

# Disappearing green: Shrubs decline and bryophytes increase with nine years of increased snow accumulation in the High Arctic

Elisabeth J. Cooper<sup>1</sup>  | Chelsea J. Little<sup>1,2</sup>  | Anna K. Pilsbacher<sup>1</sup> |  
Martin A. Mörsdorf<sup>1</sup> 

<sup>1</sup>Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Tromsø, Norway

<sup>2</sup>Department of Zoology, University of British Columbia, Vancouver, BC, Canada

## Correspondence

Elisabeth J. Cooper, Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Tromsø, Norway.  
Email: elisabeth.cooper@uit.no

## Funding information

Funding for this project came from the Norwegian Research Council ("SnoEco" project, number 230970), the FRAM Centre Terrestrial Flagship ("SnoEcoFen" project) and the Norwegian Centre for International Cooperation in Education (SIU) High North Programme ("JANATEX" project, number HNP2013/10092), all to E.J.C.

Co-ordinating Editor: Valerio Pillar

## Abstract

**Question:** How does increased snow depth affect plant community composition of High Arctic tundra, and can the Normalized Differential Vegetation Index (NDVI) detect induced changes?

**Location:** Adventdalen, Spitsbergen, Svalbard (78°10' N, 16°04' E).

**Methods:** We manipulated snow depth on the tundra using fences, resulting in *Deep*, *Medium*, and *Ambient* snow regimes. Increased snow led to warmer winter soil temperatures, a delayed onset of growing season and wetter conditions during the early growing season. Plant community composition of living and dead plant material was recorded after nine years. NDVI was measured at the plot level using a handheld sensor.

**Results:** Community composition and the abundance of typically dominant shrub species were substantially different in the *Deep* compared to the *Ambient* regime. *Deep* had lower cover of live shrubs (*Cassiope tetragona*, *Dryas octopetala* and *Salix polaris*) and *Luzula confusa*, and higher cover of dead shrubs (*Cassiope* and *Dryas*) compared to the other snow regimes. Bryophyte cover was highest in *Medium*. NDVI was positively correlated to the cover of living vascular plants and negatively correlated to cover of dead vascular plants. Accordingly, *Deep* snow regime had reduced NDVI, reflecting the contribution of dead *Cassiope* and *Dryas*.

**Conclusion:** Snow regime strongly influenced community composition in High Arctic plant communities. Enhanced snow regimes had more dead shrubs, reduced *Luzula* and increased bryophyte cover than ambient conditions. These differences were detectable by handheld NDVI sensors.

## KEYWORDS

Browning, *Cassiope tetragona*, community composition, dead plants, *Dryas octopetala*, NDVI, *Salix polaris*, snow depth, snow melt, Svalbard

## 1 | INTRODUCTION

High latitudes are already strongly affected by anthropogenic climate change. Climate warming is occurring fastest at high latitudes, but unlike at lower latitudes, precipitation is forecast to increase (IPCC 2013, Chapter 12, Bintanja & Andry, 2017) and projected to happen primarily in late autumn and winter due to the decline of sea ice (Bintanja & Selten, 2014; Kopec, Feng, Michel, & Posmentier, 2015). Increasing snowfall could lead to deeper snow, later snowmelt, and delayed start of the growing season. Projections of snowfall and snow cover duration have high uncertainty compared to projections of temperature (IPCC 2013), and this is particularly so for northernmost and non-continental areas, such as Svalbard (addressed also in López-Moreno, Boike, Sanchez-Lorenzo, & Pomeroy, 2016). Snow cover is extremely important for species' distributions and ecosystem function (Cooper, 2014; Niittynen & Luoto, 2018), and thus any changes in precipitation could have substantial consequences for tundra ecosystems. Of particular interest is a proposed feedback loop deemed the "snow–shrub hypothesis" (Sturm et al., 2005) whereby deeper snow leads to increased microbial activity (Schimel, Bilbrough, & Welker, 2004), thus faster decomposition (Blok, Elberling, & Michelsen, 2016), higher nitrogen availability, and hence increased shrub growth. Shrubs trap drifting and windblown snow, leading to even deeper snow cover and creating a positive feedback. This has been suggested as the mechanism for observed landscape-scale shrub expansion in the Low Arctic (Hallinger, Manthey, & Wilmking, 2010).

Changes in winter climate affect environmental conditions well into the growing season. Snowmelt timing affects plant phenology (Bjorkman, Elmendorf, Beamish, Vellend, & Henry, 2015; Semenchuk, Gillespie, Rumpf, Baggessen, Elberling, & Cooper 2016) and has species-specific effects on plant size in the High Arctic (Blok et al., 2015; Rumpf, Semenchuk, Dullinger, & Cooper, 2014; Semenchuk et al., 2015). Delays in growing season onset can also hinder plant reproduction (Cooper, Dullinger, & Semenchuk, 2011; Mallik, Wdowiak, & Cooper, 2011) through a decrease in floral abundance (Semenchuk, Elberling, & Cooper, 2013) and germination success (Semenchuk, Gillespie et al., 2016).

Plant community composition provides a link between ecosystem-level and species-specific responses to snow cover and has implications throughout the food web (Cooper, 2014; Gillespie, Baggessen, & Cooper, 2016). Thus, it is crucial to understand the dynamics of plant community composition in relation to snow conditions. For instance, increased snow depth in Alaska was shown to alter tundra communities more than summer warming did (Wahren, Walker, & Bret-Harte, 2005). Yet in contrast to the many assessments of plant community composition with regard to experimental warming, there are few assessments of compositional responses to experimental snow manipulations in Arctic tundra (but see Leffler, Klein, Oberbauer, & Welker, 2016; Scott & Rouse, 1995; Wahren et al., 2005). This is especially true in the High Arctic, where, to our knowledge, snow depth manipulations have only taken place at three High Arctic areas (northwest Greenland, central Greenland,

and different locations on Svalbard) and vegetation composition has rarely been measured (except in Leffler & Welker, 2013; Scott & Rouse, 1995).

Here, we report plant community composition after nine years of a manipulative snow depth experiment in High Arctic Svalbard. In addition, we sought to assess whether local-scale measurements of normalized differential vegetation index (NDVI) reflected the responses that we documented. This greenness index reliably indicates the proportion of green leaves in a study plot (Natali, Schuur, & Rubin, 2012, using an on-site camera) and relates to the biomass (Hope, Kimball, & Stow, 1993, using hand-held radiometers) of Arctic tundra plant communities. It is therefore useful in situations where plants cannot be harvested for biomass measurements (e.g., long-term monitoring/experiments). Changes in greenness and brownness of tundra have been recorded from satellite imagery assessment of NDVI (Epstein et al., 2016). However, such datasets have pixels which may encompass several square kilometers and may not offer sufficient spatial resolution. Given environmental heterogeneity and differences of vegetation types within tundra landscapes, finer-scale measurements ("near remote sensing") are required in order to link local changes of populations and communities to greening or browning trends (Anderson et al., 2016). Thus, we sought to validate whether a handheld sensor (previously used primarily for agricultural applications) can aid in understanding changes to tundra communities. We hypothesized that after nine years of increased snow depth:

(1a) Community composition would differ between snow regimes and especially (1b) shrub cover would be greater under deep snow compared to plots with ambient snow depth

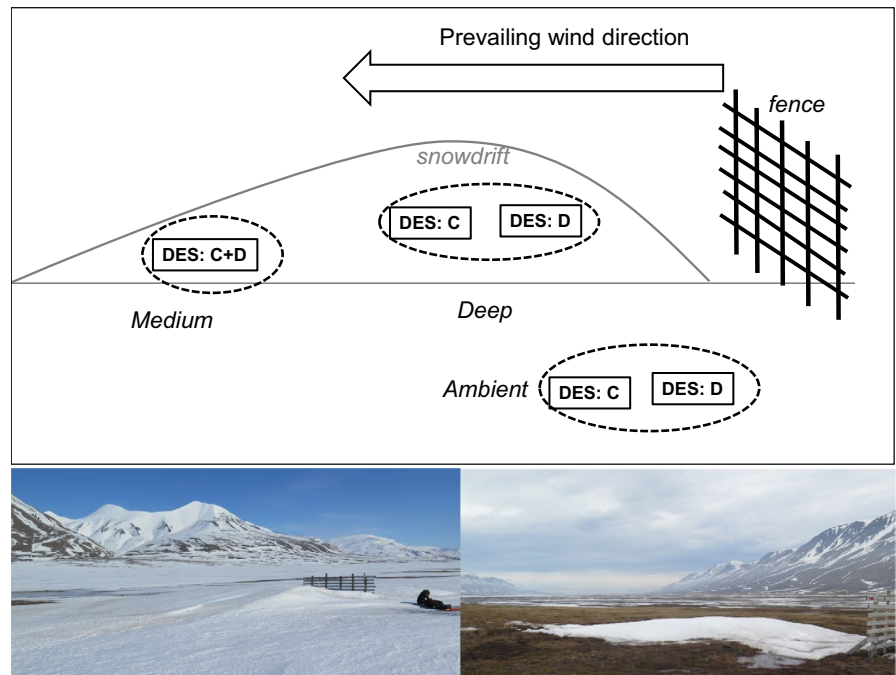
(2) Any differences in community composition would be detectable by plot-level NDVI measurements.

## 2 | METHODS

### 2.1 | Study site and experimental design

The study was conducted in Adventdalen, western Spitsbergen (78°10' N, 16°04' E). This area is underlain by permafrost with an active layer depth of ~100 cm (Schuh, Frampton, & Christiansen, 2017). The mean annual temperature (2000–2011) is –3.8°C with an annual precipitation of 180.5 mm (<http://www.eklima.no>), most of which falls in winter. Mean temperature has increased 2.5°C in the period from 2000 to 2015 compared to the preceding three decades (Isaksen et al., 2016). Abiotic conditions are further described in Cooper et al. (2011), Morgner, Elberling, Strebel, & Cooper (2010), and Semenchuk et al. (2015). The common vegetation is described in Appendix S1, but briefly, well-drained stony heaths in the valley are characterized by high abundance of the dwarf shrubs *Dryas octopetala* on slight ridges, and *Cassiope tetragona* in hollows. *Salix polaris* is a common plant species across those topographical units. The flatter mesic meadows are characterized by higher proportional cover of graminoids with *Salix polaris* and *Dryas octopetala* common throughout, and some patches of *Cassiope tetragona*. All vegetation at this site is <10 cm in height.

**FIGURE 1** Experimental design, with plots located different distances behind a snowfence under *Deep* and *Medium* additional snowpack in 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: *Dryas octopetala* (D) or *Cassiope tetragona* (C). The system was replicated five times in a heath area and five times in a meadow [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



Snow regime was manipulated using ten snowfences, five in stony heaths and five in mesic meadows. Twelve fences were originally built (Morgner et al., 2010) but two were not used for this study due to subsequent breakage and surface subsidence. The snowfences (1.5 m high, 6 m long) were erected at the site in 2006 perpendicular to the prevailing winter wind direction, in order to create snow-drifts on their lee sides (Figure 1 and photos in Appendix S1). At each fence location, areas were identified in 2006 in which the vegetation initially appeared visually similar, and to which three different snow regimes were applied: a fenceless, unmanipulated “*Ambient*” regime, where snow depth reached a maximum of roughly 35 cm; a “*Deep*” regime 3–12 m behind the fences, with maximum 1.5 m snow depth; and further on up to 20 m behind the fences, a “*Medium*” regime with 60–100 cm maximum snow depth (Semenchuk et al., 2013). Snowmelt timing is affected by snow regimes; even though there is large annual variation, the order of melting is the same every year, with average dates (for the six years 2008–2012 & 2015) being *Ambient*: 2 June, *Medium*: 12 June and *Deep*: 18 June (Semenchuk, Gillespie et al., 2016). Near-surface soil temperature at 1 cm depth was recorded hourly using Tinytag data loggers model TGP-4020 (Gemini) and soil moisture was measured twice a week throughout the summer at all four edges of the plots using a Theta ML 2× probe (Delta-T Devices), and averaged to give a mean plot value.

Vegetation plots (75 cm × 75 cm) in the *Ambient* and *Deep* regimes were defined immediately after snowmelt in 2007, following the first winter of the experiment. At each fence location, six *Deep* and six *Ambient* plots were established by the researchers so that in each regime, three plots had *Dryas* and the other three had *Cassiope* as the Dominant Evergreen Shrub (DES), that is, the evergreen shrub species which visually appeared to be the most abundant. Three *Medium* plots per fence were established in 2010 to include both *Dryas* and *Cassiope* (Figure 1). Plots were defined in this way to

ensure both common shrubs were represented in the experiment, in case they should react differently to increased snow (Cooper et al., 2011). However, having one species as the dominant shrub did not preclude the other species from being present in the plot at a moderate abundance. DES was not considered a factor of interest but was controlled for as a conditional factor in our data analyses (see below in Section 2.2).

For this study, we used a subset of the vegetation plots, due to time constraints. For each fence location, we randomly selected one plot from each DES and snow regime to survey, i.e., five plots per fence location (*Ambient Dryas*, *Ambient Cassiope*, *Medium*, *Deep Dryas* and *Deep Cassiope*). This experimental design has 50 plots; however, from the start of the experiment, one fence lacked *Cassiope* in the area where the snow accumulated. Therefore two planned plots were missing i.e., one *Medium* plot and also one of *Deep Cassiope*, and so the total number of plots used in this study was 48 (Appendix S1).

Plant communities were surveyed 3–7 August 2015, nine years after the erection of the fences. Percent cover of different species/groups, including bare ground, was estimated visually such that the sum of all categories totaled 100% for each plot. Two researchers assessed cover of each species/group and then agreed on a value, spending ~15 min per plot. Nomenclature used for vascular species was the Pan-Arctic Flora (Elven, Murray, Razzhivin, & Yurtsev, 2011). Vascular plant material was defined as alive or dead. Dead material from *Cassiope*, *Dryas*, and *Luzula* is persistent, while dead material from grasses, forbs and *Salix* decomposes very fast, thus not much remains from previous years. Woody shrub stems are brown when alive; those that were grey were considered to be dead. Bryophytes and lichen were not classified as alive or dead.

NDVI was measured at all plots twice at the peak of the growing season (16 and 23 July 2015, i.e., before the onset of senescence) using a handheld Greenseeker sensor (Trimble AG Field Solutions).

**TABLE 1** Effect sizes of snow regimes on the cover of plant groups in our experiment, together with the mean cover for *Ambient* treatment. For vascular plants, this refers to the live cover

Response variable	Treatment comparison	Effect strength	SE	t-Ratio	p-Value
% <i>Dryas</i> (in Ambient 23.27%)	Ambient → Medium	-11.30	6.54	-1.72	0.21
	Ambient → Deep	-17.80	6.54	-2.72	0.03
	Medium → Deep	-6.50	7.47	-0.87	0.66
% <i>Cassiope</i> (in Ambient 34.42%)	Ambient → Medium	-14.22	7.60	-1.87	0.17
	Ambient → Deep	-22.96	5.96	-3.85	<0.01
	Medium → Deep	-8.75	7.70	-1.14	0.50
% <i>Salix</i> (in Ambient 9.58%)	Ambient → Medium	0.56	2.00	0.28	0.96
	Ambient → Deep	-5.71	1.83	-3.12	0.01
	Medium → Deep	-6.28	2.28	-2.75	0.03
% <i>Bistorta</i> (in Ambient 3.88%)	Ambient → Medium	0.12	1.28	0.09	1.00
	Ambient → Deep	1.88	1.07	1.76	0.20
	Medium → Deep	1.76	1.28	1.37	0.37
% <i>Alopecurus</i> (in Ambient 6.18%)	Ambient → Medium	-1.82	2.03	-0.90	0.65
	Ambient → Deep	-2.35	1.78	-1.32	0.40
	Medium → Deep	-0.53	2.06	-0.26	0.96
% <i>Luzula</i> (in Ambient 7.24%)	Ambient → Medium	-2.66	2.28	-1.17	0.48
	Ambient → Deep	-5.36	1.91	-2.81	0.02
	Medium → Deep	-2.70	2.41	-1.12	0.51
% bryophytes (in Ambient 8.20%)	Ambient → Medium	15.47	4.05	3.818	<0.01
	Ambient → Deep	6.59	3.33	1.98	0.13
	Medium → Deep	-8.87	4.16	-2.133	0.10
% lichens (in Ambient 1.23%)	Ambient → Medium	-0.19	0.56	-0.34	0.94
	Ambient → Deep	0.06	0.43	0.14	0.99
	Medium → Deep	0.25	0.56	0.44	0.90

The sensor was held 90 cm above the plot center, thus scanning an oval-shaped area of roughly 38 cm width. Each measurement took only a few seconds to make.

## 2.2 | Data analysis

All data analyses were conducted in R version 3.3.2 (R Core Team 2016, Vienna, Austria). We examined the effects of snow regime on plant community composition using distance-based redundancy analysis dbRDA (Legendre & Anderson, 1999), applying the *capscale* function of the “vegan” package 2.4-1 (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). This method is a constrained ordination approach, allowing us to use non-Euclidean distance measures, which is essential since we did not want the absence of the same species in two different plots to influence the ecological distance between those two plots (Faith, Minchin, & Belbin, 1987). Here we used the Bray–Curtis distance, which also takes the abundance of plants into account when calculating the distance measure. As opposed to unconstrained ordinations, the constrained approach allowed us to test explicitly how much of the total variation in community composition (total inertia) is explained by the snow manipulation. Based on a priori understanding of the

experimental design, we therefore considered the snow regime to be a constraining variable. The location of each fence and DES were defined as conditional variables, to exclude variation in community composition not of primary experimental interest. Our choice of constraints to include in the dbRDA model was supported by comparison of different candidate models in terms of their residual variation and parsimony (Appendix S1). Based on the final model, we used permutation tests to assess the significance of snow regime for community composition. Those tests were based on the generation of “pseudo-*F*” values, which use the ratio of constrained and unconstrained total inertia. We conducted 999 permutations.

To identify a possible affiliation of evergreen shrub species in the site to each snow regime, presence/absence of live plants of *Dryas* and *Cassiope* across all plots was analyzed using generalized linear models for binomially distributed data, where we defined the snow regime as a fixed factor. In the subset of plots where these species were present, their percentage cover was analyzed using linear models for normally distributed data with the same model structure. The same type of analysis was also performed for cover of other common plants in the site, such as *Salix* (present in 79% of plots), *Bistorta* (present in 94% of plots), *Alopecurus* (present in 67% of plots), *Luzula* (present in 81% of plots), bryophytes (present in all plots) and lichens

**TABLE 2** Effect sizes of snow regimes on cover of combined plant groups and dead vascular plant material and soil moisture in our snowfence experiment in Adventdalen, together with the mean cover for *Ambient* treatment

Response variable	Treatment comparison	Effect strength	SE	t-Ratio	p-Value
% Shrubs alive (in Ambient 51.1%)	Ambient → Medium	-18.40	7.11	-2.59	0.03
	Ambient → Deep	-38.10	5.67	6.72	<0.01
	Medium → Deep	-19.70	7.17	-2.75	0.02
% Graminoids and herbs alive (in Ambient 17.4%)	Ambient → Medium	-3.25	4.74	-0.68	0.77
	Ambient → Deep	4.42	3.78	1.17	0.48
	Medium → Deep	7.68	4.78	1.61	0.25
% All vascular plants alive (in Ambient 68.5%)	Ambient → Medium	-21.7	5.89	-3.68	<0.01
	Ambient → Deep	-36.4	4.77	7.63	<0.01
	Medium → Deep	-14.7	5.99	-2.45	<0.05
% Live vascular + bryophytes + lichens (in Ambient 77.9%)	Ambient → Medium	-6.52	6.44	-1.01	0.57
	Ambient → Deep	-21.54	5.14	-4.19	<0.01
	Medium → Deep	-15.01	6.49	-2.31	0.06
% Dead shrubs (in Ambient 7.45%)	Ambient → Medium	5.22	6.23	0.84	0.68
	Ambient → Deep	18.81	4.97	3.79	<0.01
	Medium → Deep	13.6	6.28	2.17	0.09
% Dead vascular plants (in Ambient 17.8%)	Ambient → Medium	2.94	6.06	0.49	0.88
	Ambient → Deep	17.98	4.83	3.72	<0.01
	Medium → Deep	15.04	6.11	2.46	<0.05
% Soil moisture (in Ambient 47.63)	Ambient → Medium	3.82	4.72	0.81	0.70
	Ambient → Deep	1.50	3.77	0.40	0.92
	Medium → Deep	-2.32	4.76	-0.49	0.88

(present in 98% of plots; see Table 1). We also analyzed snow regime effects on the cover of combinations of these plants, including the cover of dead vascular plant material.

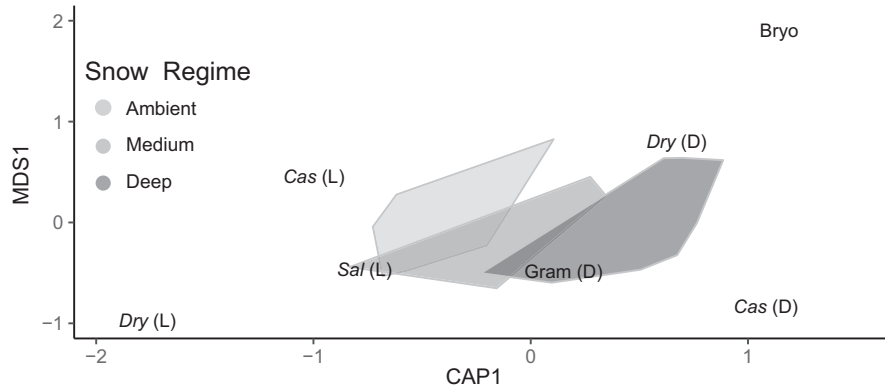
Potential differences in NDVI with regard to the snow regimes were analyzed using linear fixed effects models as described above. As tundra NDVI may be affected by soil moisture (May, Parker, Unger, & Oberbauer, 2018), we also tested for correlation between NDVI and average soil moisture at peak growing season in our plots (average of soil moisture values taken on 16 and 23 July at the same time as NDVI measurements). Since NDVI might indicate plant responses to the snow regime, it was tested for correlation towards all plant cover variables outlined above.

We used the *lm/glm* functions of the base package to fit all linear fixed effects models. Model assumptions, in terms of homogeneous and normally distributed residuals and influential outliers, were assessed using diagnostic plots. We compared pairwise differences between treatment levels using Tukey's Honestly Significant Differences (HSD), and retrieved estimated marginal means (Searle, Speed, & Milliken, 1980) using the "emmeans" package version 1.3.4 (<https://www.rdocumentation.org/packages/emmeans/versions/1.3.5.1>). Significance tests, which are based on models with binomial data, are thereby based on a logarithmic odds ratio scale, and not the measurement scale. Significant effect sizes of NDVI regression models were assessed through *t*-test statistics.

### 3 | RESULTS

#### 3.1 | Effect of the fences on soil temperature and moisture

The fences collected snow throughout the winter in a similar way to previous years, and the snow regime affected soil temperature and moisture (Appendix S2), with the greatest effects on temperature during winter. *Deep* snow insulated the ground (minimum -10°C) from the cold winter air and kept it warmer and more stable than in *Ambient* (minimum -23.5°C) for 175 of the 227 days with sub-zero temperatures. Snow regime affected the date of spring snowmelt in 2015, with *Ambient* melting first (1 June), followed by *Medium* (5 June) and then *Deep* (14 June). After snowmelt was complete, summer soil temperatures did not vary much between regimes, but on the warmest days, *Ambient* plots had slightly warmer soils than the other treatments. Immediately following snowmelt the soils were saturated; subsequently, their moisture levels dropped until the start of August. From soon after snowmelt until mid-July, *Ambient* soil moisture was lower than both *Medium* and *Deep*, but there was little consistent difference between the enhanced snow treatments. At peak growing season (16–23 July 2015) the soil moisture did not differ between snow regimes (Table 2; Appendix S2).



**FIGURE 2** Distance-based redundancy analysis (dbRDA) ordinations of plots (contained within convex hulls shaded by snow regime) and species in plant communities in the experimental snow regime plots at Adventdalen, Svalbard. Only species with high loadings on the capscale and first MDS axis are shown; the center of the text is in the position in ordination space occupied by the species, and the following abbreviations were used: “Dry”, “Cas”, “Sal”, “Gram” and “Bryo” respectively for *Dryas*, *Cassiope*, *Salix*, graminoids and bryophytes. In addition, (L) indicates live material and (D) indicates dead material

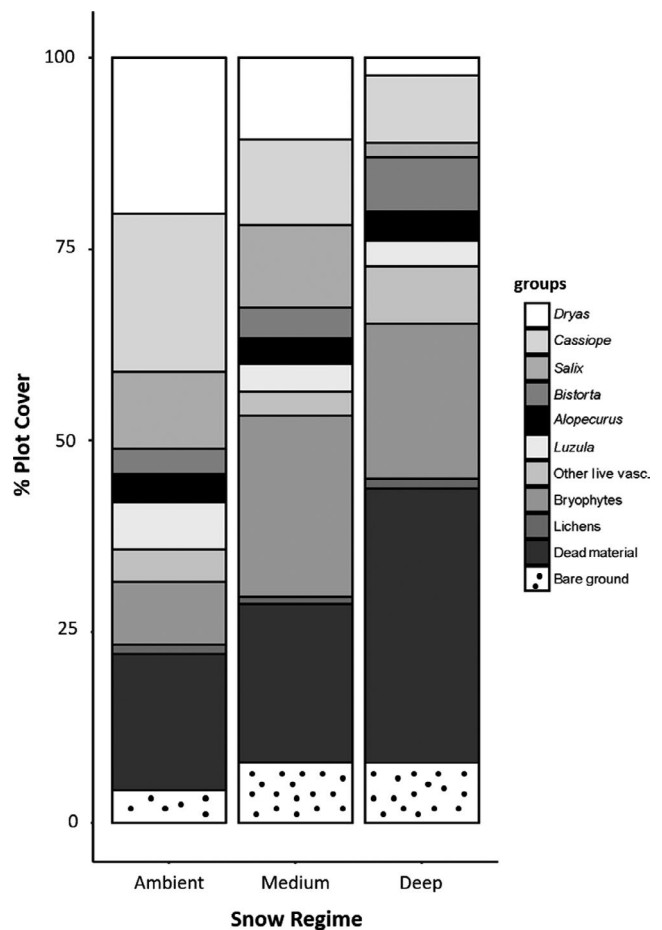
### 3.2 | Plant community composition in differing snow regimes

Snow regime was responsible for 11.5% of the variation in community composition (total inertia), which was a statistically significant proportion based on the permutation tests ( $F_{1,35} = 11.631$ ,  $p = 0.001$ ). The conditional variables fence location and DES accounted for 42.5% of the total inertia, leaving an unexplained residual variation of 45.7%. Due to the strong influence of the snow regime, the community composition clearly sorted along the first ordination axis (Figure 2 CAP 1); bryophytes as well as dead *Dryas* and *Cassiope* had heavy positive loadings on this axis, while live *Dryas*, *Cassiope* and *Salix* had strong negative loadings.

Living *Dryas* was present in 80% of *Ambient* plots but only 42% of *Deep* plots ( $-1.71$ ,  $SE = 0.73$ ,  $z\text{-ratio} = 2.35$ ,  $p < 0.05$ ). There was no significant difference in occurrence between *Ambient* and *Medium* ( $-0.69$ ,  $SE = 1.20$ ,  $z\text{-ratio} = -0.58$ ,  $p = 0.83$ ) or *Medium* and *Deep* plots ( $-2.40$ ,  $SE = 1.16$ ,  $z\text{-ratio} = -2.07$ ,  $p = 0.10$ ). For live *Cassiope*, we found no statistically significant differences in occurrence between *Ambient* and *Deep* ( $+0.13$ ,  $SE = 0.66$ ,  $z\text{-ratio} = 0.20$ ,  $p = 0.98$ ), *Ambient* and *Medium* ( $-0.18$ ,  $SE = 0.81$ ,  $z\text{-ratio} = 0.23$ ,  $p = 0.97$ ), or *Medium* and *Deep* ( $0.32$ ,  $SE = 0.82$ ,  $z\text{-ratio} = 0.38$ ,  $p = 0.92$ ).

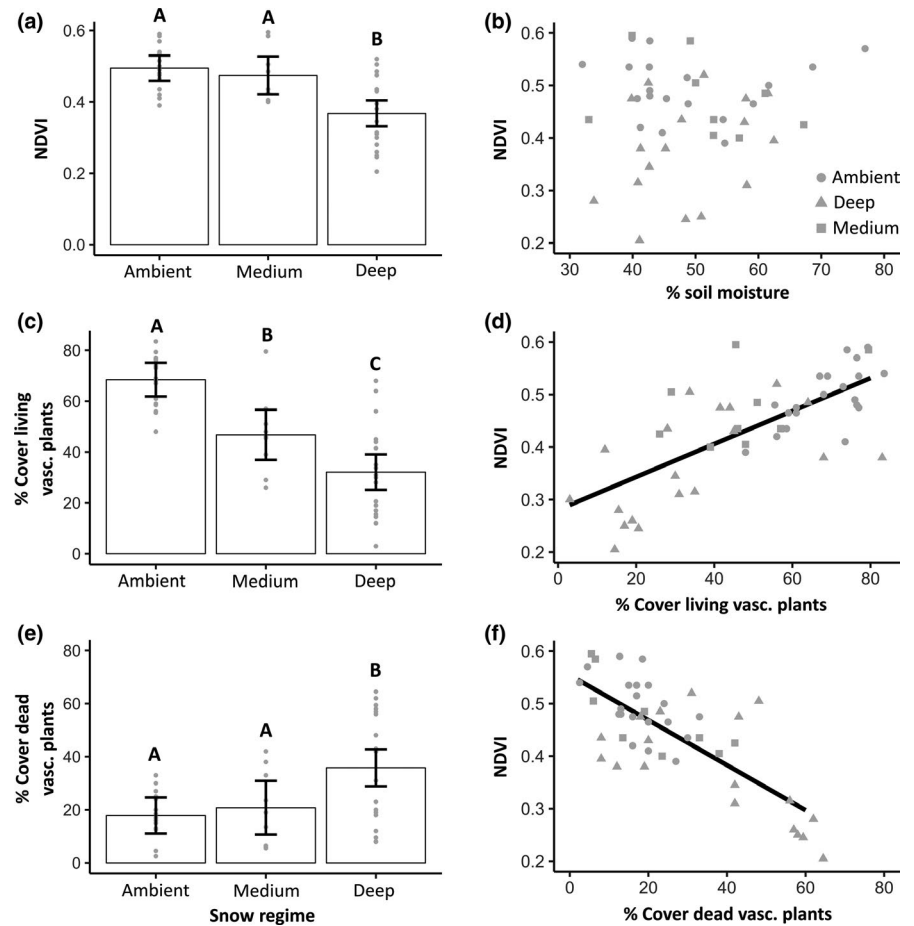
The snow regimes influenced the plot cover of some plant groups, but not others (Figure 3, Table 1). Cover of live *Dryas*, *Cassiope* and *Salix* were all significantly lower in *Deep* than *Ambient* plots, and live *Salix* cover was also lower in *Deep* than in *Medium*. The cover of the forb *Bistorta* and the graminoid *Alopecurus* did not differ significantly between snow regimes, whilst *Luzula* had significantly lower cover in *Deep* than *Ambient*. Bryophytes increased in *Medium* compared to *Ambient*, but there was no effect of snow regime on lichen cover within the plots. Live shrub cover declined from *Ambient* towards *Medium* and *Deep* regimes (Table 2). This effect was reflected in lower live vascular plant cover in *Deep* than in *Ambient* or *Medium* (Figure 4c), and a decline in the category live vascular plant, bryophyte and lichen cover in enhanced snow regimes (Table 2). Despite a reduction in the

cover of *Luzula* with deep snow, cover of the category “live graminoids and herbs” was unaffected by snow regime. The cover of bare ground (including soil, biological crust and stones) could not be tested



**FIGURE 3** Live cover of common plant species and groups, in addition to dead vascular plant material and bare ground (including soil, biological crust, stones), in the experimental plots in Adventdalen, Svalbard 2015

**FIGURE 4** NDVI, living and dead vascular plant cover and moisture relationships in the snowfence experiment Adventdalen 2015. (a) Peak-season NDVI for plots of different snow regimes, bars with means and 95% confidence intervals from the model; grey dots show plot-level observations. Significant differences ( $p < 0.05$ ) between regimes are shown by different capital letters. Percentage plot cover of (c) live vascular plant material, and (e) dead vascular plant material for each snow regime. Correlations of plot NDVI to (b) soil moisture, (d) live vascular plant cover and (f) cover of dead plant vascular material



**TABLE 3** Linear regression models, relating NDVI (Y) to a set of plant community variables and soil moisture content (X)

Y	X % cover	Intercept	Effect strength	SE	t	p	Pearson R
NDVI	<i>Dryas</i> alive	0.44	0.002	0.001	3.26	<.01	0.52
NDVI	<i>Dryas</i> dead	0.51	-0.005	0.001	-5.71	<.01	-0.77
NDVI	<i>Cassiope</i> alive	0.36	0.003	0.001	3.22	<.01	0.53
NDVI	<i>Cassiope</i> dead	0.49	-0.003	0.001	-4.30	<.01	-0.65
NDVI	<i>Salix</i> alive	0.43	0.006	0.002	3.31	<.01	0.50
NDVI	<i>Salix</i> dead	0.50	0.016	0.028	0.57	.59	0.21
NDVI	<i>Bistorta</i> alive	0.48	-0.005	0.003	-1.66	.10	-0.29
NDVI	<i>Alopecurus</i> alive	0.45	0.000	0.003	-0.14	.89	0.05
NDVI	<i>Luzula</i> alive	0.45	0.001	0.002	0.25	.81	-0.29
NDVI	bryophytes	0.45	-0.001	0.001	-0.72	.48	-0.11
NDVI	Lichens	0.46	-0.013	0.011	-1.22	.23	-0.18
NDVI	Shrubs alive	0.35	0.003	0.000	6.23	<.01	0.676
NDVI	Graminoids & herbs alive	0.48	-0.001	0.001	-1.12	.27	-0.167
NDVI	All vascular plants alive	0.28	0.003	0.000	6.93	<.01	0.71
NDVI	Live vasc. + bryo. + lichens	0.159	0.0042	0.000	9.25	<.01	0.809
NDVI	Dead shrubs	0.05	-0.004	0.001	-5.95	<.01	-0.68
NDVI	Dead vascular plants	0.55	-0.004	0.001	-7.82	<.01	-0.76
NDVI	% moisture	0.43	0.000	0.001	0.19	.89	0.03

Note: R represents Pearson's product moment correlation coefficient.

statistically due to too many zeros and too many outliers. Bare ground data for the three snow regimes are presented in Appendix S2.

### 3.3 | Relationships between plant community properties and NDVI

NDVI at peak growing season was significantly lower in the *Deep* than in the *Ambient* ( $-0.13$ ,  $SE = 0.03$ ,  $t$ -ratio =  $-5.02$ ,  $p < 0.01$ ) or *Medium* ( $-0.11$ ,  $SE = 0.03$ ,  $t$ -ratio =  $-3.35$ ,  $p < 0.01$ ) snow regimes (Figure 4a). There was no significant difference in NDVI between *Ambient* and *Medium* ( $-0.02$ ,  $SE = 0.03$ ,  $t$ -ratio =  $-0.64$ ,  $p = 0.80$ ). In relation to plant cover within plots, NDVI showed significant positive correlations to the cover of living *Dryas*, *Cassiope* and *Salix*, and negative correlations to the cover of dead *Dryas* and *Cassiope* (Table 3). In more general terms, NDVI was positively correlated to the cover of living shrubs, and the total living vascular plant material (Figure 4d), as well as the category living plants including bryophytes and lichens (Table 3). On the other hand, NDVI was negatively correlated to cover of dead vascular plant material (Table 3, Figure 4f). NDVI values were not correlated to soil moisture at peak growing season (Table 3, Figure 4b).

## 4 | DISCUSSION

As hypothesized (Hypothesis 1a), plant community composition was substantially altered by enhanced snow regimes, and especially by *Deep* snow regime. However, in contrast to Hypothesis 1b, deeper snow due to fences led to a reduction of live shrub abundance in our site. *Luzula* also decreased in *Deep*, whilst bryophytes appeared to be the only plant group that profited from enhanced snow, significantly so in the *Medium* but not the *Deep* regime. NDVI measurements could reliably detect these differences, thus we can accept Hypothesis 2. Our results indicate that aspects of enhanced snow regimes may contribute towards vascular plant death – commonly termed “arctic browning” (Phoenix & Bjerke, 2016), and is discussed further below.

### 4.1 | Snow regime effects on plant community composition

Several studies have examined the physiological responses of plants of various species to changing snow depth in the High Arctic. For example, leaf and/or stem nitrogen increased in *Salix arctica*, *Salix polaris*, *Luzula confusa*, and *Cassiope tetragona* behind snowfences (Blok et al., 2015; Leffler & Welker, 2013; Van der Wal et al., 2000). While this might suggest that vascular plant growth should increase with enhanced snow, such conditions also shorten the growing season. In Svalbard, delayed onset of the growing season decreased the vegetative and reproductive success of *Cassiope* (Mallik et al., 2011). In this study, we found that *Cassiope* and *Salix* cover was lower in the *Deep* snow regime than in the *Ambient*. Thus, even if increases in nutrient availability did provide some benefit to plants, other changes associated with our deep snow regimes led to a decline of dominant species.

This indicates that the empirical implications of the snow–shrub hypothesis depend on the balance between the positive and negative effects of the enhanced snow layer (Blok et al., 2016; Sturm et al., 2005); the balance of these effects may play out differently in the High Arctic, where we worked, than in the Low Arctic where the snow–shrub hypothesis was initially developed (Sturm et al., 2001). Positive effects of deeper snow include increased mineralization and nutrient availability (Mörsdorf et al., 2019; Semenchuk et al., 2015). Negative effects resulting from deeper snow include increased winter soil and plant respiration due to warmer temperatures under the snow (Morgner et al., 2010; Semenchuk, Christiansen, Grogan, Elberling, & Cooper, 2016), increased early growing season soil moisture, and later phenology (Cooper et al., 2011; Semenchuk, Gillespie et al., 2016). In addition, tradeoffs resulting from increased allocation for growth may leave plants vulnerable to other threats such as pathogens (Pandey, Irulappan, Bagavathiannan, & Senthil-Kumar, 2017), leading to negative outcomes over longer timeframes. In our site, negative impacts of deeper snow seemed to outweigh the positive, since we generally found a lower cover of living plants in enhanced snow regimes, whilst cover of dead plant material increased. This balance also has consequences at the food web level: some herbivores choose patches with the highest abundance of favored forage species, regardless of whether the plants in these patches are the most nutrient-rich (Van der Wal et al., 2000). Thus shifts in species dominance have strong implications for ecosystems.

Influx of species associated with nearby snow banks to the area behind a snowfence established in 1959 in alpine New Zealand was reported by Mark et al. (2015). An increase in cover of plants characteristic for snow beds, such as bryophytes at *Medium* in our experiment, may therefore not be surprising. Conditions accompanying deeper snow increase the prevalence of fungal and other disease vectors (Graae, Alsos, & Ejrnaes, 2008; Olofsson, Ericson, Torp, Stark, & Baxter, 2011). The presence of snow fungi (*Pythium* spp.), which can eventually kill moss, was more common in the *Deep* than the *Ambient* regime in our experiment (Tojo and Cooper, in prep.), and may explain why we did not find enhanced bryophyte cover also in our *Deep* regime.

Dead plant material, especially stemming from shrubs, increased substantially in our *Deep* snow regime, similarly to findings by Mark et al. (2015) who reported that some dominant species had a rapid negative response to experimentally increased snow. Besides the presence of fungi and plant pathogens, there are several other possible explanations for increased plant mortality. Although part of the increased winter respiration may come from microbial processes, a large proportion (37%–65%) can be attributed to root respiration (Bhupinderpal-Singh et al., 2003; Ryan & Law, 2005). Roots have a strong influence on the temperature sensitivity of soil respiration (Boone, Nadelhoffer, Canary, & Kaye, 1998), and roots of arctic plants have high respiration rates, which are particularly temperature sensitive (Cooper, 2004); plants under deep snow may have lost so much carbon through winter respiration that they were unable to survive. The *Medium* and *Deep* regimes often had high soil moisture, especially in the early season (Mörsdorf et al., 2019). Even though



some High Arctic plants have been shown to be tolerant to anoxia (Crawford, Chapman, & Hodge, 1994) those were mostly herbs and graminoids; dwarf shrubs, such as those in our experiment, are generally found in well-drained soils, and so may not be able to survive the enhanced moisture levels experienced here.

## 4.2 | NDVI as a measurement tool

Plot-level NDVI was a useful way to detect differences between communities in different snow regimes, and we infer that this is due to the difference in the amount of living versus dead material. Interestingly, NDVI did not show any association with bryophyte or lichen cover, and thus, NDVI should be used here primarily as a metric of vascular plant communities. In our study, NDVI was not affected by short-term changes in soil moisture. While this may be the case for vascular plants, changes in moss water content have been shown to induce rapid and large changes in NDVI, and the relationship between NDVI and water content is nonlinear (May et al., 2018). However, in our study, neither moisture content nor bryophyte cover affected the NDVI values. Either our mid-season moisture levels were too low for bryophyte NDVI reflectance (May et al., 2018 show a change in NDVI at 70%–80% saturation for their study moss species) or bryophytes at our site were fully saturated at c. 35%, and therefore their reflectance did not vary with moisture content above that. In our study, we did not characterize the species and percentage cover of each bryophyte, and yet it would be reasonable to assume that species of differing habitat would show individual responses to moisture, and bryophyte color differences may affect NDVI values. It may simply be that in a mixed plot, the vascular plants dominate the contribution to NDVI. This study shows that there is a need to better understand the contribution of bryophyte species composition and cover as well as their moisture content, and their interaction with vascular species in order to more clearly interpret NDVI values.

In general, the Arctic has been considered to be “greening” while lower latitude boreal regions have been “browning” (for example, Verbyla, 2008). This paradigm was established based on satellite measurements of NDVI made at a much coarser spatial grain; in contrast, measurements from a handheld NDVI sensor much better reflect what is occurring in a local vegetation patch, potentially even providing process-based explanations for the larger regional patterns. The greening/browning paradigm has recently been developed into a more nuanced picture where a mosaic of greening and browning occurs regionally and locally across all latitudes, partly due to extreme weather events from which ecosystems take varying amounts of time to recover (Phoenix & Bjerke, 2016). Our finding that local communities accumulate dead vascular plant material and show reduced greenness in response to increased snow depth is in line with recent assessments showing substantial browning even at high latitudes (Epstein et al., 2016), perhaps caused partly by delayed growing season onset (Bieniek et al., 2015). However, there are also other potential drivers of arctic browning, such as extreme weather events (Phoenix & Bjerke, 2016).

## 5 | CONCLUSIONS

In this study, we assessed for the first time compositional change in response to increased snow depth in High Arctic tundra plant communities. Contrary to our hypothesis, dominant shrub species had lower live cover in plots with enhanced snow, likely due to one or more of the following reasons: the negative effect of late melt-out dates on vegetative growth and reproductive success; higher respiration rates in winter; fungal and plant pathogen attacks; and/or greatly increased soil moisture and anoxia immediately after snowmelt. Conversely, bryophytes increased with moderately deeper snow.

The increase in dead vascular plant material in the *Deep* snow regime was reliably detected by a handheld NDVI sensor. Such local NDVI measures provide the opportunity to link community dynamics in a site or vegetation type of interest to more regional patterns of browning in the Arctic. Our findings suggest that winter processes, such as deeper snow and longer snow cover into the spring, may be among the causes of arctic browning.

## ACKNOWLEDGMENTS

We thank Yuko Kusama (National Institute of Polar Research, Tokyo, Japan) for collecting plant cover data, and Saskia Bergmann, Nanna Baggesen and Mark Gillespie for field assistance. We are grateful to the University Centre in Svalbard (UNIS) for field logistics. Frans-Jan Parmentier provided helpful comments on an initial draft of the manuscript. Funding for this project came from the Norwegian Research Council (“SnoEco” project, number 230970), the FRAM Centre Terrestrial Flagship (“SnoEcoFen” project) and the Norwegian Centre for International Cooperation in Education (SIU) High North Programme (“JANATEX” project, number HNP2013/10092), all to EJC.

## AUTHOR CONTRIBUTIONS

EJC conceived of the research idea and collected data; MAM and AKP prepared data; MAM and CJL performed statistical analyses; EJC, CJL and MAM wrote the paper; all authors discussed the results and commented on the manuscript.

## DATA AVAILABILITY STATEMENT

The primary data are available in Appendix S3 and S4, and the program codes for analysis in R are available in Appendix S5.

## ORCID

Elisabeth J. Cooper  <https://orcid.org/0000-0002-0634-1282>

Chelsea J. Little  <https://orcid.org/0000-0003-2803-7465>

Martin A. Mörsdorf  <https://orcid.org/0000-0002-3903-2021>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Supporting information for Methods

**Table S1.** Number of plots in each snow regime of the snowfence experiment, sorted according to dominant evergreen shrub (DES) and vegetation type

**Table S2.** Comparison of candidate models for dbRDA, relating community composition to snow regime and other design variables (fence location and DES)

**Appendix S2.** Supporting information for Results

**Figure S1.** Environmental conditions within snow regimes (a) soil surface temperatures during the year 2014–2015, and (b) soil moisture during growing season 2015

**Figure S2.** Peak-season soil moisture for plots of different snow regimes in the snowfence experiment in Adventdalen

**Figure S3.** Cover of bare ground in each experimental snow regime

**Appendix S3.** Primary data: percentage plant cover

**Appendix S4.** Primary data: NDVI and soil moisture

**Appendix S5.** Program codes for analysis in R

**How to cite this article:** Cooper EJ, Little CJ, Pilsbacher AK, Mörsdorf MA. Disappearing green: Shrubs decline and bryophytes increase with nine years of increased snow accumulation in the High Arctic. *J Veg Sci.* 2019;30:857–867. <https://doi.org/10.1111/jvs.12793>