

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

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31
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114

115 **Abstract**

116

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

134

135 **Keywords**

136

137 vegetation change, phenology, Arctic, experimental warming, long-term monitoring

138

139 **Introduction**

140

141 A major goal of global change ecology is to document and predict the impacts of environmental
142 change on species, communities and ecosystems worldwide. In the Arctic, exceptionally rapid
143 warming (IPCC 2013) has the potential to lead to dramatic changes in vegetation through longer
144 growing seasons, increased thaw depth, and altered snow regimes. High latitudes contain up to 50%

145 of the world's soil carbon stored in permafrost soils; this carbon is vulnerable to loss with warming
146 (Schuur et al. 2015; Crowther et al. 2016; van Gestel et al. 2018). Thus, change in vegetation carbon
147 and nutrient inputs to tundra soils could have potentially global impacts. For example, shifts in
148 species composition could lead to changes in aboveground carbon storage, nutrient cycling,
149 decomposition rates, (Callaghan et al. 2004), potentially leading to global climate feedbacks (Chapin
150 et al. 2005; Pearson et al. 2013). Changing vegetation could also alter trophic interactions (Post et al.
151 2009; Gauthier et al. 2013) and thus influence Arctic wildlife populations and the human communities
152 that rely on them for resource provision or cultural purposes (Weller et al. 2004; Henry et al. 2012;
153 Stern and Gaden 2015).

154
155 A key source of information about the consequences of climate warming for Arctic vegetation comes
156 from plot-based research at sites across the Arctic (Henry and Molau 1997). This includes both long-
157 term monitoring of species composition, diversity, and phenology over time (up to four decades), as
158 well as experimental manipulation of key abiotic and biotic drivers (e.g., temperature, snow, nutrients,
159 grazing). Community composition, diversity, and phenology have all been identified as “Focal
160 Ecosystem Components” (FECs) by the international Circumpolar Biodiversity Monitoring Program
161 (Christensen et al. 2013), as monitoring of these attributes facilitates a more rapid detection,
162 communication, and response to significant biodiversity-related trends and pressures affecting the
163 circumpolar world. In addition, comparing the results of observed trends over time with experimental
164 studies can help to elucidate the drivers of observed trends and inform predictions of future change
165 (Elmendorf et al. 2015).

166
167 Here, we synthesize what is currently known about plot-based changes in vegetation composition
168 (abundance), phenology, diversity, and functional traits. We compiled information from single-site
169 studies of composition and phenological change to document 1) the direction and significance of
170 change over time, and 2) the direction and significance of responses to experimental warming. We
171 compare these results to published syntheses of long-term monitoring and experimental warming. We
172 additionally review studies of plot-based changes in plant functional traits and diversity, for which
173 published observations are relatively scarce. Finally, we discuss the broader implications of observed
174 and predicted Arctic vegetation change and recommend priorities for future monitoring efforts.

175 176 **Materials and Methods**

177
178 *Literature review of vegetation trends*
179

180 We conducted a literature review to identify single-site studies of changes in plant community
181 composition (abundance) and phenology both over time and in response to experimental warming.
182 Our search included combinations of the terms “tundra”, “arctic”, “vegetation”, “plot”, “change”,
183 “ITEX”, “cover”, “abundance”, “phenology”, “diversity”, “functional trait”, “warming”, and
184 “experiment”. These terms encompasses two Focal Ecosystem Components included in the
185 Circumpolar Biodiversity Monitoring Program terrestrial monitoring plan: i) diversity, composition
186 and abundance and ii) phenology. We do not include the attributes “diversity and spatial structure”,
187 “productivity”, “Rare species, species of concern”, or “food species” in this review due to a paucity of
188 published plot-based monitoring and/or experimental studies on these topics. The attribute “non-
189 native species” is addressed in a separate article in this issue [WASOWICZ ET AL., THIS ISSUE].

190

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

199

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

208

209 For all studies we recorded the direction (increase/stable/decrease for abundance change, or
210 earlier/stable/later for phenological change) and significance (yes/no) of responses for all species and
211 functional groups identified. A response could be recorded as directional (increase/decrease or
212 earlier/later) and non-significant if the authors identified it as such, or if the p-value provided was
213 between 0.05 and 0.1. We adopted this approach in order to standardize alpha levels across all studies
214 (e.g. if some studies used an alpha level cut-off of 0.05 to assess significance while others used an
215 alpha level of 0.1). If a response was identified by the authors as directional but no indication of

216 significance was given (either in the text or in a figure/table), the response was categorized as non-
217 significant. The difference between significant and non-significant directional changes is shown in the
218 figures and provided in the supplementary data table. We used this “vote-counting” approach, rather
219 than a traditional meta-analysis, in order to include the many studies that do not provide response
220 effect sizes or estimates of error. In addition, this approach allows us to visualize the full distribution
221 of vegetation responses to ambient and experimental warming, as a meta-analysis finding of “no-
222 change” could in fact be made up of multiple significant changes in different directions (e.g. context
223 dependency).

224

225 Experimental warming was generally conducted through the use of clear-sided, open-top chambers
226 that passively warm air temperatures by ~1.5-3 °C, with most of the studies following International
227 Tundra Experiment (ITEX) protocols (Molau and Mølgaard 1996; Marion et al. 1997), though some
228 experiments used greenhouses or other warming methods (Chapin and Shaver 1996; Wang et al.
229 2017). The seasonal duration of warming also varies by study; some warming chambers were in place
230 only during the summer, while others were present year-round. Both warming chambers and
231 greenhouses can influence environmental factors other than temperature (e.g. soil moisture, wind,
232 snow accumulation), though the magnitude and significance of these effects are variable among sites
233 (Marion et al. 1997).

234

235 *Comparison to tundra-wide syntheses*

236

237 In order to evaluate the consistency of patterns revealed by the literature review, we compared the
238 results of our review with tundra-wide syntheses of community composition and phenological change
239 (Arft et al. 1999; Walker et al. 2006; Elmendorf et al. 2012a; Elmendorf et al. 2012b; Oberbauer et al.
240 2013), both over time and in response to experimental warming. These syntheses used primary data
241 and were not based on published studies, though some data included in the syntheses may be from the
242 same sites as the single-site studies included in our literature review. However, the synthesis and
243 single-site studies likely include different combinations of sites and years, and use different statistical
244 methods to analyze responses. In addition, many of the synthesis studies included both Arctic and
245 alpine tundra sites, while here we focused exclusively on Arctic and sub-Arctic locations. Thus,
246 evidence that synthesis studies found trends consistent with those documented in this literature review
247 can help evaluate the robustness of observed patterns in Arctic vegetation change.

248

249 **Results**

250

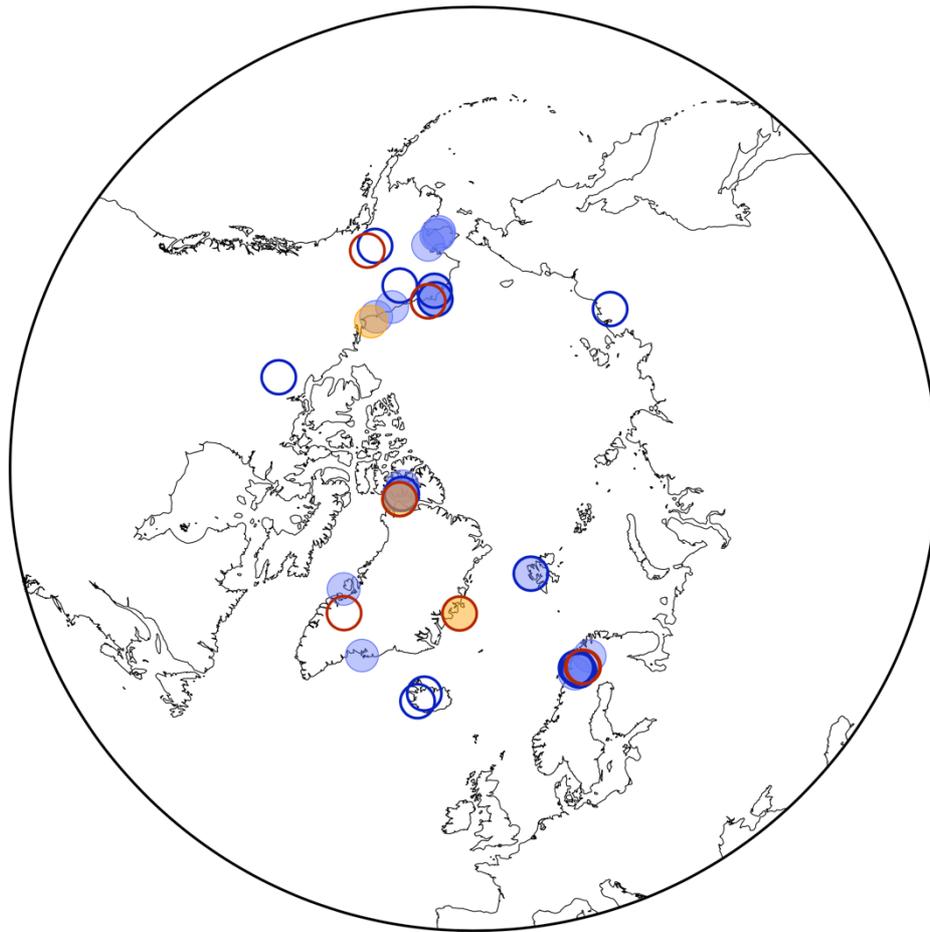
251 We identified a total of 560 vegetation composition/abundance observations (species or functional
252 group) from 19 studies of long-term monitoring and 209 observations from 14 studies of responses to
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version is available online at: <http://dx.doi.org/10.1007/s13280-019-01161-6>

253 experimental warming (Figure 1, Table 1). The duration of monitoring studies ranged from five to 43
254 years, with a median duration of 19 years. We additionally identified long-term monitoring of
255 phenology for 17 species in three studies and responses to experimental warming of 52 species from
256 nine studies (Figure 1, Table 1). Phenological monitoring studies ranged from nine to 21 years in
257 duration, with a median duration of 16 years.

258

259 Our literature review reveals geographical gaps in both long-term monitoring and experimental
260 warming studies. The FEC (Christensen et al. 2013) encompassing composition and abundance is
261 better represented than that encompassing phenology, but both lack published records of change from
262 Siberia and wide swaths of the Canadian Arctic. Intensive, multivariate monitoring is concentrated
263 primarily in Alaska and Scandinavia, with the exception of one site in high-Arctic Canada (Muc et al.
264 1989; Freedman and Svoboda 1994; Hudson and Henry 2009; Hill and Henry 2011; Bjorkman et al.
265 2015).

266



267

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

272

273 *Vegetation composition change*

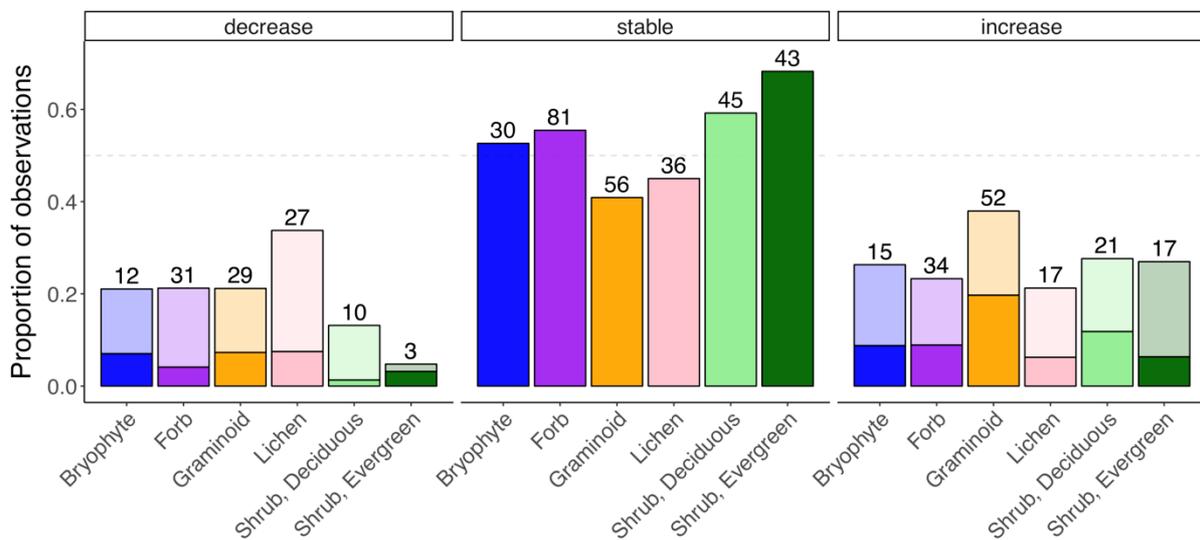
274 In all cases, the most common response documented by long-term monitoring of compositional
 275 change was one of no trend (52-84% of trends did not differ from zero, depending on the significance
 276 cutoff used; Figure 2). This is likely an underestimate of the proportion of no-change responses, as
 277 some studies reported results only for species that changed significantly over time (Tømmervik et al.
 278 2004). Forbs, graminoids and both evergreen and deciduous shrubs were slightly more likely to
 279 increase in abundance over time than decrease, but were most likely to remain stable. Experimental
 280 warming led to more dramatic responses, particularly in lichens, which were far more likely to
 281 decrease in abundance in response to experimental warming (46-63%) than to increase (0%) or
 282 remain stable (37%). Bryophytes also had a tendency to respond negatively to experimental warming,
 283 while evergreen and deciduous shrubs were more likely to respond positively.

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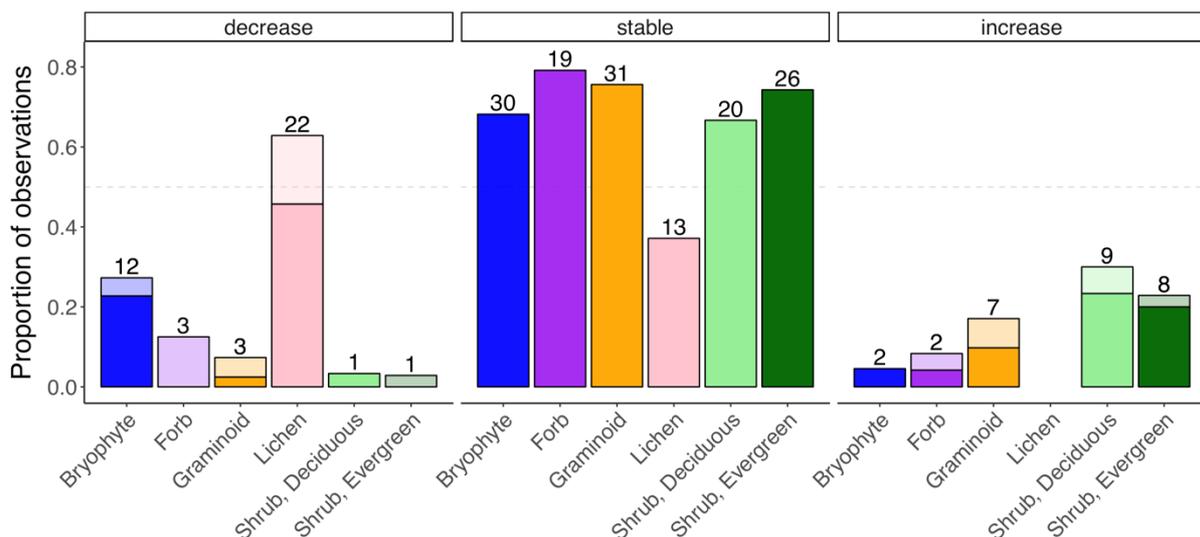
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Few studies included both above- and below-ground measurements; of those that did, above- and below-ground responses were not always consistent. Above-ground responses to experimental warming in northern Alaska were greater than below-ground responses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

a) Direction of abundance change over time



b) Abundance response to experimental warming



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Figure 2. Summary of studies investigating abundance change over time (a) and abundance change in response to experimental warming (b) by species or functional group. Panels represent, from left to right, the proportion of observations decreasing in abundance, stable, or increasing in abundance over time (median 20.5 years) or in response to experimental warming. Species-specific trends were grouped into the relevant functional group category. The darker portions of each bar represent “significant” ($p < 0.05$) change (decrease or increase) or

299 *insignificant (stable; $p > 0.1$) results, while lighter colors represent borderline or marginally significant change*
300 *(e.g., p -values between 0.05 and 0.1). The numbers above each bar represent a count of the number of*
301 *observations included in that group. The proportion of “stable” species is underrepresented in this figure, as*
302 *some studies only reported results for species that changed in abundance.*

303 These responses are largely in line with those revealed in tundra-wide syntheses of vegetation change
304 at the functional group level. In a recent thirty-year study of vegetation change across 46 Arctic,
305 alpine and Antarctic tundra locations (Elmendorf et al. 2012b), only evergreen shrubs (but not
306 deciduous) increased significantly over time. Bryophytes were more likely to decrease than increase,
307 but the response was not significant. Similar to results from our literature review, responses to
308 experimental warming were more dramatic. Deciduous but not evergreen shrubs increased
309 significantly in abundance in response to experimental warming, while both lichens and bryophytes
310 decreased significantly (Elmendorf et al. 2012a). In both monitoring and experimental synthesis
311 studies, the quantity of dead material (litter and attached dead) increased over time or with warming
312 (Elmendorf et al. 2012a; Elmendorf et al. 2012b).

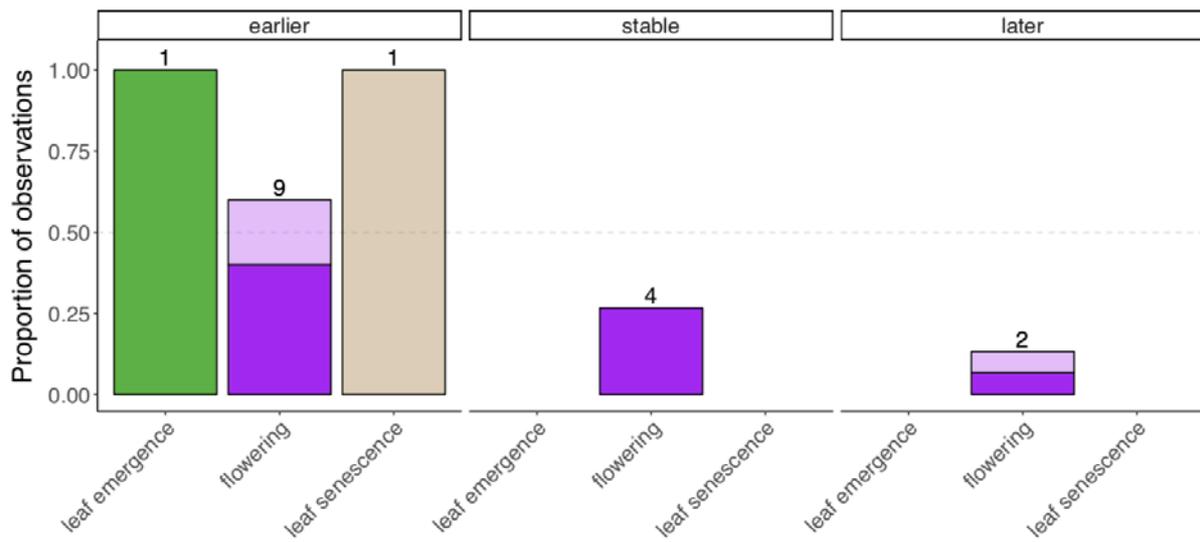
313

314 *Phenological change*

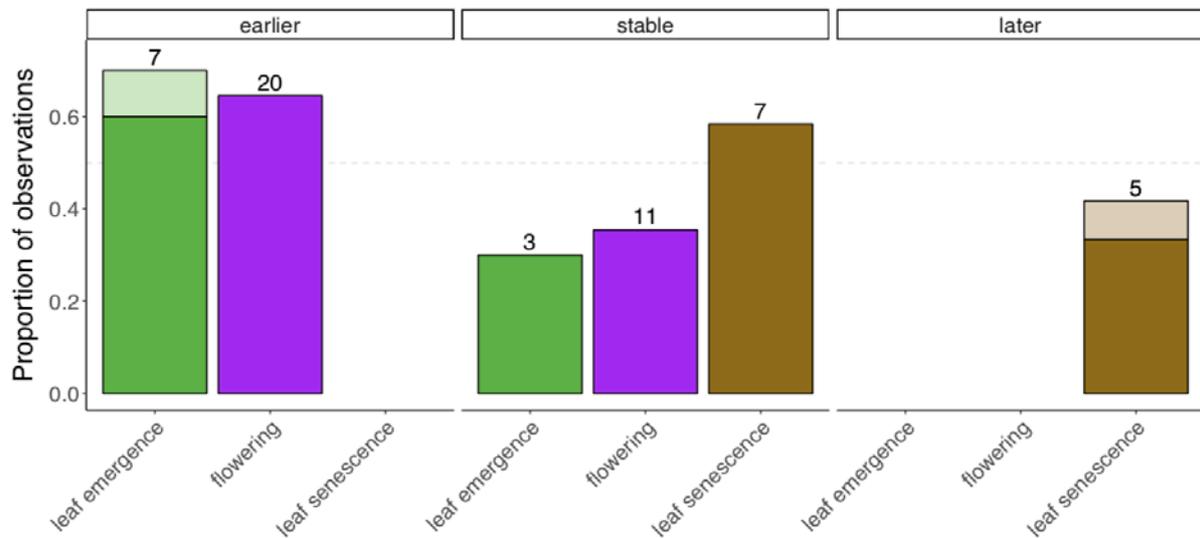
315 In general, the timing of leaf emergence and flowering advanced both over time and with
316 experimental warming, though a minority of species experienced stable or even delayed flowering
317 over time (Figure 3). Interestingly, experimental warming led to later leaf senescence in all cases,
318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

320

a) Direction of phenological change over time



b) Phenological response to experimental warming



321

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

329

330 In a 17-year synthesis of phenological trends at 12 tundra sites (including two alpine locations), there
 331 was no significant change in the timing of flowering or leaf senescence, though both events tended to
 332 advance over time (Oberbauer et al. 2013), as we also found in the literature review. Surprisingly, this
 333 same synthesis study found that leaf emergence was significantly delayed over time despite increasing
 334 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

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

337

338 **Discussion**

339

340 Studies of plot-based vegetation change reveal that while some sites and species or functional groups
341 have experienced substantial shifts in vegetation and phenology in response to ambient or
342 experimental warming, the most common response overall is one of no change. Furthermore,
343 vegetation changes over time did not always match responses to experimental warming. One pattern
344 emerges: both long-term monitoring and experimental studies suggest that the graminoid and shrub
345 functional groups respond positively to warming and are slightly more likely to increase in abundance
346 over time. This is in line with studies of shrub infilling and expansion across much of the tundra
347 (Sturm et al. 2001; Myers-Smith et al. 2011a; Martin et al. 2017). Even so, the majority of graminoid
348 and shrub abundance responses in our literature review were that of no significant trend over time and
349 no significant response to experimental warming. Further exploration of these trends reveals that
350 increasing shrub abundance primarily occurs in relatively warm tundra regions with mesic or wet
351 soils, while colder and dry tundra sites have not experienced increasing shrub abundance (Elmendorf
352 et al. 2012b) consistent with patterns in the climate sensitivity of shrub growth (Myers-Smith et al.
353 2015). Grazing may also influence shrub responses to summer temperature change (Bråthen et al.
354 2017). The lack of strong trends over time in many sites and for many species suggests that tundra
355 plant communities are remarkably resilient to moderate warming, at least over decadal time spans,
356 and that site-specific factors such as moisture availability and grazing may limit vegetation responses
357 to warming (Elmendorf et al. 2012b; Myers-Smith et al. 2015; Ackerman et al. 2017).

358

359 Differing responses to experimental and ambient (natural) warming highlight both the benefits and the
360 challenges of using experimental approaches to understand tundra vegetation responses to climate
361 change. When experimental and monitoring results agree, experimental studies enable us to pinpoint
362 the likely drivers of change over time (Elmendorf et al. 2015), and improve our confidence in
363 predictions of the impacts of warming on vegetation (e.g., increasing shrub abundance). Diverging
364 responses can challenge our understanding of tundra vegetation change. For example, while
365 experimental warming led to fairly dramatic declines in lichen abundance (Walker et al. 2006;
366 Elmendorf et al. 2012a and this study), lichen abundance did not decline over time in long-term
367 monitoring studies (Elmendorf et al. 2012b and this study). Similarly, while experimental warming
368 generally led to later leaf senescence (Arft et al. 1999 and this study), monitoring studies indicate that
369 senescence is in fact advancing over time, though not significantly (Oberbauer et al. 2013 and this

370 study). Trends in the timing of flowering and leaf emergence are also varied despite a relatively
371 consistent advance in these variables in response to experimental warming.

372

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

386

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

394

395 *Other vegetation trends: functional traits and diversity*

396

397 While trends in composition and phenology are perhaps the most studied plot-based responses to
398 global change, a handful of studies document changes in other vegetation parameters. Of these,
399 increasing height is likely the most well-documented. Increases in community height have been
400 documented by synthesis studies of responses to experimental warming (Elmendorf et al. 2012a) and
401 over time (Bjorkman et al. 2018), a change driven primarily by the influx of taller species into the
402 monitoring plots (Bjorkman et al. 2018). Some single-site studies have also documented increasing
403 height over time (Hollister et al. 2015) and in response to experimental warming (Hudson et al. 2011;
404 Hollister et al. 2015; Baruah et al. 2017). Changes in other plant traits have also been documented.
405 Experimental warming at Alexandra Fiord in high Arctic Canada resulted in greater leaf size, lower

406 specific leaf area (the ratio of leaf area to leaf dry mass), and decreased leaf carbon content for at least
407 some species-site combinations (Hudson et al. 2011) but did not affect leaf nitrogen (N) content, leaf
408 dry matter content, or nitrogen isotope signatures. Other studies have documented mixed responses of
409 leaf size to experimental warming in the Swedish subarctic tundra (Graglia et al. 1997; Baruah et al.
410 2017) and one study found trends toward reduced leaf size over time (Barrett et al. 2015). Additional
411 studies of leaf N content responses to experimental warming are also mixed; leaf N content increased
412 in response to winter but not summer warming across six species at Eight Mile Lake, Alaska (Natali
413 et al. 2012) but was either unaffected by temperature or declined in response to warming at Toolik
414 Lake, Alaska (Chapin and Shaver 1996) and Alexandra Fiord, Canada (Tolvanen and Henry 2011). A
415 synthesis of community-weighted mean functional trait change across the tundra biome (including
416 alpine sites) over 27 years found no significant change in leaf area, leaf N content, leaf dry matter
417 content, or specific leaf area (Bjorkman et al. 2018). Overall, species composition has shifted toward
418 more thermophilic (warm-loving) species both over time and in response to experimental warming
419 (Elmendorf et al. 2015).

420

421 Over the long term, climate warming may lead to increased diversity in the Arctic as southern,
422 species-rich floras move northward (Parmesan 2006). However, short-term responses to warming
423 might differ substantially from long-term trends, as immigration is likely to be slow relative to local
424 assembly processes (e.g. competition; Walker et al. 2006). Thus far, evidence of plot-scale diversity
425 change in Arctic ecosystems is mixed. A multi-site synthesis found a significant decline in both
426 Shannon diversity and species richness after three to six years of experimental warming (Walker et al.
427 2006), but a more recent, longer-term synthesis found no response (Elmendorf et al. 2012a). Lichen
428 diversity was found to decline significantly in response to long-term experimental warming at three
429 sites in northern Sweden and Alaska (Lang et al. 2012). Among monitoring studies, a recent synthesis
430 found no change in vascular plant diversity over three decades of monitoring across dozens of tundra
431 sites (Elmendorf et al. 2012b). This is in stark contrast to ongoing changes in European mountaintop
432 plant communities, which have experienced rapid and accelerating increases in richness over the past
433 century (Steinbauer et al. 2018). This difference could indicate that diversity change in non-alpine
434 tundra communities is limited by dispersal rates of southerly, warm-adapted species, or that strong
435 gradients in environmental variables other than temperature (e.g. photoperiod) across latitudes limit
436 the establishment success of warm-adapted species from farther south (Bjorkman et al. 2017).

437

438 *Consequences of Arctic vegetation change*

439

440 Changes in tundra vegetation could have far-reaching impacts across trophic levels and to human
441 societies (Weller et al. 2004). Shifts in plant phenology and reproductive success influence individual-

442 and population-level fitness (Berteaux et al. 2004; Cleland et al. 2012) and could lead to trophic
443 mismatches of resources for pollinators (Høye et al. 2013; Wheeler et al. 2015; Prevéy et al. 2018),
444 breeding birds (McKinnon et al. 2012; Gauthier et al. 2013; Boelman et al. 2015) and mammals
445 (Hertel et al. 2017). For example, one long-term study at Zackenberg, Greenland documented a
446 shortening of the flowering season with climate warming over time and a concurrent decline in the
447 abundance of insect visits to flowers (Høye et al. 2013). Berry-producing (Hertel et al. 2017) and
448 other tundra plants provide forage for hunted or domestic wildlife (Post and Stenseth 1999; Kerby and
449 Post 2013) and represent culturally important resources for Arctic peoples (Henry et al. 2012).

450

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

465

466 Due to the large amount of carbon stored in tundra permafrost soils (Koven et al. 2011; Schuur et al.
467 2015; Crowther et al. 2016) and well-established links between vegetation and carbon storage,
468 vegetation change in the Arctic can influence regional carbon cycling and feedbacks to the global
469 climate (Callaghan et al. 2004; Sturm and Douglas 2005; Petrenko et al. 2016). For example,
470 increasing shrub abundance and/or plant height can lead to increased winter snow trapping, greater
471 insulation of underlying soils, warmer winter soil temperatures (Myers-Smith and Hik 2013), and
472 potentially increased active layer depth and decomposition (Blok et al. 2016). Taller shrubs may also
473 extend above the snowpack, decreasing winter albedo and increasing absorbed solar radiation (Sturm
474 and Douglas 2005). Bryophytes have also been shown to play an important role in soil insulation and
475 energy fluxes; experimental removal of bryophytes leads to increased evapotranspiration and ground
476 heat flux (Blok et al. 2011). Thus, future declines in bryophytes – observed in warming experiments

477 but not yet in monitoring studies – could also lead to deeper summer permafrost thaw and soil carbon
478 release, representing another positive feedback to climate warming.

479

480 Changing vegetation can also impact carbon cycling through changes in the quantity and
481 decomposability of litter (Callaghan et al. 2004), as litter decomposition contributes nearly 70% of
482 global CO₂ fluxes from soils (Raich and Potter 1995). A long-term increase in shrubs, which have
483 relatively recalcitrant litter, could lead to reduced litter decomposability and a negative feedback to
484 climate warming (Cornelissen et al. 2007). A change in litter composition can also indirectly
485 influence soil carbon storage by driving changes in soil microbial communities (Christiansen et al.
486 2018) or altering tundra fuel loads. For example, increased woody litter inputs from shrub expansion
487 might also increase flammability, which could lead to positive feedbacks through fire-induced soil
488 carbon loss (Cornelissen et al. 2007; van Altena et al. 2012).

489

490 **Conclusions**

491

492 Rapid warming in the Arctic has the potential to cause substantial shifts in vegetation, potentially
493 driving widespread changes across trophic levels and altering tundra ecosystem functions. While our
494 review identifies significant shifts at some sites and in some species, the large variation in the
495 magnitude and even direction of responses illustrates the high degree of context dependency in tundra
496 vegetation change. This context dependency highlights the importance of maintaining multiple
497 monitoring sites in many different habitat types across the entire Arctic, as well as increasing
498 monitoring of local ecological and environmental conditions that would improve our understanding of
499 how factors other than temperature influence Arctic vegetation change. Thus, we recommend that
500 international bodies such as the Circumpolar Biodiversity Monitoring Program (Christensen et al.
501 2013) prioritize monitoring efforts that i) fill current geographical gaps, particularly in Canada and
502 Siberia, and ii) enable us to better disentangle the relative importance of climate warming and other
503 environmental factors on the diverging responses reported here.

504

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

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