

1 **Environmental correlates of peatland carbon fluxes in a**  
2 **thawing landscape: do transitional thaw stages matter?**

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22 **Abstract**

23 Peatlands in discontinuous permafrost regions occur as a mosaic of wetland types, each with  
24 variable sensitivity to climate change. Permafrost thaw further increases the spatial heterogeneity  
25 in ecosystem structure and function in peatlands. Carbon (C) fluxes are well characterized in  
26 end-member thaw stages such as fully intact or fully thawed permafrost but remain  
27 unconstrained for transitional stages that cover a significant area of thawing peatlands.  
28 Furthermore, changes in the environmental correlates of C fluxes, due to thaw are not well  
29 described: a requirement for modeling future changes to C storage of permafrost peatlands. We  
30 investigated C fluxes and their correlates in end-member and a number of transitional thaw  
31 stages in a sub-arctic peatland. Across peatland lumped CH<sub>4</sub> and CO<sub>2</sub> flux data had significant  
32 correlations with expected correlates such as water table depth, thaw depth, temperature,  
33 photosynthetically active radiation and vascular green area. Within individual thaw states,  
34 bivariate correlations as well as multiple regressions between C flux and environmental factors  
35 changed variably with increasing thaw. The variability in directions and magnitudes of correlates  
36 reflects the range of structural conditions that could be present along a thaw gradient. These  
37 structural changes correspond to changes in C flux controls, such as temperature and moisture,  
38 and their interactions. Temperature sensitivity of CH<sub>4</sub> increased with increasing thaw in bivariate  
39 analyses, but lack of this trend in multiple regression analyses suggested confounding effects of  
40 substrate or water limitation on the apparent temperature sensitivity. Our results emphasize the  
41 importance of incorporating transitional stages of thaw in landscape level C budgets and  
42 highlight that end-member or adjacent thaw stages do not adequately describe the variability in  
43 structure-function relationships present along a thaw gradient.

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## 51 **1 Introduction**

52 Northern permafrost regions contain approximately 50% (1672 Pg) of the world's soil carbon  
53 (C) pool and peatlands store 277 Pg of this C (Schuur et al., 2008; Tarnocai et al., 2009).

54 Thawing permafrost is projected to act as a positive feedback to climate change via the release of  
55 soil C to the atmosphere and the magnitude of this feedback remains uncertain (Schuur et al.,  
56 2013). Peatlands in the permafrost regions are currently experiencing increased rates of thaw and  
57 related changes to abiotic and biotic components (structure) and elemental cycling (function;  
58 Camill, 2005; Osterkamp, 2005). Thawing peatlands are a mosaic of different wetland types,  
59 ranging from permanently frozen (*e.g.* *palsa*) to permafrost-free and minerotrophic fens (Luoto et  
60 al., 2004). Each component of these heterogeneous landscapes has distinct C function,  
61 contributing to uncertainties in estimating landscape level C budgets. Constraining the spatial  
62 variability in peatland C fluxes and related abiotic and biotic factors, is an essential step toward  
63 estimating the positive feedback potential of thawing permafrost on climate change.

64 Permafrost thaw in peatlands is associated with marked changes in ecosystem structure and  
65 function. Initial ground subsidence from thaw results in wet habitats due to a high water table  
66 (Smith et al., 2012). Relative to dry areas, the seasonal frost table thaws faster in wet areas,  
67 further increasing lateral flow of water to wet areas (Quinton et al., 2009). The increase in water  
68 table depth (WTD) leads to a vegetation shift toward wetter communities and an increase in  
69 graminoid species (Camill, 1999; Camill et al., 2001; Malmer et al., 2005). Rapid changes also  
70 occur in the microbial community, notably an increased activity of methane (CH<sub>4</sub>) and nitrogen  
71 cycling (Mackelprang et al., 2011). Associated with structural shifts, several functional changes  
72 have been observed in thawed permafrost peatlands. Typically plant productivity increases  
73 (Vogel et al., 2009), but so does autotrophic and heterotrophic respiration (Hicks Pries et al.,  
74 2013). Organic matter decomposition may decrease due to increased anoxic conditions after  
75 ground subsidence (Camill et al., 2001). Thus, there could be an initial increase in organic matter  
76 accumulation as a result of permafrost thaw (Turetsky et al., 2007; Vitt et al., 2000).  
77 Subsequently, decomposition may increase due to the increase in easily decomposable litter from  
78 community shifts toward more vascular plants (Hodgkins et al., 2014; Turetsky, 2004) and  
79 quantity of litter (Malmer et al., 2005). Regardless of the initial increase in C accumulation, the  
80 net radiative forcing of a recently thawed area is offset by an increase in CH<sub>4</sub> emissions  
81 (Johansson et al., 2006; Sitch et al., 2007; Turetsky et al., 2007). This increase in CH<sub>4</sub> emissions

82 may be a direct result of increased temperature on microbial processes or indirect consequences  
83 such as increases in plant mediated transport of CH<sub>4</sub> by increased graminoid abundance and  
84 increased anaerobic decomposition due to a high water table (Christensen et al., 2004). In  
85 addition to magnitude, the dominant pathway of methane production is also altered after thaw,  
86 shifting from CO<sub>2</sub> reduction (hydrogenotrophic) to acetate cleavage (acetoclastic; Hodgkins et  
87 al., 2014; McCalley et al., 2014). The change in pathway is likely related to shifts in vegetation,  
88 for example, a decrease in *Sphagnum* abundance could lead to an increase in pH and related  
89 increase in acetoclastic methanogens (Hines et al., 2008; Ye et al., 2012). Dissolved organic  
90 matter (DOM) is also more labile in the more thawed stages and there is increased export of  
91 DOM out of the peatland catchment (Hodgkins et al., 2014; Olefeldt and Roulet, 2012, 2014).  
92 Recent studies highlight the interactive controls on C fluxes, emphasizing that net radiative  
93 forcing of a thawing ecosystem depends on non-linear interactions among temperature, degree of  
94 anoxia and organic matter chemistry (Lee et al., 2012; Treat et al., 2014). For example, while  
95 temperature sensitivity of CH<sub>4</sub> flux increases in wet habitats (Olefeldt et al., 2013), ecosystem  
96 respiration is more sensitive in dry conditions (McConnell et al., 2013). Interactive controls on C  
97 fluxes are further complicated by the variable structural conditions as thaw progresses, and the  
98 overall effect on landscape level fluxes remains unconstrained.

99 Changes to peatland structure and function due to permafrost degradation have been studied  
100 using a chronosequence approach with sites that have intact permafrost, completely thawed  
101 permafrost and one or two intermediate stages (e.g., Bäckstrand et al., 2010; Turetsky et al.,  
102 2007; Vogel et al., 2009). While end-member and major thaw stages of the permafrost gradient  
103 have been well characterized for plant community structure and carbon cycling, the same is not  
104 true for the transitional vegetation communities. Carbon cycling in thawing permafrost regions is  
105 spatially heterogeneous (e.g. Belshe et al., 2012; Morrissey and Livingston, 1992; Zhang et al.,  
106 2012) and a significant portion of the landscape is in varying stages of thaw. Spatial  
107 heterogeneity and transitional stages are therefore important to the ecosystem level C exchanges.  
108 It is unclear whether 3 to 5 thaw classes of intact, intermediate and fully thawed permafrost can  
109 be used to adequately extrapolate landscape scale C fluxes and their abiotic and biotic correlates.  
110 Additional thaw stages may help resolve landscape scale C fluxes in models.

111 Our study aims to identify the abiotic and biotic factors (hereafter, correlates) that relate to C  
112 function and investigate how these correlates change along end-member and transitional  
113 permafrost thaw stages. Our research questions are: 1) which correlates best explain the CH<sub>4</sub> and  
114 CO<sub>2</sub> fluxes across all thaw stages at a peatland where permafrost is thawing? 2) How does the  
115 importance of these correlates change along a gradient of increasing thaw? Our selection of  
116 measured correlates was based on current understanding of C flux relationships with  
117 temperature, moisture, pH, nutrients and plant biomass. Given the interactive nature of controls  
118 on C fluxes and variable structural changes after thaw, we expected to see no relationship  
119 between dominant correlates of C flux and degree of thaw.

## 120 **2 Methods**

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### 122 **2.1 Study site**

123 The study site, Stordalen mire is located 10 km east of Abisko in Sweden (68°22' N, 19°03' E).  
124 The Stordalen peatland complex consists of several landscape units and wetland types.  
125 Permafrost is present in the dry hummocky sections of the peatland (palsa mire). Also present are  
126 areas where permafrost is thawing or has disappeared with vegetation communities that have  
127 been classified as semi-wet, wet, and tall graminoid (Johansson et al., 2006; Kvillner and  
128 Sonesson, 1980). Generally, the drier areas of the peatland complex are composed of species  
129 such as *Empetrum hermaphroditum*, *Betula nana*, *Rubus chamaemorus*, *Eriophorum vaginatum*,  
130 *Dicranum elongatum* and *Sphagnum fuscum*. The wetter areas consist of species such as *E.*  
131 *vaginatum*, *Carex rotundata*, *S. balticum*, *E. angustifolium*, *C. rostrata*, *S. lindbergii*, and *S.*  
132 *Riparium*. The long term (1912-2003) mean precipitation measured at the Abisko Scientific  
133 Research Station (10 km from the site) is 303.3 mm, of which 150 mm occurs between June and  
134 September. The long term (1912-2009) mean annual temperature at the site is -0.5°C but has  
135 surpassed 0°C in the recent decades (summarized in Olefeldt and Roulet (2012) from  
136 observations made at Abisko Scientific Research Station). Smoothed mean annual temperature  
137 trends suggest a 2.5°C increase between 1913 and 2006. (Callaghan et al., 2010).

## 138 **2.2 Vegetation community and thaw stage selection**

139 Ten vegetation communities were selected across Stordalen to represent major stages along the  
140 thaw gradient. Selection of communities was based on an across site survey of dominant  
141 vegetation communities, coupled with characterization of water table depth and active layer  
142 thickness. The sequence of the 10 thaw stages was based on a survey of spring thaw depth and  
143 previously established vegetation community relationships with permafrost thaw (Johansson et  
144 al., 2006; Kvillner and Sonesson, 1980).

## 145 **2.3 Gas flux measurements**

146 Within each of the 10 selected communities 3 collars of 0.05 m<sup>2</sup> area [each](#) were inserted in the  
147 peat surface and served as a seal for the manual gas flux measurements; with the exception of 2  
148 communities that had only 2 collars each as they represent a small area in the mire (Table 1).  
149 Each community also had a PVC dip well installed to measure the water table depth.

150 Methane flux was measured using opaque chambers of volume 9 or 18 liters. [Five headspace](#)  
151 [gas samples of 20 ml each were collected every 5 min over 20 min.](#)~~Headspace gas samples were~~  
152 ~~collected every 5 minutes over 25 minutes.~~ Prior to collecting each sample, the headspace was  
153 mixed using a syringe. The collected headspace samples were analyzed within 24 hours for  
154 concentrations of CH<sub>4</sub> using a Shimadzu GC-2014 gas chromatograph with a flame ionization  
155 detector, after separation on a HayeSep-Q packed column at the Abisko Scientific Research  
156 Station. Helium was used as a carrier gas at the flow rate of 30 ml min<sup>-1</sup>. Injector, column and  
157 detector temperatures were 120, 40 and 120 °C, respectively. A 10-repetition run of known CH<sub>4</sub>  
158 standard (2 ppm concentration) was used to calibrate the GC before and after each sample run.  
159 Accuracy of the analysis (calculated with the standard deviation of the 10 standard replicates)  
160 was ±0.1 to 0.75%. Flux rates were then calculated using the slope of the linear relationship  
161 between gas concentrations and time. Only the relationships with a significant (p<0.05) R<sup>2</sup> above  
162 0.85 for the 5 time points were kept to calculate fluxes. If one of the five samples deviated from  
163 the linear fit, flux was calculated without it as long as the R<sup>2</sup> was greater than 0.95. Methane was  
164 measured on 7 days and 12 days in the 2012 and 2013 growing seasons, respectively.

165 For carbon dioxide flux measurements on the 28 collars, we used clear cylindrical polycarbonate  
166 chambers (13 liter volume). The air enclosed within the chambers was mixed by fans and

167 circulated through an infrared gas analyzer (PP Systems, Model EGM-4) that measured changes  
168 in CO<sub>2</sub> over 3-min measurement intervals (recording every 10 seconds for the first minute, and  
169 then every 30 seconds for the last 2 minutes). [Over the 3 minute measurement period, on](#)  
170 [average, temperature in the chamber only increased by 1.9 °C.](#) Measurements were performed  
171 for full sun, with a mesh cover and finally with a black shroud, so that data from varying light  
172 intensities could be collected. Photosynthetically active radiation (PAR) was measured (Model  
173 LI-190SA, LI-COR<sup>®</sup>, NE, USA) within each chamber over the sample interval. Fluxes were  
174 calculated using a linear regression of CO<sub>2</sub> concentration change over time. CO<sub>2</sub> was sampled on  
175 10 days during the 2013 growing season.

## 176 **2.4 Ancillary measurements**

177 Each flux measurement of CO<sub>2</sub> or CH<sub>4</sub> was coupled with simultaneous measurements of soil  
178 temperature at 10 cm, air temperature, thaw depth and water table depth (WTD). Once during the  
179 2012 growing season, elevation (above sea level) of each collar was measured using a RTK-  
180 GPS.

181 Vegetation composition for vascular plants was surveyed once every growing season in each of  
182 the collars recording the percent cover of each species. In 2013, vascular green area (VGA) was  
183 also measured on 4 days during the growing season using species specific formulae based on  
184 leaf-geometry (Lai, 2012; Wilson et al., 2006). For each collar, the total number of green leaves  
185 per species was recorded along with width and length of 10 leaves for each species. The  
186 seasonality of VGA was modeled using a Gaussian fit and combined with a quadratic fit with  
187 elevation to extrapolate a spatially and temporally higher resolution dataset for VGA.

188 [Throughout the manuscript we only use the modeled VGA, referred to as modeled VGA in the](#)  
189 [text.](#)

190 Surface water was sampled near the collars on each CH<sub>4</sub> sampling day in thaw stages that had  
191 persistent water table throughout the growing season (Thaw stages 5, 7, 8, 9 and 10). Surface  
192 water samples were analyzed for pH and conductivity (Oakton<sup>®</sup> portable pH conductivity meter)  
193 and reduced conductivity was calculated by removing H ion concentrations from the  
194 conductivity. Subsequently, samples were filtered using Whatman<sup>®</sup> Glass Fiber Filters (0.45 μm

195 pore size) and analyzed for dissolved organic carbon and total nitrogen using a Shimadzu TOC-  
196 V series Analyzer.

## 197 **2.5 Data analysis**

198 *CH<sub>4</sub> flux*- Each flux measurement was log<sub>10</sub> transformed after adding 12 mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup> to the  
199 original value (to account for all the negative fluxes). [Log<sub>10</sub> transformation decreased the skew in](#)  
200 [the raw data and improved the linear relationship between methane and other variables, allowing](#)  
201 [for the use of multiple linear regressions.](#) Bivariate relationships with abiotic and biotic factors  
202 were explored with Spearman's rank-order correlations. To explore the relationship between  
203 environmental correlates and CH<sub>4</sub> flux, we used stepwise multiple linear regression. [We used](#)  
204 [both additive and interactive effects to explore a best fit model, but found that interactive effects](#)  
205 [were either insignificant or had a weak contribution to the overall model. For ease of](#)  
206 [interpretation, given that our variables are already proxies for several interacting controls on](#)  
207 [methane fluxes, we only included additive effects in our final model.](#) The best fit model met the  
208 necessary assumptions of normality and homoscedasticity of model residuals. Multicollinearity  
209 was checked using variance inflation factors (VIF), wherein any explanatory variable with VIF  
210 greater than 2 was removed from the model.

211 Arrhenius plots were utilized to study the temperature sensitivity of CH<sub>4</sub> flux, regressing the log  
212 of CH<sub>4</sub> flux with inverse of temperature in Kelvin.

213 *CO<sub>2</sub> flux*- We combined all CO<sub>2</sub> flux data using nonlinear regression of a rectangular hyperbola  
214 to describe the relationship of NEE and PAR (Bubier et al., 2003)-

$$215 \quad NEE = \frac{GP_{MAX} \times PAR \times \alpha}{PAR \times \alpha + GP_{MAX}} + A \quad (1)$$

216

217 Where the parameters are:

218 GP<sub>MAX</sub> - the maximum gross photosynthetic CO<sub>2</sub> capture at maximum PAR (μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>)

219 α - the photosynthetic quantum efficiency (μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> per μmol PAR m<sup>-2</sup> s<sup>-1</sup>)

220 A - the dark respiration at 0 °C (μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>)



221 Other than PAR, we expected to see non-linear relationships between CO<sub>2</sub> flux and WTD, thaw  
222 depth, soil temperature and VGA, but we did not find significant relationships. Instead we found  
223 linear relationships to be significant. Since our data were non-parametric, we used Spearman's  
224 correlation coefficients to quantify the link between CO<sub>2</sub> flux with abiotic and biotic  
225 variables. Linear regressions were performed between the CO<sub>2</sub> flux data as well as WTD, thaw  
226 depth, soil temperature and VGA.

227 *Thaw gradient analyses-* above analyses for CH<sub>4</sub> and CO<sub>2</sub> were repeated independently for each  
228 of the 10 thaw stages. Subsequently, strength (adjusted R<sup>2</sup> or Spearman's ρ) and direction of  
229 relationships between correlates and function variables were organized by thaw stage to observe  
230 whether there is a significant trend in changing correlates of CH<sub>4</sub> and CO<sub>2</sub> fluxes along the thaw  
231 gradient. The sequence of thaw stages along the gradient was based on a survey of spring thaw  
232 depth, as discussed in section 2.2. Multiple regressions were also performed for each thaw stage  
233 since CH<sub>4</sub> and CO<sub>2</sub> fluxes are not typically estimated using bivariate models. While the bivariate  
234 correlations identified how the dominant correlates change across the thaw gradient, multiple  
235 regressions across the thaw gradient provide a better idea of the changing interactive effects of  
236 abiotic and biotic correlates on CH<sub>4</sub> or CO<sub>2</sub> fluxes.

237 Lastly, we evaluated the relationship between CH<sub>4</sub> and CO<sub>2</sub> fluxes using a simple CH<sub>4</sub>: CO<sub>2</sub> flux  
238 ratio. To use a standardized measure of CO<sub>2</sub> flux we use the GP<sub>MAX</sub> from each thaw stage.

### 239 **3 Results**

#### 240 **3.1 Across peatland C fluxes and correlates**

241 Mean and standard error of CH<sub>4</sub> flux across all collars from 2 years of sampling was 91.25±8.17  
242 mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup>, ranging from -1.1±0.3 to 370.2±52.1 mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup> (Table 1).

243 Strongest bivariate relationships between CH<sub>4</sub> flux and abiotic variables were with elevation,  
244 water table depth, pH, VGA, thaw depth and surface water C:N (Fig. 1). Significant but weaker  
245 relationships were also found with soil temperature and Julian day. TC, TN, conductivity and  
246 reduced conductivity did not have a significant relationship with CH<sub>4</sub> flux.

247 The best fit multiple regression model for CH<sub>4</sub> fluxes across the peatland included elevation,  
248 thaw depth, VGA and soil temperature, in decreasing order of contribution to the overall model,  
249 and these variables were able to explain 73% of the variance in CH<sub>4</sub> flux (Table 2). [An  
250 alternative model that excluded elevation wherein the adjusted R<sup>2</sup> drops to 0.62, is also reported  
251 as it better isolated the effects of VGA, soil temperature and thaw depth. The contribution \(beta  
252 weights reported in brackets\) of soil temperature \(0.16\) and thaw depth \(-0.27\) are similar in the  
253 model with or without elevation. The contribution of VGA increases from 0.26 to 0.58 when  
254 elevation is removed from the model.](#)

255 Photosynthetically active radiation showed the strongest relationship with CO<sub>2</sub> fluxes, explaining  
256 55% of the variance observed in the flux data (Fig. 2). The rectangular hyperbola fit of NEE  
257 against PAR, Eq. (1), provided the following parameter estimates and standard errors for the  
258 across site lumped data: GP<sub>MAX</sub> was 4.24±0.26 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>, α was 0.027±0.005 μmol CO<sub>2</sub>  
259 m<sup>-2</sup> s<sup>-1</sup> per μmol PAR m<sup>-2</sup> s<sup>-1</sup> and A was -1.78±0.09 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>.

260 Water table depth and thaw depth showed weak relationships with NEE and GPP (calculated  
261 using NEE minus R<sub>eco</sub>; Table 3). Soil temperature was also related to R<sub>eco</sub> and NEE. NEE and  
262 R<sub>eco</sub> were most strongly related to the mean growing season VGA (Table 3).

### 263 **3.2 Correlate-function relationships within the thaw stages**

264 Along the thaw gradient, the strength and direction of bivariate relationships among  
265 environmental variables and CH<sub>4</sub> flux changed variably (Fig. 3). No significant trend along the  
266 thaw gradient was observed for the relationship between CH<sub>4</sub> flux and elevation, VGA (vascular  
267 green area) and WTD. Significant trends were observed with the water chemistry variables of  
268 pH, C:N, TC, TN and conductivity and strength of correlations between correlate and CH<sub>4</sub> flux  
269 increased as the permafrost thawed. However, these data were only available for thaw stages  
270 with a water table (thaw stages 5 to 10). Soil temperature, thaw depth and Julian day, with data  
271 available for each of the 10 thaw stages, showed significant trends along the thaw gradient in  
272 their correlation with the CH<sub>4</sub> flux (Fig. 4 a, b, and c). There was an increase in the amount of  
273 variance explained in the CH<sub>4</sub> flux by temperature as well as the slope of this relationship (Fig.  
274 5).

275 The parameter estimates from the best fit model of across peatland lumped flux data, as shown in  
276 Table 2, were used as inputs for individual multiple regression models for each thaw stage. The  
277 interactive effects of elevation, soil temperature, thaw depth and vascular green area (VGA)  
278 showed varying results across the thaw gradient (Fig. 6). The model  $R^2$  values ranged from 0.09  
279 (insignificant) to 0.79 (significant with  $p < 0.0001$ ). Generally, elevation, soil temperature, thaw  
280 depth and VGA were better predictors of variance in  $CH_4$  fluxes in the later stages of thaw.

281 Model fit was non-significant for stages 2 and 3, and therefore their slope coefficients are not  
282 reported in Fig 6.

283 The relationship of NEE with temperature and with PAR varied across the thaw gradient without  
284 a statistically significant trend. Generally there is a trend of increasing,  $GP_{MAX}$ ,  $\alpha$  and A, going  
285 from less thawed to more thawed stages (Table 4). Furthermore, the amount of variance of NEE  
286 explained by PAR was typically higher in the more thawed stages.

### 287 3.3 The relationship between $CO_2$ and $CH_4$

288  $GP_{MAX}$  and  $CH_4$  were positively correlated ( $\rho = 0.56$ ,  $p = 0.0021$ ; Fig. 7). We found that the best  
289 explanatory variables for  $CH_4$ :  $GP_{MAX}$  ratio were *Sphagnum* percent cover ( $\rho = -0.72$ ,  $p = 0.008$ ;  
290 and graminoid VGA ( $\rho = 0.63$ ,  $p = 0.0004$ ). While graminoid VGA did not have any interactive  
291 effects with abiotic variables in explaining  $CH_4$ :  $GP_{MAX}$  ratio, *Sphagnum* cover and soil  
292 temperature had a significant interactive effect (Table 5)

293

## 294 **4 Discussion**

295 We identified the major abiotic and biotic correlates of the ecosystem – atmospheric exchanges  
296 of  $CO_2$  and  $CH_4$  across Stordalen mire and found that, as per our expectation, these environment-  
297 function relationships changed variably across the thaw gradient, suggesting that correlates of  
298  $CO_2$  and  $CH_4$  fluxes in transitional stages are not necessarily represented well by correlates of  
299 the end-member or adjacent thaw stages. Contrary to our expectation, we did see significant  
300 trends with thaw in certain bivariate correlations of  $CH_4$  fluxes such as temperature sensitivity,  
301 seasonality and effect of deepening frost table during the growing season. However, these trends

302 were absent when multiple correlates were considered together, suggesting that dominant  
303 controls on C fluxes and their interactions, change variably as thaw progresses.

#### 304 **4.1 Across peatland correlates of C fluxes**

305 Strongest environmental factors associated with the CH<sub>4</sub> flux across all sampled collars were-  
306 elevation, water table depth, pH, VGA, thaw depth and surface water C:N. Each of these  
307 correlates is a possible proxy of one or more controls of temperature, moisture and substrate  
308 quantity and quality on CH<sub>4</sub> flux. Our correlations support previous findings from various  
309 wetland types (as reviewed in Lai, 2009; Olefeldt et al., 2013; Turetsky et al., 2014). The  
310 multiple regression of lumped data across Stordalen also showed similar trends to other  
311 temperate, boreal or arctic peatlands. For example, a peatland complex sampled in the  
312 discontinuous permafrost region of Manitoba, Canada by Bubier et al. (1995) showed a best fit  
313 model including WTD, water chemistry and vegetation variables explaining 81% of the variance  
314 in CH<sub>4</sub> fluxes. Bubier et al. (1995) reported WTD as being the strongest individual correlate with  
315 the CH<sub>4</sub> fluxes, but in our best fit model, WTD was not an important variable likely because the  
316 stages with little or no thaw had no water table. Elevation seems to be a better proxy for soil  
317 moisture (and other CH<sub>4</sub> controls), showing the highest contribution to the best fit model (Table  
318 2). Elevation has been previously recognized as an integrator of multiple structural changes  
319 resulting from permafrost thaw and is a potentially useful component of models estimating C  
320 flux in permafrost landscapes (Lee et al., 2011). [Rerunning the best fit model without elevation  
321 decreases the overall model fit by 10% but increases the contribution of VGA to the model,  
322 while the contribution of thaw depth and soil temperature remain the same. Removal of elevation  
323 from the model better isolates the relative effects of thaw depth, temperature and VGA on  
324 methane fluxes and suggests that the strongest contribution is from VGA, followed by thaw  
325 depth and soil temperature. VGA is likely a strong effect as it is linked with spatial and seasonal  
326 changes in substrate availability, litter input and root exudates and thus relates to both spatial and  
327 temporal variability in CH<sub>4</sub> flux \(Whiting and Chanton 1993\).](#)

328 Soil temperature and thaw depth are significant variables in our multiple regression model of  
329 CH<sub>4</sub> flux, while Julian day is not. It may be that across the permafrost gradient, Julian day does  
330 not capture seasonality as well as a combination of thaw depth and soil temperature (Table 2),

331 suggesting the role of the variable seasonal trajectories of thaw depth and soil temperature in the  
332 different thaw stages, for predicting CH<sub>4</sub> flux.

333 As expected, PAR was the strongest correlate of NEE both in across peatland lumped data and  
334 within thaw stage data. Using the rectangular hyperbola fit, Frohking et al. (1998) reported  
335 parameters from 13 peatland sites wherein PAR explained, on average, 68% (ranging from 47 to  
336 89%) of the variance in NEE. [Comparatively our across peatland lumped data fit to the  
337 rectangular hyperbola model explain a lower percent of the variance \(52 %\) in NEE, likely due  
338 to biases introduced by the high spatial heterogeneity on our site](#) (Laine et al., 2009).  
339 ~~Comparatively our across peatland lumped data fit to the rectangular hyperbola model explain a  
340 lower percent of the variance (52%) in NEE, likely due to the structural heterogeneity on our  
341 site.~~ WTD, thaw depth and soil temperature also show significant but weak relationships with  
342 CO<sub>2</sub> fluxes. Vascular green area seems to be a better proxy than WTD, thaw depth and soil  
343 temperature for controls on CO<sub>2</sub> fluxes, which ~~was~~ makes sense as VGA represents the amount  
344 of photosynthesizing area as well as approximates above and belowground biomass which is  
345 related to autotrophic and heterotrophic respiration (Schneider et al., 2011; Wilson et al., 2006).

#### 346 **4.2 Trends with increasing thaw**

347 Bivariate relationships between correlates and CH<sub>4</sub> flux progress variably as the permafrost  
348 thaws although some significant trends of increasing correlations are seen in soil temperature,  
349 thaw depth and Julian day, as thaw progresses (Fig. 3, 4 and 5). We found that as the permafrost  
350 thaws, temperature sensitivity increases (Fig. 4a), increasing thaw depth has an increasing effect  
351 on CH<sub>4</sub> fluxes (Fig. 4b) and there is a stronger seasonality effect (Fig. 4c). This trend of  
352 increasing correlation could be partly due to the increasing magnitude and variance of not only  
353 CH<sub>4</sub> fluxes but also the environmental variables with thawing permafrost. [Additionally, higher  
354 VGA later in the growing season could also be result in a stronger seasonality effect \(Fig. 4c\) in  
355 the later stages of thaw, especially as these stages had the highest sedge VGA.](#) The Arrhenius  
356 plots of soil temperature and CH<sub>4</sub> fluxes showed increased temperature sensitivity from less  
357 thawed to more thawed stages, with the slope and R<sup>2</sup> of this regression increasing (Fig. 5).  
358 Changing temperature sensitivity in our results contradicts results from Yvon-Durocher et al.  
359 (2014) that suggest a consistent temperature sensitivity of CH<sub>4</sub> fluxes across scales. Apparent  
360 temperature sensitivity can be confounded due to changes in substrate availability (Kirschbaum,

2006). Increasing temperature sensitivity with thaw in our results could be related to higher substrate availability (supported by higher VGA) in thawed stages switching CH<sub>4</sub> production from being substrate limited to becoming temperature limited. Lower temperature sensitivity in the intact permafrost could also be related to DOC quality. Olefeldt et al. (2012) report higher aromaticity in DOC exported from palsas and bog catchments at Stordalen compared to fen catchments and a high proportion of aromatic compounds in litter is generally associated with decreased temperature sensitivity (eg. Erhagen et al., 2013). High temperature sensitivity in wetter sites has also been reported by Olefeldt et al. (2013) in a meta-analysis of CH<sub>4</sub> emissions from terrestrial ecosystems worldwide. Christensen et al. (2003) found that temperature is a limiting factor only when the WTD is 10 cm or less below the surface, whereas a lower WTD is more sensitive to WTD fluctuations than to soil temperature fluctuations. This is generally supported in our results with stages 4 to 6 that have growing season mean WTD greater than 10 cm (Table 1) having lower sensitivity to WTD than stages 7 to 10, though there is variability in both classes (Fig. 3). [Our estimated temperature sensitivity for each thaw stage is the net effect of temperature on methanogenesis and methanotrophy and since we only measure the net CH<sub>4</sub> flux we cannot isolate the relative temperature sensitivities for the two processes.](#) Also interesting is the effect of the increasing thaw, over the growing season, on CH<sub>4</sub> flux- more significant in the wetter more thawed stages than the drier intact permafrost stages (Fig. 3 and 4b). A similar trend was also emphasized in Olefeldt et al. (2013). The deepening frost table is related to temperature and thus could also represent the larger temperature sensitivity of CH<sub>4</sub> in later thaw stages. Additionally, larger variance in thaw depths of later thaw stages could explain the larger effect of thaw depth in these stages. The larger variance in thaw depth could be attributed to a steeper drop in thaw depths as the growing season progresses in the wetter thaw stages due to the dependence of thermal conductivity of peat on the degree of wetness (Quinton et al. 2009).

While bivariate relationships between correlates and C flux provide insight into the possible controls on these fluxes, multiple regressions better demonstrate the interactive nature of these correlates. Re-running the best fit model of the lumped data (Table 2) for each thaw stage showed that the strength of the overall model and the parameter estimates are variable along the thaw gradient (Fig. 6). While elevation had a strong effect in across peatland lumped data, it makes sense that it was a significant effect only for a few within thaw stage analyses (thaw

392 stages 1, 4, 8 and 9) because these stages had diverse habitats with spatially varying elevations.  
393 Soil Temperature was not a statistically significant estimate for any of the thaw stages, possibly  
394 because elevation and thaw depth [are better proxies for the long term thermal regime and also](#)  
395 [relate to several other controls of CH<sub>4</sub> flux, as previously mentioned.](#)~~(significant for stages 1, 4,~~  
396 ~~5, 7, 8 and 10) better accounted for thermal regimes.~~ VGA was only a significant effect within  
397 thaw stages 8 and 9. These results emphasize that spatial differences in elevation are not as  
398 important within thaw stages as they were in across peatland lumped data. Also, thaw depth and  
399 VGA have variable effects but generally stronger in the thawed stages.

400 Similar to CH<sub>4</sub> flux, the strength of the major correlate for CO<sub>2</sub> flux (PAR) changes variably  
401 across the thaw gradient. While the across peatland relationship of NEE with temperature and  
402 PAR is weaker than that found in other peatland sites (e.g. Bubier et al., 2003), when broken  
403 down into thaw stages, the percent variance of NEE explained increases (up to 91%; Table 4) for  
404 many thaw stages. The sample size for each thaw stages is different making it problematic to  
405 statistically compare the thaw stages. However, we found that the R<sup>2</sup> is not significantly  
406 correlated to the sample size for that thaw stage, suggesting that there are other factors increasing  
407 the control of PAR on NEE as permafrost thaws such as increased photosynthesizing biomass  
408 (reflected by increasing VGA and GPP). If VGA is no longer limiting, PAR sensitivity could be  
409 increasing as permafrost thaws. This is supported in the parameter fitting for each thaw stage  
410 (Table 4), the general trends observed are that the CO<sub>2</sub> fixed at maximum PAR (GP<sub>MAX</sub>)  
411 increases as permafrost thaws as does the amount of CO<sub>2</sub> fixed per unit of PAR ( $\alpha$ ), both of  
412 which could be related to increase in VGA but also the photosynthetic capacity change from  
413 plant species changes. The amount of respiration at 0°C generally increases with thaw, which  
414 could be related to increasing substrate availability. Trends of increasing GPP and ecosystem  
415 respiration with permafrost thaw have been reported in previous studies (eg. Dorrepaal et al.,  
416 2009; Hicks Pries et al., 2013). However, in our results these trends are not significant along the  
417 thaw gradient and progress variably.

### 418 **4.3 Relationship between NEE and CH<sub>4</sub>**

419 NEE is thought to be related to CH<sub>4</sub> emissions due to the shared association with recently  
420 produced substrate availability, root exudates and turnover and litter input, and this link has been  
421 observed in several studies (Bellisario et al., 1999; Ström and Christensen, 2007; Whiting and

422 Chanton, 1993, etc.). In our thaw stages, there was also an overall significant and positive  
423 relationship between growing season averages of  $GP_{MAX}$  and  $CH_4$  ( $\rho=0.56$ ,  $p=0.0021$ ; Fig. 7).  
424 Interestingly, thaw stages 8 to 10 (graminoid dominated) have a different relationship of  $GP_{MAX}$   
425 and  $CH_4$  compared with thaw stages 1 to 7 (moss dominated) suggesting a shift in the  
426 partitioning of C loss from the system as  $CO_2$  or  $CH_4$  with increasing thaw and changing  
427 vegetation. We ~~further expected this shift to be related to an increase in graminoid VGA~~  
428 ~~(increase in lability and  $CH_4$  emission via aerenchyma) investigated whether this shift is related,~~  
429 ~~which was supported by our data. Surprisingly, we also found the shift to be related to a loss of~~  
430 ~~*Sphagnum* cover, (perhaps due to an increase in pH and decrease in organic matter lability.) or~~  
431 ~~increase in graminoid species (increase in lability and  $CH_4$  emission via aerenchyma). Both~~  
432 ~~percent cover of *Sphagnum* ( $\rho=0.72$ ,  $p=0.008$ ) as well as VGA of graminoid species ( $\rho=0.63$ ,~~  
433  ~~$p=0.0004$ ) in the collar were significantly related to  $CH_4:CO_2$ . Additionally~~ Furthermore, there  
434 was a significant interaction between soil temperature and *Sphagnum* cover in a linear model  
435 explaining  $CH_4:CO_2$ , suggesting that the relationship of  $CH_4$  and  $CO_2$  depends on *Sphagnum*  
436 abundance but the effect of *Sphagnum* varies by temperature (Table 5).

#### 437 **4.4 Variable changes in ecosystem relationships with increasing thaw**

438 Permafrost thaw increases magnitude and variance of  $CO_2$  and  $CH_4$  fluxes as well as changes the  
439 abiotic and biotic correlates of these fluxes. As a result, the relationships between the correlates  
440 and C fluxes change. While in the lumped across peatland data, spatially variable factors are the  
441 dominant correlates of  $CO_2$  and  $CH_4$  fluxes (elevation being the best proxy for thermal regime,  
442 soil moisture, VGA, etc.), within thaw stages it is the correlates with high temporal variations  
443 that play a critical role (Julian day, deepening frost table and soil temperature). The changing  
444 correlates of  $CO_2$  and  $CH_4$  fluxes are important to consider from a context of upscaling these  
445 processes from within thaw stage to site to landscape scales. Changing sensitivity of  $CH_4$  fluxes  
446 to temperature, likely related to a shift from substrate to temperature limitation going from low  
447 biomass and low nutrient tundra stages to high biomass and high nutrient thawed stages. Based  
448 on the range of temperature response curves of  $CH_4$  flux across the thaw gradient (Fig. 4a),  
449 applying one activation energy value to estimate landscape level  $CH_4$  fluxes at Stordalen would  
450 not be appropriate and would likely require a set of parameterizations for the various thaw  
451 stages. Variable temperature sensitivities to C fluxes have been recognized in major thaw stages



452 in the past (eg. Lupascu and Wadham, 2012), but our study demonstrates that this variability is  
453 present even in the transitional stages. Furthermore, the multiple regression analyses for each  
454 thaw stages (Fig. 6) demonstrated the changing relative importance and interactive effects of  
455 dominant correlates of CH<sub>4</sub> flux highlighting that controls in transitional stages of permafrost  
456 thaw are not necessarily related to controls in adjacent or end-member stages.

457 Paleo-ecological methods were not employed to confirm the actual thaw status of the thaw stages  
458 used in our analyses. Rather, our space for time approach was employed to sample the major  
459 stages of thaw at Stordalen acknowledged in previous studies (Bäckstrand et al., 2010; Johansson  
460 et al., 2006; Svensson et al., 1999, etc.)- encompassing palsa (our stages 1 to 3), internal fen (our  
461 stages 4 to 6), completely thawed flow through fen (our stages 7 to 10) type habitats- while  
462 capturing the wide range of structural conditions within each one of these 3 broad thaw stages.  
463 We acknowledge that structural changes due to thaw may progress variably and tried to capture  
464 each of these pathways. For example, palsa may collapse abruptly into a wet sedge dominated  
465 habitat that then switches to a *Sphagnum* lawn (our thaw stage 1 progressing into stage 8 and  
466 then to stage 5). Alternatively, this progression can be gradual with a decrease in elevation of  
467 palsa (stage 1 to 2 and then 3), followed by progression into *Sphagnum* lawn (stage 4 and 5).  
468 Regardless, the focus of our study was the changing correlates of C fluxes along the thaw  
469 gradient and a proposed sequence of thaw stages was required to analyze these changes.

## 470 **5 Conclusions**

471 Our results on the environmental correlates of C fluxes interacting and changing variably with  
472 thaw suggest that using process based models or relationships between NEE and CH<sub>4</sub> flux to  
473 derive landscape level C fluxes would require additional information about transitional thaw  
474 stages.

475 Peatlands in the discontinuous permafrost zone are highly heterogeneous, especially if they are  
476 actively thawing. Our research highlights the variability observed in structure-function  
477 relationships with permafrost thaw. Additionally, by identifying across peatland structure-  
478 function relationships that are maintained across the heterogeneous landscape our results will  
479 assist in improving regional estimates of the carbon balance and provide insight into the level of  
480 aggregation or disaggregation needed in models to capture ecosystem level response to change.

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676 **6 Tables**

677 **Table 1.** Details of each thaw stage- habitat description and dominant vegetation, vascular plant  
 678 green area (VGA), presence or absence of permafrost, mean growing season water table depth  
 679 (from 19 days of sampling over 2 years), mean surface water pH, reduced conductivity (Cond)  
 680 and C:N ratio, growing season mean soil temperature at 10 cm depth below surface and mean  
 681 growing season CH<sub>4</sub> fluxes. Details on CO<sub>2</sub> flux for each thaw stage can be found in Table 4.  
 682 WTD was only reported for stages with a water table on more than 5 sampled days. All values  
 683 reported after ± are standard errors.

Thaw Stage	Habitat description and dominant vegetation	Mean VGA (cm <sup>2</sup> )	Perma-frost	Mean WTD (cm)	pH	Cond (mg L <sup>-1</sup> )	C:N	Mean Soil temperature (°C)	Mean CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )
1	Intact palsa, <i>Dicranum elongatum</i> , <i>Vaccinium uliginosum</i>	279.6	✓	-	-	-	-	6.2±0.2	-1.3±0.2
2	Slightly thawing palsa, <i>D. elongatum</i> , <i>Eriophorum vaginatum</i> , <i>Ptillidium ciliare</i>	232.7	✓	-	-	-	-	6.7±0.2	7.1±1.1
3	Collapsing palsa, desiccated <i>Sphagnum fuscum</i> , lichens, <i>Andromeda polifolia</i>	66.7	✓	-	-	-	-	6.6±0.2	-1.1±0.3
4	<i>Sphagnum</i> lawn in transition between stage 3 and 5	54.0	-	-11.6±1.3	-	-	-	8.3±0.3	7.6±1.4
5	<i>Sphagnum</i> lawn	60.3	-	-10.1±0.7	4.0	8.0	35.8	7.2±0.3	18.7±2.7
6	<i>Sphagnum</i> lawn, <i>Betula nana</i>	312.1	-	-11.5±0.6	-	-	-	8.1±0.4	29.5±4.8
7	<i>E. vaginatum</i> , <i>S. cuspidatum</i> , open water	334.4	-	-2.3±0.6	4.1	17.0	45.3	9.9±0.3	56.5±3.5
8	<i>E. vaginatum</i> , <i>Drepanocladus schulzei</i> , open water	322.0	-	1.8±0.9	4.0	76.2	47.9	10.4±0.3	102.4±7.5
9	<i>Eriophorum angustifolium</i> , open water	1136.3	-	2.3±0.6	4.5	30.0	46.6	7.6±0.3	370.2±52.1
10	<i>Polytrichum jensenii</i> , <i>Carex rostrata</i>	1528.7	-	-5.8±1.3	4.7	22.6	53.0	7.2±0.3	266.2±22.7

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689 **Table 2.** Multiple regression model between environmental variables and CH<sub>4</sub> flux across the  
 690 site. Listed environmental variables explain 73% of the variance in CH<sub>4</sub> flux ( $R^2 = 0.73$ ,  $F_{4,391}$   
 691  $=267.1$ ,  $p < 0.0001$ )

Term	Estimate	Std Error	t Ratio	Prob> t
Intercept	344.38	26.94	12.8	<.0001
Elevation	-0.98	0.077	-12.8	<.0001
Soil temp	0.031	0.007	4.43	<.0001
Thaw depth	-0.005	0.001	-8.50	<.0001
VGA	0.001	0.000	7.09	<.0001

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711 **Table 3.** Abiotic and biotic relationships with Gross Primary Production ( $GPP = NEE - R_{eco}$ ), Net  
 712 Ecosystem Exchange (NEE) and Ecosystem Respiration ( $R_{eco}$ ).  $R_{eco}$  has negative values and  
 713 therefore, negative correlation signifies that larger VGA or Soil temp have higher  $R_{eco}$ . Similarly,  
 714 since thaw depth has negative values, negative correlations with GPP and NEE mean that deeper  
 715 frost tables relate to greater GPP and NEE.

Function	Correlate	Spearman's $\rho$	p-value
NEE	Thaw Depth	-0.21	0.0058
NEE	Soil Temp	0.14	0.0112
NEE	WTD	0.24	0.0002
NEE	VGA	0.58	0.0180
GPP	Thaw Depth	-0.29	0.0020
GPP	WTD	0.20	0.0177
$R_{eco}$	Soil Temp	-0.16	0.0226
$R_{eco}$	VGA	-0.56	0.0250

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731 **Table 4.** Parameter estimates  $\pm$  standard error from rectangular hyperbola fit of NEE and PAR.  
 732 PAR dependence of NEE generally increases and becomes more significant from less to more  
 733 thawed stages as shown by the adjusted  $R^2$  ( $p < 0.0001$  for all thaw stages). There is a general  
 734 trend of increasing,  $GP_{MAX}$ , alpha and A, going from less thawed to more thawed stages.

Thaw Stage	$GP_{MAX}$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	$\alpha$ ( $\frac{\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}}{\mu\text{mol PAR m}^{-2} \text{ s}^{-1}}$ )	A ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	$R^2$	n
1	3.85 $\pm$ 1.21		-4.36 $\pm$ 0.53	0.59	26
2	3.99 $\pm$ 0.53	0.015 $\pm$ 0.004	-1.72 $\pm$ 0.16	0.71	75
3	2.82 $\pm$ 0.61	0.008 $\pm$ 0.003	-1.52 $\pm$ 0.13	0.80	26
4	2.44 $\pm$ 0.31	0.014 $\pm$ 0.005	-0.89 $\pm$ 0.11	0.76	52
5	3.87 $\pm$ 0.30	0.030 $\pm$ 0.007	-1.28 $\pm$ 0.11	0.85	78
6	5.15 $\pm$ 0.52	0.053 $\pm$ 0.021	-2.76 $\pm$ 0.25	0.89	27
7	6.28 $\pm$ 0.72	0.032 $\pm$ 0.010	-1.79 $\pm$ 0.24	0.74	78
8	2.15 $\pm$ 0.24	0.015 $\pm$ 0.005	-0.94 $\pm$ 0.09	0.82	98
9	8.16 $\pm$ 0.86	0.072 $\pm$ 0.023	-3.49 $\pm$ 0.32	0.91	27
10	6.62 $\pm$ 1.34		-5.35 $\pm$ 0.82	0.69	18

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749 **Table 5.** Multiple regression model of CH<sub>4</sub>:CO<sub>2</sub> explained by percent cover of *Sphagnum* and  
 750 soil temperature. ( $R^2=0.86$ ,  $F_{3,11} = 16.8$ ,  $p= 0.0008$ ). Estimates and standard errors (SE) are  
 751 reported along with t-ratio and p-value.

	Estimate	SE	t-ratio	p-value
Intercept	2107.1	444.1	4.75	0.0015
Soil Temperature	-232.5	58.6	-3.97	0.0041
% <i>Sphagnum</i>	-3.0	0.5	-5.71	0.0004
Soil Temp x % <i>Sphagnum</i>	11.8	3.5	3.39	0.0095

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771 **7 Figure Captions**

772 **Figure 1.** Relationship between the methane fluxes measured over two years and various  
773 environmental variables (across peatland lumped data). Methane flux across 28 sampled collars  
774 from two years (19 days of sampling) showed significant relationships with Julian day, elevation  
775 (above sea level) of collar, soil temperature at 10 cm depth below surface( $^{\circ}\text{C}$ ), modeled VGA  
776 (vascular green area; $\text{cm}^2$ ), water table depth (WTD), pH, thaw depth and C:N of surface water.  
777 Spearman's  $\rho$  of each correlation are shown on each graph ( $p < 0.0001$ ).

778 **Figure 2.** Rectangular hyperbola fit of site-level NEE with PAR ( $n = 525$ ).

779 **Figure 3.** Correlation coefficients between  $\text{CH}_4$  flux and various biotic and abiotic variables  
780 along the thaw gradient from 1 to 10, where 1 is intact permafrost and 10 is fully thawed. Each  
781 data point represents correlations analysis of  $n = 19$  days. The missing data points in WTD,  
782 Conductivity, Reduced Conductivity, pH, TC, TN and C:N (total carbon, nitrogen and C:N in  
783 surface water) are from the thaw stages that did not have a water table or had a correlation  
784 coefficient of zero.

785 **Figure 4a.** Arrhenius plots for each thaw stage. Slope and  $R^2$  of the plots increases with  
786 increased thaw (Figure 6). **b.** changing linear fit between thaw depth and  $\text{CH}_4$  flux with  
787 progressing thaw. **c.** increase in seasonality of  $\text{CH}_4$  flux as the permafrost thaws.

788 **Figure 5.** Slope and adjusted  $R^2$  of the Arrhenius plot (Figure 4a) across the thaw stages. The left  
789 y axis is the estimate and standard error of the slope of the fit (represented by the gray bars  $\pm$ SE)  
790 and the right y axis shows the  $R^2$  of each fit (represented by the black dots  $\pm$ SE). The significant  
791 regressions ( $p < 0.0001$ ) are denoted by asterisk. Variance of methane fluxes explained by soil  
792 temperature generally increases ~~(as shown by the dotted line of best fit of  $R^2$  along the thaw~~  
793 ~~gradient)~~ and becomes more significant (p-values) from less to more thawed stages. Slope of the  
794 soil temperature to methane flux relationship also increases with increased thaw.

795 **Figure 6.** Multiple regression of  $\text{CH}_4$  fluxes with elevation, thaw depth, soil temperature (Temp)  
796 and vascular green area (VGA) for each thaw stage (Thaw stage 1= intact permafrost, 10=  
797 completely thawed). Model fit  $R^2$  values are reported along with model estimates (stacked bars).  
798 Significance of the  $R^2$  is denoted by asterisk (\* for  $p < .05$ , \*\* for  $p < .01$ , and \*\*\* for  $p < .001$ ). Soil  
799 Temperature was not a statistically significant estimate for any of the thaw stages. Elevation was

800 significant for thaw stages 1, 4, 8 and 9; thaw depth for 1, 4, 5, 7, 8 and 10; and VGA for 8 and  
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802 **Figure 7.** Significant correlation between growing season means of CH<sub>4</sub> flux and GP<sub>MAX</sub> across  
803 all thaw stages. Thaw stage 1 (intact permafrost) to 10(thawed permafrost) are shown using blue  
804 to red colours.