

1 **Habitat determines plant community structural and diversity responses to climate change in the**
2 **High Arctic**

3

4 **Mörsdorf, MA^a and Cooper EJ^b**

5 ^aInstitute for Biology II – Geobotany, Albert-Ludwigs Universität Freiburg, 79104 Freiburg, Germany.

6 ^bDepartment of Arctic and Marine Biology, UiT The Arctic University of Norway, 9037 Tromsø,
7 Norway.

8 Corresponding author: Martin A. Mörsdorf, martin.moersdorf@biologie.uni-freiburg.de,

9 ORCID 0000-0002-3903-2021

10 EJC ORCID: 0000-0002-0634-1282

11 Competing interests: The authors declare there are no competing interests.

12

13

14

15

16

17

18

19

20

21

22 **Abstract**

23 Plant climate-responses may depend on site-specific environmental context. Using fences and open
24 top chambers (OTCs), we enhanced snow depth (identifying *Ambient*, *Medium* and *Deep* regimes) in
25 Svalbard for 11 years and increased temperatures for two summers. Comparison of growth-form live
26 abundance and diversity responses in two habitats showed that response was more limited in dry
27 Heath than moist Meadow. In both habitats, shrub abundance was lowest in *Deep*. Additionally in
28 Heath, bryophytes increased in *Deep* but OTC had no effect. In Meadow, graminoids decreased and
29 forbs increased in *Deep*. Bryophytes were high in *Medium*, and in the *Deep*- OTC combination.
30 Vascular plant species richness decreased in *Deep* in both habitats, and in *Medium* in Meadow.
31 However, in Meadow only, when combined with OTC there was no negative snow effect when
32 bryophyte taxa were included into richness measures. Bryophyte richness in Meadow was slightly
33 promoted in *Medium* and in the *Deep*- OTC combination, counteracting snow-regime reduction of
34 vascular richness. Conclusions: 1. Habitat affects plant community structure and diversity response
35 to climate; 2. Multi-year snow enhancement dramatically changes vegetation composition; 3. Even
36 two summers of warming can affect lichen and bryophyte abundance; 4. Bryophyte identification is
37 important to include in diversity assessments.

38 **Keywords: snow fence, Open Top Chamber, context dependency, plant growth form, bryophytes**

39

40 **Introduction**

41 Large Arctic areas are predicted to have increased snow and warmer temperatures during summer
42 (ACIA 2005; Saha et al. 2006). Deeper snow affects nutrient cycling (Schimel et al. 2004) and may
43 delay snowmelt and onset of growing season (Callaghan et al. 2011). Such changes affect phenology,
44 (van der Wal et al. 2000, Semenchuk et al. 2013) reproductive success (Semenchuk et al. 2013) and
45 productivity of some species (Rumpf et al. 2014), which ultimately changes the structure and
46 diversity of plant communities (Wahren et al. 2005; Wipf and Rixen 2010). Only some Arctic plants
47 profit from warmer summers (Elmendorf et al. 2012a), while others disappear (Callaghan et al. 2004;
48 CAFF 2013), thus changing vegetation. Several experimental studies tried to infer generalities of
49 Arctic plant growth form responses to climatic change, but the “winners” and “losers” are still
50 unknown, since growth forms respond differently in various habitats amongst and within study
51 areas.

52 Manipulations of Arctic snow promoted contrasting community structure responses at
53 different sites, as shown by Wipf and Rixen (2010) and Table 1. These highly site-specific outcomes
54 imply that general statements about vegetation responses to enhanced snow cannot be made, and
55 that the direction of responses may depend on environmental context, and may differ between
56 habitats within the same site as shown in Alaska (e.g. Wahren et al. 2005). Modifications of the
57 habitat- specific moisture regime during the growing season in Arctic tundra are thereby likely to play
58 a role in determining responses of community structure to enhanced snow (Leffler et al. 2016;
59 Cooper et al. 2019), as was also found in the Alpine (e.g. Knight et al. 1979). However, short-term
60 responses of community structure to experimentally enhanced snow lay may also be different from
61 long-term responses (Natali et al. 2014) and there is little experimental evidence from studies that
62 assessed changes of Arctic vegetation structure over a time period of more than a decade (Leffler et
63 al. 2016). Furthermore, long-term responses to enhanced snow depth might be modified by warmer
64 summer air temperatures (Leffler et al. 2016). Atmospheric heating during summer is associated with

65 shrub expansion throughout the Arctic (Myers-Smith et al. 2011; Elmendorf et al. 2012a), yet
66 experiments show that such trends depend on soil moisture and the manipulations duration
67 (Elmendorf et al. 2012b). Long-term responses of vegetation structure to climatic changes might also
68 affect plant diversity, because some growth forms are important niche constructors in tundra and
69 any abundance change may affect local vascular plant species richness (Bråthen and Ravolainen
70 2015). Experimental snow enhancements in Alpine tundra indicate that diversity often declines with
71 a deeper and longer snow lay (Wipf and Rixen 2010). Similar trends were shown for the Arctic, but
72 only if enhanced snow depth promotes shrub abundance, causing more shading and an exclusion of
73 small stature forb or bryophyte species (Wahren et al. 2005). However, habitat related context
74 dependencies of long-term plant diversity responses to year-round climatic changes remain poorly
75 investigated in the Arctic. Existing assessments often lack information on bryophyte diversity
76 (Elmendorf et al. 2012b), but inclusion of bryophytes into diversity measures may be important, since
77 they respond to both winter and summer changes in some Arctic sites (Elmendorf et al. 2012b;
78 Cooper et al. 2019).

79 In this study, we contributed evidence to the environmental context dependencies of long-
80 term vegetation responses to enhanced winter snow depths in the Arctic, and tested potential
81 interaction effects of long-term snow enhancement and short-term summer warming. Snow
82 manipulations were conducted for 11 years and summer air temperatures were increased for two
83 summers during the course of the experiment, using Open Top Chambers (OTCs) (Marion et al.
84 1997). Within our study area on Svalbard, we compared plant growth form abundances and diversity
85 in two nearby habitat types: a relatively dry heath and a comparably mesic meadow. We
86 hypothesized that: H1) Long-term snow enhancement caused an abundance change of the major
87 plant growths forms within the community including shrubs, graminoids, forbs and bryophytes. Also
88 the abundance of lichens may be adversely affected by a deeper and prolonged snow lay (Scott and
89 Rouse 1995; Christiansen et al. 2018). However, based on contrasting evidence presented from the
90 literature (above) we expect the direction and magnitude of responses in each growth form to be

91 habitat-specific and potentially different between our dry heath habitat and the mesic meadow
92 habitat. H2) Responses to snow depth may interact with short-term increases in summer air
93 temperatures, but also here, effects may depend on the habitat type of investigation. H3) In
94 accordance to growth form responses to climate change scenarios, we expect changes of within-
95 community plant diversity. H4) Diversity measures using vascular plants only were expected to differ
96 from those including bryophytes.

97

98 **Materials and methods**

99 Field site and experimental setup

100 Our study was conducted in a high Arctic valley site on Svalbard (78°10'N, 16°04'E). The overall
101 vegetation in the area is classified as prostrate dwarf-shrub, herb tundra (CAVM Team, 2003).
102 However, in a more detailed classification, Elvebakk (2005) defined the vegetation as part of the
103 middle Arctic tundra, with two distinct habitat types: Heath: Relatively dry and well-drained *Cassiope*
104 *tetragona* (L.) D. Don heath sloping slightly down towards Advent River in the North; and Meadow:
105 flat, less-well drained mesic *Dryas octopetala* L. -*Tomentypnum nitens* (Hedw.) Loeske meadows
106 overlying peat and shale-derived gelifols (Lupascu et al. 2018).

107 Mean annual precipitation and temperature for 2009 - 2018 was 228 mm and -2.5°C, respectively.
108 The coldest month was March with - 10.6°C and the warmest was July with 7.4°C (www.eklima.no).
109 Geological parental material in the valley bottom consisted of basic calcareous sand, silt and shale
110 stones, which originated from Mesozoic sedimentary bedrocks (Hjelle 1993; Tolgensbakk et al. 2000).
111 Soils typically have an organic layer, which is followed by A-horizons reaching down to a depth of
112 maximum 10 cm, followed by the B/C horizons (Strebel et al. 2010). Soil pH typically ranges between
113 5 and 6.5. The area is underlain by continuous permafrost, which had an active layer depth of on
114 average 105 cm between 2000 and 2007 (Morgner et al. 2010).

115 The experiment was set up in the flat valley bottom, within an altitude between 25 and 100 m above
116 sea level. The experimental manipulations within the site were established in 2006, in order to assess
117 effects of altered winter snow regimes on Arctic vegetation (Cooper et al. 2011). Snow fences were
118 set up and placed perpendicular to the main wind direction (southeast), trapping snow in the
119 leeward side of the fence. The fences are spatially distributed within four experimental blocks. Two
120 blocks were within dry heath and two blocks within mesic meadow habitats. The blocking caused
121 fences from different blocks to be spread more than 500 m apart from each other, covering a total
122 area of approximately 2.5 x 1.5 km. Three snow fences were erected within each block, each 1.5 m
123 high and 6.2 m long. Snow accumulates to a maximum depth of approx. 150 cm within a zone of
124 three to 12 m behind the fence, an area henceforth termed *Deep*. Further away behind the fence (10
125 -20 m), snow accumulates to a maximum of approx. 100 cm, henceforth termed *Medium*. *Ambient*
126 areas with natural snow deposition (maximum of approx. 35 cm) are found adjacent to- but not
127 affected by the fences. The vegetation in the location of fences and unmanipulated areas were
128 visually estimated to be comparable, before the fences were established. Temperature loggers
129 (Gemini, Tinytag, model TGP-4020, UK) were installed just below soil surface in each snow regime
130 around each fence, and recorded temperatures in 30 min intervals since start of the experiment.
131 Previous studies showed that soils in enhanced snow regimes were warmer during the winter, and
132 melt out was delayed between 1-3 weeks, compared to *Ambient* (Semenchuk et al. 2013; Mörsdorf
133 et al. 2019). Meadow takes longer to drain after snowmelt and retains a higher soil moisture content
134 than that of Heath (Cooper et al. 2011), and enhanced snow regimes are moister than *Ambient*,
135 especially at start of growing season (Mörsdorf et al. 2019).

136 At the start of the experiment, six spots were randomly selected within *Deep* and *Ambient* snow
137 regimes, in order to establish 75 x 75 cm vegetation plots for long-term monitoring. Half of those
138 plots were stratified to contain *Dryas octopetala* as a focal plant species and the other half had to
139 contain *C. tetragona* (Cooper et al. 2011). In 2010, three further plots were established by random
140 choice within *Medium* regime, containing both of the two foci species. This study only concerns data

141 from plots with *D. octopetala* as a focal species (in *Ambient* and *Deep*) and the *Medium* plots. At
142 snowmelt 2015 and 2017, we additionally erected open top chambers (OTCs), with a two m
143 diameter, in order to enhance summer temperatures (Marion et al. 1997). OTCs were placed out
144 when plots in the respective snow regime were snow free, and removed at the end of growing
145 season. At each fence an OTC was placed on a randomly selected *Ambient* and *Deep D. octopetala*
146 plot, and a *Medium* plot.

147 The species present in the two vegetation types were quite similar but the vegetation cover and the
148 dominant species differed (Supplementary Table S1). Dominant vascular plants species in Heath plots
149 (highest live abundance first): *D. octopetala*, *Salix polaris* Wahlenb., *C. tetragona*; in Meadow plots: *D.*
150 *octopetala*, *Alopecurus borealis* Trin., *S. polaris*, *Luzula confusa* Lindeb., and *Bistorta vivipara* (L.)
151 Delarbre. Dominant mosses in Heath: *Sanionia uncinata* (Hedw.) Loeske, *Tomenthypnum nitens*
152 (Hedw.) Loeske, *Hylocomium splendens* (Hedw.) Schimp., *Dicranum* spp. and *Distichium* spp.; and in
153 Meadow: *S. uncinata*, *Polytrichum* spp., *Aulacomnium* spp., *T. nitens*, and *H. splendens*.

154

155 Recordings of plant community and environmental data

156 Between 3rd and 31st of July 2017, we assessed plant community properties within the experiment.
157 We used the Point Intercept Method (Jonasson 1988) within a 75 x 75 cm squares frame placed over
158 the permanent vegetation plot. The frame was split up into 100, regularly distributed, sub-squares
159 using strings. The strings were aligned in parallel in two horizontal levels. At each point where the
160 strings crossed, we registered vegetation by aligning the two parallel strings and recording the plant
161 species at this point. Recordings were done throughout the canopy layer, by carefully moving the
162 higher vegetation layers aside and noting species within all subsequent vegetation layers at this point
163 ('all-hits'). For the community assessment within each plot, we recorded living vascular plants to
164 species level. For woody plants, we distinguished live from dead plant material when dead branches
165 easily broke off the main plant as soon as they were touched. We were able to confidently identify

166 some bryophytes and lichens to species level in the field. Bryophytes and lichens were found below
167 the canopy of vascular plants and for each of the 100 points, we noted all species that were found in
168 an approx. radius of one cm around the respective point. Each bryophyte species could therefore get
169 up to a maximum of 100 hits in each plot. Due to practical circumstances, species within the groups
170 which could not be identified without microscopy in the lab, had to be identified to genera level only.
171 Bryophytes for which we could not guarantee a secure identification to genera level in the field, had
172 to be combined into one group of un-identified bryophytes, since we could not attain abundance
173 estimates of those plants otherwise. We followed the same approach for all lichens within the plots.
174 Crustose lichens were not further identified in our study. The taxonomic units we used in this study
175 are shown in Table 2. Nomenclature for vascular plants follows the Pan Arctic flora
176 (<http://panarcticflora.org/>). Nomenclature for bryophytes is according to Prestø et al. (2014) and
177 lichen nomenclature is according to Øvstedal et al. (2009).

178 For this study we used 10 of the original 12 fences, as two of the fences collapsed due to breakage
179 and soil subsidence. Since one of the fences (C8) had no *Medium* plots it had only 6 (three *Ambient*
180 and three *Deep*) instead of the planned 9 plots. For this study we therefore used a total of 87
181 permanent vegetation plots [10 fences x 3 snow treatments x (2 non-OTC + 1 OTC)- 3 *Medium* plots
182 missing at C8).

183 Temperature loggers (Gemini, Tinytag, model TGP-4020, UK) were additionally installed below soil
184 surface within each OTC and recorded temperatures at 30 min intervals. We extracted temperature
185 data for each snow and temperature regime for the period between 1st June to 31st July 2017 to
186 represent soil temperatures during peak growing season. Volumetric soil moisture was measured at
187 each plot corner using a Theta Probe ML 2x (Delta-T Devices, Cambridge, UK) once during 6th to 27th
188 July 2017. Vegetation was not removed prior to probing.

189

190 Statistical evaluation

191 We decided to focus on growth forms, and not species, in this study since we may not be able to
192 compare individual species responses in our, to other Arctic sites, if species are lacking there.
193 Furthermore, most species in our site were not frequently found in each plot, which would lead to
194 very unbalanced data and different replicates for different models. We first combined the hits of
195 recorded live vegetation in each plot into growth forms, which were defined as shrubs, graminoids,
196 forbs, bryophytes and lichens (see Table 2). The records of unidentified bryophytes and lichens were
197 included in the respective groups here. Pteridophytes were patchily distributed with very low
198 abundance, so we added these values to the 'forbs' group. We split the dataset according to plots
199 within the Heath and Meadow habitats. In order to estimate group abundances and the effects of
200 snow enhancement and summer warming, we used linear mixed effects models within R (version
201 3.6.0), applying lme function of the nlme package (Pinheiro and Bates 2000). For each group, we set
202 the number of hits within a plot as response variable, being representative for the abundance of
203 each growth form within plots. The treatments of snow enhancement (*Ambient, Medium, Deep*) and
204 summer warming (no OTC, OTC), including their two-way interaction were defined as fixed effects.
205 The snow fence location, and plot within fence, were defined as nested random variables, to account
206 for variation being caused by the spatial hierarchy of the experimental setup. For each model, we
207 conducted model comparisons to a simplified model structure, only including additive fixed effects of
208 both treatments, by consultation of AIC. The parsimonious model with lower AIC was finally chosen
209 to estimate parameters.

210 To estimate plant diversity within plots and the effects of snow enhancement and summer warming,
211 we defined five diversity indices: 1) The number of vascular plant species within each plot,
212 resembling vascular plant species richness; 2) the number of taxonomic bryophyte units that could
213 be identified in the field (excluding unidentified bryophytes), resembling an estimate of bryophyte
214 richness; 3) the sum of vascular plant species and bryophyte richness; as well as 4) the Shannon-
215 Index based on vascular plant species; and 4) the Shannon-Index based on all taxonomic units of
216 vascular plants and bryophytes that we were able to distinguish in the field. Each of the five diversity

217 indices was set as a response variable, and we used the same modelling approach as described for
218 growth form abundances.

219 We also assessed treatment effects on soil temperatures and moisture during the growing season
220 2017. Daily soil temperature means were averaged for the period 1st June – 31st July 2017 for each
221 logger and the four soil moisture measurements at each plot corner were averaged for each plot. We
222 used the same modelling approach as for plant growth forms and diversity. Soil temperature models
223 had only snow fence location as random effect. For soil moisture models, we used the same random
224 effects structure as for plant abundance and diversity models. We assessed all models in terms of
225 outliers, homogenous and normally distributed residuals, using diagnostic plots. For all models, we
226 declared treatment effects of snow enhancement and summer warming as statistically significant if
227 the 95% confidence intervals of effect sizes did not overlap with a value of zero.

228

229 **Results**

230 *Effects of winter and summer treatments on soil environment during growing season 2017*

231 In both habitats, growing season soil temperatures were highly affected by interactions between
232 snow treatment and summer warming. Heath soils tended to be cooler in *Deep* than *Ambient*
233 without OTC (Figure 1a), but 3.5°C warmer with OTC (Figure 1a). Meadow soils without OTCs were
234 4.3°C cooler in *Medium* and 4.6°C cooler in *Deep* than *Ambient*, whereas OTCs ameliorated this snow
235 regime response and warmed soils by 3.1°C more in *Deep* than *Ambient* (Figure 1a). This led to a
236 large temperature difference in both habitats between the OTC and non-OTC plots in *Deep*. *Ambient*
237 temperatures in Meadow appeared slightly higher than those in Heath.

238 Heath soil moisture was not affected by snow enhancement or by summer warming (Figure 1b).

239 Meadow soils were 11 % moister in *Deep* than *Ambient*, and slightly, though insignificantly drier with
240 OTC (Figure 1c). Soils in Meadow appeared moister than Heath.

241

242 *Effects of winter and summer treatments on Community Structure*

243 The two habitats differed in their vegetation composition, as well as the amount and direction of
244 change due to treatment.

245 In Heath, snow enhancement affected plant growth form abundance of some groups, but the passive
246 warming treatment during summer had no effect (Table 3). The abundance of shrubs was
247 significantly lower in *Deep* than *Ambient* (Fig 2a), whilst other vascular plant groups such as forbs
248 were not significantly affected (Fig 2b). On the contrary, bryophyte abundance was significantly
249 greater in *Deep* than in *Ambient* (Fig 2c). Lichen abundance was not affected by snow regime or OTC
250 (Table 3).

251 In Meadow, all plant growth forms responded to enhanced snow (Table 4). Shrub abundance was
252 significantly lower in both *Medium* and *Deep* than *Ambient* (Fig 3a). Forbs had significantly greater
253 abundance in *Deep* (Fig. 3b). Bryophyte response showed interaction between snow enhancement
254 and summer warming (Table 4). In plots without OTC, bryophyte abundances were higher in *Medium*
255 than *Ambient*, but not in *Deep*. In plots with OTC, bryophyte abundances were higher in both
256 *Medium* and *Deep* (Fig 3c). Lichen abundance was only affected by OTC and was higher in warmed
257 than in *Ambient* plots (Table 4). Bare ground increased with snow depth (Supplementary Figure S1).

258 Within a growth form, not all the species responded to snow regime in the same direction (See
259 Supplementary Table S1), and for some species, the size or direction of response was habitat
260 dependent. Interpretation of the responses of 52 species/ groups is complicated and must be carried
261 out with caution. However, several moss species increased with snow depth (e.g. *S. uncinata*,
262 *Polytrichum* spp.) whilst some decreased (*T. nitens*, *H. splendens*) and others increased with snow in
263 Heath but decreased in Meadow (*Aulacomnium* spp., *Dicranum* spp. and *Distichium* spp.).

264

265 *Effects of winter and summer treatments on plant diversity*

266 Heath diversity responded only to snow regime and not to short-term summer warming. However,
267 effects were dependent on the diversity measure used (Table 5). Species richness of vascular plants
268 was lower in *Deep* than *Ambient* (Fig 4a). We found the same general pattern when including
269 taxonomic units of bryophytes into the richness measure (Fig 4b), as the bryophyte richness did not
270 respond to treatment. The Shannon-Index of vascular plants, and of the whole plant community,
271 were not significantly affected by snow enhancement or summer warming (Table 5).

272 Meadow vascular plant species richness was only affected by snow enhancement and was lower in
273 both *Medium* and *Deep* than *Ambient* (Fig. 5a, Table 6). However, bryophyte richness was stable, and
274 marginally higher, in *Medium* and *Deep* when combined with OTC (Table 6). Species richness
275 including vascular plant and bryophyte taxa was thereby only lower in *Deep* without summer
276 warming (Fig. 5b, Table 6). Plots with OTCs had similar values of overall plant richness in all snow
277 regimes (Fig. 5b). Shannon-Index of vascular plants or of the whole plant community, was not
278 affected by snow enhancement or summer warming (Table 6).

279

280 **Discussion**

281 *Habitat-specific treatment effects on plant community structure*

282 Our results support our hypothesis H1 that snow enhancement would change the abundance of plant
283 growth forms and lichens and that responses would be habitat-specific. However, the interaction of
284 snow enhancement and short-term summer warming that we hypothesized in H2 were only
285 observed within the Meadow habitat.

286 The only growth forms that were consistently affected by snow enhancement in both habitats of our
287 study were shrubs and bryophytes (Table 7). In general, shrub abundance was lower with enhanced
288 snow, and bryophyte abundance was higher. These patterns of change are the opposite to that

289 found at other Arctic sites in Canada and Alaska, where experimental snow enhancement often
290 increased either evergreen or deciduous shrub abundance (Leffler et al. 2016; Christiansen et al.
291 2018). Such findings were usually related to elevated nutrient availability, which results from higher
292 depolymerization and mineralization rates with enhanced snow (Schimel et al. 2004). Arctic plant
293 communities that are dominated by shrubs were thereby predicted to accumulate even more snow,
294 causing a positive feedback loop of these mechanisms and enforcing shrub expansion (Sturm et al.
295 2005). However, several findings from our site indicate that such mechanisms cannot be generalized
296 for the Arctic. Previous assessments showed that elevated nutrient availability in enhanced snow
297 regimes are also found at our site and that vascular plants show higher nitrogen uptake (Mörsdorf et
298 al. 2019), increasing the growth of some species (Rumpf et al. 2014; Semenchuk et al. 2015).
299 However, enhanced snow can also adversely affect vascular plant growth. Cooler summer soils (due
300 to late melt and enhanced moisture especially early in the season), together with reduced growing
301 season length (due to late onset of green-up) negatively affect the vegetative- and reproductive
302 success of some vascular plants (Mallik et al. 2011; Semenchuk et al. 2013, 2016). Furthermore
303 during the winter period, soil temperatures were significantly elevated due to the insulating effect of
304 enhanced snow, and plants with overwintering organs (stems, rhizomes and roots, as well as
305 preformed leaf and flower buds) experienced increased respiration rates and carbon loss during this
306 season (Morgner et al. 2010; Semenchuk et al. 2016).

307 Another key factor that may determine responses of community structure to enhanced snow is the
308 extent to which snow regimes alter soil moisture during the growing season. Treatment related
309 alterations of soil moisture might explain the contrasting responses of community structure in our
310 site compared to others and also explain the between habitat-specific responses at our site. Long-
311 term increases of shrub abundance at Toolik Lake with enhanced snow were related to deepened
312 active layer and increased drainage (Leffler et al. 2016). This mechanism can be speculated but not
313 confirmed for our site. Although soil moisture during peak growing season only showed significant
314 increase with snow depth in Meadow, our data indicated a general increase of moisture with snow

315 enhancements of both habitats (Figure 1b, c), and high soil moisture contents in enhanced
316 treatments were shown to be especially pronounced at the start of growing season (Mörsdorf et al.
317 2019). The flat terrain in our Meadow may slow drainage especially from the enhanced snowpack.
318 Extremely high soil moisture and associated anoxia soon after snowmelt may adversely affect shrubs
319 usually found in well drained conditions (Leffler et al. 2016). Some high Arctic plants are well adapted
320 to anoxia, although these are mostly forbs, which were not adversely affected by snow
321 enhancements at our site (Crawford et al. 1994). Both small statue forbs (in Meadows) and
322 bryophytes (both habitats) may profit from reduced light competition from shrubs in enhanced snow
323 regimes. However, the extent to which snow enhancements alter moisture conditions also seems to
324 determine the extent to which changes in community structure are induced.

325 Significant increases of forbs were only registered in Meadow in our study, where also alterations of
326 soil moisture via snow enhancements seemed to be more extreme than in Heath (Figure 1b, c).
327 Further, high bryophyte abundance in Meadow was only registered in *Medium* and not *Deep*, as long
328 as no summer warming was applied. As outlined above, we generally assume that bryophytes profit
329 from a release of vascular plant competition and an increase in nutrients and moisture in enhanced
330 snow regimes (Cooper et al. 2019). However, *Deep* regime has extremely long lasting snow cover,
331 which may promote the prevalence of diseases, such as parasitic fungi that can harm plants
332 (Olofsson et al. 2011). The host-specific fungal parasites, *Exobasidium hypogenum* Nannfeldt on
333 vascular plant *C. tetragona*, and *Pythium polare* on mosses (especially *S. uncinata*), both increased
334 with enhanced snow at our site, and may be a factor driving vegetation change and increasing the
335 amount of bare ground (Moriana-Armendariz et al., *submitted, this issue*). We can only speculate
336 how short-term summer warming offsets the snow regime effect observed in *Deep* in our Meadow
337 habitat. We found that OTCs reversed the soil temperature decline from *Ambient* towards enhanced
338 snow regimes (Figure 1a). The reduced shrub abundance, and therefore soil shading in *Deep* may
339 enable the OTCs to warm the soil more effectively, providing a warmer environment which
340 bryophytes can exploit since they are not moisture-limited (Figure 1b, c) unlike in many other OTC

341 experiments (Elmendorf et al. 2012b). Ameliorated growing conditions in our experiment include
342 higher nutrient availability, which is known to be exploited by bryophytes (Sjögersten et al. 2010).
343 These factors may help to compensate for losses that are caused by fungal pathogens under such
344 conditions. These mechanisms need further research to be fully understood.

345 Since vegetation structure of the habitats was different (Supplementary Table S1), it was not totally
346 surprising that some responses were habitat-dependent, and serves to remind us of the importance
347 of including species lists for the habitats when describing experimental results. As speculated by
348 others (Leffler et al. 2016), we conclude that some Arctic plant communities may locally become
349 more wet with enhanced snow depth, and experience expansion of bryophytes (Epstein et al. 2000),
350 rather than shrubs (Aerts et al. 2006; Christiansen et al. 2018). Such “bryofication” of Arctic plant
351 communities may strongly affect ecosystem properties. Bryophytes can affect several ecosystem
352 functions in the Arctic, including alterations of C, N and water cycling (Lindo and Gonzalez 2010;
353 Turetsky et al. 2012) or soil energy budgets (Gornall et al. 2007).

354

355 *Habitat-specific treatment effects on within plant community diversity*

356 Our results support hypothesis 3 that plant diversity response to experimental treatments is
357 dependent on the habitat type and highlight that H4 the direction of response depends on the
358 taxonomic resolution of plant assessments and the diversity measures used.

359 In both Heath and Meadow, vascular plant species richness decreased in enhanced snow regimes at
360 our site. Patterns of Shannon index indicated the same direction of response, but were not
361 statistically significant, likely due to the much higher abundance of the vascular plants compared to
362 bryophyte abundances used in calculating these indices. However, the use of different diversity
363 indices is important since it demonstrates that patterns of diversity change may not be observed
364 with only one index.

365 Those results are similar to findings from other Arctic (Wahren et al. 2005) and Alpine sites (Scott and
366 Rouse 1995; Seastedt and Vaccaro 2001; Litaor et al. 2008) where vascular plant species richness
367 decreased with enhanced snow, but those studies attributed their diversity decline to increased
368 shrub growth and competitive exclusion of small stature plants (Wahren et al. 2005). Since we did not
369 find such growth form responses at our site, we assume that other mechanisms are responsible for
370 the declines in richness. Many vascular plant growth forms, including shrubs, can promote
371 biodiversity in the Arctic through being niche constructors for other species (Bråthen and Ravolainen
372 2015). A loss of such nurse plants could thereby lead to an overall loss of species within the
373 community. Furthermore, assessments in Meadow showed that treatment effects on plant diversity
374 may depend on the taxonomic resolution that is used.

375 When including bryophytes into diversity measures, there was no decline in plant richness with
376 enhanced snow regimes for plots with summer warming, indicating that bryophyte richness in the
377 Meadow was increased in *Medium* and also with OTC in *Deep* regime, thus counteracting the snow's
378 effect of reduction of vascular plant richness. These results relate to the ameliorated conditions for
379 bryophytes and indicate that responses in vascular plant diversity might not necessarily reflect
380 responses of the overall plant diversity to climatic change in the Arctic. We assume that our
381 outcomes of bryophyte richness represent a rather conservative estimate of such effects, since we
382 were not able to identify bryophytes to species level in the field. Monitoring of taxonomic
383 information on bryophytes should therefore be a key feature to predict Arctic plant diversity to
384 climatic changes. We acknowledge the fact that abundance assessments of some bryophyte species
385 are not possible in the field, and that a sensible classification of bryophytes into groups, relating to
386 essential ecosystem functions in tundra, is so far lacking but highly necessary. A current study is
387 contributing to resolve this issue in future (Lett et al., *submitted, this issue*).

388

389 **Acknowledgements**

390 We are especially thankful for Anna Katharina Pilsbacher, Katariina Elsa Maria Vuorinen, Kathrin
391 Bender and Fumino Maruo for their help in the field.

392

393 **Funding statement**

394 This study was funded by The Norwegian Research Council (“SnoEco” project # 230970), and the
395 Norwegian Centre for International Cooperation in Education (SIU) High North Programme
396 (“JANATEX” project # HNP2013/10092), both to EJC.

397

398 **References**

399 ACIA 2005. Arctic Climate Impact Assessment. Cambridge University Press, UK.

400 Aerts, R., Cornelissen, J. H. C., and Dorrepaal, E. 2006. Plant performance in a warmer world: General
401 responses of plants from cold, northern biomes and the importance of winter and spring events.
402 *Plant Ecol.* **182**: 65–77. doi:10.1007/s11258-005-9031-1

403 Bråthen, K. A., and Ravolainen, V. T. 2015. Niche construction by growth forms is as strong a
404 predictor of species diversity as environmental gradients. *J. Ecol.* **103**(3): 701–713.
405 doi:10.1111/1365-2745.12380

406 CAFF 2013. Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity. Conservation of
407 Arctic Flora and Fauna, Akureyri, IS.

408 Callaghan, T. V., Björn, L. O., Chernov, Y., Chapin, T., Christensen, T. R., Huntley, B., Ims, R. A.,
409 Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Elster, J.,
410 Henttonen, H., Laine, K., Taulavuori, K., Taulavuori, E., and Zöckler, C. 2004. Biodiversity,
411 distributions and adaptations of Arctic species in the context of environmental change. *Ambio*
412 **33**(7): 404–417. doi:10.1579/0044-7447-33.7.404

413 Callaghan, T. V., Johansson, M., Brown, R. D., Groisman, P. Y., Labba, N., Radionov, V., Barry, R. G.,
414 Bulygina, O. N., Essery, R. L. H., Frolov, D. M., Golubev, V. N., Grenfell, T. C., Petrushina, M. N.,
415 Razuvaev, V. N., Robinson, D. A., Romanov, P., Shindell, D., Shmakin, A. B., Sokratov, S. A., Warren,
416 S., and Yang, D. 2011. The changing face of Arctic snow cover: A synthesis of observed and
417 projected changes. *Ambio* **40**: 17–31. doi:10.1007/s13280-011-0212-y

418 CAVM Team. 2003. Circumpolar Arctic Vegetation Map. (1:7,500,000 Scale). U.S. Fish and Wildlife
419 Service, Anchorage, Alaska Conservation of Arctic flora and fauna (CAFF), Map No. 1.
420 <http://www.arcticatlas.org/maps/themes/cp/>.

421 Christiansen, C. T., Lafrenière, M. J., Henry, G. H. R., and Grogan, P. 2018. Long-term deepened snow
422 promotes tundra evergreen shrub growth and summertime ecosystem net CO₂ gain but reduces
423 soil carbon and nutrient pools. *Glob. Chang. Biol.* **24**(8): 3508–3525. doi:10.1111/gcb.14084

424 Cooper, E. J., Dullinger, S., and Semenchuk, P. 2011. Late snowmelt delays plant development and
425 results in lower reproductive success in the High Arctic. *Plant Sci.* **180**(1): 157–167.
426 doi:10.1016/j.plantsci.2010.09.005

427 Cooper, E. J., Little, C. J., Pilsbacher, A. K., and Mörsdorf, M. A. 2019. Disappearing green: Shrubs
428 decline and bryophytes increase with nine years of increased snow accumulation in the High
429 Arctic. *J. Veg. Sci.* **30**(5): 857–867. doi:10.1111/jvs.12793

430 Crawford, R. M. M., Chapman, H. M., and Hodge, H. 1994. Anoxia tolerance in high Arctic vegetation.
431 *Arct. Alp. Res.* **26**(3): 308–312.

432 Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J.,
433 Cornelissen, J. H. C., Day, T. A., Dorrepaal, E., Elumeeva, T. G., Gill, M., Gould, W. A., Harte, J., Hik,
434 D. S., Hofgaard, A., Johnson, D. R., Johnstone, J. F., Jónsdóttir, I. S., Jorgenson, J. C., Klanderud, K.,
435 Klein, J. A., Koh, S., Kudo, G., Lara, M., Lévesque, E., Magnússon, B., May, J. L., Mercado-Díaz, J. A.,
436 Michelsen, A., Molau, U., Myers-Smith, I. H., Oberbauer, S. F., Onipchenko, V. G., Rixen, C.,

437 Schmidt, N. M., Shaver, G. R., Spasojevic, M. J., Pórhallsdóttir, P. E., Tolvanen, A., Troxler, T.,
438 Tweedie, C. E., Villareal, S., Wahren, C.-H., Walker, X., Webber, P. J., Welker, J. M., and Wipf, S.
439 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nat.*
440 *Clim. Chang.* **2**: 453–457. doi:10.1038/nclimate1465

441 Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., Collier,
442 L. S., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Fosaa, A. M., Gould, W. A., Grétarsdóttir, J.,
443 Harte, J., Hermanutz, L., Hik, D. S., Hofgaard, A., Jarrad, F., Jónsdóttir, I. S., Keuper, F., Klanderud,
444 K., Klein, J. A., Koh, S., Kudo, G., Lang, S. I., Loewen, V., May, J. L., Mercado, J., Michelsen, A.,
445 Molau, U., Myers-Smith, I. H., Oberbauer, S. F., Pieper, S., Post, E., Rixen, C., Robinson, C. H.,
446 Schmidt, N. M., Shaver, G. R., Stenström, A., Tolvanen, A., Totland, Ø., Troxler, T., Wahren, C.-H.,
447 Webber, P. J., Welker, J. M., and Wookey, P. A. 2012. Global assessment of experimental climate
448 warming on tundra vegetation: Heterogeneity over space and time. *Ecol. Lett.* **15**(2): 164–175.
449 doi:10.1111/j.1461-0248.2011.01716.x

450 Elvebakk, A. 2005. A vegetation map of Svalbard on the scale 1:3.5 mill. *Phytocoenologia* **35**(4): 951–
451 967. doi:10.1127/0340-269X/2005/0035-0951

452 Epstein, H. E., Walker, M. D., Chapin, F. S., and Starfield, A. M. 2000. A Transient, nutrient-based
453 model of Arctic plant community response to climatic warming. *Ecol. Appl.* **10**(3): 824–841.
454 doi:10.1890/1051-0761(2000)010[0824:ATNBMO]2.0.CO;2

455 Gornall, J. L., Jónsdóttir, I. S., Woodin, S. J., and Van Der Wal, R. 2007. Arctic mosses govern below-
456 ground environment and ecosystem processes. *Oecologia* **153**: 931–941. doi:10.1007/s00442-
457 007-0785-0

458 Hjelle, A. 1993. *Geology of Svalbard*. Available from Norwegian Polar Institute, Tromsø, Norway.
459 *Polarhåndbok* 7.

460 Johansson, M., Callaghan, T. V., Bosiö, J., Åkerman, H. J., Jackowicz-Korczynski, M., & Christensen, T.
461 R. 2013. Rapid responses of permafrost and vegetation to experimentally increased snow cover in
462 Sub-Arctic Sweden. *Env. Res. Lett.* **8**(3): 035025. doi:10.1088/1748-9326/8/3/035025

463 Jonasson, S. 1988. Evaluation of the point intercept method for the estimation of plant biomass.
464 *Oikos* **52**(1): 101–106. doi:10.2307/3565988

465 Knight, D. H., Weaver, S. W., Starr, C. R., and Romme, W. H. 1979. Differential response of subalpine
466 meadow vegetation to snow augmentation. *J. Range Manage.* **32**(5): 356–359.

467 Leffler, A. J., Klein, E. S., Oberbauer, S. F., and Welker, J. M. 2016. Coupled long-term summer
468 warming and deeper snow alters species composition and stimulates gross primary productivity in
469 tussock tundra. *Oecologia* **181**: 287–297. doi:10.1007/s00442-015-3543-8

470 Lindo, Z., and Gonzalez, A. 2010. The bryosphere: An integral and influential component of the
471 earth's biosphere. *Ecosystems* **13**: 612–627. doi:10.1007/s10021-010-9336-3

472 Litaor, M. I., Williams, M., and Seastedt, T. R. 2008. Topographic controls on snow distribution, soil
473 moisture, and species diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado. *J.*
474 *Geophys. Res.* **113**(G2): 1–10. doi:10.1029/2007JG000419

475 Lupascu, M., Czimczik, C. I., Welker, M. C., Ziolkowski, L. A., Cooper, E. J., and Welker, J. M. 2018.
476 Winter ecosystem respiration and sources of CO₂ from the high Arctic tundra of Svalbard:
477 Response to a deeper snow experiment. *Journal of Geophysical Research: Biogeosciences* **123**(8):
478 2627–2642. doi:10.1029/2018JG004396

479 Mallik, A. U., Wdowiak, J. V., and Cooper, E. J. 2011. Growth and reproductive responses of *Cassiope*
480 *tetragona*, a circumpolar evergreen shrub, to experimentally delayed snowmelt. *Arct., Antarct.,*
481 *Alp. Res.* **43**(3): 404–409. doi:10.1657/1938-4246-43.3.404

482 Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., Lévesque, E.,
483 Molau, U., Mølgaard, P., Parsons, A. N., Svoboda, J., and Virginia, R. A. 1997. Open-top designs for

484 manipulating field temperature in high-latitude ecosystems. *Glob. Chang. Biol.* **3**(S1): 20–32.
485 doi:10.1111/j.1365-2486.1997.gcb136.x

486 Morgner, E., Elberling, B., Strebel, D., and Cooper, E. J. 2010. The importance of winter in annual
487 ecosystem respiration in the High Arctic: Effects of snow depth in two vegetation types. *Polar Res.*
488 **29**(1): 58–74. doi:10.1111/j.1751-8369.2010.00151.x

489 Mörsdorf, M. A., Baggesen, N. S., Yoccoz, N. G., Michelsen, A., Elberling, B., Ambus, P. L., and Cooper,
490 E. J. 2019. Deepened winter snow significantly influences the availability and forms of nitrogen
491 taken up by plants in high Arctic tundra. *Soil Biol. Biochem.* **135**: 222–234.
492 doi:10.1016/j.soilbio.2019.05.009

493 Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-
494 Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A.,
495 Collier, L. S., Weijers, S., Rozema, J., Rayback, S. A., Schmidt, N. M., Schaepman-Strub, G., Wipf, S.,
496 Rixen, C., Ménard, C. B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V.,
497 Welker, J., Grogan, P., Epstein, H. E., and Hik, D. S. 2011. Shrub expansion in tundra ecosystems:
498 Dynamics, impacts and research priorities. *Env. Res. Lett.* **6**(4): 045509. doi:10.1088/1748-
499 9326/6/4/045509

500 Natali, S. M., Schuur, E. A. G., Webb, E. E., Pries, C. E. H., and Crummer, K. G. 2014. Permafrost
501 degradation stimulates carbon loss from experimentally warmed tundra. *Ecology* **95**(3): 602–608.
502 doi:10.1890/13-0602.1

503 Olofsson, J., Ericson, L., Torp, M., Stark, S., and Baxter, R. 2011. Carbon balance of Arctic tundra
504 under increased snow cover mediated by a plant pathogen. *Nat. Clim. Chang.* **1**: 220–223.
505 doi:10.1038/NCLIMATE1142

506 Øvstedal, D., Tønsberg, T., and Elvebakk, A. 2009. The lichen flora of Svalbard. *Sommerfeltia* **33**(1): 1-
507 393. doi:10.2478/v10208-011-0013-5

508 Pinheiro, J.C., and Bates, D.M. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer
509 Science+Business Media New York, US.

510 Prestø, T., Lüth, M. and Hassel, K. 2014. Bryophytes of the Longyearbyen area. Available from NTNU
511 Vitenskapsmuseet, Trondheim, NOR. *Naturhistorisk notat* 10: 1-68.

512 Rumpf, S. B., Semenchuk, P. R., Dullinger, S., and Cooper, E. J. 2014. Idiosyncratic responses of high
513 Arctic plants to changing snow regimes. *PloS One* **9**(2): e86281.
514 doi:10.1371/journal.pone.0086281

515 Saha, S. K., Rinke, A., and Dethloff, K. 2006. Future winter extreme temperature and precipitation
516 events in the Arctic. *Geophys. Res. Lett.* **33**(15): 1–4. doi:10.1029/2006GL026451

517 Schimel, J. P., Bilbrough, C., and Welker, J. M. 2004. Increased snow depth affects microbial activity
518 and nitrogen mineralization in two Arctic tundra communities. *Soil Biol. Biochem.* **36**(2): 217–227.
519 doi:10.1016/j.soilbio.2003.09.008

520 Scott, P. A., and Rouse, W. R. 1995. Impacts of increased winter snow cover on upland tundra
521 vegetation: A case example. *Clim. Res.* **5**(1): 25–30.

522 Seastedt, T. R., and Vaccaro, L. 2001. Plant species richness, productivity, and nitrogen and
523 phosphorus limitations across a snowpack gradient in Alpine tundra, Colorado, U.S.A. *Arct.,
524 Antarc., Alp. Res.* **33**(1): 100–106. doi:10.2307/1552283

525 Semenchuk, P. R., Elberling, B., and Cooper, E. J. 2013. Snow cover and extreme winter warming
526 events control flower abundance of some, but not all species in high Arctic Svalbard. *Ecol. Evol.*
527 **3**(8): 2586–2599. doi:10.1002/ece3.648

528 Semenchuk, P. R., Elberling, B., Amtorp, C., Winkler, J., Rumpf, S., Michelsen, A., and Cooper, E. J.
529 2015. Deeper snow alters soil nutrient availability and leaf nutrient status in high Arctic tundra.
530 *Biogeochemistry* **124**: 81–94. doi:10.1007/s10533-015-0082-7

531 Semenchuk, P. R., Christiansen, C. T., Grogan, P., Elberling, B., and Cooper, E. J. 2016. Long-term
532 experimentally deepened snow decreases growing-season respiration in a Low- and High-Arctic
533 tundra ecosystem. *Journal of Geophysical Research: Biogeosciences* **121**(5): 1236-1248.
534 doi:10.1002/2015JG003251

535 Semenchuk, P. R., Gillespie, M. A. K., Rumpf, S. B., Baggesen, N., Elberling, B., and Cooper, E. J. 2016.
536 High Arctic plant phenology is determined by snowmelt patterns but duration of phenological
537 periods is fixed: An example of periodicity. *Env. Res. Lett.* **11**(12): 125006. doi:10.1088/1748-
538 9326/11/12/125006

539 Sjögersten, S., Kuijper, D. P. J., van der Wal, R., Loonen, M. J. J. E., Huiskes, A. H. L., and Woodin, S. J.
540 2010. Nitrogen transfer between herbivores and their forage species. *Polar Biol.* **33**: 1195–1203.
541 doi: 10.1007/s00300-010-0809-9

542 Strebel, D., Elberling, B., Morgner, E., Knicker, H. E., and Cooper, E. J. 2010. Cold-season soil
543 respiration in response to grazing and warming in High-Arctic Svalbard. *Polar Res.* **29**(1): 46–57.
544 doi:10.1111/j.1751-8369.2010.00154.x

545 Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., Fahnestock, J.,
546 and Romanovsky, V. E., 2005. Winter biological processes could help convert Arctic tundra to
547 shrubland. *BioScience* **55**(1): 17–26. doi:10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2

548 Tolgensbakk, J., Soerbel, L., and Hoegvard, K., 2000. Adventdalen, Geomorphological and Quaternary
549 Geological Map, Svalbard 1:100000. Spitsbergen Sheet C9Q. Norsk Polarinstitut, Tromsø,
550 Norway. Temakart Nr. 32.

551 Turetsky, M. R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frohking, S., McGuire, A. D., and Tuittila,
552 E. S. 2012. The resilience and functional role of moss in boreal and Arctic ecosystems. *New Phytol.*
553 **196**(1): 49–67. doi:10.1111/j.1469-8137.2012.04254.x

554 van der Wal, R., Madan, N., van Lieshout, S., Dormann, C., Langvatn, R., and Albon, S. D. 2000.
555 Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer.
556 *Oecologia* **123**: 108–115. doi:10.1007/s004420050995

557 Wahren, C.-H. A., Walker, M. D., and Bret-Harte, M. S. 2005. Vegetation responses in Alaskan Arctic
558 tundra after 8 years of a summer warming and winter snow manipulation experiment. *Glob.*
559 *Chang. Biol.* **11**(4): 537–552. doi:10.1111/j.1365-2486.2005.00927.x

560 Wipf, S., and Rixen, C. 2010. A review of snow manipulation experiments in Arctic and Alpine tundra
561 ecosystems. *Polar Res.* **29**(1): 95–109. doi:10.1111/j.1751-8369.2010.00153.x

562

563 **Table Captions**

564 Table 1. Plant growth form response to experimentally increased winter snow depth, with habitat,
565 site and reference.

566

567 Table 2. Vascular plants, bryophytes and lichens, which were identified during the field campaign and
568 the corresponding grouping into growth forms. All vascular plants could be identified to species in
569 the field. Since we did not sample destructively, some bryophytes and lichens could only be
570 identified to genera level.

571

572 Table 3. **Dry Heath**: Model estimates for live growth form abundances (based on average number of
573 hits per plot). The first line of values represents means in unmanipulated conditions (i.e. *Ambient*
574 snow regime and no summer warming) including their lower and upper 95% confidence interval
575 limits. Values on subsequent lines represent effect sizes of experimental treatments in comparison to
576 *Ambient*. Statistically significant effects at the 5% level are marked with “*”.

577

578 Table 4. **Mesic Meadow:** Model estimates for live growth form abundances (based on average
579 number of hits per plot). The first line of values represents means in unmanipulated conditions (i.e.
580 *Ambient* snow regime and no summer warming) including their lower and upper 95% confidence
581 interval limits. Values on subsequent lines represent effect sizes of experimental treatments in
582 comparison to *Ambient*. Statistically significant effects at the 5% level are marked with “*”.

583

584 Table 5. **Dry Heath:** Model estimates of diversity. The first line of values represents means in
585 unmanipulated conditions (i.e. *Ambient* snow regime and no summer warming) including their lower
586 and upper 95% confidence interval limits. Values on subsequent lines represent effect sizes of
587 experimental treatments in comparison to unmanipulated. Statistically significant effects at the 5%
588 level are marked with “*”.

589

590 Table 6. **Mesic meadow:** Model estimates of diversity. The first line of values represents means in
591 unmanipulated conditions (i.e. *Ambient* snow regime and no summer warming) including their lower
592 and upper 95% confidence interval limits. Values on subsequent lines represent effect sizes of
593 experimental treatments in comparison to unmanipulated. Statistically significant effects at the 5%
594 level are marked with “*”.

595

596 Table 7. Summary showing the context dependencies of climate change effects on plant community
597 properties. The effects of either *Deep* or *Medium* are summarized as effect of "enhanced winter
598 snow". Those and the effects of summer warming are compared to unmanipulated conditions.
599 Effects are presented for the Dry Heath and Mesic Meadow habitats separately. The "+" sign

600 represents positive effects of the respective parameter, i.e. an increase of values in the respective
601 community property. "-" represents negative effects and "0" represent no significant effects.

602

603 **Figure Captions**

604 Fig 1. Estimates of soil environmental conditions within treatment categories during growing season
605 2017. a) Significant interaction effects between snow enhancement and summer warming affected
606 temperatures below soil surface in both habitats after snowmelt (1st June to 31 July 2017). Effects of
607 snow enhancement and summer warming were independent for volumetric soil moisture content
608 and are presented for b) Dry Heath and c) Mesic Meadows. Statistically significant effects of snow
609 enhancement in comparisons to *Ambient* without OTC are marked with "*" and are separately
610 presented for plots without (dark grey) and with summer warming (light grey).

611

612 Fig 2. Estimates of growth form abundances (average number of hits within each plot) in the Dry
613 Heath habitat according to snow enhancement and summer warming. Estimates are presented for a)
614 shrubs, b) forbs and c) bryophytes. Statistically significant differences compared to *Ambient* without
615 OTC are marked with "*" .

616

617 Fig 3. Estimates of growth form abundances (based on average number of hits within each plot) in
618 Mesic Meadows according to snow enhancement and summer warming. Estimates are presented for
619 a) shrubs, b) forbs and c) bryophytes. Statistically significant effects of snow enhancement in
620 comparisons to *Ambient* without OTC are marked with "*" and are separately presented for plots
621 without (dark grey) and with summer warming (light grey).

622

623 Fig 4. Estimates of community diversity in the Dry Heath habitat according to snow enhancement and
624 summer warming. Estimates are presented for a) richness of vascular plant species and b) richness of
625 all taxonomic units including bryophytes. Statistically significant differences compared to *Ambient*
626 without OTC are marked with “*”.

627

628 Fig 5. Estimates of community diversity in Mesic Meadow habitat according to snow enhancement
629 and summer warming. Estimates are presented for a) richness of vascular plant species and b)
630 richness of all taxonomic units including bryophytes. Statistically significant effects of snow
631 enhancement in comparisons to *Ambient* without OTC are marked with “*” and are separately
632 presented for plots without (dark grey) and with summer warming (light grey).