plattner, M Tignor, S K Allen, J Boschung, A Nauels, Y Xia, et al.
549 Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

550 J. Kummerow. 1992. Phenology, resource allocation, and growth of Arctic vascular plants. In *Arctic*
551 *ecosystems in a changing climate: an ecophysiological perspective*, eds. F. S. Chapin III, R.
552 Jefferies, J. Reynolds, G. R. Shaver, and J. Svoboda, 193–211. Arctic Ecosystems in a Changing
553 Climate: an Ecophysiological Perspective. San Diego, CA: Academic Press, Inc.

554 Jandt, R., K. Joly, C. R. Meyers, and C. Racine. 2008. Slow Recovery of Lichen on Burned Caribou
555 Winter Range in Alaska Tundra: Potential Influences of Climate Warming and Other Disturbance
556 Factors. *Arctic, Antarctic, and Alpine Research* 40: 89–95. doi:10.1657/1523-0430(06-
557 122)[jandt]2.0.co;2.

558 Jägerbrand, A. K., J. M. Alatalo, D. Chrimes, and U. Molau. 2009. Plant community responses to
559 5 years of simulated climate change in meadow and heath ecosystems at a subarctic-alpine site.
560 *Oecologia* 161: 601–610. doi:10.1007/s00442-009-1392-z.

561 Joly, K., R. R. Jandt, C. R. Meyers, and M. J. Cole. 2007. Changes in vegetative cover on Western
562 Arctic Herd winter range from 1981 to 2005: potential effects of grazing and climate change.
563 *Rangifer* 17: 199–207.

564 Jonasson, S., A. Michelsen, I. K. Schmidt, and E. V. Nielsen. 1999. Responses in microbes and plants
565 to changed temperature, nutrient, and light regimes in the Arctic. *Ecology* 80. John Wiley &
566 Sons, Ltd: 1828–1843. doi:10.1890/0012-9658(1999)080[1828:RIMAPT]2.0.CO;2.

567 Jones, M. H., C. Bay, and U. Nordenhäll. 1997. Effects of experimental warming on arctic willows
568 (*Salix* spp.): a comparison of responses from the Canadian High Arctic, Alaskan Arctic, and
569 Swedish Subarctic. *Global Change Biology* 3. John Wiley & Sons, Ltd (10.1111): 55–60.
570 doi:10.1111/j.1365-2486.1997.gcb135.x.

571 Jorgenson, J. C., M. K. Reynolds, J. H. Reynolds, and A.-M. Benson. 2015. Twenty-Five Year
572 Record of Changes in Plant Cover on Tundra of Northeastern Alaska. *Arctic, Antarctic, and*
573 *Alpine Research* 47: 785–806. doi:10.1657/AAAR0014-097.

574 Jónsdóttir, I. S., B. Magnússon, J. Gudmundsson, A. Elmarsdóttir, and H. Hjartarson. 2005. Variable
575 sensitivity of plant communities in Iceland to experimental warming. *Global Change Biology* 11:
576 553–563. doi:10.1111/j.1365-2486.2005.00928.x.

577 Kerby, J., and E. Post. 2013. Capital and income breeding traits differentiate trophic match-mismatch
578 dynamics in large herbivores. *Philosophical transactions of the Royal Society of London. Series*
579 *B, Biological sciences* 368: 20120484. doi:10.1098/rstb.2012.0484.

580 Klady, R. A., G. H. R. Henry, and V. Lemay. 2011. Changes in high arctic tundra plant reproduction
581 in response to long-term experimental warming. *Global Change Biology* 17: 1611–1624.
582 doi:10.1111/j.1365-2486.2010.02319.x.

583 Koven, C. D., B. Ringeval, P. Friedlingstein, P. Ciais, P. Cadule, D. Khvorostyanov, G. Krinner, and
584 C. Tarnocai. 2011. Permafrost carbon-climate feedbacks accelerate global warming. *Proceedings*
585 *of the National Academy of Sciences of the United States of America* 108. National Academy of
586 Sciences: 14769–14774. doi:10.1073/pnas.1103910108.

587 Lang, S. I., J. H. C. Cornelissen, G. R. Shaver, M. Ahrens, T. V. Callaghan, U. Molau, C. J. F. Ter
588 Braak, A. Hölzer, et al. 2012. Arctic warming on two continents has consistent negative effects
589 on lichen diversity and mixed effects on bryophyte diversity. *Global Change Biology* 18.
590 Wiley/Blackwell (10.1111): 1096–1107. doi:10.1111/j.1365-2486.2011.02570.x.

591 Marchand, F. L., I. Nijs, M. Heuer, S. Mertens, F. Kockelbergh, J.-Y. Pontailier, I. Impens, and L.
592 Beyens. 2004. Climate warming postpones senescence in high arctic tundra. *Arctic, Antarctic,*
593 *and Alpine Research* 36: 390–394.

594 Marion, G. M., G. H. R. Henry, D. W. Freckman, J. Johnstone, G. Jones, M. H. Jones, E. Lévesque,
595 U. Molau, et al. 1997. Open- top designs for manipulating field temperature in high- latitude
596 ecosystems. *Global Change Biology* 3. Wiley Online Library: 20–32.

597 Martin, A. C., E. S. Jeffers, G. Petrokofsky, I. Myers-Smith, and M. Macias-Fauria. 2017. Shrub
598 growth and expansion in the Arctic tundra: an assessment of controlling factors using an
599 evidence-based approach. *Environmental Research Letters* 12. IOP Publishing: 085007–14.
600 doi:10.1088/1748-9326/aa7989.

601 McKinnon, L., M. Picotin, E. Bolduc, C. Juillet, and J. Bêty. 2012. Timing of breeding, peak food
602 availability, and effects of mismatch on chick growth in birds nesting in the High Arctic.
603 *Canadian Journal of Zoology* 90. NRC Research Press: 961–971. doi:10.1139/z2012-064.

604 Molau, U. 2010. Long-term impacts of observed and induced climate change on tussock tundra near
605 its southern limit in northern Sweden. *Plant Ecology & Diversity* 3: 29–34.
606 doi:10.1080/17550874.2010.487548.

607 Molau, U., and P. Mølgaard. 1996. *International Tundra Experiment (ITEX) Manual*. 2nd ed.
608 Copenhagen, Denmark: Danish Polar Center.

609 Muc, M., B. Freedman, and J. Svoboda. 1989. Vascular plant communities of a polar oasis at
610 Alexandra Fiord (79 N), Ellesmere Island, Canada. *Canadian Journal of Botany* 67: 1126–1136.

611 Myers-Smith, I. H., and D. S. Hik. 2013. Shrub canopies influence soil temperatures but not nutrient
612 dynamics: An experimental test of tundra snow-shrub interactions. *Ecology and Evolution* 3:
613 3683–3700. doi:10.1002/ece3.710.

614 Myers-Smith, I. H., B. C. Forbes, M. Wilmsking, M. Hallinger, T. Lantz, D. Blok, K. D. Tape, M.
615 Macias-Fauria, et al. 2011a. Shrub expansion in tundra ecosystems: dynamics, impacts and
616 research priorities. *Environmental Research Letters* 6. IOP Publishing: 045509.

617 Myers-Smith, I. H., D. S. Hik, C. Kennedy, D. Cooley, J. F. Johnstone, A. J. Kenney, and C. J. Krebs.
618 2011b. Expansion of Canopy-Forming Willows Over the Twentieth Century on Herschel Island,
619 Yukon Territory, Canada. *Ambio* 40: 610–623. doi:10.1007/s13280-011-0168-y.

620 Myers-Smith, I. H., M. M. Grabowski, H. J. D. Thomas, S. Angers-Blondin, G. N. Daskalova, A. D.
621 Bjorkman, A. M. Cunliffe, J. J. Assmann, et al. 2018. *Eighteen years of ecological monitoring*
622 *reveals multiple lines of evidence for tundra vegetation change. Ecological Monographs.*

623 Myers-Smith, I. H., S. C. Elmendorf, P. S. A. Beck, M. Wilmsking, M. Hallinger, D. Blok, K. D. Tape,
624 S. A. Rayback, et al. 2015. Climate sensitivity of shrub growth across the tundra biome. *Nature*
625 *Climate Change* 5: 887–891. doi:10.1038/nclimate2697.

626 Natali, S. M., E. A. G. Schuur, and R. L. Rubin. 2012. Increased plant productivity in Alaskan tundra
627 as a result of experimental warming of soil and permafrost. *Journal of Ecology* 100.
628 Wiley/Blackwell (10.1111): 488–498. doi:10.1111/j.1365-2745.2011.01925.x.

629 Oberbauer, S. F., S. C. Elmendorf, T. G. Troxler, R. D. Hollister, A. V. Rocha, M. S. Bret-Harte, M.
630 A. Dawes, A. M. Fosaa, et al. 2013. Phenological response of tundra plants to background
631 climate variation tested using the International Tundra Experiment. *Philosophical Transactions*
632 *of the Royal Society B: Biological Sciences* 368: 20120481. doi:10.1126/science.1108142.

633 Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review*
634 *of Ecology, Evolution, and Systematics* 37: 637–669.

635 Pattison, R. R., J. C. Jorgenson, M. K. Reynolds, and J. M. Welker. 2015. Trends in NDVI and
636 Tundra Community Composition in the Arctic of NE Alaska Between 1984 and 2009.
637 *Ecosystems*. Springer US: 1–13. doi:10.1007/s10021-015-9858-9.

638 Pearson, R. G., S. J. Phillips, M. M. Lorant, P. S. A. Beck, T. Damoulas, S. J. Knight, and S. J.
639 Goetz. 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature*
640 *Climate Change* 3. Nature Publishing Group: 673–677. doi:10.1038/nclimate1858.

641 Petrenko, C. L., J. Bradley-Cook, E. M. Lacroix, A. J. Friedland, and R. A. Virginia. 2016.
642 Comparison of carbon and nitrogen storage in mineral soils of graminoid and shrub tundra sites,
643 western Greenland. *Arctic Science* 2: 165–182. doi:10.1139/as-2015-0023.

644 Post, E., and C. Pedersen. 2008. Opposing plant community responses to warming with and without
645 herbivores. *Proceedings of the National Academy of Sciences of the United States of America*
646 105: 12353–12358.

647 Post, E., and N. C. Stenseth. 1999. CLIMATIC VARIABILITY, PLANT PHENOLOGY, AND
648 NORTHERN UNGULATES. *Ecology* 80: 1322–1339. doi:10.1890/0012-
649 9658(1999)080[1322:CVPPAN]2.0.CO;2.

650 Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A.
651 D. Fox, O. Gilg, et al. 2009. Ecological dynamics across the Arctic associated with recent climate
652 change. *Science* 325: 1355–1358. doi:10.1126/science.1173113.

653 Prevéy, J. S., C. Rixen, N. Rüger, T. T. Høye, A. D. Bjorkman, I. H. Myers-Smith, S. C. Elmendorf, I.
654 W. Ashton, et al. 2018. Warming shortens flowering seasons of tundra plant communities. *Nature*
655 *ecology & evolution*. Nature Publishing Group. doi:10.1038/s41559-018-0745-6.

656 Prevéy, J., M. Vellend, N. Rüger, R. D. Hollister, A. D. Bjorkman, I. H. Myers-Smith, S. C.
657 Elmendorf, K. Clark, et al. 2017. Greater temperature sensitivity of plant phenology at colder
658 sites: implications for convergence across northern latitudes. *Global Change Biology* 23: 2660–
659 2671. doi:10.1111/gcb.13619.

660 Raich, J. W., and C. S. Potter. 1995. Global patterns of carbon dioxide emissions from soils. *Global*
661 *Biogeochemical Cycles* 9. Wiley-Blackwell: 23–36. doi:10.1029/94GB02723.

662 Richardson, S. J., M. C. Press, A. N. Parsons, and S. E. Hartley. 2002. How do nutrients and warming
663 impact on plant communities and their insect herbivores? A 9-year study from a sub-Arctic heath.
664 *Journal of Ecology* 90: 544–556. doi:10.1046/j.1365-2745.2002.00681.x.

665 Robinson, C. H., P. A. Wookey, J. A. Lee, T. V. Callaghan, and M. C. Press. 1998. Plant Community
666 Responses to Simulated Environmental Change at a High Arctic Polar Semi-Desert. *Ecology* 79:
667 856. doi:10.2307/176585.

668 Rundqvist, S., H. Hedenås, A. Sandström, U. Emanuelsson, H. Eriksson, C. Jonasson, and T. V.
669 Callaghan. 2011. Tree and Shrub Expansion Over the Past 34 Years at the Tree-Line Near
670 Abisko, Sweden. *Ambio* 40: 683–692. doi:10.1007/s13280-011-0174-0.

671 Schuur, E. A. G., A. D. McGuire, C. Schädel, G. Grosse, J. W. Harden, D. J. Hayes, G. Hugelius, C.
672 D. Koven, et al. 2015. Climate change and the permafrost carbon feedback. *Nature* 520: 171–
673 179. doi:10.1038/nature14338.

674 Starr, G., S. F. Oberbauer, and E. W. Pop. 2000. Effects of lengthened growing season and soil
675 warming on the phenology and physiology of *Polygonum bistorta*. *Global Change Biology* 6.
676 Wiley Online Library: 357–369.

677 Steinbauer, M. J., J.-A. Grytnes, G. Jurasinski, A. Kulonen, J. Lenoir, H. Pauli, C. Rixen, M. Winkler,
678 et al. 2018. Accelerated increase in plant species richness on mountain summits is linked to
679 warming. *Nature* 556: 231–234. doi:10.1038/s41586-018-0005-6.

680 Stenström, A., and I. S. Jónsdóttir. 1997. Responses of the clonal sedge, *Carex bigelowii*, to two
681 seasons of simulated climate change. *Global Change Biology* 3. John Wiley & Sons, Ltd
682 (10.1111): 89–96. doi:10.1111/j.1365-2486.1997.gcb134.x.

683 Stern, G. A., and A. Gaden. 2015. *From Science to Policy in the Western and Central Canadian*
684 *Arctic: An Integrated Regional Impact Study (IRIS) of Climate Change and Modernization*.
685 Quebec City: ArcticNet.

686 Sturm, M., and T. Douglas. 2005. Changing snow and shrub conditions affect albedo with global
687 implications. *Journal of Geophysical Research* 110: G01004. doi:10.1029/2005JG000013.

688 Sturm, M., C. Racine, and K. Tape. 2001. Increasing shrub abundance in the Arctic. *Nature* 411: 546–
689 547.

690 Tolvanen, A., and G. H. R. Henry. 2011. Responses of carbon and nitrogen concentrations in high
691 arctic plants to experimental warming. *Canadian Journal of Botany*. NRC Research Press
692 Ottawa, Canada. doi:10.1139/b01-052.

693 Tømmervik, H., B. Johansen, I. Tombre, D. Thannheiser, K. A. Høgda, E. Gaare, and F. E.
694 Wielgolaski. 2004. Vegetation Changes in the Nordic Mountain Birch Forest: the Influence of
695 Grazing and Climate Change. *Arctic, Antarctic, and Alpine Research* 36: 323–332.
696 doi:10.1657/1523-0430(2004)036[0323:vcitnm]2.0.co;2.

697 van Altena, C., R. S. P. van Logtestijn, W. K. Cornwell, and J. H. C. Cornelissen. 2012. Species
698 composition and fire: non-additive mixture effects on ground fuel flammability. *Frontiers in*
699 *plant science* 3. Frontiers: 63. doi:10.3389/fpls.2012.00063.

700 van Gestel, N., Z. Shi, K. J. van Groenigen, C. W. Osenberg, L. C. Andresen, J. S. Dukes, M. J.
701 Hovenden, Y. Luo, et al. 2018. Predicting soil carbon loss with warming. *Nature* 554. Nature
702 Publishing Group: E4–E5. doi:10.1038/nature25745.

703 Villarreal, S., R. D. Hollister, D. R. Johnson, M. J. Lara, P. J. Webber, and C. E. Tweedie. 2012.
704 Tundra vegetation change near Barrow, Alaska (1972–2010). *Environmental Research Letters* 7:
705 015508–11. doi:10.1088/1748-9326/7/1/015508.

706 Vowles, T., C. Lovehø, U. Molau, and R. G. Björk. 2017. Contrasting impacts of reindeer grazing in
707 two tundra grasslands. *Environmental Research Letters* 12: 034018–10. doi:10.1088/1748-
708 9326/aa62af.

709 Walker, M. D., C. H. Wahren, R. D. Hollister, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P.
710 Calef, T. V. Callaghan, et al. 2006. Plant community responses to experimental warming across
711 the tundra biome. *Proceedings of the National Academy of Sciences of the United States of*
712 *America* 103: 1342–1346. doi:10.1073/pnas.0503198103.

713 Wang, P., J. Limpens, L. Mommer, J. van Ruijven, A. L. Nauta, F. Berendse, G. Schaepman-Strub, D.
714 Blok, et al. 2017. Above- and below-ground responses of four tundra plant functional types to
715 deep soil heating and surface soil fertilization. Edited by Etienne Laliberté. *Journal of Ecology*
716 105: 947–957. doi:10.1111/1365-2745.12718.

717 Welker, J. M., U. Molau, A. N. Parsons, C. H. Robinson, and P. A. Wookey. 1997. Responses of
718 *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar
719 comparisons. *Global Change Biology* 3. Wiley Online Library: 61–73.

- 720 Weller, G., E. Bush, T. V. Callaghan, R. Corell, S. Fox, C. Furgal, A. H. Hoel, H. Huntington, et al.
721 2004. Summary and Synthesis of the ACIA. In *Impacts of a Warming Arctic: Arctic Climate*
722 *Impact Assessment*, ed. S. J. Hassol, 990–1020. Cambridge, UK: Cambridge University Press.
- 723 Wheeler, H. C., T. T. Høye, N. M. Schmidt, J.-C. Svenning, and M. C. Forchhammer. 2015.
724 Phenological mismatch with abiotic conditions - implications for flowering in Arctic plants.
725 *Ecology* 96: 775–787.
- 726 Wilson, S. D., and C. Nilsson. 2009. Arctic alpine vegetation change over 20 years. *Global Change*
727 *Biology* 15: 1676–1684. doi:10.1111/j.1365-2486.2009.01896.x.
- 728 Wookey, P. A., A. N. Parsons, J. M. Welker, J. A. Potter, T. V. Callaghan, J. A. Lee, and M. C. Press.
729 1993. Comparative responses of phenology and reproductive development to simulated
730 environmental change in sub-arctic and high Arctic plants. *Oikos* 67. JSTOR: 490–502.
- 731 Zamin, T. J., M. S. Bret-Harte, and P. Grogan. 2014. Evergreen shrubs dominate responses to
732 experimental summer warming and fertilization in Canadian mesic low arctic tundra. Edited by
733 Rien Aerts. *Journal of Ecology* 102: 749–766. doi:10.1111/1365-2745.12237.
- 734