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1 **Phenological responses to small-scale spatial variation in snowmelt timing reveal**
2 **compensatory and conservative strategies in subarctic-alpine plants**

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26 **Abstract**

27 **Background:** In tundra ecosystems, the adjustment of phenological events, such as bud burst, to
28 snowmelt timing is crucial to the climatic adaptation of plants. Natural small-scale variations in
29 microclimate potentially enable plant populations to persist in a changing climate.

30 **Aims:** To assess how plant phenology responds to natural differences in snowmelt timing.

31 **Methods:** We observed the timing of eight vegetative and reproductive phenophases in seven dwarf-
32 shrub species in relation to differences in snowmelt timing on a small spatial scale in an alpine
33 environment in subarctic Finland.

34 **Results:** Some species and phenophases showed accelerated development with later snowmelt, thus
35 providing full or partial compensation for the shorter snow-free period. Full compensation resulted in
36 synchronous occurrence of phenophases across the snowmelt gradient. In other species, there was no
37 acceleration of development. The timing of phenophases varied between two consecutive years and
38 two opposing mountain slope aspects.

39 **Conclusions:** The results have shown three distinct patterns in the timing of phenophases in relation to
40 snowmelt and suggest alternative strategies for adaptation to snowmelt timing. These strategies
41 potentially apply to other species and tundra ecosystems and provide a framework, enabling one to
42 compare and generalise phenological responses to snowmelt timing under different future climate
43 scenarios.

44 **Keywords:** climate change; compensation; conservative strategy; natural snowmelt gradient;
45 phenophases; plant phenology; subarctic; tundra

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52 **Introduction**

53 In high latitude and high elevation ecosystems, snow cover can last for several months, profoundly
54 affecting seasonal dynamics and plant life (Jonas et al. 2008; Estilow et al. 2015). Snow cover
55 protects plants from harsh winter conditions such as low temperatures, ice blast, winter desiccation,
56 frost damage and photoinhibition (Körner 2003; Zhang 2005; Bennie et al. 2010; Saarinen and
57 Lundell 2010). During the growing season, the progression of snowmelt and the amount of
58 snowpack also determine local soil moisture and nutrient conditions near the melting snowbeds
59 (Björk and Molau 2007; Clement et al. 2012). The timing of snowmelt, along with a changing
60 photoperiod and temperature, largely determines the onset of plant growth. Snowmelt directly
61 increases the light and water available to the plant and coincides with higher temperatures and
62 longer days (Billings and Mooney 1968; Jonas et al. 2008). Recently, it has further been suggested
63 that the timing of spring snowmelt affects the timing of autumn senescence (Abbandonato 2014;
64 Keenan and Richardson 2015). Thus year-round plant growth appears to be influenced by the
65 duration of snow cover.

66 Climate change is predicted to affect the amount and duration of snow cover, especially at
67 high latitudes (ACIA 2005; Callaghan et al. 2011; IPCC 2013). Higher temperatures, leading to
68 earlier snowmelt in the spring have already been recorded in the western North American and the
69 Northern European Arctic (e.g. Serreze et al. 2000; Stone et al. 2002). This can potentially alter the
70 growing season length and can lead to shifts in the timing of seasonal events in plants
71 (phenophases), flowering synchrony with the presence of pollinators, exposure to spring frost, and
72 eventually to plant fitness (Inouye 2008; Wipf et al. 2009; Kudo and Ida 2013; Gillespie et al.
73 2016).

74 Snow manipulation experiments (addition or removal of snow) have been used in arctic,
75 subarctic tundra and in alpine vegetation to study the short- and mid-term effects of simulated
76 changes in winter climate on the timing of phenophases in plants (Henry and Molau 1997; Walker

77 et al. 1999; Wipf and Rixen 2010; Cooper 2014; Wipf et al. 2015). In most studies, phenophases
78 were affected by differences in snowmelt timing, for example they occurred on an earlier day of the
79 year (DOY) when the snow melted earlier (Wipf et al. 2009; Wipf and Rixen 2010; Cooper et al.
80 2011; Livensperger et al. 2016); but in others, the DOY remained the same regardless of snowmelt
81 timing (Dunne et al. 2003; Aerts et al. 2004). The photoperiod at a given location is always the
82 same for a given DOY, so those phenophases found always to occur on the same DOY might be
83 responding to photoperiod, i.e. they may be photoperiodic. Photoperiodism enables plants to delay
84 phenophases until later in the season when temperature conditions are more stable if a longer day
85 length is a signal for a later onset of development (Keller and Körner 2003). On the other hand,
86 plants with less photoperiodism have the capacity to commence growth as a function of snowmelt,
87 and this, in case of earlier melt-out, has the advantage of a longer growing season (Wipf et al.
88 2009). Phenological timing can also be assessed as the number of days required after snowmelt
89 (days after snowmelt; DAS) until the beginning of growth or a new phenophase. The DAS may
90 either remain the same (Borner et al. 2008) or vary (Petraglia et al. 2014; Bienau et al. 2015) for
91 plants growing along snowmelt gradients. DAS can be used to characterise the rate of plant
92 development after snowmelt, i.e. how fast a phenophase is attained (assuming that developmental
93 processes begin on snowmelt). The rate of development is determined by genetic requirements and
94 current environmental conditions, such as temperature, and can therefore give additional insights
95 into the mechanisms that control the timing of phenology (Bliss 1962). How the timing of
96 phenophases is affected by snowmelt timing depends on whether they are controlled by photoperiod
97 alone or by other factors, such as temperature and soil moisture.

98 Limited conclusions can be drawn from experimental simulations of snowmelt timing alone
99 since they can only capture immediate and short-term acclimation responses of plants, but not their
100 long-term adaptation to existing variations in local conditions (Wolkovich et al. 2012; Blume-
101 Werry et al. 2016). In arctic and alpine ecosystems with uneven terrain, large variations in

102 snowmelt timing can occur naturally on a scale of a few metres, so that early-, mid- and late-
103 melting areas are adjacent to each other (Körner 2003). A plant population occurring along such a
104 gradient has adapted to the microclimatic variation, either genetically or through strong phenotypic
105 plasticity, as seen in its successful establishment. This capacity to exist along gradients in snowmelt
106 timing means that plant populations may be pre-adapted to the potential variations created by
107 climate change in the future, i.e. plants with the capacity to adjust to future climatic changes may
108 exist within a distance of just a few metres (Crawford and Abbott 1994). As short-term experiments
109 may over-predict adverse effects of environmental changes due to the lack information about long-
110 term adaptive responses, understanding natural variations of populations to snowpack duration is
111 important (Blume-Werry et al. 2016). Reports from *in situ* observations of phenological events
112 along natural snow duration gradients are relatively few (but see for example Kudo 1991; Kudo and
113 Suzuki 1999; Dunne et al. 2003; Kudo and Hirao 2006; Sedlacek et al. 2015; Wheeler et al. 2015,
114 2016; Carbognani et al. 2016) compared to experimental studies. However, they are important for
115 indicating the natural limitations of a species and whether a plant population is pre-adapted to
116 diverse microclimates and therefore may be buffered against future climate change (Crawford
117 2008). Studying over the long term of natural small-scale environmental variations is therefore
118 needed alongside experimental studies to assess the long-term success of a population.

119 This study aimed to evaluate how natural differences in the timing of spring snowmelt on a
120 small spatial scale affected plant phenology. We studied how many days after snowmelt (DAS) and
121 on which day of year (DOY) four vegetative and four reproductive phenophases began in three
122 evergreen and four deciduous subarctic-alpine dwarf shrubs and examined how DAS and DOY
123 were related to the timing of snowmelt. We also tested whether the relationship between the timing
124 of phenophases and the timing of snowmelt varied between two years. Differences in snowmelt
125 timing between the two years may be reflected in changes in DAS if this factor affects the rate of
126 development. The study was conducted at two mountain slopes with different aspects (northeast- vs.

127 southwest-facing) to investigate whether the phenological responses are consistent across two
128 sampling locations. Different years and slope aspects involve differences in local surface
129 temperature, one of the possible drivers of phenology, so including these variables in a study can
130 give an insight into whether the effect of snowmelt timing is dependent on changes in temperature.

131 Specifically, we aimed to answer the following research questions addressing the
132 phenological timing of phenophases (Day of year, DOY) and their timing in relation to snowmelt
133 (Days after snowmelt, DAS):

134 (1) How do the DOY and DAS of different phenophases of seven subarctic alpine dwarf shrubs
135 respond to snowmelt timing?

136 (2) Is the response of DOY and DAS the same across two years and two slope aspects with
137 different snowmelt timing?

138 **Materials and methods**

139 *Study site*

140 The study was conducted on Saana mountain (69°02'37" N, 20°51'22" E), Scandes Range, north-
141 western Finland. At the Kilpisjärvi Biological Station (1.5 km away from the study site), the annual
142 mean temperature is -1.9 °C and January and July mean temperatures are -12.9 °C and 11.2 °C,
143 respectively (means from 1981-2010; Pirinen et al. 2012). The average annual precipitation is 487
144 mm and the average peak snow depth reaches 99 cm in March (Pirinen et al. 2012). The first snow-
145 free patches appear in April-May, but light snowfall can remain on the ground for up to 2 days
146 especially at higher altitudes until late June. The mountain birch (*Betula pubescens* ssp.
147 *czerepanovii*) treeline on Saana is formed at 600 m a.s.l. Above the treeline, the vegetation is a
148 subarctic alpine vegetation dominated by ericaceous dwarf shrubs such as *Empetrum nigrum* and
149 *Vaccinium* spp., and *Betula nana* and *Salix* spp. The humus layer is shallow (ca. 7-15 cm deep) and
150 the soil moisture is usually low (Eskelinen et al. 2009; Le Roux et al. 2013a). The bedrock consists

151 of siliceous and dolomitic rock resulting in nutrient-poor, acidic soils in some areas and calcium-
152 rich, non-acidic soils in other areas. The study was restricted to acidic areas as these dominated the
153 landscape.

154 We selected two areas (hereafter called 'Site') located at 700-770 m a.s.l. on the north-
155 eastern (hereafter called 'North') and the south-western (hereafter called 'South') slopes of Saana
156 (Supplementary Figure S1). The small differences in elevation did not appear to cause temperature
157 differences (data not shown). These areas have previously been characterised by Le Roux et al.
158 (2013b) and they are known to consist of representative heath vegetation. The progression of
159 snowmelt was observed from early May 2014 and three groups of sequential timing of spring
160 snowmelt (hereafter called 'Snowmelt') termed 'Early', 'Mid' and 'Late' were identified. In each
161 group, three plots (two plots in South Mid) of 2 m × 2 m² area each were marked in 2014. An
162 additional plot (two additional plots in South Mid) was added at each Site-Snowmelt combination
163 in spring 2015 (Figure S1). Plots within the same Site were between ca. 3 and 200 m apart.

164 Reindeer were sometimes observed in the area, but they did not appear to disturb the study
165 plots.

166 *Temperature and snowmelt measurements*

167 Air temperature at ca. 20 cm above the ground and soil surface temperature were logged at hourly
168 intervals in duplicates at each plot with iButtons® (DS1922L-F5 thermochrons; Homechip Ltd.,
169 UK). The loggers measuring air temperature were protected from direct sunlight with a cylindrical
170 radiation shield (height = 15 cm, diameter = 6 cm) made of white PVC. To calculate the air
171 temperature for May 2014, before the loggers were placed, we correlated air temperatures from the
172 Saana weather station (International identification number WMO 02701) with our temperature data
173 from the summer 2014 and extrapolated temperatures backwards until snowmelt. The sum of
174 average daily temperatures above 0 °C (accumulated thawing degree days, TDDs) was calculated
175 for each Site and Snowmelt level from the date of snowmelt until 2 September in 2014 and 2015.

176 Accumulated TDDs measure the magnitude and duration of above-zero temperatures and are
177 therefore an indication of the warmth and length of the growing season.

178 In 2014, the day of snowmelt of early melting plots was estimated from two visits to the site.
179 On the first visit on 8 May, the area was covered completely with snow and on the second visit on
180 26 May, it was snow-free, so snowmelt was estimated to have occurred in the middle of this period,
181 i.e. 17 May or DOY 137. For the other plots, the day of snowmelt in 2014 was noted as the day
182 when a plot was completely snow-free. This method was not possible in 2015 because some early-
183 melting plots were already snow-free when the observations started on 20 May . Instead, the day at
184 which the logged topsoil temperatures started fluctuating by about 5 °C was used as the day of
185 snowmelt for those plots in 2015 (see Wipf 2010). Soil temperature fluctuations are a good
186 indicator of snowmelt as the snow cover keeps the soil surface temperature at approximately 0 °C
187 regardless of the air temperature (Havas 1966; Körner 2003). In 2014-2015, Early plots melted out
188 between the beginning and middle of May, Mid plots between the end of May and the beginning of
189 June and Late plots between mid-June and the beginning of July (Table 1). The plots therefore
190 represented three phases in a natural gradient of snowmelt timing of five to seven weeks on the two
191 opposing slopes.

192 *Phenological observations*

193 Phenological observations were made on the most commonly occurring species in the area. Four
194 deciduous species *Betula nana* L., *Salix herbacea* L., *Vaccinium myrtillus* L., *Vaccinium*
195 *uliginosum* L. and three evergreen species *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup)
196 Böcher, *Phyllodoce caerulea* (L.) Bab., and *Vaccinium vitis-idaea* L were observed in each plot. A
197 plastic tie (width = 2.4 mm) was loosely attached to the base of 24 individual shoots of each of the
198 examined species present in a plot. Due to species-specific affinities to snow, some species were not
199 sufficiently abundant or were not present at all in some plots. *V. vitis-idaea* was present in all plots.
200 *S. herbacea* and *V. myrtillus* only grew in late-melting plots, whereas *B. nana* did not grow in late-

201 melting plots and *E. nigrum* only grew in late-melting plots in the North. *P. caerulea* was not
202 present in any early-melting plots and *V. uliginosum* was only present across the whole snowmelt
203 gradient in the South Site.

204 Each marked shoot was observed every three to seven days and the DOY at which the first
205 bud on the shoot reached a new phenophase was noted. Observations were made from 31 May to 2
206 September in 2014 and from 20 May to 4 September in 2015. Five vegetative and six reproductive
207 phenophases were defined individually for each species (Figure S2):

208 Vegetative phases

- 209 · Bud green (first evidence of green colour can be seen on the bud)
- 210 · Leaf unfolded (the bud has broken open and the first leaf has separated from the bud)
- 211 · Leaf expanded (the leaf is fully unfolded and the leaf angle is similar to mature leaves)
- 212 · Leaf senescence (first evidence of autumn colouration is visible on the adaxial leaf surface;
213 the colour depends on the species)

214 Reproductive phases

- 215 · Flower open (the petals have fully opened; stamens and styles are fully extended)
- 216 · Flower senescence (the petals are dry or have fallen off and stamens and styles have
217 withered)
- 218 · Fruit set visible (first evidence that the ovary is swollen)
- 219 · Fruit ripe (the fruit is completely ripe).

220 For practical reasons, not every phenophase was recorded in all species, e.g. leaf senescence
221 was not observed in evergreen species and bud greening was not observed in *P. caerulea* as its buds
222 look green as soon as they become visible. In a small number of cases, some phenophases had
223 already been reached before the beginning of the study period or had not been reached by the end of

224 it so they were excluded from the dataset as the exact timing of the phenophase was unknown in
225 those cases. The final sample size for each species also varied due to the loss of tags and lack of
226 flowers or leaf development on individual shoots.

227 *Statistical analyses*

228 The DOY at the onset of each phenophase was recorded individually for each shoot. The DAS was
229 then calculated as the number of days from the day of snowmelt to the measured DOY. The effect
230 of the factors Snowmelt (levels 'Early', 'Mid' and 'Late'), Site (levels 'North' and 'South') and
231 Year (levels '2014' and '2015') on DOY and DAS was evaluated separately for each species and
232 phenophase with a linear mixed-effects model with Plot as a random effect. All factors and all
233 possible interactions were included. In cases where there were no data for a species in all
234 combinations of factor levels, separate models were fitted for subsets of the data which included the
235 remaining possible interactions (see supplementary tables S1 and S2 for a list of all fitted models).
236 The optimal model was determined using the maximum likelihood ratio test. Main effects and
237 interactions of variables were tested for significance ($P < 0.05$) with an analysis of variance
238 (ANOVA). Normality, homogeneity and independence assumptions of ANOVA were evaluated by
239 visual inspection of residual plots. In some cases, a constant variance function was applied to one or
240 several variables to achieve homogeneity. Variation in the timing of phenophases with the timing of
241 snowmelt, between the two years and slope aspects was evaluated based on the significance of
242 Snowmelt, Year or Site as main effects. When a significant interaction was present, pairwise
243 comparisons of least square means were carried out with t-tests within each year and site and the P -
244 values were adjusted using the Holm's method (Holm 1979) and a general trend was assumed to be
245 present when most pair-wise interactions were significant. Where the ANOVA assumptions were
246 not fulfilled, (see model results in Tables S1 and S2 marked as 'Could not be tested'), the trend was
247 estimated visually from the figures. All analyses were carried out in R (R Core Team 2016, version
248 3.3.1) using the packages *nlme* (Pinheiro et al. 2016), *lsmeans* (Lenth 2015) and *stats* (R Core Team

249 2016).

250 **Results**

251 *Temperature conditions*

252 The accumulated thawing degree days indicated that the growing season was generally warmer in
253 2014 than in 2015 and on south-facing than on north-facing slopes in both years (Table 1).

254 Accumulated thawing degree day at the end of the season was always highest in early melting plots
255 and lowest in late melting plots (Table 1).

256 *Timing of phenophases across species*

257 The number of DAS until bud greening was lowest for *S. herbacea* and *V. myrtillus* which only
258 grew in late-melting snowbeds, followed by the deciduous species *B. nana* and *V. uliginosum* and
259 was greatest in the two evergreen species, *E. nigrum* and *V. vitis-idaea* (Figures 1 and 2). This
260 ranking of species according to number of DAS was largely conserved across all vegetative
261 phenophases. The ranking of species from earliest to latest was different for the DOY at which
262 vegetative phenophases occurred: *V. uliginosum* < *B. nana* < *E. nigrum* < *S. herbacea* < *V. myrtillus*
263 < *V. vitis-idaea* < *P. caerulea* (Figures 1 and 2).

264 *E. nigrum* required the smallest number of DAS for almost all reproductive phenophases
265 among the studied species, followed by *V. myrtillus*, *P. caerulea*, *V. uliginosum* and *V. vitis-idaea*
266 (Figures 3 and 4). The order of species according to the phenological timing in DAS remained
267 almost the same throughout later reproductive phenophases except for fruit ripening in *V. myrtillus*,
268 which occurred within the smallest number of DAS among all species (Figure 4). When arranging
269 the species according to the DOY on which reproductive phenophases occurred, the order was
270 similar except that *V. myrtillus* and *V. uliginosum* were in reverse order.

271 Ripe fruits were rarely observed, partially because some fruits did not reach this phase
272 before the end of the fieldwork period, so data are only presented from a few cases.

273 *The effect of snowmelt on phenological timing*

274 The shifts in phenophases due to snowmelt timing could, in several cases, be described by
275 generalised patterns indicated schematically by solid red lines in Figures 1 and 3. The conditions on
276 which the schematic lines are based are described in the section “Statistical analysis” of the
277 Materials and methods section. Most phenophases in the late-developing evergreen species *V. vitis-*
278 *idaea* (except bud greening) and late phenophases in *P. caerulea*, such as fruit set and leaf
279 expansion, responded similarly to snowmelt timing. They usually required more DAS to occur in
280 early vs. late snowmelt (Figures 1b,e and 3b,d, Tables S1 and S2). These phenophases occurred
281 synchronously on the same DOY. The reproductive phenophases and most vegetative phenophases
282 of the deciduous species *V. uliginosum* (Figures 1c and 3c), which was among the early-flowering
283 species, and the early phenophases of *P. caerulea* (flower opening and leaf unfolding; Figures 1b
284 and 3b), also required more DAS to begin in early vs. late snowmelt (Tables S1 and S2). However,
285 these phenophases occurred on a later DOY in late vs. early snowmelt (Tables S1 and S2).
286 Conversely, most vegetative phenophases of *B. nana* and some in 2014 also of *V. uliginosum* and
287 bud greening in *V. vitis-idaea* required a fixed number of DAS to occur, regardless of snowmelt
288 timing (Figures 1a,c). These phenophases usually occurred on an earlier DOY in early vs. late
289 snowmelt (Tables S1). These results fall into three patterns of 1) more DAS and the same DOY, 2)
290 more DAS and later DOY and 3) the same DAS and later DOY in late vs. early snowmelt.

291 In *E. nigrum*, snowmelt timing did not cause any clear response in the timing of
292 phenophases (Figures 1d and 3a, Tables S1 and S2). Most vegetative phenophases occurred after
293 more DAS in early vs. late snowmelt, but there were some exceptions (for example, leaf unfolding
294 and leaf expansion in the South in 2014). Some phenophases occurred on the same DOY whilst
295 others occurred later in late vs. early snowmelt (Figure 1d). The effect of snowmelt was also

296 inconsistent in reproductive phenophases of *E. nigrum* (Figure 3a). Depending on year and site,
297 some of its phenophases required more DAS in early vs. late snowmelt and occurred on the same
298 DOY, while others took a fixed number of DAS but occurred on an earlier DOY in early vs. late
299 snowmelt. Only fruit set in the North in 2014 occurred within more DAS in early vs. late snowmelt,
300 causing an earlier DOY of fruit set in those plots (Figure 3a).

301 *Variation in phenological timing between slope aspects*

302 In *V. vitis-idaea*, vegetative and reproductive phenophases began within fewer DAS at the North vs.
303 the South site (Figures 1e and 3d, Table S1). Other species and phenophases usually required the
304 same number of DAS to attain vegetative phenophases, regardless of the Site (Figures 1 and 2,
305 Table S1) with the exceptions of leaf expansion in *E. nigrum*, which took significantly fewer DAS
306 in the South vs. the North and senescence in *B. nana*, which required more DAS in the South vs. the
307 North in 2015 (Figure 1a,d). *Vaccinium myrtillus* and *E. nigrum* began bud greening and leaf
308 unfolding on an earlier DOY in the South vs. the North and the same effect was seen in leaf
309 unfolding and leaf expansion in *B. nana* (Figures 1a,d and 2b).

310 The effect of Site on the number of DAS required by reproductive phenophases was only
311 consistent in the species which took a relatively high number of DAS until flowering (Figures 3 and
312 4, Table S2). In *V. uliginosum*, flowers from early-melting plots in 2015 took more DAS to open
313 and to senesce in the South vs. the North site and the effect was the same in all phenophases of *V.*
314 *vitis-idaea* (Figure 3c,d). A significant effect of Site remained in the DOY of flower opening in *V.*
315 *vitis-idaea* but the site at which the phenophases occurred later varied with snowmelt timing (Table
316 S2). Reproductive phenophases of *V. uliginosum* and *V. myrtillus* did not differ strongly between
317 sites, but flower phenophases of *E. nigrum* and *P. caerulea* (in 2015) and fruit ripening in *E. nigrum*
318 (in 2014) usually occurred on an earlier DOY in the South vs. the North (Figures 3a,b,c and 4).

319 *Variation in phenological timing between years*

320 Reproductive phenology responded more strongly to variation between the years compared to
321 vegetative phenology. Reproductive phenophases always required more numbers of DAS in 2015
322 vs. 2014, approximately the same value, regardless of snowmelt timing (Figures 3 and 4). This was
323 significant in almost all possible pair-wise comparisons of the two years and apparent in all species
324 and phenophases, apart from *E. nigrum* (Table S2). This difference between the years persisted in
325 the DOY at which flowering phases occurred.

326 Inter-annual differences in the DAS needed to reach vegetative phenophases increased in the
327 late phenophases compared to earlier phenophases of evergreen species (Figures 1 and 2). Leaf
328 expansion always took significantly more DAS for these species and occurred on a later DOY in
329 2015 vs. 2014 (Table S1). The vegetative phenology of deciduous species was affected less by
330 inter-annual variations than that of evergreen species. The only significant delay in 2015 vs. 2014
331 was in the leaf senescence of *V. myrtillus* and *V. uliginosum* (Table S1, Figures 1c and 2b). Some
332 inter-annual differences could be seen in the DOY at which vegetative phenophases were reached,
333 but the year during which phenophases occurred later varied by phenophase and site. Differences
334 between the years in the DOY of attaining vegetative phenophases were irregular and often varied
335 by phenophases and site, except in the case of a significantly later occurrence of senescence in *V.*
336 *uliginosum* in 2014 (Figure 1c).

337 **Discussion**

338 *Patterns in the phenological response to snowmelt*

339 Our results for plant phenology along a natural snowmelt gradient are consistent with results from
340 experimental systems in comparable arctic and alpine environments (delayed DOY: Wipf et al.
341 2009; Wipf 2010; Cooper 2014; or unaltered DOY: Bienau et al. 2015). We additionally examined
342 the number of DAS required to begin a phenophase and found similar responses to those reported

343 by, for example, Petraglia et al. (2014) (increased DAS) and Cooper et al. (2011) (unaltered DAS)
344 for various arctic and alpine dwarf shrubs in similar ecosystems.

345 Some studies found that responses of phenological timing to earlier snowmelt cluster
346 according to life form with graminoid phenology advancing the most, followed by deciduous and
347 then evergreen dwarf shrubs (Khorsand Rosa et al. 2015; Livensperger et al. 2016). In other cases,
348 the relative timing of phenology among species (for example, early-flowering versus late-flowering
349 species) determined how a species responded to differences in snowmelt timing (Wipf 2010;
350 Petraglia et al. 2014). However, the detailed results we present from four deciduous and three
351 evergreen dwarf-shrub species and eight phenophases cannot confirm that growth form or temporal
352 niche correspond to a particular response to snowmelt timing (Figure 5).

353 The discrepancy between our findings and results from earlier research may be due to the
354 fact that previous studies either included only a few species or few phenophases, or focused only on
355 one response variable for phenological timing, limiting the possibility to identify more general
356 response patterns. In contrast, we compared how the timing of several phenophases of several
357 species corresponded to snowmelt timing in terms of both DAS and DOY. This indicated a novel
358 clustering of phenophases into three distinct patterns according to their responses to snowmelt
359 timing:

360 (1) *Compensation*: The number of DAS required to reach a certain phenophase decreases with
361 later snowmelt timing. This reduction translates into acceleration of growth and
362 compensates for the delay caused by the late snowmelt, leading to synchronous occurrence
363 of phenophases in plots with different snowmelt timing (Figure 5a). This response was
364 mostly seen in *V. vitis-idaea* and in the late phenophases of *P. caerulea*.

365 (2) *Under-compensation*: The number of DAS required to reach a certain phenophase decreases
366 with later snowmelt timing, but this acceleration is not sufficient to compensate for the
367 delayed start of the growing season caused by late snowmelt. Therefore, phenophases are

368 reached at a later DOY in late-melting plots compared to early-melting plots, but this
369 difference is smaller than the corresponding difference in the snowmelt timing (Figure 5b).
370 This response was seen in most phenophases of *V. uliginosum* and the early phenophases of
371 *P. caerulea*.

372 (3) *Conservativeness (no compensation)*: The number of DAS required to reach a certain
373 phenophase is the same along the snowmelt gradient. Late snowmelt poses a natural delay to
374 development so that phenophases occur at a later DOY in late- compared to early-melting
375 plots and this difference is equal to the corresponding difference in the snowmelt timing
376 (Figure 5c). This response was mostly seen in the vegetative phenophases of *B. nana* and in
377 2015 in some phenophases of *V. uliginosum*.

378 The only species which did not tend to follow any of these patterns was *E. nigrum*. Its
379 patterns of phenological timing along the snowmelt gradient varied greatly with site and year within
380 the same phenophase. *E. nigrum* grows ubiquitously in the study area and it can be found on wind-
381 blown ridges and in places with thick snow cover (authors' pers. observation; Bell and Tallis 1973).
382 This suggests that it can cope with a large range of variation in snow depth and snowmelt timing. *E.*
383 *nigrum* always developed earliest after snowmelt among the studied species and its flower bud
384 break had often already begun prior to snowmelt (authors' pers. observation), showing a strong
385 adjustment to snowmelt timing. Large trait variation along natural snow depth gradients has also
386 been found in *Empetrum* by Bienau et al. (2014) as well as in a snow removal experiment in alpine
387 *Empetrum*, which showed plasticity in developmental timing of bud greening and flowering after
388 one or two years (Wipf et al. 2009; Wipf 2010). This suggests at least partial plasticity in the
389 response of *E. nigrum* to snowmelt which we observed. It is likely that its divergent responses to
390 snowmelt timing seen in different years, sites or phenophases are modulated by, for example,
391 prevailing temperatures.

392 While these patterns show that the timing of snowmelt affects the timing of phenophases,
393 the variation in the responses within and between species indicate a more complex control on
394 phenology than snowmelt alone can explain. This is likely, at least partially, due to the confounding
395 effects of snowmelt with other environmental variables which affect phenology, such as soil
396 moisture variation during snowmelt and higher temperatures in late-melting plots at the time of
397 snowmelt. Snowmelt as a predictor of phenology is also partially limited by the preferences of
398 species for certain snow depth niches, so that some of our species studied did not grow along the
399 whole gradient and hence were not exposed to all snowmelt timings. A finer snowmelt gradient and
400 additional species with a broad habitat range could be used in future studies to avoid the limitations
401 we encountered. Mating systems can also influence the timing of phenophases beyond the influence
402 of snowmelt timing, as strictly outcrossing species must flower synchronously for successful
403 reproduction. In our study, only *E. nigrum* can commonly self-fertilise due to its bisexual flowers in
404 northern populations (Bell and Tallis 1973) which may explain the great variability in the timing of
405 its phenophases, but does not explain why there is great variation among the other species with
406 obligatory or preferentially outcrossing mating systems.

407 *Modulation of phenological timing by environmental variations between years and slope*
408 *aspects*

409 In those cases where the phenological timing varied between the years, phenophases usually
410 developed on a later DOY or required more DAS in the relatively colder year of 2015, suggesting
411 that low temperatures limit phenological development in these subarctic-alpine plant species. This
412 accelerating effect of warm years has also been found in the dwarf shrub *Cassiope tetragona* in a
413 similar subarctic-alpine ecosystem (Molau 1997) and in several other arctic plant species, which
414 had a shorter pre-floration period in years with higher spring temperatures (Bjorkman et al. 2015).
415 Semenchuk et al. (2016) also report that the timing of phenophases varied between years, but this
416 could not be explained by temperature sums because the cumulative TDDs until the occurrence of

417 each phenophase was not constant between the years. This indicates that other factors, for example
418 variation in soil moisture, modulate the responses in different years, as has been suggested by
419 Oberbauer et al. (2013). In our comparison between years, we found the strongest responses in the
420 reproductive phenology and stronger effects on late- vs. early-developing species, suggesting a
421 higher flexibility in responding to short-term environmental fluctuations, in particular phenophases
422 of certain species. Hence, reproductive phenophases and late-developing species have a greater
423 advantage as they can respond to favourable conditions, for example they can extend the available
424 time for reproductive processes by developing earlier in a warmer year. This could also hold future
425 advantages when acclimatising to changing conditions.

426 The response of phenology to the aspect of the mountain slope was inconsistent within
427 almost all species and phenophases, apart from *V. vitis-idaea*. Overall, Site mainly appeared to
428 modulate developmental timing in the colder year of 2015. The slope aspect has rarely been
429 included in previous studies of phenological timing and Iversen et al. (2009) found only a small
430 effect of slope aspect on the timing of phenology when comparing north-, south- and east-facing
431 slopes. In their study, phenological development was slower in the South compared to the North but
432 slope aspect was overall a poor predictor of phenology. In addition to our own results, the findings
433 of Iversen et al. (2009) suggest that environmental or genetic differences between the two sites not
434 accounted for in our study are likely to have caused the variation that we observed.

435 *Limitations and adaptations of phenology*

436 Plants which follow the compensatory pattern (Figure 5a) respond flexibly to snowmelt timing.
437 This indicates an adjustment to the environmental differences at the time of snowmelt, such as
438 higher temperatures later in the season when late-melting plots become snow free, compared to the
439 lower temperatures in spring when early-melting plots melt out. Indeed, Livensperger et al. (2016)
440 found that the timing of leaf appearance in *V. vitis-idaea* and other shrubs was advanced both by
441 warming and by early snowmelt, but warming usually had no additional effect on the timing of leaf

442 expansion later in the season. In the same study, early snowmelt slowed down rates of leaf
443 development in many species, suggesting that early-season development may be slowed down by
444 the colder temperatures and a slower accumulation of temperature sums. Later phenophases, on the
445 other hand, may be regulated by other physiological requirements, as temperatures are already high
446 when they occur and are unlikely to be restricting. Specific temperature accumulation requirements
447 to phenophases are not uncommon in subarctic and alpine species, as evident in the studies by
448 Wheeler et al. (2016) and Huelber et al. (2006) in which the growing degree days above 5 °C until
449 the onset of reproductive phenophases in several alpine plant species were identical along an
450 elevational and snowmelt gradient. However, variations in the degree-day sensitivity are also
451 common with respect to habitat, growth form or latitude (Kudo and Suzuki 1999; Molau et al. 2005;
452 Prevéy et al. 2017). The photoperiod reaches 24 h on DOY 142 at our study site, so the occurrence
453 of phenophases on the same DOY as seen in this pattern is unlikely to be caused by day length.

454 The under-compensating pattern (Figure 5b) follows a similar concept of flexibility as the
455 compensatory pattern. However, in this case there is more limitation on how strongly phenology
456 responds to snowmelt, as the number of DAS does not vary as strongly along the snowmelt gradient
457 compared to the first pattern.

458 In conservative, group (Figure 5c), the number of DAS required to reach a phenophases is
459 the same along the snowmelt gradient. This implies that despite the environmental differences, such
460 as temperature differences upon snowmelt, these phenophases do not respond flexibly to snowmelt
461 timing, likely due to an internal physiological requirement or a genetic regulation which is
462 independent of the environmental differences between plots with different snowmelt timing. This
463 was also suggested by Borner *et al.* (2008), who likewise found no differences in the rates of
464 phenological development in *B. nana* or in other arctic plant species along an experimental
465 snowmelt gradient.

466 *The role of small-scale spatial differentiation and developmental strategy in a changing*
467 *climate*

468 Climate simulations for northern Finland predict a decrease in the amount of snowfall and the
469 duration of snow cover for the period 2070-2099 (Jylhä et al. 2009; Räisänen and Eklund 2012).
470 However, small-scale variability in snow cover may retain diverse environments in the future, likely
471 including suitable habitats for plants under changed conditions (Friedel 1961). The potential of
472 microhabitat variability to prevent habitat loss in the future and provide buffers against climate
473 change has been recognised previously especially with respect to thermal differentiation by Scherrer
474 and Körner (2010, 2011) and Scherrer et al. (2011). In our study, the microclimatic conditions at
475 our current mid-melting plots would correspond to those of the current early-melting plots if climate
476 change causes an overall advance in snowmelt. Similarly, current late-melting plots will correspond
477 to mid-melting plots. Although we cannot say whether the strategies we have identified are
478 genotypic or phenotypic in nature, the plants overall show differential responses to snowmelt timing
479 within the same population.

480 In some of our studied species, the timing of phenology varied significantly between the two
481 years. In addition, tundra and alpine species in general are known to mainly reproduce vegetatively.
482 These characteristics make it likely that the responses of these species are at least partially due to
483 phenotypic plasticity. Sedlacek *et al.* (2015) confirmed that phenotypic acclimation rather than
484 genotypic adaptation to snowmelt timing was present in the leaf phenology of *S. herbacea* in an
485 alpine ecosystem. Patterns which can describe the phenotypic plasticity of phenology in response to
486 snowmelt timing, such as those we present here, can indicate the capacity of plants to respond to
487 these differences in general, and therefore give us an idea of how climate change-induced advances
488 in snowmelt might affect them specifically. We cannot conclude how plants in the early-melting
489 plots might respond to even earlier snowmelt, as these plots constituted the earliest area of our
490 snowmelt gradient and were also one of the earliest areas to melt out in the region. However, plants

491 in currently late- or mid-melting habitats will experience a forward shift in snowmelt timing and
492 therefore can be expected to respond similarly to those in currently mid- or early-melting habitats,
493 respectively, if phenotypic plasticity is present. Phenophases following the first pattern (Figure 5a)
494 will likely still occur on the same DOY, whilst phenophases following the second or third pattern
495 (Figure 5b, c) will probably occur on an earlier DOY. In reproductive phenophases, this possible
496 shift in phenology may cause a mismatch of peak flowering time with the peak abundance of
497 pollinators if the pollinators do not shift to the same extent with consequences for reproductive
498 success (Kudo and Ida 2013; Gillespie et al. 2016). A study from the Arctic showed that late
499 flowering individuals advance faster than early flowering individuals in the case of an advance in
500 snowmelt timing, causing a contraction in the flowering period and an associated decline in
501 resource availability for pollinators (Høye et al. 2007, 2013). However, Cortés et al. (2014) found
502 that gene flow in *S. herbacea* continues between microhabitats with different snowmelt due to seed
503 dispersal so that sub-populations are not genetically separated.

504 **Conclusions**

505 Our results suggest that the extent to which a plant population shows variable phenological timing
506 in response to the timing of snowmelt can be inferred from the length of the period after snowmelt
507 individual subpopulations require to attain phenophases under current natural conditions.
508 Comparing this requirement of DAS to the response of phenology measured as the DOY allowed us
509 to define three patterns of species' responses which correspond to distinct developmental strategies
510 reflecting species' means of adaptation to variations in the timing of snowmelt. Contrary to
511 previous classifications of phenological responses, the patterns we found are not dependent on any
512 particular functional classification (such as growth form), number of species studied, or a particular
513 type of ecosystem. This framework facilitates the comparison of phenological responses among
514 various studies and would even potentially allow previous results to be classified according to these
515 patterns. Achieving a greater uniformity in reporting research results would improve our

516 understanding of how plant phenology responds to the environment. Furthermore, these strategies
517 raise ideas about the underlying physiological processes and environmental factors which control
518 plant phenology and are not fully understood yet.

519

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539 biodiversity and global change.

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541 plants, and the effects of warming winters on invasive plant species.

542

543 **Disclosure statement**

544 The authors declare no conflicts of interest.

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760 **Supplemental data**

761 Supplemental data for this article can be accessed here.
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775 Table 1. Average date and day of year (DOY; with standard errors) of snowmelt timing and average
 776 accumulated thawing degree days (TDD) after snowmelt at two Sites (North and South) and three
 777 levels of snowmelt timing (Early, Mid and Late) in 2014 and 2015. Accumulated TDDs were
 778 calculated as the sum of average daily temperatures above 0 °C from the date of snowmelt until 2
 779 September. Each average was calculated from one or two temperature loggers per plot from three
 780 plots (two in South Mid) in 2014 and from four plots in 2015. See main text for how snowmelt
 781 timing was estimated.

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	Snowmelt date (DOY±SE)	TDD±SE
2014		
North		
Early	17/5 (137±0)	1041±16
Mid	05/6 (156±0)	963±23
Late	26/6 (177±1.7)	803±22
South		
Early	17/5 (137±0)	1071±19
Mid	05/6 (156±0)	1004±2
Late	30/6 (181±0)	805±10
2015		
North		
Early	22/5 (142±1.4)	927±15
Mid	03/6 (154±1.2)	850±12
Late	28/6 (179±0.8)	700±23
South		
Early	01/5 (121±5.3)	1007±32
Mid	28/5 (148±0.8)	954±19
Late	18/6 (169±3.4)	813±24

802 Figure 1. Number of days after snowmelt and day of year on which four vegetative phenophases
803 (Bud green, leaf unfolded, leaf expanded, leaf senescence) in five subarctic dwarf shrubs (a–e)
804 occurred for the first time along a natural gradient of snowmelt timing (Early, Mid and Late). The
805 phenophases were observed at two mountain slope aspects (North and South). Closed symbols
806 denote observations from 2014 and open symbols observations from 2015. The solid schematic
807 lines (in red) indicate the generalised trend in the phenophase shifts along the snowmelt gradient. A
808 flat line corresponds to no shift along the snowmelt gradient in all or most pairwise comparisons.
809 No red line indicates that no clear pattern was identified. For full species' names and description of
810 the snowmelt gradient see "Methods". Note that overlapping points have been dodged sideways.

811 Figure 2. Number of days after snowmelt and day of year on which four vegetative phenophases
812 (Bud green, leaf unfolded, leaf expanded, leaf senescence) in two subarctic dwarf shrubs (a–b)
813 occurred for the first time. The phenophases were observed at two mountain slope aspects (North
814 and South) in a late-melting snowbed. Closed symbols denote observations from 2014 and open
815 symbols observations from 2015. For full species' names and description of the snowmelt gradient
816 see "Methods". Note that overlapping points have been dodged sideways.

817 Figure 3. Number of days after snowmelt and day of year on which four reproductive phenophases
818 (Flower open, flower senescence, fruit set visible, fruit ripe) in four subarctic dwarf shrubs (a–d)
819 occurred for the first time along a natural gradient of snowmelt timing (Early, Mid and Late). The
820 phenophases were observed at two mountain slope aspects (North and South). Closed symbols
821 denote observations from 2014 and open symbols observations from 2015. The solid schematic
822 lines (in red) indicate the generalised trend in the phenophase shifts along the snowmelt gradient. A
823 flat line corresponds to no shift along the snowmelt gradient in all or most pairwise comparisons.
824 No red line indicates that no clear pattern was identified. For full species' names and description of
825 the snowmelt gradient see "Methods". Note that overlapping points have been dodged sideways.

826 Figure 4. Number of days after snowmelt and day of year on which four reproductive phenophases
827 (Flower open, flower senescence, fruit set visible, fruit ripe) in *V. myrtillus* occurred for the first
828 time. The phenophases were observed at two mountain slope aspects (North and South) in a late-
829 melting snowbed. Closed symbols denote observations from 2014 and open symbols observations
830 from 2015. For full species' names and description of the snowmelt gradient see "Methods". Note
831 that overlapping points have been dodged sideways.

832 Figure 5. Schematic representation of patterns in plant phenology with regards to snowmelt timing.
833 Phenological timing is represented as days after snowmelt (DAS) until the onset of a phenophase
834 (continuous line) and as the day of year (DOY) of the onset of a phenophase (dashed line). The
835 occurrence of phenophases in response to snowmelt timing clustered in the present study into three
836 patterns:

837 (a) *Compensation*: The number of DAS required to reach a certain phenophase decreases with later
838 snowmelt timing. This reduction translates into acceleration of growth and compensates for the
839 delay caused by the late snowmelt, leading to synchronous occurrence of the observed phenophases
840 in plots with different snowmelt timing.

841 (b) *Under-compensation*: The number of DAS required to reach a certain phenophase decreases
842 with later snowmelt timing but this acceleration is not sufficient to compensate for the delayed start
843 of the growing season caused by late snowmelt. Therefore, phenophases are reached at a later DOY
844 in late-melting plots compared to early-melting plots, but this difference is smaller than the
845 corresponding difference in the snowmelt timing.

846 (c) *Conservativeness (no compensation)*: The number of DAS required to reach a certain
847 phenophase is the same along the snowmelt gradient. Late snowmelt poses a natural delay to
848 development so that phenophases occur at a later DOY in late- compared to early-melting plots and
849 this difference is equal to the corresponding difference in the snowmelt timing.

850 Note the different slopes in the solid lines in (a) and (b) and the dashed lines in (b) and (c).