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# Increased snow and cold season temperatures alter High Arctic parasitic fungi – host plant interactions[1]

Mikel Moriana-Armendariz, Holly Abbandonato, Takahiro Yamaguchi, Martin A. Mörsdorf, Karoline H. Aares, Philipp R. Semenchuk, Motoaki Tojo, and Elisabeth J. Cooper

**Abstract:** In the Arctic, fungal mycelial growth takes place mainly during the cold season and beginning of growing season. Climate change induced increases of cold season temperatures may, hence, benefit fungal growth and increase their abundance. This is of particular importance for parasitic fungi, which may significantly shape Arctic vegetation composition. Here, we studied two contrasting plant parasitic fungi's occurrences (biotrophic *Exobasidium hypogenum* Nannf. on the vascular plant *Cassiope tetragona* (L.) D. Don., and necrotrophic *Pythium polare* Tojo, van West & Hoshino on the moss *Sanionia uncinata* (Hedw.) Loeske) in response to increased snow depth, a method primarily used to increase cold season temperatures, after 7–13 years of snow manipulation in Adventdalen, Svalbard. We show that enhanced snow depth increased occurrences of both fungi tested here and indicate that increased fungal infections of host plants were at least partly responsible for decreases of host occurrences. Although bryophyte growth, in general, may be influenced by increased soil moisture and reduced competition from vascular plants, *Pythium polare* is likely enhanced by the combination of milder winter temperatures and moister environment provided by the snow. The relationships between host plants and fungal infection indicate ongoing processes involved in the dynamics of compositional adjustment to changing climate.

*Key words:* *Exobasidum hypogenum*, *Cassiope tetragona*, *Pythium polare*, *Sanionia uncinata*, winter.

**Résumé :** Dans l'Arctique, la croissance mycélienne des champignons a lieu principalement pendant la saison froide et au début de la saison de croissance. L'augmentation des

**M. Moriana-Armendariz, K.H. Aares, and E.J. Cooper.** Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT- The Arctic University of Norway, N-9037 Tromsø, Norway.
**H. Abbandonato.** Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT- The Arctic University of Norway, N-9037 Tromsø, Norway; Department of Geography and Environment, Mount Allison University, Sackville, NB, E4L 1A7, Canada.
**T. Yamaguchi.** Graduate School of Life and Environmental Sciences, Osaka Prefecture University, Sakai, Japan; Nara Plant Protection Center, Sakurai, Nara, Japan.
**M.A. Mörsdorf.** Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT- The Arctic University of Norway, N-9037 Tromsø, Norway; Faculty of Biology – Geobotany, University of Freiburg, Schaenzlestr. 1, D-79104 Freiburg, Germany.
**P.R. Semenchuk.** Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT- The Arctic University of Norway, N-9037 Tromsø, Norway; Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria.
**M. Tojo.** Graduate School of Life and Environmental Sciences, Osaka Prefecture University, Sakai, Japan.
**Corresponding author:** Elisabeth J. Cooper (e-mail: elisabeth.cooper@uit.no).

températures de la saison froide induite par les changements climatiques peut donc favoriser la croissance des champignons et accroître leur abondance. Ceci revêt une importance particulière pour les champignons parasites, qui peuvent façonner de manière significative la composition de la végétation arctique. Ici, les auteurs ont étudié la présence de deux champignons opposés parasites de plantes (*Exobasidium hypogenum* Nannf. biotrophe sur la plante vasculaire *Cassiope tetragona* (L.) D. Don., et *Pythium polare* Tojo, van West & Hoshino nécrotrophe sur la mousse *Sanionia uncinata* (Hedw.) Loeske) en réponse à l'augmentation de l'épaisseur de neige, une méthode principalement utilisée pour accroître les températures de la saison froide, après 7–13 ans de manipulation de la neige à Adventdalen, Svalbard. Ils montrent que l'augmentation de l'épaisseur de la neige augmentait la présence des deux champignons testés ici, et indiquent que l'augmentation des infections fongiques des plantes hôtes était au moins partiellement responsable de la diminution de la présence des hôtes. Alors que la croissance des bryophytes en général peut être influencée par l'augmentation de l'humidité du sol et la réduction de la concurrence des plantes vasculaires, *Pythium polare* est probablement favorisé par la combinaison des températures hivernales plus douces et d'un environnement plus humide fourni par la neige. Les relations entre les plantes hôtes et l'infection fongique indiquent des processus continus impliqués dans la dynamique de l'adaptation compositionnelle aux changements climatiques. [Traduit par la Rédaction]

*Mots-clés :* Exobasidium hypogenum, Cassiope tetragona, Pythium polare, Sanionia uncinata, hiver.

## Introduction

Plant parasitic fungi and snow moulds may benefit from milder cold season temperatures, brought about by increased air temperature (Callaghan et al. 2011; Cooper 2014; Hoegh-Guldberg et al. 2018) and the stabilizing effect of an insulative snow layer (Wipf and Rixen 2010), as mycelial growth takes place mainly under the snow (Jung et al. 2007; Hoshino et al. 2009). Climate change is especially pronounced in high latitude and elevation regions and may therefore promote infections of plants by parasitic fungi in these cold-dominated ecosystems (Olofsson et al. 2011). For instance, increased occurrence of snow moulds in northern regions render golf course grass unsightly (Hsiang et al. 1999; McBeath 2003; Jung et al. 2007), and fungal infection reduces commercial blueberry crops in eastern North America (Brewer et al. 2014; Stewart et al. 2015), both with important economic implications. The response of native vegetation to changing warm and cold season conditions in these biomes is well documented (Wipf and Rixen 2010; Elmendorf et al 2012*a*, 2012*b*; Cooper 2014), but the role played by parasitic fungi is understudied thus far.

Long-term snow enhancement in the High Arctic with corresponding milder winter temperatures reduced the cover of dwarf shrub *Cassiope tetragona* (L.) D. Don. and increased that of moss (Cooper et al. 2019). Infections with parasitic fungi may have contributed to the *C. tetragona* decline, as infected individuals may have been more vulnerable to disturbances and thereby less likely to adapt to changing conditions. *Exobasidium hypogenum* Nannf. (Fig. 1) is a prominent, highly specialized biotrophic parasitic fungi only growing in *C. tetragona* (Nannfeldt 1981; Elvebakk and Prestrud 1996), a dominant hemi-prostrate dwarf shrub with circumpolar distribution (Walker et al. 2005). Due to *C. tetragona*'s susceptibility to frost damage (Semenchuk et al. 2013; Milner et al. 2016), this plant is common in areas with relatively deep snow cover (Mallik et al. 2011; Semenchuk et al. 2016*a*), but an increased occurrence of the easily recognized infected leaves was noted in areas of experimentally increased snow depth (own observations; Abbandonato 2014).

*Sanionia uncinata* (Hedw.) Loeske is one of the dominant moss species in many Arctic ecosystems (Smith 1996; Virtanen et al. 1997), and is infected, weakened, and killed by *Pythium polare* Tojo, van West & Hoshino (synonym *Globisporangium polare*), a necrotrophic oomycete (Tojo et al. 2012; Tojo and Newshman 2012). *Pythium polare* is highly dependent

**Fig. 1.** Shoots of *Cassiope tetragona*, showing healthy shoots (small green leaves, tightly packed, shown within the black ellipses) and shoots infected by *Exobasidium hypogenum* (big red leaves, long internodes between them, shown within the white ellipses). Photo credit: Karolina Paquin.



on *Sanionia uncinata* in polar regions; thus, potentially affecting both *Sanionia uncinata*'s occurrence and its ability to respond to increased snow depth in the same way as other bryophyte species. *Pythium polare* infection can be easily seen by the presence of light-coloured circles of dead tissue within moss colonies (Fig. 2, Tojo and Newsham 2012). Rings of dead *Sanionia uncinata* observed in our study site on Svalbard indicated increased *Pythium polare* infection in response to experimentally increased snow (Cooper et al. 2019).

In general, the effect of parasitic fungi on their hosts depends on their mode of nutrition; biotrophs, such as our study organism *E. hypogenum*, acquire nutrients from the living host plant cells, whereas necrotrophs kill the host plant and feed on the dead tissues (Ingold and Hudson 1993). As biotrophic fungi require their host to be alive to obtain nutrients, they avoid damaging the plant (Barnett and Binder 1973). They establish very specialized structures for compatibility (Mendgen and Hahn 2002; Duplessis et al. 2011), usually through coevolution with the host plant (Schulze-Lefert and Panstruga 2003), even evolving mechanisms to keep their host cells alive (Struck 2006) to reduce their impact on their host (Ingold and Hudson 1993). Over time, however, these impacts may accumulate and increase mortality over large areas, with further effects at a community level (Olofsson et al. 2011).

To investigate the effect of increased snow on these two contrasting plant parasitic fungi in the High Arctic (biotrophic *E. hypogenum* on *C. tetragona*, and necrotrophic *Pythium polare* on the moss *Sanionia uncinata*), we collected occurrence data of each species from a long-term snow fence experiment in Adventdalen, Svalbard. Snow fences were erected in 2006, i.e., 7–13 years prior to this study, and affected both abiotic and biotic conditions, including increased cold season temperatures, increased soil moisture during the early growing season, and species composition changes, among others (Semenchuk et al. 2013; Cooper et al. 2019; Mörsdorf et al. 2019). We recorded the occurrence of *E. hypogenum* and *Pythium polare* and hypothesized that each parasite's presence in its respective host was higher with increased snow depth, a potential mechanism contributing to the documented (*C. tetragona*) and potential (*Sanionia uncinata*) decline of both hosts (Cooper et al. 2019).

## Materials and methods

### Study site

The study took place in Adventdalen, Svalbard (78°10′N, 16°04′E), 30–80 m above sea level. Weather data from Svalbard airport, located approximately 15 km from the study site,

**Fig. 2.** Rings (5–10 cm in diameter) of dead *Saniona uncinata* killed by *Pythium* spp. observed in Svalbard. Photo credit: Motoaki Tojo.



show that average temperature for the 2010–2019 period was −2.4 °C, the coldest month being March (−10.9 °C) and the warmest July (7.4 °C) (eKlima 2020). Precipitation is low, with an average of 229 mm per year, and spread throughout the year (eight months of monthly precipitation between 19 and 28 mm), although values in the period March–June are lower (between 6 and 14 mm/month). On average (2010–2019) 173 mm falls in the period September–May, inclusive, and 56 mm in June–August, so 76% falls in the non-growing season.

The vegetation is classified as part of the middle Arctic tundra (Elvebakk 2005), dominated by *C. tetragona* heaths and moister meadows, with abundant *Salix polaris* Wahlenb. throughout. More details about soil and vegetation at the site is given in Appendix A.

### Experimental set-up

Snow fences were established in Adventdalen in 2006 to study the environmental and biological response of a High Arctic ecosystem to increased snow. Four blocks were established, two in Heath vegetation and two in a moister Meadow (Morgner et al. 2010). Each block consisted of three fences (6 m long and 1.5 m high) perpendicular to the prevalent wind direction: the fence disturbs the wind flow and leads to the accumulation of snow on the lee side creating different snow depths (see Appendix A, Fig. A1). For each fence six plots were established in the unmanipulated "Ambient" regime (10–30 cm snow depth) and six at the "Deep" snow regime (1.2–1.5 m deep). In three of the plots at each regime the dominant evergreen shrub species was *C. tetragona*, and in the three others it was *Dryas octopetala* L. In 2010 further plots were marked in a third snow regime, "Medium", farther from the fence than Deep but still influenced by it (60–100 cm snow depth). Three Medium plots were established per fence, and where possible each contained a mixture of *C. tetragona* and *D. octopetala.* Two fences were not used for this study (one collapsed and the other lacked *C. tetragona* behind the fence). As snow bed plants, such as bryophytes, may benefit from the decrease of shrub cover in deep snow regimes (Mark et al. 2015; Cooper et al. 2019), for the purpose of the current study only plots with *C. tetragona* as the dominant evergreen shrub were chosen. For Ambient and Deep regimes, this resulted in three plots studied at each fence. For the Medium regime, only plots that had *C. tetragona* when they were established were chosen, but some of them had to be discarded as they

**Fig. 3.** Soil temperature and soil moisture at each snow regime for the 2014–2015 period. Winter is defined here as the period from 1 September 2014 to 31 May 2015, and summer from 1 June to 31 August 2015. Soil moisture was measured manually, and thus could not be recorded until the first day of sampling (12 June 2015).
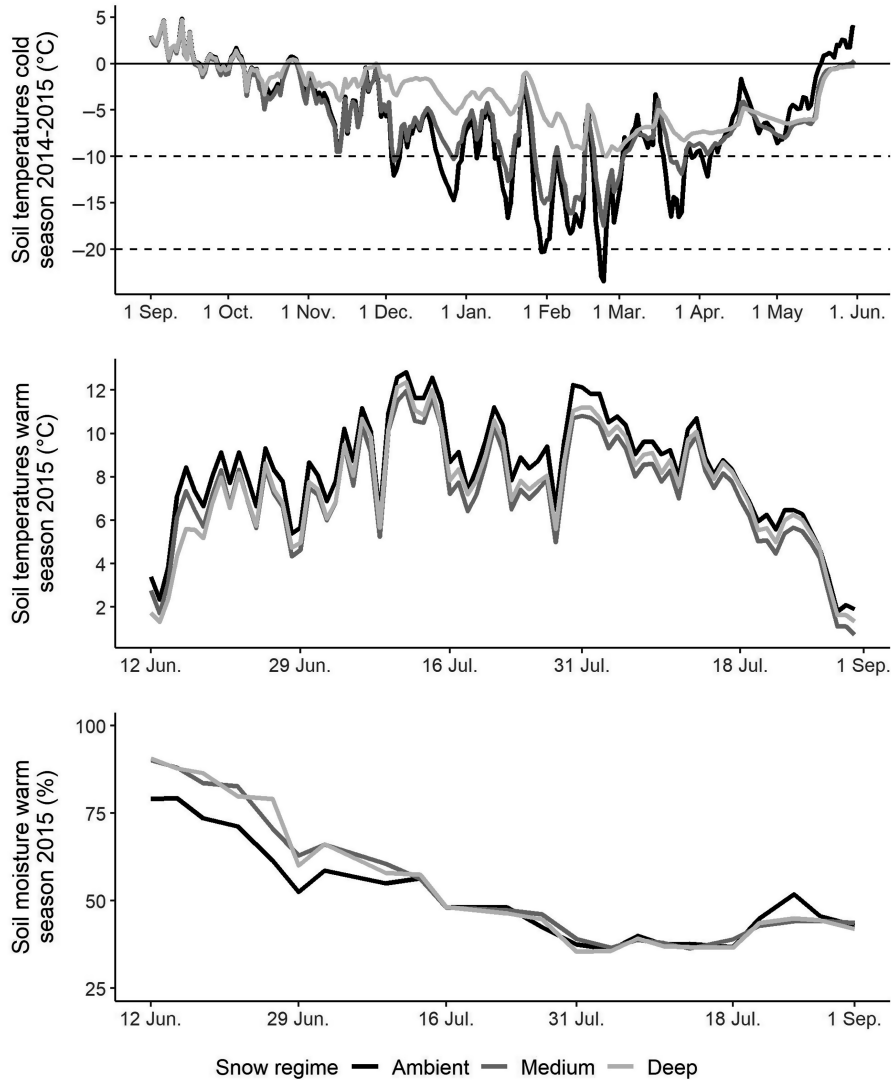


had been the focus of an open-top chamber (OTC) study. See Appendix A, Fig. A1 and Table A1 for an overview of the experimental design and the plots used.

The fences increased snow depth and the length of snow lie, delaying snowmelt and affecting both winter and summer temperature and soil moisture (Fig. 3). During winter 2014–2015, soils were warmer within Deep than Ambient snow regime, for approximately 77% of the time (i.e., 175 days of the 227 days of sub-zero temperatures, Mörsdorf et al. 2019). Soil in Medium was also warmer than in Ambient, but for a shorter duration. Minimum temperatures during winter were milder in Deep (−10 °C) and Medium (−17.5 °C), and they were more stable than the highly fluctuating Ambient soil temperatures (min. −23.5 °C). Soil moisture was very high directly after snowmelt, especially for the enhanced snow regimes. This gradually decreased throughout the growing season, so that

by mid-July there was little difference between the regimes. This pattern of temperature and moisture was similar for all study years (e.g., Morgner et al. 2010; Cooper et al. 2011; Gillespie et al. 2016). Heaths accumulated significantly more snow than Meadows between mid-November and late May; consequently, both early and late winter surface soil temperatures were higher in Heath than Meadow for both Ambient and Deep (Morgner et al. 2010). A vegetation survey in the experiment was carried out in 2015 after nine winters of manipulated snow and reported by Cooper et al. (2019). In summary, deeper snow behind the fences resulted in shrub death (mostly *C. tetragona* and *D. octopetala*), reducing the cover of live shrubs and increasing that of bare ground and dead shrub material. Bryophyte cover also increased with deeper snow, especially in the Medium regime in Meadow and in the Deep regime in Heath.

**Soil moisture and temperature**

During the summer of 2015, soil moisture was measured at the centre of each plot using a Theta ML 2x Probe (Delta-T Devices, Cambridge, UK). Near soil surface temperature was recorded hourly throughout the experiment using Tinytag data logger model TGP-4020 (Gemini Data Loggers, Chichester, UK), with one logger per fence and snow regime combination. Summaries of temperature data were made from the Ambient, Medium, and Deep regimes for all years 2010–2018. The date (day of year) the plots were snow free was recorded in the field and (or) found by examination of the temperature data during earlier studies. For the years where these data were missing (2014, 2016–2018), we used rounded medians across all other years, for each fence and treatment separately. The remaining summary statistics were run on block means, so snow free dates and logger temperature data were averaged within blocks. From the within-block averaged temperature data, daily averages were calculated and used thereafter. The initial freezing date was defined as the first day after 31 August (day of year 243) when the daily average temperature was less than zero. We defined the year into two seasons based on this temperature data: "warm season", the period between snow free date and initial freezing date; and "cold season", the period between initial freezing date and snow free date. We obtained the following values from these data: Thawing and Freezing Degree Days of the soil calculated as an accumulation of daily (positive and negative, respectively) temperature means as well as Annual Degree Day sums, together with season lengths. We present means of these data as averages across the whole experiment.

**Vegetation cover**

We recorded the percentage cover of plants in the plots in two field campaigns and used the 2019 *C. tetragona* data and 2017 bryophyte data for this study. Briefly, the percentage cover of *C. tetragona*, classified as alive or dead, was estimated together with that of other plants in the plot making a total plot cover of 100%, following the method outlined by Cooper et al. (2019), on 12–13 August 2019.

Detailed vegetation analysis carried out in July 2017 using the point-frame method (Jonasson 1988; Walker et al. 1996) in which we identified the bryophytes to species where possible. We later separated the bryophyte data into two groups: *Sanionia uncinata*, and "non-*Sanionia* bryophytes", composed of *Anthelia juratzkana* (Limpr.) Trevis., *Aulacomnium* spp., *Dicranum* spp. and *Distichium* spp., *Hylocomium splendens* (Hedw.) Schimp., *Polytrichum* spp., *Ptilidium ciliare* (L.) Hampe, *Racomitrium* spp., *Tomentypnum nitens* (Hedw.) Loeske, and unidentified bryophytes. Here we only used the "first/top-hits" giving a total number of possible hits of 100 per plot. From the 2017 field campaign we only used the bryophyte data for this study (total bryophytes, only *Sanionia uncinata*, non-*Sanionia* bryophytes, and proportion of bryophytes that are *Sanionia uncinata*).

### *Exobasidium hypogenum*

Plots from all regimes (Ambient $n = 30$, Medium $n = 14$, Deep $n = 29$) were checked for live *C. tetragona* and the occurrence of *E. hypogenum* infection on two occasions: 7–27 August 2013, and 14–15 August 2019. Infected shoots have elongated internodes and malformed leaves, which are easily identifiable (Nannfeldt 1981, Fig. 1). Leaves grow to up to $10 \times 6$ mm, more than double their normal size, are triangular and the adaxial side is blood-red or whitish. No connections have been found between attacks of consecutive seasons, which suggests that each affected shoot usually develops from a new infection (Nannfeldt 1981). Having data from two different years, seven and thirteen years after establishing the fences, can give some indication of infection development through time.

### *Pythium* spp.

During August 2014 and 2015, $1 \times 1$ m$^2$ plots were established for the study of *Pythium* species. One *Pythium* plot was established at each fence (10 fences) and snow regime, totalling 30 *Pythium* plots. At each *Pythium* plot, five samples of 3–5 g (wet weight) of *Sanionia uncinata* were collected and later stored at 2–4 °C until use.

Four *Sanionia uncinata* shoots per *Pythium* plot and year were washed in tap water and dried with paper towels. They were later brought to a clean bench (an enclosure that provides filtered air across the work surface to protect against contamination) and buried equidistantly in a petri dish with *Pythium* selective NARM medium (Morita and Tojo 2007). The petri dishes were then sealed with Parafilm and brought to a cold room, where they were incubated at 4 °C for 1–2 weeks. After this period any present *Pythium* mycelium would have reached a size of 2–3 cm, and the number of such mycelia per petri dish was noted (usually 0 or 1, and very occasionally 2). This procedure was performed five times per plot, using four different *Sanionia uncinata* shoots each time, resulting in a theoretical maximum of 20 isolates per plot, 600 per year, and 1200 total.

### Statistical analyses

All data were analysed in R (R Core Team 2019), applying linear mixed models.

Vegetation cover was analysed using the function glmmTMB from the glmmTMB package (Brooks et al. 2017). This function uses beta distribution and logit link function. Beta distribution requires values between 0 and 1. Therefore, percentage values were divided by 100, live and dead covers equal to 0 were changed to 0.0001, and proportions equal to 0 and 1 were changed to 0.001 and 0.999 respectively.

In the case of *C. tetragona* using cover data from 2019 three models were established: live cover of *C. tetragona*, dead cover of *C. tetragona*, and proportion of dead cover (dead/(dead + live)). Here we used all permanent vegetation plots containing live *C. tetragona* at the start of the experiment. One plot was removed from the analysis as it was under water in 2019, and six of the Medium plots were removed from analysis as they did not contain live *C. tetragona* when established. For live and dead cover analyses all plots originally containing live *C. tetragona* were used ($n = 73$), although for proportion of dead cover only those plots with some *C. tetragona* in 2019 (dead and (or) alive) were used ($n = 72$). For analysis of bryophyte cover obtained in 2017 in relation to snow regime we used four models: total bryophyte cover, *Sanionia uncinata* cover, non-*Sanionia* bryophytes cover, and proportion of bryophyte cover that was *Sanionia uncinata* (i.e., *Sanionia uncinata*/total bryophyte cover). For this last analysis only plots that had bryophytes were used ($n = 62$).

For each of these models the explanatory variables were vegetation type and snow regime, and fence identifier was included as a random factor. A stepwise reduction approach was employed for the election of the best candidate model, which allows the retention of all important factors and avoids over-fitting. First, the response variable was

modelled according to the explanatory variables (including all interactions), and then the different terms were progressively removed, and the remaining models compared (first the interaction, then the single variables). Models were compared by means of analysis of variance, obtaining Akaike's information criterion and calculating the chi-squared test.

Infection by *E. hypogenum* and *Pythium* spp. was analysed using the function glmer from the lme4 package (Bates et al. 2015). In the case of *E. hypogenum*, only plots with live *C. tetragona* were considered in the analysis ($n = 142$: 75 in 2013, 67 in 2019), and a binomial error distribution was used (presence/absence data, where each plot was assigned a value of 1 if *E. hypogenum* was present, or 0 if it was not present). The response variable was, therefore, the presence or absence of *E. hypogenum* within a plot, and logit transformation was applied for modelling. In the case of *Pythium* a Poisson error distribution was used, where the response variable was the abundance of *Pythium* per fence (the number of individual *Pythium* mycelia in the petri dishes, i.e., count data, ($n = 56$: 26 in 2014 and 30 in 2015)). For this analysis, all *Pythium* species were grouped together in a single variable, as most species were too rare for statistical analysis, and log-transformation was applied for modelling. The explanatory variables for these two models were year, vegetation type and snow regime, and fence was included as a random factor. A stepwise reduction approach was also employed, aiming at the simplest model with all significant variables.

Fungal occurrence was then modelled against the cover of the host plants. In the case of *E. hypogenum* the presence/absence data from 2019 was modelled against *C. tetragona* (live and dead cover, and proportion of dead, all in 2019) by means of glmer. We used binomial distribution and logit transformation, and fence was included as random factor. In the case of *Pythium*, the abundances from 2014 and 2015 were summed (and those of the two plots that were only sampled in one year were doubled), and the resulting values were modelled against bryophyte cover from 2017 (total bryophyte cover, *Sanionia uncinata* cover and proportion of *Sanionia uncinata*), using a mean bryophyte value for each fence–snow regime combination ($n = 30$). We used Poisson distribution and log-transformation, and fence was included as a random factor. As we used different plots within a fence–snow regime combination for *Pythium* sampling and bryophyte cover, we tested the *Pythium*–bryophyte relationship using mean bryophyte values from two different sets of plots for the bryophyte cover: (1) the plots used in the other analyses described here (i.e., *Cassiope*-focussed plots, $n = 71$), (2) all plots within these 10 fences in the whole experiment (*Cassiope* and *Dryas* focussed, without OTCs, $n = 119$).

We applied post-hoc analysis to all models, to get the relationships between the different levels and factors. This was done using the function emmeans from the emmeans package (Length 2020).

## Results

### Abiotic conditions

Deep and Medium had significantly milder cold seasons than Ambient (Table 1, Fig. 3). These enhanced snow regimes became snow free later, had shorter warm seasons and, thus, fewer days available to collect Thawing Degree Days, a cold season with higher (less negative) Freezing Degree Day values, and more stable and significantly higher soil temperatures during the cold season. These effects were stronger in Deep than in Medium. In the Ambient regime Heath was slightly colder than Meadow, in both cold and warm seasons (Appendix A, Table A2, and Figs. A2A and A2B). This pattern was reversed by snow enhancement, so that Heath was warmer than Meadow for Medium and Deep. The largest differences in temperature sums between the snow regimes was during the cold season.

Although the majority of the snow melted and ran off while the soil was still frozen without the formation of obvious pools of meltwater, soil moisture levels were elevated during

**Table 1.** Seasonal data from snow fence experiment, Adventdalen, Svalbard, obtained from continuous hourly temperature records from 32 Tinytag data loggers, during the period from 2010 to 2018.

| Snow Regime | SF | IF | Warm season No. days | Cold season No. days | Annual TDDsoil | Annual FDD soil | Annual DD sum |
|---|---|---|---|---|---|---|---|
| Ambient | 153 | 263 | 110 | 255 | 721 | −1604 | −883 |
| Medium | 161 | 259 | 98 | 267 | 604 | −1326 | −722 |
| Deep | 167 | 262 | 95 | 270 | 600 | −808 | −208 |

**Note:** SF, snow-free date (day of year); IF, initial freezing date (day of year); No. days, season length in warm season and cold season. Annual Thawing and Freezing Degree Days of the soil (TDDsoil and FDDsoil, respectively) calculated as an accumulation of daily (positive and negative, respectively) temperature means, together with the Degree Day Sum (DD sum) for the whole year.

**Table 2.** Effect strengths of vegetation type and snow regime on cover of live *Cassiope tetragona*, dead *C. tetragona*, and proportion of dead *C. tetragona*. Non-significant variables were removed from the models and are not shown in the table. The first row of each model indicates the intercept. Values are presented in the logit scale. Significant *p* values (<0.05) are indicated in bold text.

| | | Effect size | Standard error | z | p |
|---|---|---|---|---|---|
| % cover live *C. tetragona* | Heath: Ambient | −1.14 | 0.14 | — | — |
| | Meadow | −0.22 | 0.20 | −1.09 | 0.27 |
| | Medium | −0.54 | 0.25 | −2.21 | **0.03** |
| | Deep | −0.60 | 0.21 | −2.82 | **0.005** |
| | Meadow: Medium | −1.58 | 0.50 | −3.14 | **0.002** |
| | Meadow: Deep | −1.66 | 0.37 | −4.55 | **<0.001** |
| % cover dead *C. tetragona* | Heath: Ambient | −2.26 | 0.24 | — | — |
| | Meadow | −0.57 | 0.30 | −1.90 | 0.06 |
| | Medium | 0.15 | 0.23 | 0.64 | 0.52 |
| | Deep | 0.88 | 0.18 | 3.95 | **<0.001** |
| Proportion dead *C. tetragona* | Heath: Ambient | −0.78 | 0.35 | — | — |
| | Meadow | −0.57 | 0.49 | −1.16 | 0.25 |
| | Medium | 0.38 | 0.33 | 1.14 | 0.26 |
| | Deep | 1.05 | 0.28 | 3.68 | **<0.001** |
| | Meadow: Medium | 2.17 | 0.53 | 4.06 | **<0.001** |
| | Meadow: Deep | 2.47 | 0.46 | 5.42 | **<0.001** |

the first third of the growing season in Deep and Medium (Fig. 3), with Deep and Medium not differing from each other. Meadow was moister than Heath in Ambient and Medium (Appendix A, Fig. A2C) but there were no differences between the vegetation types in Deep.

### Vegetation cover

The cover of live *C. tetragona* decreased with enhanced snow depth, was lower in Meadow than Heath, and both cover and proportion of dead *C. tetragona* were significantly much higher in Deep than in Ambient (Table 2, Fig. 4). Of the five plots where *C. tetragona* was completely dead, one was in Medium and four were in Deep (see Table 3, year 2019).

Total bryophyte cover and cover of non-*Sanionia* bryophytes was higher in Meadow than Heath (Table 4, Fig. 5). Total bryophyte cover increased with snow depth in both habitats, although for both *Sanionia uncinata* and non-*Sanionia* bryophytes this occurred only in Meadow. Proportion of *Sanionia uncinata* did not differ between snow regimes in Heath, but was higher in Deep than Ambient in Meadow.

**Fig. 4.** Cover of live (A) and dead (B) *Cassiope tetragona*, in 2019 plots, and proportion of dead to total *C. tetragona* (C). Results are shown for Heath and Meadow at each snow regime (Ambient, Medium, Deep). Error bars indicate confidence intervals. Bars with the same letter do not differ at a 5% significance level.
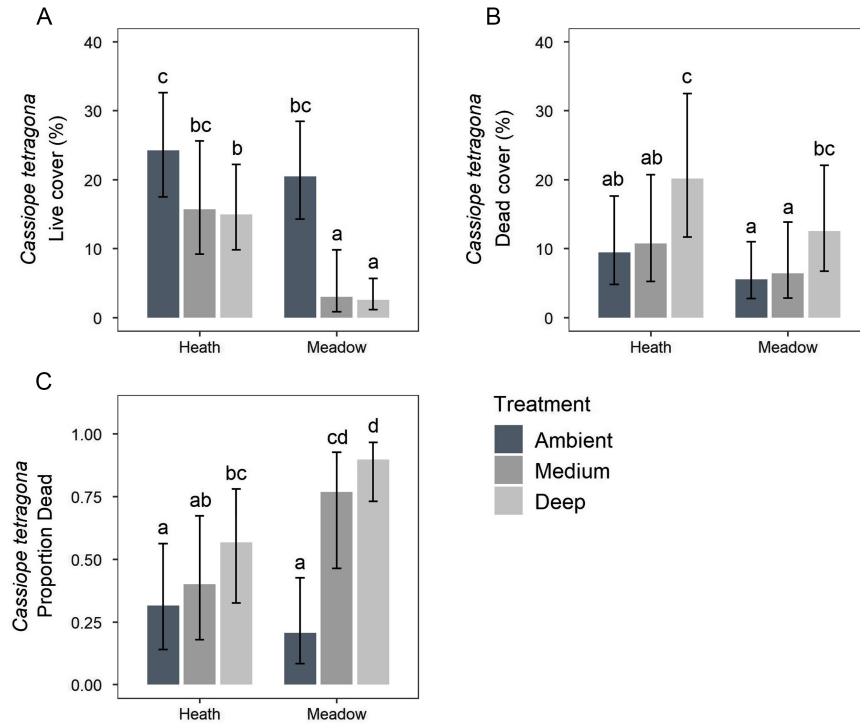


### Infection of *Cassiope tetragona* by *Exobasidium hypogenum*

In both Heath and Meadow, the proportion of plots with live *C. tetragona* that were infected by *E. hypogenum* increased with snow depth, with the clearest increases in Deep (Table 3, Appendix A, Table A3). The likelihood of infection of *C. tetragona* by *E. hypogenum* did not differ between vegetation types and years, with *C. tetragona* in Deep being more frequently infected than in Ambient and Medium (Table 5, Fig. 6).

The increase of infection in Deep was slightly, although insignificantly, higher in 2019 than in 2013 (Table 3 and Appendix A, Fig. A3), suggesting an increased fungal response as the experiment progressed. In four plots *C. tetragona* died out between 2013 and 2019, one in Medium and three in Deep, of which two (one at each snow regime) were infected by *E. hypogenum* (Table 3).

The fungus/host plant model showed that the presence of *E. hypogenum* was significantly positively related to the cover of dead *C. tetragona* in a plot, and had no relationship to live *C. tetragona* cover or proportion of *C. tetragona* that was dead (Table 5).

### Infection of *Sanionia uncinata* by *Pythium* spp.

From the incubation trials a total of 103 isolates of *Pythium* spp. were obtained (Appendix A, Table A4). Two shoots gave two mycelia, the rest produced only one each. A fifth of the mycelia could not be discerned to the species level. Among the other isolates we obtained five different species of fungal mycelia; four *Pythium* species are new discoveries (and, therefore, we lack information about specificity). *Pythium polare* (synonym *Globisporangium polare*), was the most abundant, accounting for 60% of the mycelial growth.

**Table 3.** Presence of *Cassiope tetragona* and *Exobasidium hypogenum* in the plots in 2013 and 2019. Note that plots are not ordered by position, but to give a better impression of the differences.

| 2013 | Ambient | | | Medium | | Deep | | |
|---|---|---|---|---|---|---|---|---|
| Fence | 1 | 2 | 3 | 1 | 2 | 1 | 2 | 3 |
| A1 | black | black | black | gray | gray | black | black | gray |
| A3 | black | black | gray | black | black | black | black | black |
| B4 | black | black | light gray | black | white | black | gray | gray |
| B5 | black | black | gray | black | black | gray | gray | gray |
| B6 | black | black | black | black | black | black | black | gray |
| C7 | black | black | black | black | white | gray | gray | white |
| C9 | black | black | gray | black | white | black | gray | gray |
| D10 | black | black | black | black | white | black | black | black |
| D11 | black | black | gray | white | white | black | gray | light gray |
| D12 | black | black | light gray | black | gray | black | black | gray |

| 2019 | Ambient | | | Medium | | Deep | | |
|---|---|---|---|---|---|---|---|---|
| Fence | 1 | 2 | 3 | 1 | 2 | 1 | 2 | 3 |
| A1 | black | black | black | black | black | black | black | gray |
| A3 | black | black | black | black | black | black | black | gray |
| B4 | black | black | black | gray | white | black | gray | gray |
| B5 | black | black | black | black | black | black | black | gray |
| B6 | black | black | gray | black | gray | gray | gray | gray |
| C7 | black | black | black | black | white | light gray | white | white |
| C9 | black | black | black | black | white | light gray | gray | gray |
| D10 | black | black | gray | black | white | black | gray | gray |
| D11 | black | black | black | white | white | gray | gray | light gray |
| D12 | black | black | black | black | light gray | black | light gray | black |

| Colour | Meaning |
|---|---|
| black | Live *Cassiope tetragona*, not infected by *Exobasidium hypogenum* |
| gray | Live *Cassiope tetragona*, infected by *Exobasidium hypogenum* |
| light gray | Only dead *Cassiope tetragona* |
| white | No *Cassiope tetragona* |

**Table 4.** Effect strengths of vegetation type and snow regime on bryophyte cover in 2017. Four models were established: total bryophyte cover, *Sanionia uncinata* cover, non-*Sanionia* cover, and proportion of bryophyte cover that is *Sanionia uncinata*. Non-significant variables were removed from the models and are not shown in the table. The first row of each model indicates the intercept. Values are presented in the logit scale. Significant *p* values (<0.05) are indicated in bold text.

| | | Effect size | Standard error | $z$ | $p$ |
|---|---|---|---|---|---|
| Total bryophyte cover (%) | Ambient | −3.19 | 0.35 | — | — |
| | Meadow | 0.88 | 0.40 | 2.20 | **0.03** |
| | Medium | 0.94 | 0.30 | 3.10 | **0.002** |
| | Deep | 0.76 | 0.23 | 3.25 | **0.001** |
| *Sanionia uncinata* cover (%) | Heath: Ambient | −3.32 | 0.36 | — | — |
| | Meadow | −0.33 | 0.46 | −0.72 | 0.47 |
| | Medium | 0.15 | 0.43 | 0.34 | 0.73 |
| | Deep | −0.30 | 0.35 | −0.84 | 0.40 |
| | Meadow: Medium | 1.68 | 0.62 | 2.73 | **0.006** |
| | Meadow: Deep | 1.62 | 0.51 | 3.18 | **0.001** |
| Non-*Sanionia* bryophyte cover (%) | Heath: Ambient | −3.41 | 0.31 | — | — |
| | Meadow | 0.50 | 0.39 | 1.27 | 0.20 |
| | Medium | 0.00 | 0.40 | 0.00 | 1.00 |
| | Deep | 0.50 | 0.35 | 1.44 | 0.15 |
| | Meadow: Medium | 1.07 | 0.56 | 1.93 | 0.05 |
| | Meadow: Deep | −0.05 | 0.47 | −0.10 | 0.92 |
| Proportion *Sanionia uncinata* | Heath: Ambient | −0.60 | 0.43 | — | — |
| | Meadow | −0.62 | 0.57 | −1.10 | 0.27 |
| | Medium | −0.01 | 0.61 | −0.01 | 0.99 |
| | Deep | −0.80 | 0.49 | −1.63 | 0.10 |
| | Meadow: Medium | 1.14 | 0.89 | 1.27 | 0.20 |
| | Meadow: Deep | 2.04 | 0.67 | 3.03 | **0.002** |

In the model reduction of the *Pythium* analysis the year variable was discarded, leaving snow regime, vegetation type, and their interaction as explanatory variables (Table 5). *Pythium* was generally more abundant in Heath than Meadow (Fig. 6). In Meadow, both Deep and Medium had significantly higher abundance of *Pythium* than Ambient, whereas in Heath, Deep had a higher abundance than both Ambient and Medium.

The fungus/host plant model showed that *Pythium* was significantly more abundant when total bryophyte cover was greater (Table 5). In addition, there was a significant inverse relationship between *Pythium* abundance and cover of *Sanionia uncinata*, and this relationship was independent of the plot selection used to calculate bryophyte cover fence–snow regime mean values.

## Discussion

This study verifies our hypothesis that enhanced snow regimes increase the pathogenetic fungal occurrences of *E. hypogenum* and *Pythium polare* in their respective host organisms. The higher occurrences of both parasites may be caused by the altered abiotic microclimate under a prolonged, deeper snow cover with higher cold season soil temperatures and elevated early growing season soil moisture. Both of these factors potentially influence fungal growth and infection rates of host organisms.

Enhanced snow cover increases cold season soil temperatures, thus increasing the activity of most heterotrophic organisms (e.g., Semenchuk et al 2016*a*; Semenchuk et al. 2019). At this time of the year when mycelial growth is most active, higher temperatures may, therefore, promote fungal growth. This phenomenon seemed to have occurred in our Deep treatment, where the soil remained warmer than −5 °C for the first half of the cold season, and never became colder than −10 °C. Both of these temperature thresholds are

**Fig. 5.** Total bryophyte cover in 2017 (A), cover of *Sanionia uncinata* (B) and non-*Sanionia* bryophytes (C), and proportion of bryophyte cover that is *Sanionia uncinata* (D) in 2017. Results are shown for Heath and Meadow for each snow regime (Ambient, Medium, and Deep). Error bars indicate confidence intervals. Bars with the same letter do not differ at a 5% significance level.
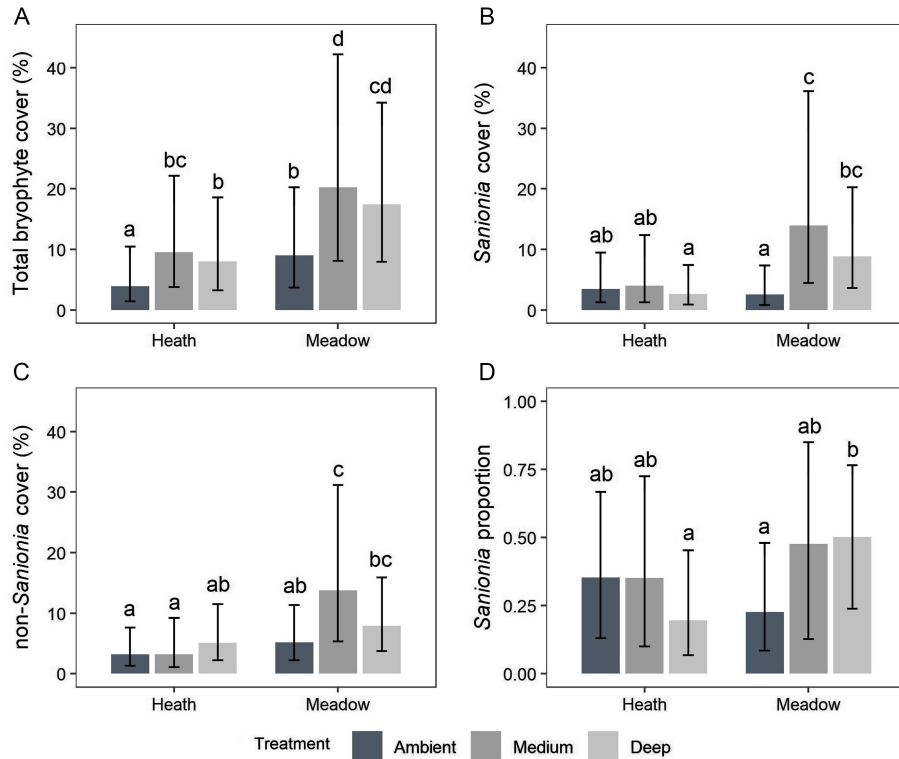


commonly exceeded in most parts of all cold seasons in the unmanipulated Ambient regime, which typically reached temperatures below −15 °C for prolonged periods of time.

Arctic soil microbes have high activity in cold conditions (Mikan et al. 2002), but are dependent on the availability of liquid water in winter (Mikan et al. 2002), as frozen soil water limits microbial activity (Öquist et al. 2009). Frozen soils have films of liquid water persisting around the soil particles, especially when temperatures remain above −10 °C. Fungal mycelia can possibly access this water film, and spores might also be able to travel within it. Thus, snow accumulation enables such activity during winter.

The effect of experimentally increased snow depth on the amount of melt water locally entering the soil system may interact with the temperature effects described above. Although most of the melt water runs off prior to soil thaw and cannot enter or waterlog it (own observations; water-logging only happens when thermokarst forms), soil moisture remains slightly elevated in both of our snow manipulation treatments during the first part of the growing season with possible effects on the pathogens' life cycle stages in that period. In fact, moisture increase has been documented to increase spore germination and infection success in various plant pathogenic fungi species (Huang et al. 1998; Manandhar 1998; Biddulph et al. 1999; Green and Bailey 2000, as cited by Pehkonen et al. 2002).

**Table 5.** Effect strengths of vegetation type, snow regime and host plant cover on parasite infection. *Exobasidium hypogenum* was modelled against cover of *Cassiope tetragona*, and *Pythium* against cover of bryophytes (using (a) bryophyte cover data from only the plots with *C. tetragona* used in the rest of the study, and (b) bryophyte data from all plots in the experimental set-up, except those used in a passive warming study). Non-significant variables were removed from the model and are not shown in the table. The first row of each model indicates the intercept. Values are presented in the logit scale for *E. hypogenum* and log scale for *Pythium*. Significant *p* values (<0.05) are indicated in bold text.

| | | Effect size | SE | *z* value | *Pr* > \| *z* \| |
|---|---|---|---|---|---|
| **Exobasidium hypogenum** | | | | | |
| Snow regime | Ambient | −2.16 | 0.43 | — | — |
| | Medium | 0.47 | 0.65 | 0.73 | 0.47 |
| | Deep | 2.24 | 0.51 | 4.36 | **<0.001** |
| Cover | Intercept | −4.82 | 1.38 | — | — |
| *Cassiope tetragona* | Dead | 25.53 | 7.95 | 3.21 | **0.001** |
| **Pythium spp.** | | | | | |
| Vegetation type snow regime | Heath: Ambient | 0.42 | 0.29 | — | — |
| | Meadow | −1.19 | 0.60 | −1.99 | **0.05** |
| | Medium | 0.00 | 0.35 | 0.00 | 1.00 |
| | Deep | 0.69 | 0.30 | 2.28 | **0.02** |
| | Meadow: Medium | 1.52 | 0.65 | 2.34 | **0.02** |
| | Meadow: Deep | 0.53 | 0.64 | 0.84 | 0.40 |
| Bryophyte cover (a) (using data only from plots with *Cassiope tetragona*) | Intercept | 0.39 | 0.30 | — | — |
| | *Sanionia uncinata* | −11.92 | 3.46 | −3.44 | **<0.001** |
| | Total bryophyte | 11.26 | 2.50 | 4.50 | **<0.001** |
| Bryophyte cover (b) (using data from all plots in the study site) | Intercept | 0.13 | 0.35 | — | — |
| | *Sanionia uncinata* | −11.45 | 3.45 | −3.32 | **<0.001** |
| | Total bryophyte | 10.90 | 2.14 | 5.09 | **<0.001** |

*Exobasidium hypogenum*

The response of *E. hypogenum* to increased temperature and soil water content is unknown. However, *Exobasidium splendidum* Nannf., a related species found in boreal and subarctic ecosystems, has been shown to have higher prevalence in forest habitats after tree clearing, where increased soil moisture due to deeper snow was suggested as causation for this pattern (Pehkonen et al. 2002). Likewise, in our study, enhanced soil moisture during the first part of the growing season may have increased the likelihood of *E. hypogenum* spread, thereby infecting more *C. tetragona* individuals.

The co-occurrence of the host plant *C. tetragona*'s reduced occurrence and cover supports the idea that this pathogen may play a role in the dieback of this species during climate change. To grow and survive within its host, the biotrophic fungus *E. hypogenum* may suppress its host plant *C. tetragona*'s systemic acquired resistance (Mur et al. 2015), making it more vulnerable to other possible pathogens. At the same time, biotrophs also entail an energy burden, as they take nutrients from the plant (Barnett and Binder 1973). This can have further consequences, including shoot death (Wolfe and Rissler 2000) and reduced flower production (Hildebrand et al. 2000), leading to an overall reduction of the plant's performance (Nannfeldt 1981) as studied on another *Exobasidium* species in tea cultivars (Muraleedharan and Chen 1997; Premkumar et al. 2008; Ponmurugan et al. 2016). These observations imply that infected plants, even though not necessarily killed by the pathogen, are in a weakened or stressed state and may have difficulties dealing with other possible disturbances caused by our experimental treatment, such as increased respiration rates during the cold season (Cooper 2004; Semenchuk et al. 2016b), shortened growing seasons (Semenchuk et al 2016a) and, perhaps, increased soil moisture.

**Fig. 6.** Frequency of infection of *Cassiope tetragona* by *Exobasidium hypogenum* for the year 2019 at each snow regime (Ambient, Medium, Deep) (A). *Pythium* abundance obtained from *Sanionia uncinata* growing at each habitat (Heath, Meadow) and snow regime (Ambient, Medium, Deep) (B). Error bars represent the 95% confidence interval. Data with the same letter do not differ at a 5% significance level.
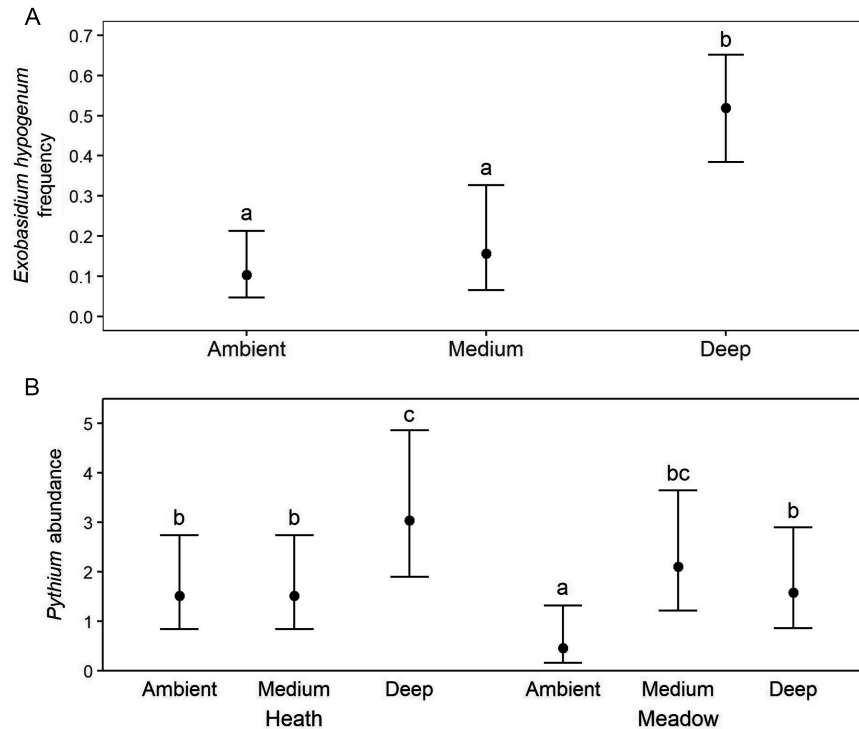


The high proportion of dead *C. tetragona* in the Deep regime may negatively impact *E. hypogenum*, as future fungal distribution and infection may be impacted by the reduced cover of live *C. tetragona* remaining. Further field surveys and analysis would be required to assess this temporal aspect, considering a more detailed quantification of the parasite together with *C. tetragona* cover. Experimental work specifically on this host–parasite–snow regime relationship is needed to elucidate the role of *E. hypogenum* in the death of *C. tetragona* plants under conditions of enhanced snow.

### *Pythium* spp.

Similar to *E. hypogenum*, we found a higher abundance of *Pythium* in response to increased snow cover. This fungus is classified as a cold-tolerant species (Hoshino et al. 1999; Hoshino et al. 2002; Tojo et al. 2012; Murakami et al. 2015) as its mycelial growth and infection of its host organism occur during the cold season taking advantage of the dormant stage of the moss (Jung et al. 2007; Hoshino et al. 2009). We managed to grow *Pythium* at −0.5 °C (own observations), an indicator for its capability to grow at sub-zero temperatures. A longer exposure to close to zero temperatures may, thus, have been beneficial, although a more thorough study of its growth pattern at sub-zero temperatures would help understand these results. Hoshino et al. (2009) demonstrated that the mycelial growth of several snow moulds including *Pythium iwayamai* Ito was stopped by exposure to −20 °C for 24 h. Our experimental snow enhancement raised the minimum soil temperatures experienced during the cold season, and soil in our Deep regime was maintained above

−10 °C all year, which may have enabled more *Pythium* mycelia to survive and grow, and therefore, have a higher abundance in this regime.

Furthermore, *Pythium* increases zoospore production after the addition of melt water suggesting that this species utilizes melt water to spread its zoospores (Lipps 1980), thereby increasing the likelihood of infecting its host. The increased soil moisture in our enhanced snow regimes may thereby promote the spread of zoospores to new host individuals.

Bryophytes generally react positively to enhanced snow in our study site, either due to dieback of competing vascular plants such as *C. tetragona* (Cooper et al. 2019 and this study) or due to the slightly increased soil moisture or both, with *Sanionia uncinata* even reacting disproportionally strongly in Meadows. The inverse relationship between *Pythium* abundance and cover of *Sanionia uncinata* should be interpreted with caution as a causal relationship can only be confirmed by further experimental studies, including inoculation of *Pythium* into different moss species and subsequent measurements of the host's survival. However, this relationship suggests that increased *Pythium* weakens and kills more of its host, leading to a decline in *Sanionia uncinata* cover.

## Conclusions

This study showed that enhanced snow considerably reduced the severity of winter soil surface temperatures and increased the infection of *C. tetragona* by *E. hypogenum* and *Sanionia uncinata* by *Pythium polare* and other *Pythium* species. These fungal interactions contribute to changes in vegetation composition, and so have consequences at the community level.

We recommend that sub-zero temperature responses of *Pythium* should be investigated, and fungal inoculation experiments carried out to better understand the dynamics of these relationships. Furthermore, the temporal aspect of fungal infection is not well understood and should be the focus of future studies.

## Author contributions

The project was initiated and designed by E.J.C. Field work was carried out by all authors, M.T and T.Y. carried out the mycelial growth lab study, P.R.S summarised soil temperature data and M.M.A. carried out statistical analyses. M.M.A. and E.J.C. wrote the manuscript with contributions from the other authors.

## Acknowledgements

## Data accessibility

The data set for this study is available at DataverseNO UiT Open Research Data https://dataverse.no/dataset.xhtml?persistentId=doi:10.18710/QHTCPC.

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## Appendix A

### Site Description: Soil, vegetation, and herbivory

Calcareous sand, silt, and shale originating during the Mesozoic era compose the main parent material (Tolgensbakk et al. 2000). Soils are poorly developed and moderately acidic (5–6.5), with a thin top part (usually 2 cm) consisting of lightly decomposed organic material and live plant roots (O horizon). Below that is a dark-brown A horizon of a similar thickness (2 cm, 1–5 cm), and a B/C horizon of grey silt (Strebel et al. 2010). The concentration of soil organic carbon and total nitrogen are highest at the top and decrease through the soil profile.

The most common species are the deciduous shrub *Salix polaris* Wahlenb. and evergreen shrubs *Dryas octopetala* and *Cassiope tetragona*, the graminoids *Luzula confusa* Lindeb., *Alopecurus borealis* Trin., and *Carex rupestris* All., and the herbs *Bistorta vivipara* L., *Pedicularis hirsuta* L., and *Stellaria longipes* Goldie. Common mosses in the area are *Aulacomnium* spp., *Distichium* spp., *Dicranum* spp., *Hylocomium splendens*, *Polytrichum* spp., *Racomitrium* spp., *Sanionia uncinata*, *Tomentypnum nitens*, and liverworts including *Anthelia juratzkana* and *Ptilidium ciliare* were also present. *Stereocaulon* and *Rhizocarpon geographicum* L. are the most common lichens, together with *Thamnolia vermicularis* Sw. and *Cetrariella delisei* Bory ex Schaer. Lichen abundance is low in this valley due to continual grazing pressure from Svalbard reindeer (*Rangifer tarandus* subsp. *platyrhynchus* (Vrolik, 1829)). All treatments were equally available for herbivory.

**Fig. A1.** Experimental design, with plots located different distances behind a snow fence under Deep and Medium enhanced snow in Adventdalen, High Arctic Svalbard. Ambient plots were located next to the fences and were unaffected by the experimental snowdrifts. Within each regime, plots were stratified to include different types of dominant evergreen shrubs (DES) at the start of the experiment: *Cassiope tetragona* (C) or *Dryas octopetala* (D). The system was replicated five times in Heath and five times in Meadow vegetation. Photos show the fence effect on snow accumulation in March (bottom left) and snow melt timing in June (bottom right).
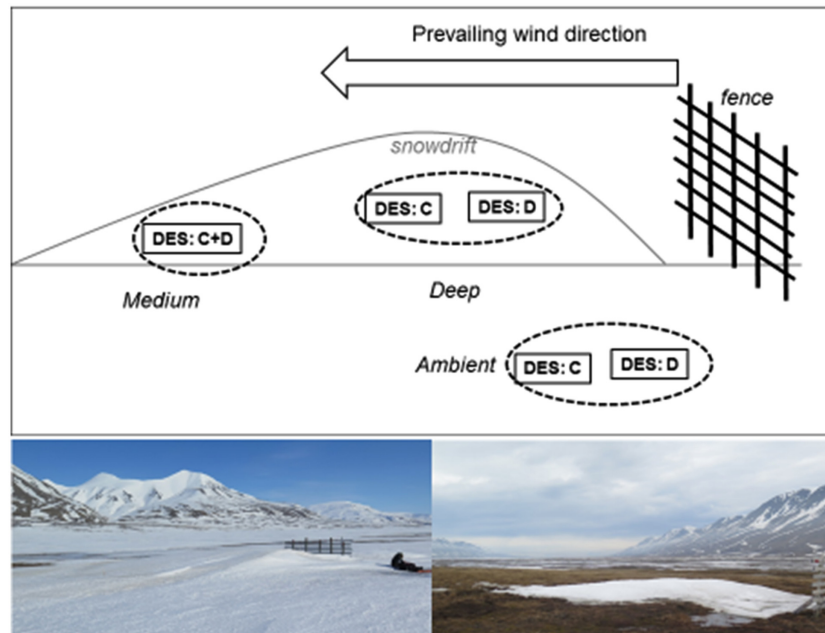


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### Extra background concerning microbes especially fungi

Arctic soil microbes have high activity in cold conditions (Mikan et al. 2002), with bacteria more susceptible to freeze–thaw cycles than fungi (Skogland et al. 1998; Sharma et al. 2006). Soil microorganisms are involved in decomposition of organic material and most of the microbial growth in our system occurs during the snow-covered months (Jonasson et al. 1999; Schimel and Bennett 2004; Brooks et al. 2011). Microbial processes such as soil respiration have been shown to happen faster in higher sub-zero temperatures (Morgner et al. 2010; Semenchuk et al. 2016). Deeper snow also increases the fungal richness of ectomycorrhizae and reduces that of saprotrophs (Mundra et al. 2016).

Smut fungi are parasites characterized by highly specialized plant–parasite interactions (Begerow et al. 1997). In the order Exobasidiales, these close interactions have evolved into species that can survive well within the host, without the need for resting spores (Begerow et al. 2002). As a result, these fungi are extremely species-specific, and their phylogeny can reflect the diversification of their hosts (Jackson 2004; Begerow and Kemler 2018). Although not much is known ecologically about *E. hypogenum*, the genus

**Fig. A2.** Soil temperature for Heath and Meadow separately during (A) cold season and (B) warm season summer, together with (C) warm season soil moisture at each snow regime for the 2014–2015 period. Cold season is defined here as the period from 1 September 2014 to 31 May 2015, and warm season from 1 June to 31 August 2015. Soil moisture was measured manually, and thus could not be recorded until the first day of sampling (12 June 2015).
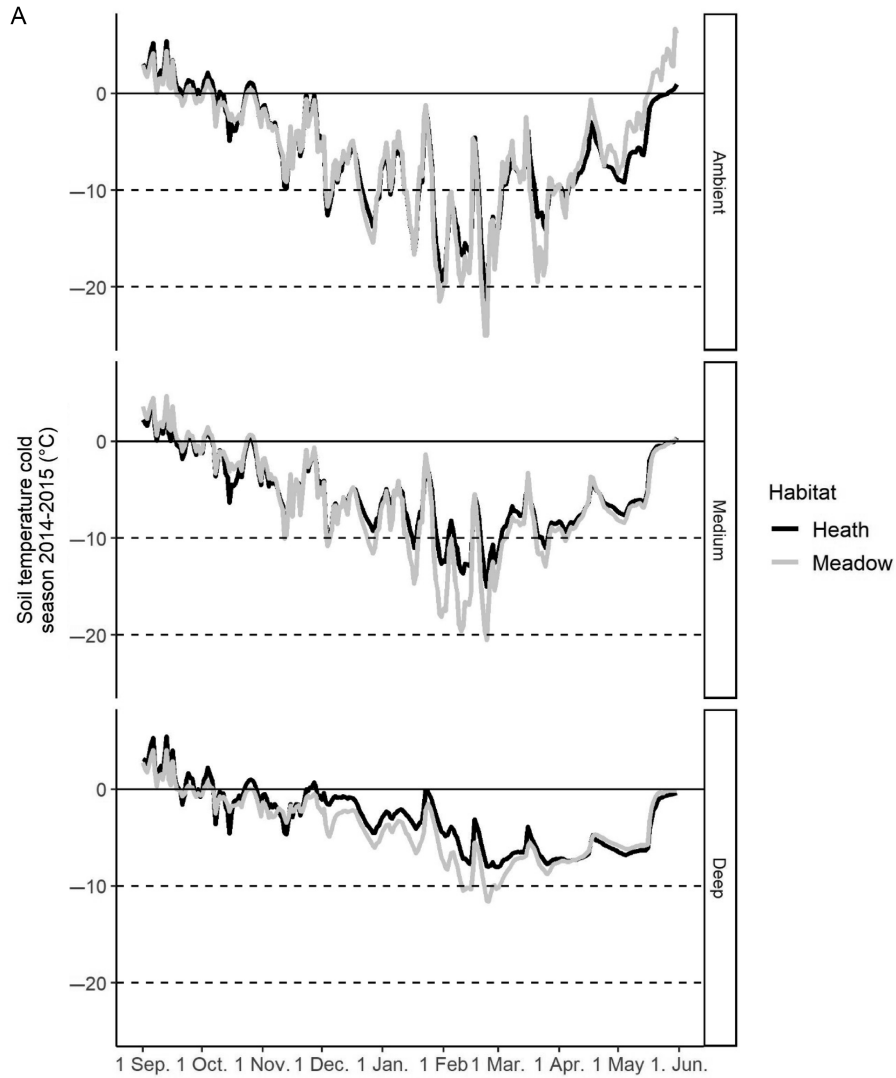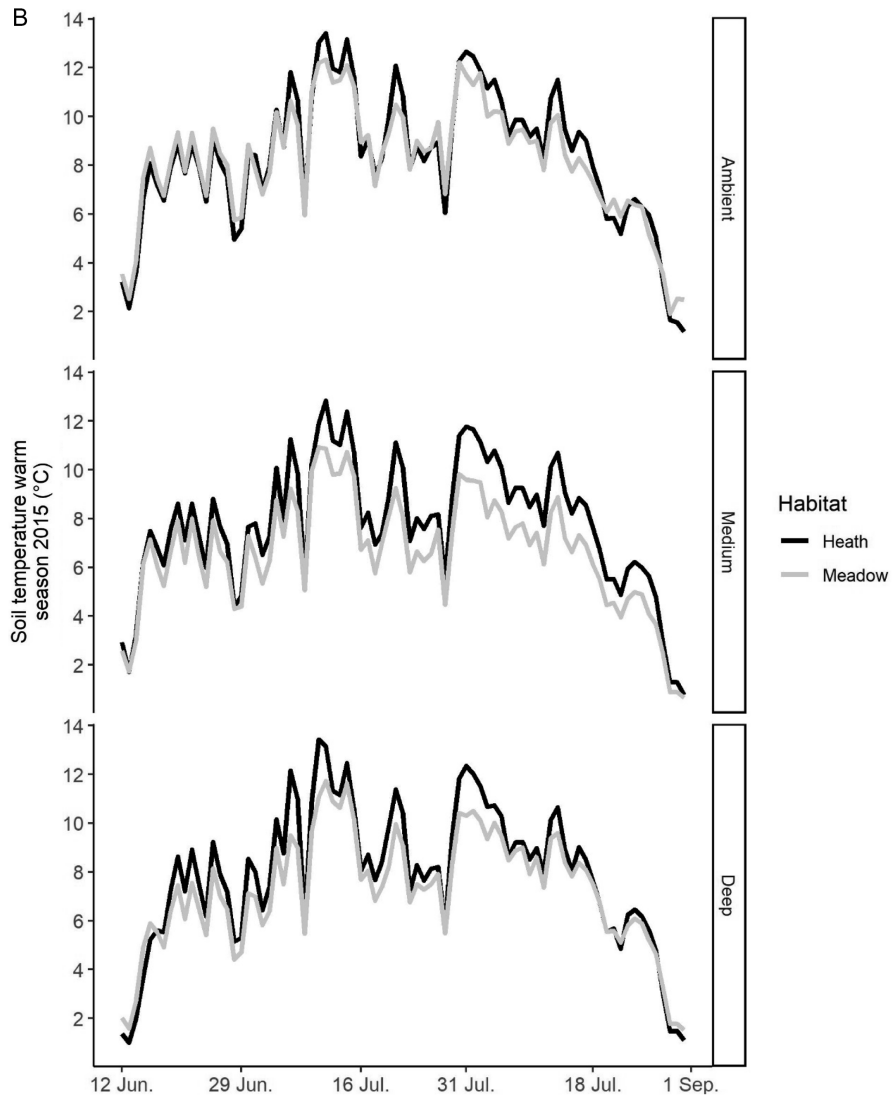
**Fig. A2** (*continued*).
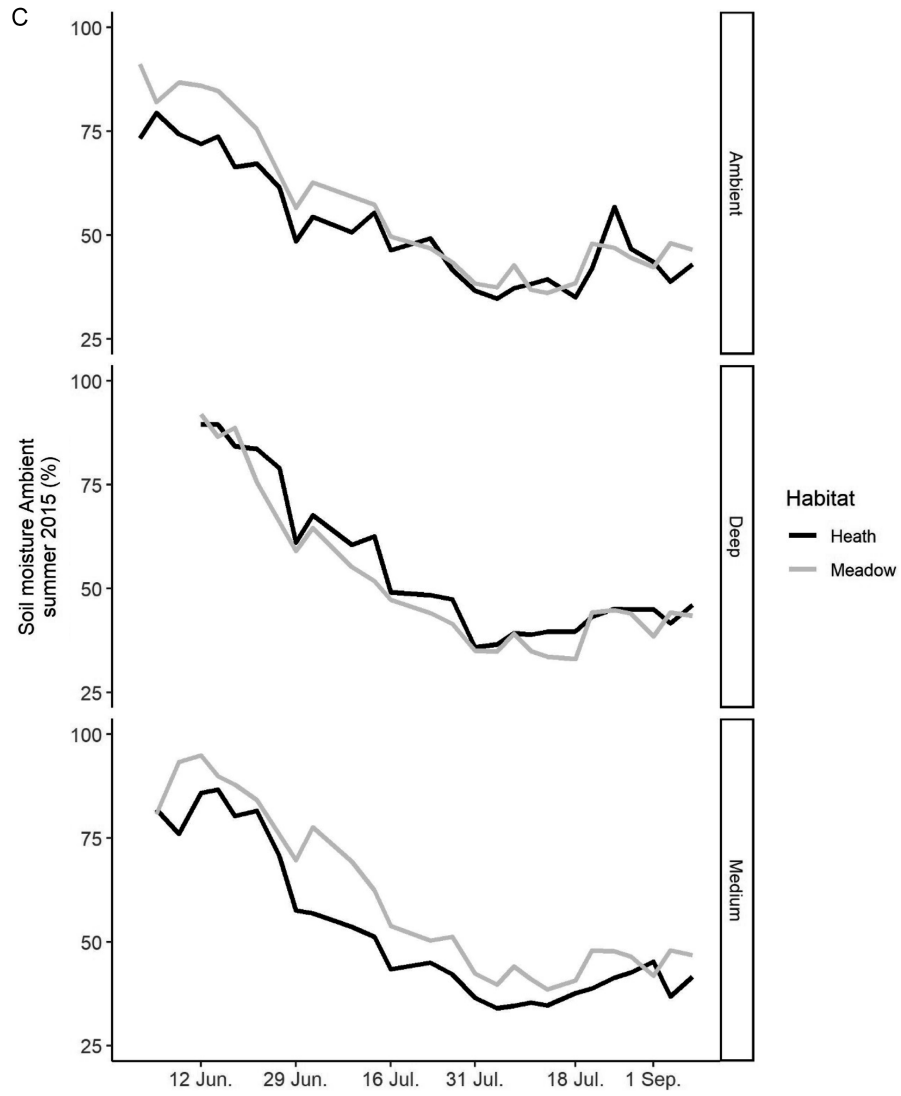
**Fig. A2** (*concluded*).

**Fig. A3.** Frequency of infection of *Cassiope tetragona* by *Exobasidium hypogenum* at the different snow depths and years. Error bars represent the 95% CI. Data with the same letter do not differ at a 5% significance level. During the model reduction of *Exobasidium hypogenum* against vegetation type, snow regime and year, the interaction between snow regime and year was discarded. As can be seen in the figure, keeping it results in a wider difference between Deep and Ambient in 2019 than in 2013, whereas in 2019 Medium also seems to have a slightly higher frequency of *Exobasidium* than Ambient. This trend can also be seen in Table 3, and indicates a possible temporal trend, where the parasite benefits from enhanced snow conditions.
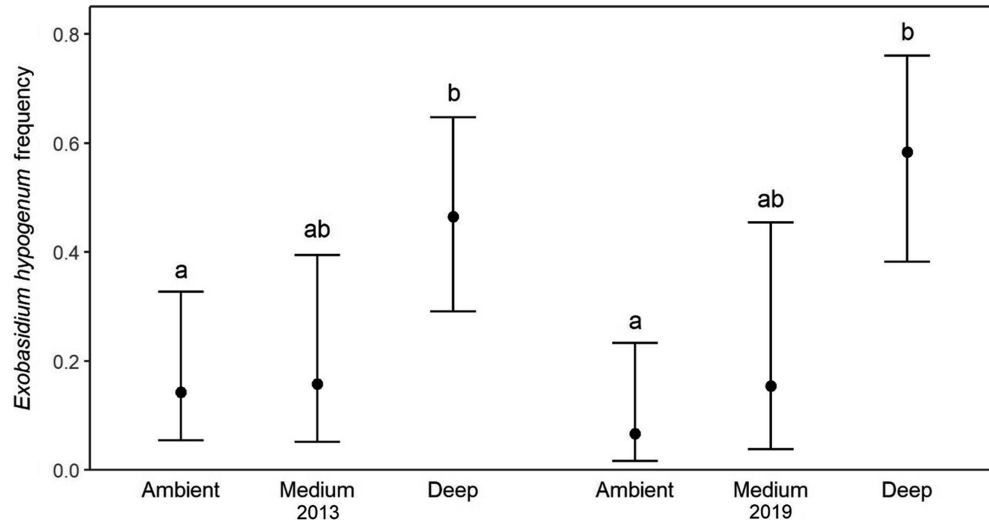


**Table A1.** Number of plots used of at each vegetation type and snow regime for each of the analyses. Explanation behind plot selection can be found in the Materials and Methods section.

| Analysis | | Heath | | | Meadow | | | Total |
|---|---|---|---|---|---|---|---|---|
| | | Ambient | Medium | Deep | Ambient | Medium | Deep | |
| *C. tetragona* live and dead | | 15 | 9 | 15 | 15 | 5 | 14 | 73 |
| *C. tetragona* proportion[a] | | 15 | 9 | 15 | 15 | 5 | 13 | 72 |
| *Exobasidium* frequency[b] | 2013 | 14 | 13[c] | 15 | 14 | 6[c] | 13 | 75 |
| | 2019 | 15 | 9 | 15 | 15 | 4 | 9 | 67 |
| *Exobasidium* ~ *C. tetragona* cover | | 15 | 9 | 15 | 15 | 4 | 9 | 67 |
| Total bryophyte, *Sanionia* and non-*Sanionia* cover | | 15 | 9 | 15 | 15 | 5 | 14 | 73 |
| *Sanionia* proportion[d] | | 11 | 6 | 13 | 15 | 5 | 14 | 64 |
| *Pythium* abundance | 2014 | 5 | 5 | 5 | 3 | 4 | 4 | 26 |
| | 2015 | 5 | 5 | 5 | 5 | 5 | 5 | 30 |
| *Pythium* ~ Bryophyte cover | | 5 | 5 | 5 | 5 | 5 | 5 | 30 |

[a]One Deep plot did not have any *Cassiope tetragona* by 2019 (neither alive nor dead), so it could not be used for the analysis of dead to total *C. tetragona* cover.

[b]Only plots with live *C. tetragona* were considered when analysing the frequency of *Exobasidium*, as it was not possible to discern whether the dead remains of the plant had been infected or not.

[c]The OTC study started in 2015, so it had no effect on the 2013 data. Thus, more plots were available for analysis from this year.

[d]Plots with no bryophyte cover (neither *Sanionia uncinata* nor other bryophytes) could not be used for the analysis of *Sanionia* to total bryophyte cover.

**Table A2.** Seasonal data from snow fence experiment, Adventdalen, Svalbard, obtained from continuous hourly temperature records from 32 Tinytag data loggers, during the period 2010–2018.

| Vegetation Type | Snow Regime | SF | IF | Warm S No. days | Cold S No. days | Annual TDDsoil | Annual FDDsoil | Annual DD sum |
|---|---|---|---|---|---|---|---|---|
| Heath | Ambient | 154 | 257 | 103 | 262 | 696 | −1621 | −925 |
| | Medium | 161 | 257 | 96 | 269 | 613 | −1278 | −665 |
| | Deep | 166 | 263 | 96 | 269 | 658 | −798 | −140 |
| Meadow | Ambient | 151 | 268 | 118 | 247 | 747 | −1587 | −840 |
| | Medium | 161 | 260 | 99 | 266 | 595 | −1374 | −779 |
| | Deep | 168 | 262 | 94 | 271 | 542 | −818 | −276 |
| All | Ambient | 153 | 263 | 110 | 255 | 721 | −1604 | −883 |
| | Medium | 161 | 259 | 98 | 267 | 604 | −1326 | −722 |
| | Deep | 167 | 262 | 95 | 270 | 600 | −808 | −208 |

**Note:** SF, snow-free date (day of year); IF, initial freezing date (day of year); No. days, season length in warm season (WarmS) and cold season (ColdS). Annual Thawing and Freezing Degree Days of the soil (TDDsoil and FDDsoil, respectively) calculated as an accumulation of daily (positive and negative, respectively) temperature means, together with the Degree Day Sum (DD sum) for the whole year. Data are presented for Heath and Meadow separately and combined.

**Table A3.** Number of plots that had live *Cassiope tetragona*, number of plots that showed infection by *Exobasidium hypogenum*, and percentage of the plots with live *Cassiope tetragona* that were infected by *Exobasidium hypogenum*. Data are compared by year, vegetation type, and snow regime.

| Vegetation type | Snow Regime | 2013 | | | 2019 | | |
|---|---|---|---|---|---|---|---|
| | | *Cassiope* | *Exobasidium* | % | *Cassiope* | *Exobasidium* | % |
| Heath | Ambient | 14 | 2 | 14 | 15 | 1 | 7 |
| | Medium | 13 | 2 | 15 | 9 | 2 | 22 |
| | Deep | 15 | 7 | 47 | 15 | 8 | 53 |
| Meadow | Ambient | 14 | 2 | 14 | 15 | 1 | 7 |
| | Medium | 6 | 1 | 17 | 4 | 0 | 0 |
| | Deep | 13 | 6 | 46 | 9 | 6 | 67 |

**Table A4.** Abundance of mycelia of the different *Pythium* species found in this study, sorted by sampling year and snow regimes. Note that not all isolated mycelia were identified to species level (not ID).

| | | 2014 | | | 2015 | | |
|---|---|---|---|---|---|---|---|
| | | Ambient | Medium | Deep | Ambient | Medium | Deep |
| *Pythium* | *polare* | 11 | 10 | 15 | 3 | 15 | 8 |
| | New 1 | 0 | 0 | 5 | 1 | 0 | 1 |
| | New 2 | 0 | 0 | 0 | 0 | 0 | 1 |
| | New 3 | 0 | 1 | 1 | 2 | 0 | 2 |
| | New 4 | 1 | 1 | 0 | 2 | 1 | 0 |
| | not ID | 0 | 3 | 7 | 0 | 5 | 7 |
| Total | | 12 | 15 | 28 | 8 | 21 | 19 |

*Exobasidium* generally parasitizes plants the Ericaceae family including cultivated blueberry and cranberry crops (Brewer et al. 2014; Stewart et al. 2015). *Exobasidium* infections can manifest in the stem, flower, shoot, and buds of their hosts, although exact

deformities may vary per fungal species and host plant (Nannfeldt 1981; Brewer et al. 2014; Stewart et al. 2015).

*Pythium* is a genus of oomycetes within the commonly known snow moulds: psychrophilic or psychrotrophic fungal pathogens that actively attack dormant plants under the snow cover (Hsiang et al. 1999; Hoshino et al. 2009). The systematics of this genus is in a transitional period, as a phylogenetic study in 2010 suggested its division into five different genera (Uzuhashi et al. 2010) and *Pythium polare* may be renamed as *Globisporangium polare*. However, the term *Pythium* for the genus is still currently more accepted and is used throughout this paper. *Pythium* has a world-wide distribution (Lévesque and De Cock 2004; Kirk et al. 2008), and some of the species have been found to infect and weaken mosses in both the Arctic and Antarctic (Hoshino et al. 1999; Hoshino et al. 2002; Bridge et al. 2008).

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