

1 **Climatic and biotic extreme events moderate long-term responses of above-**  
2 **and belowground sub-Arctic heathland communities to climate change**

3 *Running head: Interacting drivers of Arctic communities*

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## 26 **Abstract**

27 Climate change impacts are not uniform across the Arctic region because interacting factors  
28 causes large variations in local ecosystem change. Extreme climatic events and population  
29 cycles of herbivores occur simultaneously against a background of gradual climate warming  
30 trends and can redirect ecosystem change along routes that are difficult to predict. Here, we  
31 present the results from sub-Arctic heath vegetation and its belowground micro-arthropod  
32 community in response to the two main drivers of vegetation damage in this region: extreme  
33 winter warming events and subsequent outbreaks of the defoliating autumnal moth caterpillar  
34 (*Epirrita autumnata*).

35 Evergreen dwarf shrub biomass decreased (30%) following extreme winter warming events and  
36 again by moth caterpillar grazing. Deciduous shrubs that were previously exposed to an extreme  
37 winter warming event were not affected by the moth caterpillar grazing while those that were  
38 not exposed to warming events (control plots) showed reduced (23%) biomass from grazing.  
39 Cryptogam cover increased irrespective of grazing or winter warming events. Micro-arthropods  
40 declined (46%) following winter warming but did not respond to changes in plant community.  
41 Extreme winter warming and caterpillar grazing suppressed the CO<sub>2</sub> fluxes of the ecosystem.

42 Evergreen dwarf shrubs are disadvantaged in a future sub-Arctic with more stochastic climatic  
43 and biotic events. Given that summer warming may further benefit deciduous over evergreen  
44 shrubs, event and trend climate change may both act against evergreen shrubs and the  
45 ecosystem functions they provide. This is of particular concern given that Arctic heath  
46 vegetation is typically dominated by evergreen shrubs. Other components of the vegetation  
47 showed variable responses to abiotic and biotic events, and their interaction indicates that sub-

48 Arctic vegetation response to multiple pressures is not easy to predict from single factor  
49 responses. Therefore, while biotic and climatic events may have clear impacts, more work is  
50 needed to understand their net effect on Arctic ecosystems.

51

## 52 **Introduction**

53 The Arctic regions are undergoing particularly rapid climate change compared to the rest of the  
54 world, but predicting the impacts of climate change on Arctic ecosystems is challenging. These  
55 challenges arise (in part) because (i) changes in the gradual climate are not uniform across the  
56 Arctic (AMAP 2011), and (ii) at local scales, ecosystem responses to warming are not  
57 necessarily the same due to variation driven by other biotic and climatic factors (Post *et al.*  
58 2009; Callaghan *et al.* 2013). For example, the northward expansion of shrubs resulting in  
59 Arctic ‘greening’ that has arisen from gradual warming over the last decade has been observed  
60 in many locations but has not been uniform at local scales (Tape *et al.* 2006; Myers-Smith *et*  
61 *al.* 2011). This site specificity in plant community responses to climate warming is confirmed  
62 by a number of observations in northern Scandinavia (Hedenås *et al.* 2012; Callaghan *et al.*  
63 2013). Warming of the Arctic is also **expected to result** in an increasing frequency of stochastic  
64 climatic events (Saha *et al.* 2006), such as extreme winter warming events. Such extreme events  
65 severely damage Arctic and sub-Arctic vegetation and can therefore, halt or reverse these  
66 ‘greening’ trends (Bokhorst *et al.* 2009; 2011; Callaghan *et al.* 2013; Bjerke *et al.* 2014). In  
67 addition, unpredictable population cycles of herbivores and fungal pests can severely affect the  
68 competitive interactions between plant species and readily change vegetation composition  
69 (Lehtonen and Heikkinen 1995; Malmström and Raffa 2000; van der Wal 2006; Jepsen *et al.*  
70 2008; Van Bogaert *et al.* 2009; Olofsson *et al.* 2012; Jepsen *et al.* 2013; Karlsen *et al.* 2013).  
71 Plant community changes may affect belowground communities such as micro-arthropods that

72 in turn affect ecosystem processes. All these changes in community composition can alter  
73 feedbacks to the global carbon cycle (Cornwell *et al.* 2008; De Deyn *et al.* 2008). Predicting  
74 ecosystem change over northern lands is therefore particularly challenging given that these  
75 stochastic climatic events and herbivore outbreaks occur against a background of gradual  
76 warming trends.

77 To address the complexity of different drivers for communities and ecosystem processes in the  
78 Arctic we need to adapt our research to incorporate stochastic extreme events, as has been called  
79 for more generally in climate change research (Jentsch *et al.* 2007; Smith 2011) and in long-  
80 term monitoring programmes. Here we present the results from a sub-Arctic ecosystem that -  
81 following simulated extreme winter warming events in 2007, 2008 and 2009 (Bokhorst *et al.*  
82 2011; 2012c)- was then subject to natural regional outbreaks of the defoliating autumnal moth  
83 (*Epirrita autumnata*) in 2012 and 2013. The extreme winter warming events were simulations  
84 of abrupt warm spells during winter, which are becoming more frequent in northern  
85 Scandinavia (Phoenix and Lee 2004; Johansson *et al.* 2011; Bjerke *et al.* 2014). These events  
86 can raise the mid-winter temperature to 10 °C and lead to snow melt across large (>1000 km<sup>2</sup>)  
87 areas (Bokhorst *et al.* 2009). Due to the loss of snow cover the vegetation and soil are exposed  
88 to colder freezing temperatures on the return of winter temperatures. This freezing leads to  
89 severe damage to the dominant dwarf shrubs *Empetrum nigrum*, *Vaccinium myrtillus*, and *V.*  
90 *vitis-idaea*, while other plant species such as the dwarf shrub *V. uliginosum*, and the grass  
91 *Deschampsia (Avenella) flexuosa* are much more tolerant (Bokhorst *et al.* 2011).

92 Aboveground, winter warming events may interact with outbreaks of the autumnal moth. This  
93 herbivore, in caterpillar form, typically feeds on leaves of birch (especially the widespread trees  
94 *Betula pubescens*), but once these have been consumed, dwarf shrubs are targeted (Jepsen *et al.*  
95 2008) indicating that the shrub species are dually susceptible to climatic extreme events and  
96 herbivore outbreaks. Mosses – often a major component of high latitude ecosystems – also

97 show damage including reductions in growth (50 %) arising from extreme winter warming  
98 events (Bjerke *et al.* 2011). Mosses, however, are not a food source for the autumnal moth  
99 (Jepsen *et al.* 2008) and so are likely to show differential responses to shrubs should climatic  
100 and herbivore outbreak events occur concurrently. Lichens were not affected by the extreme  
101 winter warming events and are not known to be grazed upon by the caterpillars. Therefore,  
102 lichens may benefit the most from extreme winter events and herbivore outbreaks. This  
103 contrasts sharply with the negative response observed in many summer warming studies  
104 (Cornelissen *et al.* 2001).

105 Belowground, soil frost following winter warming events reduces micro-arthropod abundance  
106 and changes their community composition (Bokhorst *et al.* 2012b) as species differ in cold  
107 tolerance. In addition, the negative effects of frost damage to dominant dwarf shrubs and mosses  
108 will also affect the micro-arthropod community (Salmane and Brumelis 2008; Bokhorst *et al.*  
109 2014). Changes in plant and soil fauna community composition affects the carbon balance of  
110 an ecosystem as different plant functional types differ in their carbon sequestration rates and  
111 the decomposability of their litter (Cornelissen 1996; Bokhorst *et al.* 2007; De Deyn *et al.* 2008;  
112 Lang *et al.* 2009), while shifts in soil fauna community composition drive decomposition rates  
113 (Heemsbergen *et al.* 2004; Handa *et al.* 2014). In addition, shifts in the soil biota as a result of  
114 repeated extreme events can influence plant competition (Meisner *et al.* 2013). Therefore,  
115 changes in the soil and plant community as a result of these extreme events are likely to impact  
116 on the carbon balance of these sub-Arctic ecosystems. The direction of such changes is less  
117 clear as a previous autumnal moth outbreak in the Abisko area during 2004 reduced the CO<sub>2</sub>  
118 sink strength of the birch forest by 89 % (Heliasz *et al.* 2011), while a moth outbreak in a  
119 Siberian taiga caused increases in CO<sub>2</sub> release from the soil due to the qualitative changes in  
120 the litter composition (Baranchikov *et al.* 2002). Thus, it is unclear what the combined effects  
121 of extreme weather events and herbivore peaks will be for the carbon balance of these sub-

122 Arctic ecosystems. By comparing the impacts of climatic and biotic events within one study  
123 system we are able to identify potential synergistic and antagonistic interactions between these  
124 events for ecosystem change. This may provide a better understanding of the driving factors  
125 behind long-term trends and spatial heterogeneity in sub-Arctic heath communities.

126 We studied the response of the above- and belowground communities to the multiple stresses  
127 of extreme winter warming and autumnal moth outbreaks to improve our understanding on how  
128 sub-Arctic ecosystems respond to multiple and interacting stress events. We expect that 1) the  
129 impact of moth grazing will increase the damage to plants previously exposed to extreme winter  
130 warming events. However, this effect will be plant-type-specific, and therefore we expect that:  
131 2) dwarf shrubs will decline following the combined effects of winter warming events and moth  
132 defoliation and that graminoids will become dominant as the competition by the dwarf shrubs  
133 will be greatly reduced. 3) Cryptogams will benefit from the high vascular plant mortality as  
134 shading will be reduced (Bonan and Korzuhin 1989; van der Wal *et al.* 2005), and because  
135 cryptogams are not targeted by the autumnal moth (Jepsen *et al.* 2008). 4) Soil micro-arthropods  
136 will respond most strongly to the temperature extremes of the winter event while micro-  
137 arthropod responses to vegetation shifts will be more subtle. 5) As a result of the extreme winter  
138 warming events, CO<sub>2</sub> efflux during the following growing season will be negative for the  
139 ecosystem (net carbon source) due to high plant mortality, and this will be exacerbated by the  
140 occurrence of the autumnal moth grazing. However, declines in soil micro-arthropods, may  
141 limit CO<sub>2</sub> loss from the ecosystem, potentially leading to no net-effect on the CO<sub>2</sub> efflux rates.

142

## 143 **Materials and Methods**

144 *Field site and experimental simulations*

145 Simulations of winter warming events in the field were performed on a sub-Arctic heathland in  
146 open mountain birch forest close to the Abisko Scientific Research Station (ANS) in northern  
147 Sweden (68° 21' N, 18° 49' E) during March 2007, 2008 and 2009. Details of the research site  
148 and experimental set-up are described in Bokhorst *et al.* (2008; 2010). In brief, the experiment  
149 consisted of 18 plots (2.1 m × 1.0 m), consisting of 6 control plots (Cn) that remained under  
150 their natural snow cover throughout the winter, 6 that were exposed to a week-long winter  
151 warming event called canopy warming (CW) using infrared heating lamps (800 W emitting at  
152 3 µm; HS 2408, Kalglo Electronics Co., Bethlehem, USA), and 6 where warming from infrared  
153 heating lamps was combined with soil warming from cables at 5 cm soil depth called canopy  
154 and soil warming (CSW). Soil warming cables (LS-TXLP, Nexans, Norway, producing 120 W  
155 m<sup>-2</sup>) were switched on two days after the lamps to simulate the delay in soil thaw during a real  
156 event. Temperatures were monitored with thermistors placed in each plot at canopy height and  
157 at the soil surface, with logging at 6-h intervals recorded on a data logger (CR10 X, Campbell  
158 Scientific, UK). Details on the temperature effects of the treatment are provided in Bokhorst *et*  
159 *al.* (2011; 2012b); in summary, temperatures rose on average to 5 °C during the events, while  
160 for the remainder of winter temperatures fluctuated in tandem with the ambient conditions  
161 (ranging from -17 °C to 4 °C) due to the diminished snow cover meaning there was no  
162 insulation from air temperatures. In contrast, control plots remained well insulated under snow  
163 and experienced temperatures between -7 °C and 0 °C until snowmelt. The simulation of  
164 extreme winter warming events and ecosystem responses were supported by observations of  
165 very similar impacts arising from a natural extreme event in the same region (Bokhorst *et al.*  
166 2009).

167

168 *Autumnal moth densities*

169 The autumnal moth typically reaches population peaks approximately every 10 years (Tenow  
170 *et al.* 2004) with the Abisko outbreak of the moth caterpillars occurring during the 2012 and  
171 2013 spring. The 2012 outbreak coincided with a very cool first half of the growing season,  
172 which caused a strong delay in plant phenology (Bjerke *et al.* 2014). Hence, birch leaf biomass  
173 was low by the start of the outbreak, and this probably accentuated the grazing pressure on  
174 understory plants since the caterpillars drop down onto the understory following consumption  
175 of the tree leaf resource. Vole and lemming population peaks also occurred in the Abisko region  
176 during the summers of 2010 and 2011 (Olofsson *et al.* 2013). However, there were no  
177 indications of grazing on any of the plants by these herbivores during those years, indicating  
178 that our study site was not visited by lemming and vole in sufficient numbers to affect the  
179 vegetation.

#### 180 *Vegetation composition, shoot mortality and reproductive output*

181 Vegetation surveys were made by point quadrat measurements in permanent, randomly  
182 assigned squares (30 cm × 30 cm) in each plot of the winter warming experiment during mid-  
183 July (peak biomass) each year (2007-2013, except 2011). These surveys were therefore in the  
184 summers after the second and third winters of warming events and in the 4 subsequent summers  
185 (summers following winters with no simulated warming events). 121 point counts at 2.5 cm  
186 intervals were made of the vegetation in each square by counting the number of times a vertical  
187 pin touched plant parts. Cryptogam species were counted as present or absent, while vascular  
188 plants could be hit more than once by each vertical pin. For *E. nigrum*, only shoots were counted  
189 rather than every leaf hit to avoid over-representation due to the high number of tightly packed  
190 needle-like leaves. Correlations between point quadrat hits and biomass were made for the  
191 dominant study species on quadrats outside the experimental plots by quantifying hits in the  
192 same way and afterwards harvesting all aboveground parts. These correlations were used to  
193 quantify species biomass in each experimental plot (Jonasson 1988). Species cover was

194 quantified from point count surveys based on presence or absence at each point. Shannon  
195 diversity index ( $H'$ ) was quantified as a measure of plant diversity for each plot using the point  
196 intercept data.

197 Shoot mortality of three dominant dwarf shrub species (*E. nigrum*, *V. myrtillus* and *V. vitis-*  
198 *idaea*) was quantified by counting the number of dead and alive shoots in a randomly assigned  
199 30 cm  $\times$  30 cm quadrat in each plot during mid-June every year from 2008 to 2013 (except  
200 2011 when a survey was not undertaken). A shoot was considered dead when all leaves on its  
201 stem were brown and had died. A berry count was done during July 2013 by quantifying the  
202 number of shoots with berries for each of the three dwarf shrub species in a 1 m  $\times$  1 m quadrat  
203 in each plot.

204

#### 205 *Micro-arthropod community composition*

206 To monitor the abundance and diversity of soil micro-arthropods, an intact soil core (10 cm  
207 diameter, 5 cm long) was sampled from each experimental plot as soon as the first 5 cm of soil  
208 had thawed in spring, which generally occurred in early May. Sampling was done following  
209 the third extreme winter warming simulation in 2009 and after three years without events  
210 (2012). Samples were individually stored in sealed plastic containers and kept at 5 °C until  
211 extracted from the core in a Tullgren heat extractor (Van Straalen and Rijninks 1982) for three  
212 weeks. Extracted arthropods were preserved in alcohol (70 % ethanol). Collembola were  
213 identified to species level following Fjellberg (1998; 2007). Acari were determined to family  
214 level following Karg (1993), Krantz and Walter (2009) and Weigmann (2006), with the  
215 exception of the Prostigmata and Astigmata which were grouped together. The Shannon  
216 Diversity Index ( $H'$ ) was quantified as a measure of Collembola species diversity and at the  
217 family level for the Acari (also including higher taxonomic levels). Collembola species were  
218 grouped according to their typical association with the different soil layers. As such, there were

219 eu-edaphic species that tend to live deeper in the soil, hemi-edaphic species that live in the litter  
220 layer and epi-edaphic species living among the aboveground parts of plants (Gisin 1943).  
221 Collembola size tends to decrease further down the soil profile. This information was not  
222 available for the studied Acari in this study.

### 223 *Ecosystem CO<sub>2</sub> fluxes*

224 Ecosystem CO<sub>2</sub> fluxes were measured once during the growing seasons (mid-July) of 2012 and  
225 2013 in the same way as previously done in these experimental plots (Bokhorst *et al.* 2011).  
226 Measurements were made by placing a transparent chamber (20 cm × 20 cm × 20 cm) made  
227 from polymethyl methacrylate (PMMA) over the vegetation and by quantifying CO<sub>2</sub> change  
228 using an Infrared Gas Analyzer (EGM-4, PP-systems, Amesbury, MA, USA). Net Primary  
229 Production (NPP) was quantified by monitoring the rate of change in the headspace CO<sub>2</sub>  
230 concentration at 10 second intervals over a 3 minute period while Ecosystem Respiration (ER)  
231 was quantified by darkening the chamber with black plastic sheeting. The difference between  
232 ER and NPP determined Gross Primary Production (GPP). To minimize internal chamber air  
233 exchange with the external environment, plastic skirts (20 cm wide) weighed down with chains  
234 were attached to a square frame, onto which the chamber could be attached (Street *et al.* 2007).  
235 An internal fan was used to mix air inside the chamber. Photosynthetic Active Radiation (PAR)  
236 was measured (SKP 215 Skye Instruments, Powys, UK) at the start and end of each  
237 measurement and was on average 1000 μmol m<sup>-2</sup> s<sup>-1</sup>.

### 238 *Data and statistical analyses*

239 Repeated measures ANOVA were used to identify changes across years and between treatments  
240 for species richness, diversity (H'), plant biomass (individual species, evergreen biomass,  
241 deciduous biomass, dwarf shrubs and (hemi) cryptophytes), cryptogam cover and the ratio of  
242 alive-to-dead shoot counts of *E. nigrum*, *V. myrtillus* and *V. vitis-idaea*. Plant reproductive

243 output and CO<sub>2</sub> efflux rates were compared across treatment plots using one-way ANOVAs.  
244 Micro-arthropod responses to the winter warming events were determined with one-way  
245 ANOVA on species abundance, total Collembola and Acari abundance, species richness, and  
246 diversity (H'). In all cases, homogeneity of variance was tested with a Levene's test of equality  
247 and log-transformation was applied when necessary. All statistical analyses were done using  
248 SPSS 22.0 (IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY).

## 249 **Results**

### 250 *Vascular plant damage from climatic and biotic events*

251 The extreme winter warming events resulted in considerable shoot mortality of *E. nigrum*, *V.*  
252 *vitis-idaea* and *V. myrtillus* (Table 1, Fig. 1). Shoot damage remained high for *E. nigrum* and  
253 *V. vitis-idaea* in the Cn and CSW plots during the following years except *V. myrtillus* which  
254 showed a rapid recovery in 2010 (Fig. 1c). Following the autumnal moth peak of 2013 all three  
255 dwarf shrubs had high shoot mortality but now also in the Cn plots. In addition, there were no  
256 berries on *V. myrtillus* and *V. vitis-idaea* in any of the plots during 2013 after the moth outbreak,  
257 while *E. nigrum* had on average 1.5 ( $\pm 1.1$  SE), 0.5 ( $\pm 0.2$ ) and 0.3 ( $\pm 0.1$ ) berries per shoot for  
258 Cn, CW and CSW respectively.

### 259 *Plant functional type and growth form responses to climatic and biotic events*

260 Total deciduous shrub biomass increased (25 %) in the extreme winter warming treated plots  
261 compared to the starting conditions of 2007 and remained higher irrespective of the autumnal  
262 moth peaks (Fig. 2a). However, deciduous shrub biomass in the control plots showed a  
263 decreasing trend with time from 2007 but a large biomass decline between 2012 and 2013 (the  
264 moth outbreak years) and was different ( $F_{2,15} = 5.0$ ,  $P < 0.022$ ) from that of CSW during 2013.  
265 *Vaccinium myrtillus* biomass decreased in all plots in 2013 compared to the previous year (Fig.  
266 2b), while there was no consistent pattern for the biomass of *V. uliginosum* across the treatments

267 or years (Table 2, Fig. 2c). *Deschampsia flexuosa* increased with time irrespective of treatments  
268 (Fig. 2d). Mean species biomasses across plots for each year are presented in S1.

269 Total evergreen shrub biomass declined following the extreme winter warming treatments (Fig.  
270 2e), but increased to the initial values of 2007 by 2012. In 2013, following the autumnal moth  
271 peak, biomass decreased again, but on this occasion also in the control plots, similar to the  
272 decreases observed in treated plots following the extreme winter warming events (Fig. 2e).  
273 These biomass changes were driven by the mortality of *E. nigrum* (Figs 1d and 2f), as no  
274 consistent changes were observed in *V. vitis-idaea* (Table 1, Fig. 2g). However, biomass of  
275 *Linnaea borealis* (a much smaller component of the vegetation) increased with time reaching  
276 highest biomass change across all treatments in 2013 (Table 1, Fig. 2h, S1). The biomass of  
277 dwarf shrubs showed the same pattern as found for evergreen plants across the study period  
278 (Table 2, data not shown) since evergreens contribute the most to dwarf shrub biomass. Change  
279 in biomass of (hemi)cryptophytes increased over time showing the same pattern as *D. flexuosa*  
280 and *L. borealis* (Table 1).

281 Vascular plant diversity ( $H'$ ) did not differ between the treatment plots during any of the years,  
282 and neither was there a consistent pattern in diversity across years despite the significant year  
283 effect (Table 2). Species richness gradually increased with time; from 4.5 during 2007 to 5.1 in  
284 2013, but no differences were found between the experimental plots (Table 2). This species  
285 richness increase was mostly driven by the appearance of grasses (*Calamagrostis lapponica*  
286 and *D. flexuosa*) where they were previously absent.

#### 287 *Cryptogam community changes following climatic and biotic events*

288 Total moss (mostly *Hylocomium splendens*) and lichen cover increased, irrespective of  
289 treatments (Table 1), following the autumnal moth peaks (2012 and 2013) (Fig. 3). There were  
290 no treatment effects on cryptogam community species richness or diversity ( $H'$ ) during any of

291 the years but cryptogam richness increased ( $P < 0.001$ ) from on average 2 species per plot to 4  
292 in 2012 and 2013 following the moth outbreak. Similarly, diversity ( $H'$ ) increased ( $P < 0.001$ )  
293 from 0.4 (mean of 2007-2010) to 1.0 during 2012 and 2013. The increased species richness and  
294 diversity ( $H'$ ) were driven by the emergence of *Cladonia rangifera*, *Nephroma arcticum*,  
295 *Ptilium ciliare* and *Dicranum* sp. in plots where these were previously not observed.

#### 296 *Micro-arthropod responses to climatic and biotic events*

297 Abundance of Collembola was significantly reduced (46 %) in CSW following the third winter  
298 warming simulation event compared to control plots (Table 3). Changes in Collembola  
299 abundance were primarily the result of declines (45 %) in soil-dwelling species (*Isotomiella*  
300 *minor* 57 %). In 2012 total Collembola abundance was no longer different between treatments  
301 but surface-dwelling species abundance (notably *Lepidocyrtus lignorum*) was reduced by 70 %  
302 ( $P < 0.05$ ) in CSW compared to Cn (Table 3). Total Acari abundance was reduced in the CW  
303 and CSW treatments by 41 % and 48 %, respectively compared to the control plots in 2009  
304 (Table 3). These changes were driven by declines (43 % and 49 %, respectively) in Astigmata-  
305 Prostigmata and a 31 % and 50 % decline in total Mesostigmata and Oribatida respectively in  
306 CSW. None of the individual Oribatida families were affected by the extreme winter warming  
307 events, and in 2012, no differences were found for the total Acari and any group abundances  
308 between treatments.

309 There were no diversity ( $H'$ ) or richness differences for the Collembola between the treatments  
310 and control plots during 2009 and 2012, except for a difference ( $F_{2,15} = 5.5$ ,  $P = 0.016$ ) between  
311 CW ( $H'$ :  $1.3 \pm 0.1$ ) and CSW ( $H'$ :  $1.6 \pm 0.05$ ) in 2009. Diversity ( $H'$ ) of Acari was higher ( $F_{2,15}$   
312  $= 4.4$ ,  $P = 0.032$ ) in CW ( $1.3 \pm 0.02$ ) compared to Cn ( $1.1 \pm 0.03$ ) in 2009 and driven by changes  
313 in relative abundance. No Acari diversity ( $H'$ ) differences were found in 2012.

#### 314 *CO<sub>2</sub> efflux*

315 ER and GPP were lower in CSW (58 % and 95 % respectively) compared to Cn in 2009 while  
316 there were no differences in ER and GPP between the experimental treatment plots during 2012  
317 and 2013, (Table 4, S3). NPP was consistently lower in Cn compared to CSW across all years.

## 318 **Discussion**

319 Extreme climatic events and population outbreaks of herbivores are well known drivers of  
320 community change but these are rarely compared within one experimental study as shown here  
321 (Callaghan *et al.* 2013). There were clear responses to the climatic and biotic events and these  
322 were often species or functional group specific. As such, evergreen dwarf shrubs were  
323 negatively affected by both extreme winter warming events and moth grazing. The deciduous  
324 dwarf shrub *V. myrtillus* was only affected by the autumnal moths, in control plots, without  
325 previous exposure to winter warming events, indicating that some vegetation changes in sub-  
326 Arctic regions may depend on the history of past extreme events. Cryptogams increased during  
327 the 7 year period without major responses to the treatments. Furthermore, micro-arthropod  
328 response to extreme winter warming events was strongest among the eu-edaphic and smaller  
329 invertebrate species. In contrast, resulting shifts in the plant community composition hardly  
330 affected the soil micro-arthropod community (no response following herbivory). These  
331 different responses suggest that soil micro-arthropods respond immediately to temperature  
332 variability during winter and that changes in the plant community have much less impact in  
333 these sub-Arctic ecosystems.

334 We did not observe, as hypothesised, increased additional damage to dwarf shrubs by the  
335 autumnal moth grazing following the extreme winter warming events. Although the damage of  
336 the moth caterpillar grazing and the extreme winter warming events were similar in extent, for  
337 *E. nigrum*, the period between the events (3 years) seems long enough such that there were no  
338 synergistic impacts of both events on the plants. However, the decline of the deciduous *V.*

339 *myrtilus* following the moth caterpillars in 2013 was, however, not consistent across  
340 experimental plots: more damage was found in the control and CW treatment, while no apparent  
341 increase in shoot mortality was observed in the CSW plots, indicating that the moth caterpillars  
342 may have avoided eating from the plants in the CSW treatment. This apparent reduced feeding  
343 on *V. myrtilus* may reflect increased concentration of phenolic defence compounds or reduced  
344 nutrient availability (Herms and Mattson 1992; Awmack and Leather 2002). The damage to  
345 plants caused by extreme winter warming events is largely dependent on snow thickness  
346 (Bokhorst *et al.* 2009), which is driven by local topography and wind direction, whereas the  
347 damage caused by herbivore peaks depends on their spatial distribution across the landscape.  
348 Potentially synergistic or antagonistic effects of climatic and biotic events on vegetation change  
349 are therefore not equally distributed across the landscape, but may play a role in the spatial  
350 distribution and heterogeneity of plant communities and their response to gradual climate  
351 warming. Overall, evergreen dwarf shrubs appear the most susceptible to extreme events and  
352 therefore may experience more abiotic stress and competition than deciduous shrubs during  
353 future climate change.

354 We did not find support for our second hypothesis that the decline of dwarf shrubs would enable  
355 graminoids to dominate. The lack of response by the graminoids may be due to the afterlife  
356 effects of *E. nigrum* litter which contains high concentrations of secondary compounds that  
357 inhibits growth of other plants (Nilsson and Zackrisson 1992; Gallet *et al.* 1999; Wallstedt *et*  
358 *al.* 2000). However, *D. flexuosa* (and *L. borealis*) increased with time irrespective of extreme  
359 winter warming treatments or biomass of *E. nigrum*, suggesting that in 2010, other factors such  
360 as climatic conditions for growth had improved in combination with increased opening of  
361 micro-sites (Nathan and Muller-Landau 2000). Overall, our results indicate that graminoids and  
362 (hemi)cryptophytes are less affected by extreme climatic and biotic events than other plant  
363 functional types. Their growth strategy, with dormant buds remaining at ground level, probably

364 protects them against grazing and pre-mature winter de-hardening. However, repeated extreme  
365 events are probably required before the dominance of *E. nigrum* is broken in these sub-Arctic  
366 heathland ecosystems.

367

368 Mosses and lichens increased in cover following damage caused to dwarf shrubs supporting our  
369 third hypothesis. Critically, this increase manifested itself across all experimental plots and  
370 appears largely in response to the autumnal moth grazing. While highlighting the importance  
371 of the moth outbreak in causing major increases in the plants, it also shows that the winter  
372 warming events did not allow increased cryptogam growth in contrast to what was expected.  
373 This lack of warming event response potentially reflects the reduced growth rates (50 %)   
374 immediately following these climatic events for the dominant bryophyte *H. splendens* (Bjerke  
375 *et al.* 2011). Furthermore, the cryptogams increased despite a recovery of the dwarf shrubs  
376 between 2009 and 2012, suggesting that conditions were suitable for cryptogam growth and  
377 that there was little competition, in terms of canopy opening and light for space (Keuper *et al.*  
378 2011). The overall increased growth of cryptogams may have been promoted by higher  
379 precipitation during summer months (Tamm 1964; Vitt 1990; Potter *et al.* 1995; Sonesson *et*  
380 *al.* 2002). Precipitation recorded at the ANS research station was higher during the summers of  
381 2011 and 2012 (37 % and 17 %, respectively) than previous years (2007-2010) and the long-  
382 term mean (1913-2000). In addition, there would have been no grazing pressure on the  
383 cryptogams by the autumnal moths. Instead, there would have been an increase in nutrients  
384 from caterpillar faecal matter (Karlsen *et al.* 2013) that may have contributed to increased moss  
385 growth (Aerts *et al.* 1992; Armitage *et al.* 2012). Therefore, the observed increase of  
386 cryptogams most likely reflects a response to the wetter summers and the autumnal moth peak  
387 increasing nutrient availability, reducing competition from vascular plants and increased light  
388 through the damaged canopy.

389 In support of hypothesis four we found that the micro-arthropod community was more  
390 responsive to extreme climatic events than changes in the plant community, which is consistent  
391 with soil micro-arthropods responses to extreme climatic disturbances (Coulson *et al.* 2000;  
392 Bokhorst *et al.* 2012b). The lack of response by micro-arthropods to changes in the plant  
393 community is consistent with a study from a northern boreal forest (Bokhorst *et al.* 2014) but  
394 is inconsistent with findings from temperate grasslands (Wardle *et al.* 1999; 2005). A potential  
395 explanation between these contrasting responses lays with the quality of the soil carbon pool  
396 which is much lower and has a much slower turnover rate in northern boreal and sub-Arctic  
397 ecosystems, as compared to temperate grasslands (Carvalhais *et al.* 2014). Effects of changes  
398 in the plant community on the soil organic matter layer will therefore take years or decades  
399 before they impact on the soil micro-arthropod community and vice-versa (Hågvar 1984;  
400 Salmon *et al.* 2006; Bokhorst *et al.* 2014). In addition, the micro-arthropods in these sub-arctic  
401 ecosystems may have enough feeding plasticity that the changes in food supply and quality do  
402 not affect them overly much (Siepel and De Ruiter-Dijkman 1993; Krab *et al.* 2013). Our results  
403 indicate that soil micro-arthropod community changes as a result of extreme climate events  
404 tends to be rapid but that recovery is also quick. However, during these recovery periods the  
405 shift in soil fauna community composition may feed-back to soil carbon cycling rates  
406 {Heemsbergen, 2004 #1198;Handa, 2014 #3609}.

407 The measured declines in ER and GPP coincided with declines of Collembola and Acari  
408 abundance in the experimental plots during 2009 and may be linked but these changes in ER  
409 and GPP also coincided with high plant mortality and did not seem to extend beyond that  
410 specific growing season. The CO<sub>2</sub> fluxes measured during 2012 and 2013 were particularly low  
411 compared to reported measurements in this region (Larsen *et al.* 2007) but close to zero gas  
412 fluxes have been reported previously (Lafleur *et al.* 2003) so this may not be unusual. A  
413 continuous measuring campaign across the growing season may have shown a different pattern

414 between the experimental plots but as it is the overall consistent low measured gas flux rate  
415 probably reflect the massive defoliation caused by the autumnal moth (Heliasz *et al.* 2011;  
416 Medvigy *et al.* 2012; Simmons *et al.* 2014). Therefore, we did not find consistent support for  
417 hypothesis five.

418 Overall, these results support the notion that the response of sub-Arctic ecosystems in response  
419 to the pressures of climate change is non-linear (Callaghan *et al.* 2010; 2013). Extreme events  
420 will (at least temporarily) halt or push vegetation change away from the general ‘greening’  
421 trends driven by summer warming, but will also interact with sudden population explosions of  
422 herbivores leading to steep changes in vegetation composition (Fig. 4). Based on current  
423 evidence, it seems that evergreen dwarf shrubs appear most sensitive to extreme climatic events  
424 and grazing pressure, indicating that there is a cost associated with being evergreen in a future  
425 climate with more extreme events. Even though these *E. nigrum* heathlands are very resistant  
426 to change (Aerts 2010) future community changes are likely given the increased frequencies of  
427 extreme events expected due to climate change (Callaghan *et al.* 2010; AMAP 2011).  
428 Therefore, these sub-Arctic heath communities may shift from an evergreen and moss  
429 dominated vegetation to one dominated by deciduous dwarf shrubs and graminoids. Such  
430 changes will likely result in altered soil communities and may initiate decomposition of stored  
431 soil carbon turning these ecosystems into a net source of carbon due to the higher carbon  
432 turnover rates in these latter vegetation types (De Deyn *et al.* 2008; Hartley *et al.* 2012). Taken  
433 together, these results indicate that vegetation and soil community changes in the sub-Arctic  
434 are currently unpredictable and will be highly variable across the landscape.

435

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447

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671

672

673 **Tables**

674 Table 1. Repeated measures ANOVA statistics (F and *P* values) of alive:dead shoot ratios, plant  
 675 functional types and species-specific biomass and cryptogam cover in the experimental winter  
 676 warming event plots. N = 6 for each treatment (control, canopy warming and canopy and soil  
 677 warming). Vegetation surveys were conducted each year from 2007 to 2013 except during  
 678 2011. Ds = dwarf shrub; hemicryptophytes include: *L. borealis* and grasses.

	Treatment		Year		T × Y	
	F <sub>(2,15)</sub>	<i>P</i>	F <sub>(4,60)</sub>	<i>P</i>	F <sub>(8,60)</sub>	<i>P</i>
<i>Alive:dead shoots</i>						
<i>E. nigrum</i>	13.8	<b>0.001</b>	0.7	0.596	2.0	0.128
<i>V. vitis-idaea</i>	52.6	<b>&lt;0.001</b>	1.8	0.171	1.8	0.144
<i>V. myrtillus</i>	10.7	<b>0.002</b>	9.7	<b>&lt;0.001</b>	3.3	<b>0.004</b>
<i>Biomass</i>						
Deciduous	2.8	0.094	4.0	<b>0.006</b>	2.3	<b>0.033</b>
<i>V. myrtillus</i> (ds)	2.1	0.152	14.9	<b>&lt;0.001</b>	2.4	<b>0.028</b>
<i>V. uliginosum</i> (ds)	0.9	0.414	0.5	0.593	2.3	0.092
<i>D. flexuosa</i>	0.4	0.666	7.7	<b>0.001</b>	0.4	0.826
Evergreens	0.9	0.422	5.1	<b>0.010</b>	3.0	<b>0.029</b>
<i>E. nigrum</i> (ds)	0.9	0.426	9.9	<b>&lt;0.001</b>	2.7	<b>0.036</b>
<i>V. vitis-idaea</i> (ds)	0.7	0.510	2.1	0.122	0.5	0.797
<i>L. borealis</i>	0.8	0.449	6.4	<b>0.006</b>	0.8	0.521
Dwarf shrubs	0.9	0.427	7.3	<b>&lt;0.001</b>	3.8	<b>0.004</b>
Hemicryptophytes	0.7	0.526	11.1	<b>&lt;0.001</b>	0.8	0.537
Moss (% cover)	0.8	0.459	8.0	<b>0.001</b>	0.8	0.549
Lichen (% cover)	1.6	0.424	50.8	<b>&lt;0.001</b>	0.9	0.464

679

680

681

682 Table 2. Repeated measures ANOVA statistics (F and *P* values) of the plant and cryptogam  
 683 diversity (H') and species richness in the plots of the extreme winter warming event  
 684 simulations. The experiment included 3 treatments of 6 replicate plots each and vegetation  
 685 surveys were conducted each year from 2007 to 2013 except during 2011.

	Treatment		Year		T × Y	
	F <sub>(2,15)</sub>	<i>P</i>	F <sub>(4,60)</sub>	<i>P</i>	F <sub>(8,60)</sub>	<i>P</i>
Vascular plants						
Diversity (H')	0.8	0.467	5.4	<b>&lt;0.001</b>	1.2	0.332
Richness	0.0	0.983	3.0	<b>0.017</b>	1.3	0.266
Cryptogams						
Diversity (H')	1.6	0.237	26.4	<b>&lt;0.001</b>	0.8	0.585
Richness	1.9	0.188	23.5	<b>&lt;0.001</b>	0.7	0.734

686

687

688 Table 3. Collembola species and Acari group abundance (ind.  $\times$  1000 / m<sup>2</sup>) in the extreme winter warming event plots. 2009 data sampled following  
 689 the third winter warming simulation and the 2012 data represent sampling after three years without treatments. Data are mean of n = 6 with standard  
 690 error between parentheses. Significant differences (Tukey HSD  $P < 0.05$ ) between treatments are indicated by different letters. Cn: control, CW:  
 691 canopy warming, CSW: Canopy and soil warming. Eu-edaphic: living in the soil, hemi-edaphic: living among the litter layers, epi-edaphic: living  
 692 among the plant canopy.

Species	2009			2012		
	Cn	CW	CSW	Cn	CW	CSW
<i>Lepidocyrtus lignorum</i>	1.38 (0.024)	1.06 (0.044)	1.08 (0.28)	2.53 (0.50)a	1.40 (0.48)ab	0.68 (0.13)b
<i>Entomobrya nivalis</i>	-	-	-	0.06 (0.04)	0.06 (0.04)	0.04 (0.03)
<i>Dicyrtomina fusca</i>	0.02 (0.02)	0.06 (0.04)	0.17 (0.08)	0.76 (0.35)	0.34 (0.13)	0.30 (0.11)
epi-edaphic	1.40 (0.23)	1.12 (0.44)	1.25 (0.34)	3.35 (0.84)a	1.80 (0.42)ab	1.02 (0.17)b
<i>Pseudachorutus corticicolus</i>	-	-	-	0.19 (0.05)	0.06 (0.06)	0.08 (0.04)
<i>Folsomia quadrioculata</i>	4.22 (1.41)	2.14 (0.60)	1.51 (0.39)	1.42 (0.37)	2.42 (0.65)	2.59 (1.18)
<i>Parisotoma notabilis</i>	0.06 (0.04)	0	0	0.40 (0.14)	0.19 (0.09)	0.11 (0.05)
<i>Isotoma viridis</i>	0.06 (0.04)	0	0.11 (0.05)	0.06 (0.03)	0.28 (0.07)	0.13 (0.07)
<i>Isotoma riparia</i>	-	-	-	0	0.06 (0.04)	0.02 (0.02)
<i>Isotoma sp./Isotomurus sp.</i>	-	-	-	0.36 (0.09)	0.28 (0.04)	0.23 (0.04)
<i>Desoria sp.</i>	0.28 (0.12)	0.30 (0.10)	0.15 (0.05)	0	0.02 (0.02)	0.02 (0.02)
hemi-edaphic	4.63 (1.46)	2.44 (0.64)	1.76 (0.41)	2.44 (0.37)	3.31 (0.59)	3.18 (1.15)
<i>Protaphorura cf. gisini</i>	2.84 (0.51)	2.16 (0.67)	3.71 (0.47)	3.54 (0.87)	2.33 (0.48)	3.65 (1.05)
<i>Willemia anophthalma</i>	5.16 (1.93)	5.18 (2.78)	2.19 (0.43)	1.42 (0.79)	1.90 (0.94)	0.81 (0.23)
<i>Folsomia sensibilis</i>	0.28 (0.25)	0	0.49 (0.33)	1.80 (1.12)	0.59 (0.35)	0.87 (0.71)
<i>Paranura sexpunctata</i>	-	-	-	0.04 (0.04)	0	0.02 (0.02)
<i>Isotomiella minor</i>	15.00 (2.00)a	9.46 (1.73)ab	6.41 (1.56)b	1.68 (0.40)	1.87 (0.71)	0.81 (0.23)
<i>Megalothorax minimus</i>	0.25 (0.14)	0.13 (0.07)	0.25 (0.08)	0.02 (0.02)	0.06 (0.02)	0
eu-edaphic	23.53 (2.34)a	16.93 (3.65)ab	13.05 (1.66)b	8.51 (2.69)	6.75 (1.39)	6.15 (1.67)
Collembola total	29.56 (1.76)a	20.50 (3.18)ab	16.06 (2.08)b	14.30 (2.74)	11.86 (1.58)	10.36 (2.51)
Oribatida	68.0 (13.5)a	38.3 (3.0)ab	34.3 (7.1)b	68.8 (11.7)	51.7 (8.0)	54.2 (8.1)
Astigmata-Prostigmata	65.3 (5.6)a	37.2 (3.9)b	33.2 (4.4)b	22.0 (5.4)	46.6 (13.6)	25.6 (5.1)
Mesostigmata	10.2 (0.9)a	9.2 (0.9)ab	7.1 (0.9)b	9.5 (2.2)	6.5 (1.4)	6.9 (0.8)
Acari total	143.5 (15.7)a	84.7 (4.9)b	74.5 (8.9)b	100.3 (16.4)	104.8 (12.9)	86.6 (7.7)

693

694 Table 4. Repeated measures ANOVA statistics (F and *P* values) of the ecosystem gas flux  
 695 (CO<sub>2</sub>) measurements during 2009, 2012 and 2013. The experiment included 3 treatments of 6  
 696 replicate plots each.

	Treatment		Year		T × Y	
	F <sub>(2,15)</sub>	<i>P</i>	F <sub>(2,30)</sub>	<i>P</i>	F <sub>(4,30)</sub>	<i>P</i>
ER	3.2	0.070	40.6	<b>&lt;0.001</b>	3.2	<b>0.029</b>
NPP	4.1	<b>0.027</b>	38.8	<b>&lt;0.001</b>	1.8	0.187
GPP	4.8	<b>0.025</b>	5.9	<b>0.007</b>	3.2	<b>0.025</b>

697

698

699 **Figures**

700 Figure 1. Shoot damage to the dominant dwarf shrub species in the extreme winter warming  
701 plots and from subsequent autumnal moth outbreak. Alive:dead shoot ratios of *E. nigrum* (a), *V.*  
702 *vitis-idaea* (b) and *V. myrtillus* (c). Grey shaded area indicates years with extreme winter  
703 warming event simulations and the vertical dashed line indicates the start of the autumnal moth  
704 outbreak (2012 and 2013). Cn: control, CW: Canopy warming, CSW: Canopy and soil  
705 warming. Bars are mean of 6 replicate plots with SE as error bars. ANOVA statistics are shown  
706 in Table 1. Data up to 2009 were previously presented in Bokhorst *et al.* (2011).

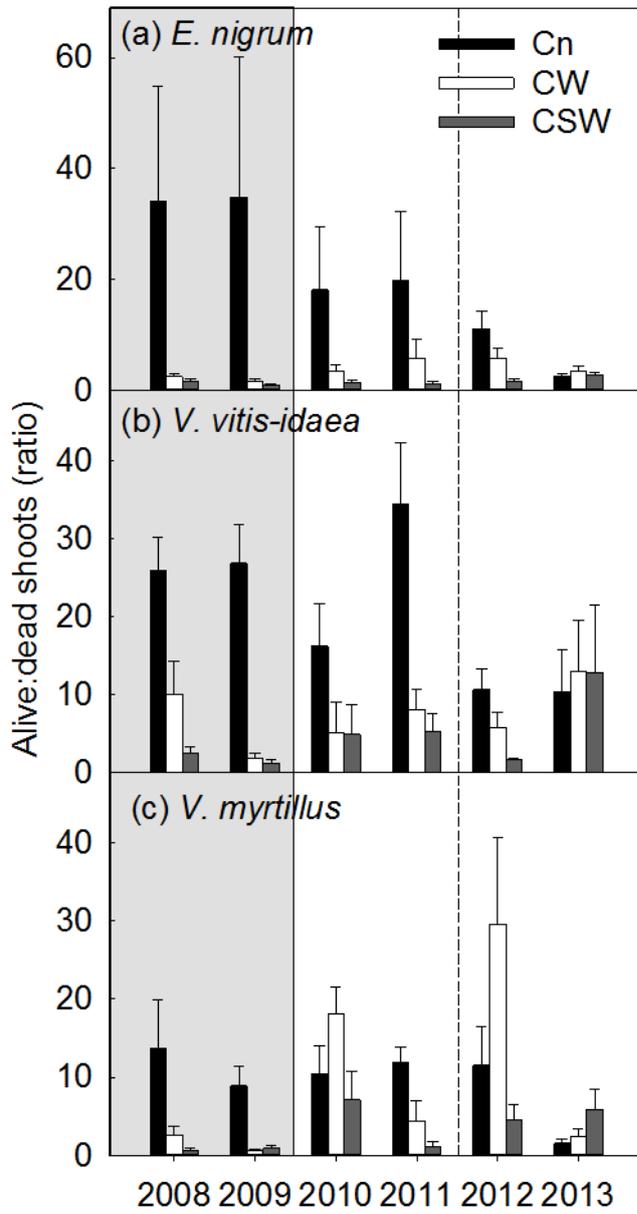
707

708 Figure 2. Change in total deciduous and evergreen plant biomass and individual species  
709 following extreme winter warming events and autumnal moth outbreaks. The percentage  
710 changes are in relation to the recorded biomass of 2007. Grey shaded area indicates period with  
711 extreme winter warming events and the vertical dashed line indicates the start of the autumnal  
712 moth peaks (2012 and 2013). Cn: control, CW: Canopy warming, CSW: Canopy and soil  
713 warming. Bars are mean of n = 6 replicate plots with SE as error bars. ANOVA statistics are  
714 shown in Table 2.

715

716 Figure 3. Changes in moss and lichen cover following extreme winter warming events (2007-  
717 2009) and the autumnal moth outbreaks (2012 and 2013). The percentage changes are in  
718 relation to the species cover measured in 2007. Cn: control, CW: Canopy warming, CSW:  
719 Canopy and soil warming. Bars are mean of n = 6 replicate plots with SE as error bars. ANOVA  
720 statistics are shown in Table 2.

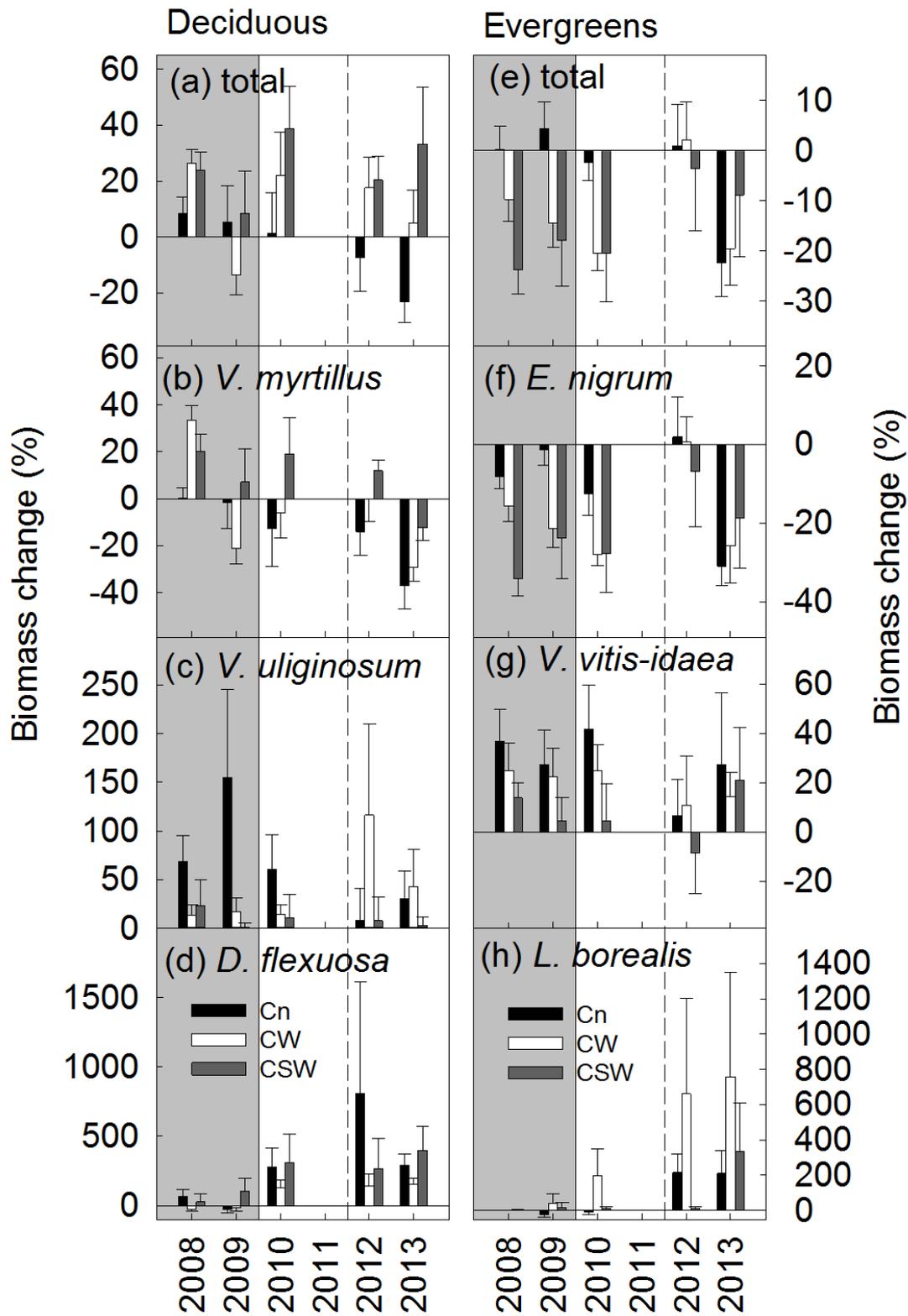
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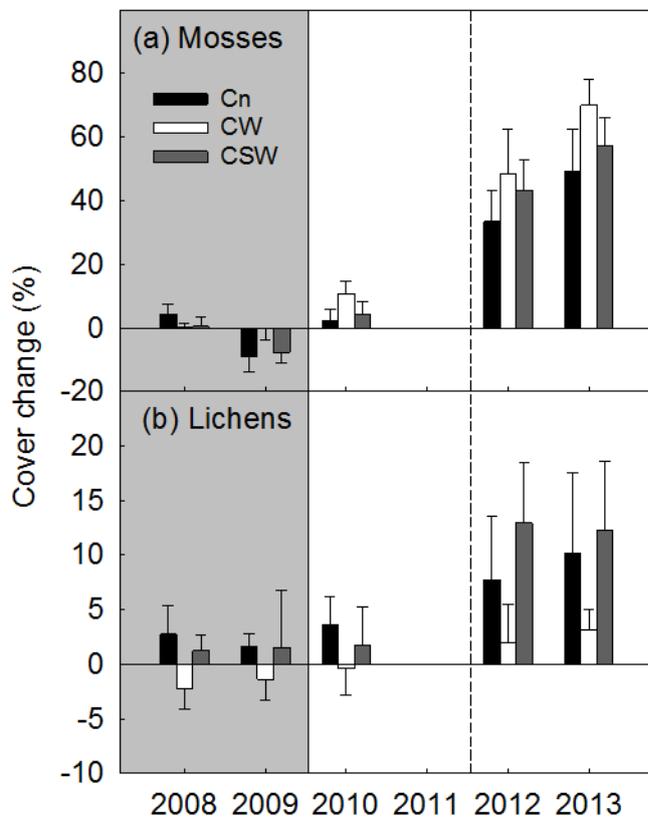


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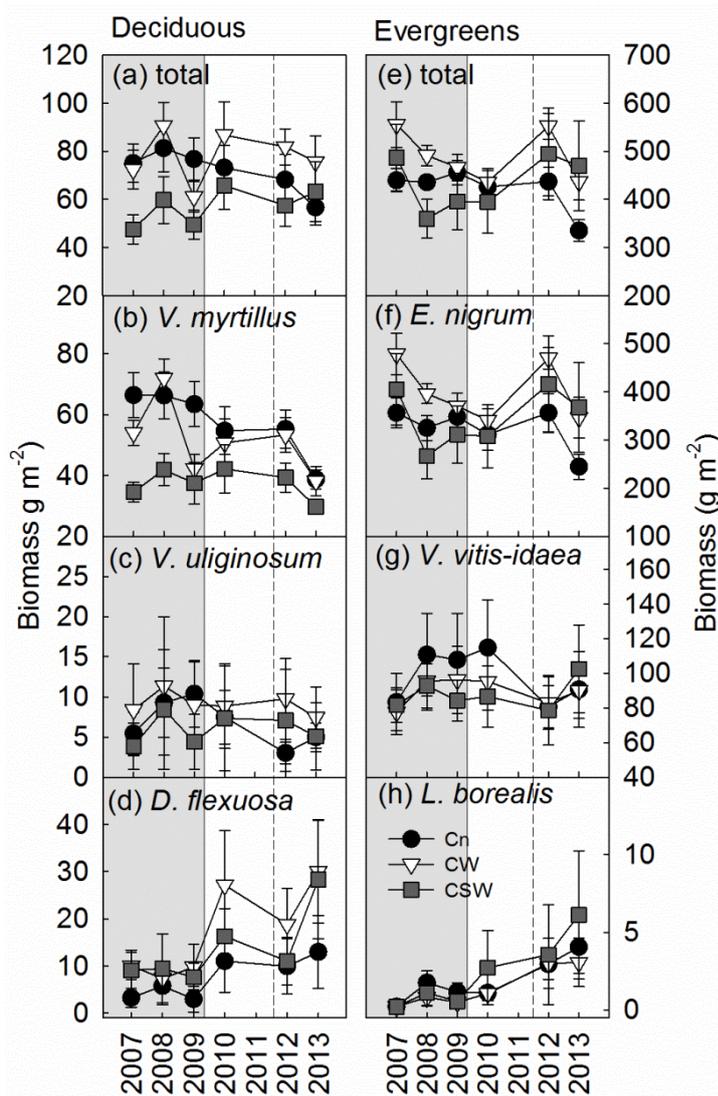


730 Figure 3.



731

732 Supporting information 1. Biomass of deciduous and evergreen plants following extreme winter  
 733 warming events and an autumnal moth outbreak (2012 and 2013). Data points are means of n  
 734 = 6 replicate plots with SE as error bars. Cn: control, CW: Canopy warming, CSW: Canopy  
 735 and soil warming. ANOVA statistics for the % changes in biomass are shown in Table 2. Grey  
 736 shaded areas indicate periods with extreme winter warming events. Vertical dashed line  
 737 indicates the start of the autumnal moth peaks (2012 and 2013).



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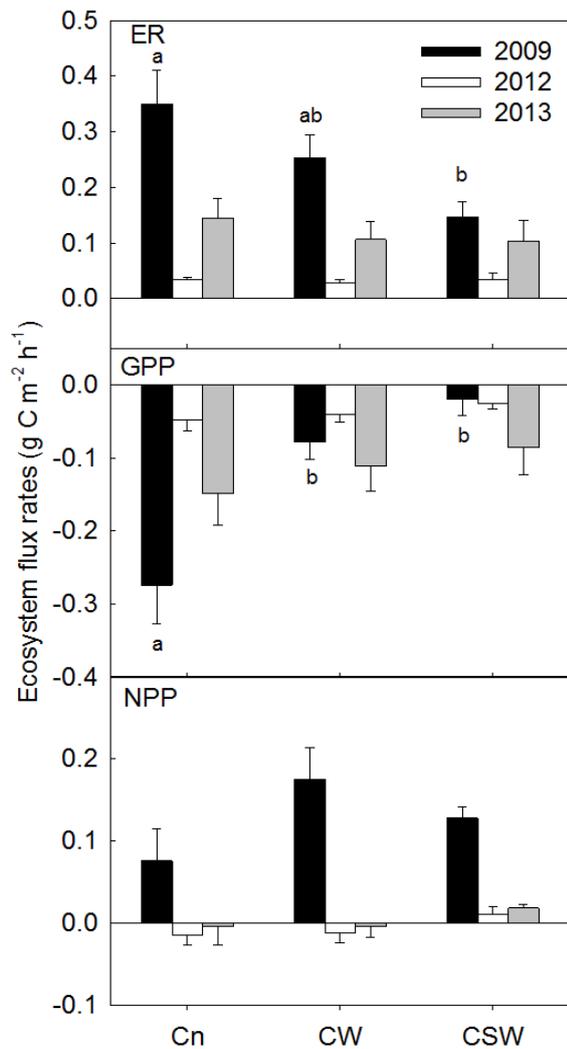
740 S2. Acari group and family abundance (ind.  $\times$  1000 / m<sup>2</sup>) in the extreme winter warming event plots. 2009 data sampled following the third winter  
 741 warming simulation and the 2012 data represent sampling after three years without treatments. Data are mean of n = 6 with standard error between  
 742 parentheses. Significant differences (Tukey HSD  $P < 0.05$ ) between treatments are indicated by different letters. Cn: control, CW: canopy warming,  
 743 CSW: Canopy and soil warming.

744

	2009			2012		
	Cn	CW	CSW	Cn	CW	CSW
Astigmata-Prostigmata	65.3 (5.6)a	37.2 (3.9)b	33.2 (4.4)b	22.0 (5.4)	46.6 (13.6)	25.6 (5.1)
Total Oribatida	68.0 (13.5)a	38.3 (3.0)ab	34.3 (7.1)b	68.8 (11.7)	51.7 (8.0)	54.2 (8.1)
Oppiidae	57.4 (14.1)	31.2 (2.2)	28.8 (7.0)	50.7 (11.2)	34.8 (5.5)	36.0 (7.7)
Phthiracaridae	0.2 (0.0)	0.3 (-)	0.1 (-)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Damaeus	0.3 (0.1)	0.2 (0.1)	0.1 (0.1)	0.3 (0.1)	0.1 (0.1)	0.2 (0.1)
Notrhidae	1.1 (0.3)	1.2 (0.3)	1.1 (0.4)	1.4 (0.6)	0.4 (0.1)	1.1 (0.3)
Brachypyliina	9.4 (3.4)	6.0 (2.1)	4.3 (0.6)	15.2 (3.7)	15.1 (5.1)	15.2 (4.3)
Total Mesostigmata	10.2 (0.9)a	9.2 (0.9)ab	7.1 (0.9)b	9.5 (2.2)	6.5 (1.4)	6.9 (0.8)
Parasitidae	6.2 (0.6)	5.6 (1.0)	4.9 (0.4)	4.9 (1.2)	3.8 (0.6)	4.3 (0.4)
Trachytidae	0.9 (0.3)	0.9 (0.3)	0.3 (0.1)	1.5 (0.6)	0.9 (0.4)	0.5 (0.2)
Uropodidae	3.1 (0.5)	2.7 (0.6)	1.9 (0.6)	3.1 (0.7)	1.8 (0.5)	2.0 (0.3)
Total Acari	143.5 (15.7)a	84.7 (4.9)b	74.5 (8.9)b	100.3 (16.4)	104.8 (12.9)	86.6 (7.7)

745

746 S3. Ecosystem CO<sub>2</sub> flux rates of experimental plots during 2009, 2012 and 2013. The 2012 and  
 747 2013 flux rates were consistently lower compared to 2009 (see table 3 for ANOVA statistics).  
 748 Gross primary production (GPP) is the difference between CO<sub>2</sub> flux measurements in full  
 749 ambient daylight (NPP) and ecosystem respiration (ER) measured in blacked-out chambers.  
 750 Positive values indicate CO<sub>2</sub> flux from the system to the atmosphere and negative CO<sub>2</sub> flux  
 751 from the atmosphere into the system. Bars with different letters indicate significant (Tukey's  
 752 HSD P < 0.05) differences between treatments. Bars are means of four to six replicate plots,  
 753 error bars are SE. The 2009 data was previously reported by Bokhorst *et al.* (2011).  
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