

1 **Non-growing season methane emissions are a significant component of annual emissions**
2 **across northern ecosystems**

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23 **Index Terms and Key Words**

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25 comparison, synthesis

26 **Abstract**

27 Wetlands are the single largest natural source of atmospheric methane (CH₄), a greenhouse
28 gas, and occur extensively in the northern hemisphere. Large discrepancies remain between
29 “bottom-up” and “top-down” estimates of northern CH₄ emissions. To explore whether these
30 discrepancies are due to poor representation of non-growing season CH₄ emissions, we
31 synthesized non-growing season and annual CH₄ flux measurements from temperate, boreal,
32 and tundra wetlands and uplands. Median non-growing season wetland emissions ranged
33 from 0.9 g m⁻² in bogs to 5.2 g m⁻² in marshes and were dependent on moisture, vegetation,
34 and permafrost. Annual wetland emissions ranged from 0.9 g m⁻² y⁻¹ in tundra bogs to 78 g
35 m⁻² y⁻¹ in temperate marshes. Uplands varied from CH₄ sinks to CH₄ sources with a median
36 annual flux of 0.0 ± 0.2 g m⁻² y⁻¹. The measured fraction of annual CH₄ emissions during the
37 non-growing season (observed: 13 to 47%) was significantly larger than was predicted by
38 two process-based model ensembles, especially between 40-60° N (modeled: 4 to 17%).
39 Constraining the model ensembles with the measured non-growing fraction increased total
40 non-growing season and annual CH₄ emissions. Using this constraint, the modeled non-
41 growing season wetland CH₄ flux from >40° north was 6.1 ± 1.5 Tg y⁻¹, three times greater
42 than the non-growing season emissions of the unconstrained model ensemble. The annual
43 wetland CH₄ flux was 37 ± 7 Tg y⁻¹ from the data-constrained model ensemble, 25% larger
44 than the unconstrained ensemble. Considering non-growing season processes is critical for
45 accurately estimating CH₄ emissions from high latitude ecosystems, and necessary for
46 constraining the role of wetland emissions in a warming climate.

47

48 **Introduction**

49 Methane (CH₄) is an important greenhouse gas with 33 times the radiative forcing of CO₂
50 (Myhre *et al.*, 2013). Wetlands are the largest natural source of methane, contributing an

51 estimated 125 - 235 Tg CH₄ to the atmosphere annually (Saunois *et al.*, 2016). Model-based
52 estimates of temperate, boreal, and tundra wetland CH₄ emissions at latitudes greater than 40°
53 N amount to 16 – 36% of global wetland emissions (Melton *et al.*, 2013). However, large
54 discrepancies remain between “bottom-up” emissions estimates using process-based or data-
55 constrained models and “top-down” emissions estimates from atmospheric CH₄ measurement
56 inversions (Kirschke *et al.*, 2013, Saunois *et al.*, 2016). Specifically, bottom-up wetland CH₄
57 emissions remain highly uncertain due to poorly constrained and highly divergent maps of
58 wetland area, a high degree of uncertainty in CH₄ process parameterization, and lack of
59 validation datasets (Melton *et al.*, 2013). Due to a relatively limited representation of wetland
60 CH₄ emission process controls, bottom-up approaches to modeling CH₄ may be missing some
61 important contributions of both non-growing season CH₄ flux (Xu *et al.*, 2016a, Zona *et al.*,
62 2016) and spatial variability in CH₄ emissions. Accounting for these factors may improve the
63 agreement between top-down and bottom-up CH₄ emissions estimates (Kirschke *et al.*, 2013,
64 Saunois *et al.*, 2016).

65 Recently, the importance of non-growing season CH₄ emissions to the annual budget
66 was shown for several tundra sites, where non-growing season fluxes comprise ~50% of the
67 annual emissions (Karion *et al.*, 2016, Mastepanov *et al.*, 2008, Zona *et al.*, 2016). However,
68 the importance of non-growing season emissions over greater temporal and spatial scales is
69 unclear. Continued measurements over several years at one tundra site showed that the high
70 non-growing season CH₄ emissions measured in one year were anomalous and were not
71 measured in any of the next four years (Mastepanov *et al.*, 2013, Pirk *et al.*, 2015). At a
72 temperate wetland site, winter CH₄ measurements over multiple years showed that the non-
73 growing season flux constituted a much smaller proportion (less than 10%) of the annual
74 emissions (Melloh & Crill, 1996). These differing results could simply reflect spatial
75 heterogeneities among sites, but also reflect a fundamental lack of understanding of what

76 processes control non-growing season emissions (including in-situ CH₄ production, inhibition
77 of CH₄ oxidation, release of CH₄ stored in peat, or some combination of the above) in both
78 individual sites and across sites. Consequently, the role of non-growing season emissions in
79 the annual wetland CH₄ budget remains highly uncertain.

80 Ecosystem CH₄ flux is the net result of CH₄ production in anaerobic soil minus CH₄
81 oxidation in aerobic soil (e.g. Blodau, 2002). Anaerobic CH₄ oxidation using alternative
82 electron acceptors, such as sulfates, nitrates, iron, manganese, and humic substances, has
83 been reported from freshwater systems (e.g., Segarra *et al.*, 2015), but its importance for CH₄
84 cycling is not yet understood. Rates of CH₄ production are dependent on temperature, pH,
85 and the availability of substrate (e.g. Moore & Dalva, 1997, Treat *et al.*, 2015). However,
86 CH₄ fluxes are highly unpredictable at daily time scales due to CH₄ oxidation and the
87 variable time lag between CH₄ production and emission. Emissions can be closely coupled to
88 CH₄ production due to efficient plant transport through aerenchymous tissue (King *et al.*,
89 1998), found in plants in the *Cyperaceae* family, or decoupled due to slower diffusive
90 transport and storage effects in anoxic soils (Blodau, 2002, Comas *et al.*, 2008, Pirk *et al.*,
91 2015). At the plot scale, CH₄ fluxes have been correlated with water table level, soil
92 temperature, productivity, and vegetation composition (Bubier, 1995, Moore & Roulet,
93 1993, Whiting & Chanton, 1993). However, these relationships differ in strength depending
94 on the time scales considered, with better correlations between environmental and plant
95 controls on CH₄ at seasonal rather than at daily scales (Blodau, 2002, Treat *et al.*, 2007,
96 Turetsky *et al.*, 2014). Furthermore, the spatial and temporal heterogeneity of CH₄ emissions
97 can obscure broader trends among different wetland classes and biomes. Given a background
98 of increasing CH₄ emissions from northern high latitudes (Nisbet *et al.*, 2014) and that
99 wetlands are the largest natural source of methane (e.g. Saunio *et al.*, 2016), it is important
100 to understand which types of wetlands and which regions (tundra, boreal, temperate) are

101 potentially the largest contributors of CH₄ to the atmosphere as well as which have the
102 greatest uncertainty. Taken together, an increasing number of CH₄ flux studies span a range
103 of high-latitude ecosystems and provide a unique opportunity to advance current
104 understanding of how net CH₄ emissions vary both spatially and temporally.

105 Here, we synthesize measurements of growing season, non-growing season, and
106 annual CH₄ fluxes from temperate, boreal, and tundra wetland and upland ecosystems from
107 191 unique sites to determine the magnitude and controls of non-growing season CH₄ and
108 annual emissions. Previous syntheses only explicitly considered CH₄ emissions during the
109 growing season and generally only from wetlands (Bartlett & Harriss, 1993, Bridgham *et al.*,
110 2006, McGuire *et al.*, 2012, Olefeldt *et al.*, 2013, Turetsky *et al.*, 2014). We use our new
111 synthesis dataset to: 1) identify trends in annual CH₄ emissions among tundra, boreal, and
112 temperate wetlands and uplands; 2) identify the contributions of non-growing season flux to
113 annual CH₄ emission; and 3) evaluate and constrain the seasonal timing and magnitude of
114 CH₄ emissions for two process-based model ensembles [WETCHIMP (Melton *et al.*, 2013)
115 and WetCHARTs (Bloom *et al.*, 2017)]. Together, the WetCHARTs and WETCHIMP model
116 ensembles effectively provide a complimentary representation of uncertainty in global-scale
117 model-based estimates of monthly wetland CH₄ emissions.

118

119 **Materials and Methods**

120 *Data compilation*

121 Annual, non-growing season, and growing season CH₄ flux measurements and
122 ancillary data were synthesized from 174 published studies that made more than one
123 measurement of CH₄ flux per month throughout the growing season (growing season) and
124 more than two measurement during the non-growing season (non-growing season, annual).
125 This resulted in 256 annual fluxes from 101 unique sites (including 48 unique sites with 131
126 explicitly differentiated non-growing season fluxes) and 853 growing season flux

127 measurements from 191 unique sites (Fig. 1) made using static chambers, automated
128 chambers, eddy covariance, and snowpack diffusion methods. Mean daily CH₄ flux, non-
129 growing season and growing season CH₄ flux, and annual CH₄ flux were extracted from
130 studies identified from Web of Science using the terms “methane” and “arctic” or “tundra” or
131 “boreal” or “temperate”, author knowledge, and from an existing synthesis dataset (McGuire
132 *et al.*, 2012). For inclusion in the analysis of growing season and annual CH₄ fluxes, studies
133 must have made more than one measurement of CH₄ flux per month throughout the growing
134 season. For inclusion in the non-growing season CH₄ flux analysis, studies must have
135 measured CH₄ flux more than twice during the non-growing season, defined as the period
136 outside the photosynthetically active period. When this was not specifically defined within a
137 study, the non-growing season included the period of mid-September through May at sites
138 between 60° and 90° N, and November through March at sites between 40° N and 60° N.

139 For all studies, we included information on the site location (latitude, longitude),
140 technique used (static/manual chamber, automated chamber, eddy-covariance), vegetation
141 composition, and other descriptive variables. Where possible, we also extracted
142 environmental variables including mean annual air temperature (n=540/853, 63%), mean
143 annual precipitation (n=556/853, 65%), mean seasonal water table position (n= 621/853,
144 73%), where positive values indicate a flooded site, pH (n=338/853, 40%), and maximum
145 active layer thickness (n=121/208 measurements in sites with permafrost, 58%). The
146 descriptive categories included biome, wetland ecosystem classification, permafrost
147 presence/absence, and categorical vegetation descriptions. Biome was extracted from Olson
148 *et al.* (2001) using the site coordinates and included tundra, boreal/taiga, temperate, and other
149 (montane grassland and shrubland, flooded grassland, subtropical). Landscape position
150 information, hydrologic descriptions, soil type, and detailed vegetation descriptions were
151 used to categorize the wetland ecosystem classes based on the Canadian Wetland

152 Classification system (Group, 1988). These categories included shallow water wetland (water
153 depth < 2 m), marsh, swamp, fen, bog, and upland (including forest and grassland). The
154 categorization of permafrost presence/absence was based on the presence or absence of
155 permafrost in the measurement location or chamber as noted by the author and occurred in 52
156 sites representing 208 flux measurements. Categorical vegetation descriptions included
157 classifying sites using the vegetation composition descriptions based on the dominance,
158 presence (minor component), or absence of different categories of vascular vegetation: trees,
159 shrubs, *Cyperaceae* (including *Carex* spp. and *Eriophorum* spp.). The CH₄ flux synthesis data
160 used in these analyses are archived and available for download from PANGAEA
161 (<https://doi.pangaea.de/10.1594/PANGAEA.886976>).

162

163 *Growing season and annual CH₄ emissions*

164 If not given by the authors, we calculated cumulative CH₄ emissions for the growing
165 season using several different approaches depending on the information included in the study,
166 but generally from integrating the mean daily CH₄ flux over the entire growing season or
167 summing the mean monthly CH₄ flux over the growing season. However, many sites did not
168 include information on the length of the growing season. For these sites and unless otherwise
169 stated by the authors, we assumed that the growing season spanned the full month of the
170 beginning and end of the measurement period. Some authors modeled annual fluxes using
171 empirical relationships; we used these for annual emissions when available (modeled fluxes,
172 n= 47/853 measurements, Fig. 1). To calculate annual emissions from the cumulative
173 growing season emissions when the authors did not measure or model the non-growing
174 season flux (n= 551/853 measurements), the empirical relationship between cumulative
175 growing season CH₄ flux and annual flux was used to estimate annual CH₄ flux (Table 1, Fig.
176 S1). Estimated annual fluxes using cumulative growing season measurements ranged from

177 40% lower (fens) to 17% lower (uplands) to 11% lower (marshes) than measured annual
178 fluxes on average, while this method resulted in substantially higher estimated annual fluxes
179 than observed fluxes in bogs (400%) and shallow water wetlands (170%; Table S1). Some of
180 this difference may be due to measurement bias in the annual measurements towards higher
181 emitting sites and wetland classes (Table S3).

182

183 *Comparison between modeled and measured growing season and annual CH₄ data*

184 We use two recent wetland CH₄ emission model ensemble studies to evaluate model-
185 based estimates of non-growing season and annual CH₄ emissions relative to measured
186 values. The wetland CH₄ emission and uncertainty dataset for atmospheric chemistry and
187 transport modelling (WetCHARTs) model ensemble approach (Bloom *et al.*, 2017) consists
188 of 324 models with 0.5° spatial and monthly temporal resolution wetland CH₄ emission
189 models, derived using a range of wetland extent maps, substrate availability models, mean
190 global wetland CH₄ emissions factors, and temperature CH₄:C dependencies. The Wetland
191 CH₄ Inter-comparison of Models Project (WETCHIMP) ensemble consists of six global-scale
192 process-based models with monthly temporal and 0.5° - 3.6° spatial resolution with a range
193 of prognostic and data-driven estimates of wetland extent and associated CH₄ emissions
194 (Melton *et al.*, 2013). Together the WetCHARTs and WETCHIMP model ensembles
195 represent a range of wetland CH₄ emission scenarios: the substantial range of modeled
196 wetland CH₄ emission rates (which typically span more than one order of magnitude at sub-
197 continental scales) are largely attributable to varying parameterizations of wetland extent and
198 net CH₄ production processes across the WetCHARTs and WETCHIMP models. For the sake
199 of brevity, we refer the reader to (Melton *et al.*, 2013) and Bloom *et al.* (2017) for additional
200 details on the model structures. The two ensembles effectively provide a complimentary

201 representation of uncertainty in global-scale model-based estimates of monthly wetland CH₄
202 emissions.

203 For the intercomparison of the timing of the CH₄ emissions between measured and
204 modeled data, the growing season, non-growing season and annual wetland fluxes for all
205 model ensemble members were summed within two latitudinal zones: 40° – 60° N and >60°
206 N. For high latitudes (> 60° N), the growing season was defined as June through mid-
207 September, while in lower latitudes (40° – 60° N), the growing season was defined as April –
208 October. As the WetCHARTs model ensembles only represent wetland emissions and do not
209 include CH₄ uptake or emission in upland soils, we included only measured non-growing
210 season and annual CH₄ fluxes from wetland sites within our synthesis dataset in the model-
211 data intercomparison. Evaluation of non-growing and annual CH₄ fluxes using zonal totals –
212 instead of model gridcell evaluation – reduced biases introduced by the large number of grid
213 cells with little or no wetland area and subsequently, negligible wetland CH₄ flux, as
214 compared to the wetland subset of the synthesis dataset that exclusively contained CH₄ flux
215 from wetland areas. We compared the synthesis and model datasets using the non-growing
216 season fraction (non-growing season flux / annual flux).

217

218 *Statistical Analysis*

219 The non-growing season, growing season, and annual CH₄ flux data were not normally
220 distributed, nor was the non-growing season fraction (non-growing season flux / annual flux).
221 Here, we use the median and 95% confidence intervals around the median to describe the
222 dataset. To calculate median and 95% confidence intervals for the measured and modeled
223 flux data, we implemented bootstrap resampling in R (Team, 2008) using the “sample”
224 command with replacement and determined the median for 10,000 simulations of resampled

225 data. We used the maximum difference between median and interquartile range as the
226 coefficient of variation when comparing variability among time scales and studies.

227 Linear mixed-effects modeling was used on the log-transformed measurement data to
228 test for significant relationships between CH₄ fluxes and both categorical variables (biome,
229 ecosystem class, dominant vegetation type, and presence/absence of permafrost) and
230 continuous variables (growing season length, mean water table position, pH, soil temperature,
231 mean annual temperature, and precipitation). Mixed-effects modeling was necessary because
232 of the bias introduced from having multiple samples from the same site, resulting from
233 measurements among distinct microtopographies and/or vegetation types, or measurements
234 over several years (e.g. repeated measures, with sites). Thus, site was included as a random
235 effect in the analyses. We implemented the mixed effects model using the lmer command
236 from the lme4 package (Bates, 2010, Bates *et al.*, 2014, Bates *et al.*, 2015) for R statistical
237 software (Team, 2008). The significance of the predictor variables were tested using a Chi²
238 test against a null model using only site as a random variable (Bates *et al.*, 2015); both
239 models were fit without reduced maximum likelihood. Interactions were tested for
240 significance against additive models without interactions. We also used this approach to test
241 the relationship between cumulative growing season and annual emissions for wetlands and
242 uplands as separate categories (Table 1). Differences among categorical variables and
243 regression parameters were determined from 95% confidence intervals of the model
244 coefficients after re-fitting the model using the reduced maximum likelihood.

245

246 **Results**

247 *Measured non-growing season CH₄ flux*

248 We compared both the magnitudes of measured non-growing season CH₄ emissions and the
249 fraction of annual emissions emitted during the non-growing season (non-growing season

250 fraction = non-growing season emissions/annual emissions) for sites with year-round
251 measurements (pink circles, Fig. 1). Non-growing season emissions ranged from -0.2 to 16.9
252 g CH₄ m⁻² y⁻¹ for wetland sites and -0.3 to 4.4 g CH₄ m⁻² y⁻¹ for upland sites. Non-growing
253 season measurements were most common at bog and fen sites (n = 38 and 58, respectively),
254 while less data were available from shallow aquatic ecosystems (n = 12), marshes (n = 19),
255 swamps (n = 1), and upland sites (n = 8; Fig. 2c).

256 Non-growing season CH₄ emissions differed significantly among ecosystem classes
257 (Chi² = 46, d.f. = 5, *P* < 0.0001; Fig. 3a) but not among biomes (Chi² = 0.9, d.f. = 2, *P* = 0.63;
258 Fig. 3b). Median non-growing season CH₄ flux in fens and marshes was more than double the
259 median emissions in bogs and uplands (Fig. 3a). The non-growing season fraction also varied
260 significantly among ecosystem classes (Chi² = 18.0, d.f. = 5, *P* = 0.003; Fig. 3c). The median
261 non-growing season fraction in upland sites was more than double the median non-growing
262 season in fens and bogs and was smallest in marshes and shallow waters (Fig. 3c).

263 While the magnitude of non-growing season CH₄ emissions did not vary significantly
264 across biomes (Fig. 3b), the non-growing season fraction did (Chi² = 11, d.f. = 2, *P* = 0.005;
265 Fig. 3d). The non-growing season fraction was largest in the tundra, averaging 42% (95% CI:
266 31- 48%) of annual emissions. In temperate sites, the non-growing season fraction was 20%
267 (14 - 27%) of annual CH₄ emissions. In the boreal biome, the non-growing season fraction
268 was significantly lower than the tundra and averaged 16% (12-17%) of annual emissions.

269 Environmental conditions had some effect on non-growing season emissions and the
270 non-growing season fraction, especially the presence/absence of permafrost. Non-growing
271 season CH₄ emissions from sites without permafrost were more than four times greater than
272 from permafrost sites (2.7 ± 0.9 g CH₄ m⁻² and 0.6 ± 0.4 g CH₄ m⁻², respectively; Fig. 4a).
273 However, the non-growing season fraction in permafrost-free sites (17 ± 3%) was less than
274 half than in permafrost sites (36 ± 16%; Fig. 4b). Water table position was positively

275 correlated with the magnitude of non-growing season emissions, where drier sites had smaller
276 non-growing season emissions than wetter sites (Fig. S2), but water table position was not a
277 significant predictor of the non-growing season fraction ($\text{Chi}^2 = 0.3$, d.f. = 1, $P=0.57$). Mean
278 annual temperature was a significant predictor of the non-growing season fraction, which was
279 higher at colder sites ($\log(\text{NGSF} (\%) + 1) = -0.054 \cdot \text{MAAT} + 2.925$, $\text{Chi}^2 = 6.7$, d.f. = 1,
280 $P=0.01$). While it is possible that the magnitude of non-growing season CH_4 emissions is
281 related to the length of the non-growing season, this relationship was not statistically
282 significant ($\text{Chi}^2 = 1.1$, d.f. = 1, $P=0.30$), nor was the relationship between the non-growing
283 season fraction and the growing season length ($\text{Chi}^2 = 0.3$, d.f. = 1, $P=0.56$).

284 The cover of different vegetation types, when combined with permafrost, was a good
285 predictor of non-growing season CH_4 fluxes. In permafrost-free sites, *Cyperacae*-dominated
286 sites had larger non-growing season CH_4 emissions ($5.2 \pm 0.7 \text{ g CH}_4 \text{ m}^{-2}$) than shrub-
287 dominated sites ($3.3 \pm 0.9 \text{ g CH}_4 \text{ m}^{-2}$) and tree-dominated sites ($0.5 \pm 0.7 \text{ g CH}_4 \text{ m}^{-2}$); trends
288 were similar in sites with permafrost but fluxes were 65-100% smaller (Fig. S3). In
289 *Cyperacae*-dominated and tree-dominated sites, the non-growing season fraction did not
290 differ between sites with and without permafrost (*Cyperacae*: 22% with vs 26%, without and
291 with permafrost, respectively; Tree: 20% for both; Fig. S3) despite the strong overall trend of
292 higher non-growing season fraction in permafrost sites.

293

294 *Annual CH₄ fluxes*

295 The dataset of annual CH_4 emissions included measured, modeled (by the original authors),
296 and estimated (Table 1) annual emissions (Fig. 1). Annual CH_4 emissions generally followed
297 a moisture, temperature, and nutrient gradient (Fig. 2b) and differed significantly among
298 ecosystem types and biomes ($\text{Chi}^2 = 107$, d.f.=13, $P<0.0001$ for the interaction). Annual
299 emissions ranged from -15 to 310 $\text{g CH}_4 \text{ m}^{-2} \text{ y}^{-1}$ for wetland sites and -23 to 73 $\text{g CH}_4 \text{ m}^{-2} \text{ y}^{-1}$

300 for upland sites. CH₄ emissions from flooded and more nutrient rich sites, such as shallow
301 waters, marshes, and fens, were greater or equal to emissions from bogs and upland sites
302 (Fig. 2b). Among wetlands, temperate marshes were the largest CH₄ sources with a median
303 flux of 78 (95% CI: 63-145) g CH₄ m⁻² y⁻¹ while tundra bogs were the smallest (0.9 g CH₄ m⁻²
304 y⁻¹; Table S1). Generally, median annual CH₄ fluxes from tundra wetlands were smaller (6.2
305 ± 1.7 g CH₄ m⁻² y⁻¹) than boreal (7.2 ± 1.4 g CH₄ m⁻² y⁻¹) or temperate (13.3 ± 5.4 g CH₄ m⁻²
306 y⁻¹) ecosystems (Fig. 2b, Table S1). However, upland CH₄ flux was similar across the biomes.
307 Upland tundra sites were a very small net source of CH₄ annually, 0.04 g CH₄ m⁻² y⁻¹, while
308 upland temperate sites were a net sink of CH₄ (-0.4 g CH₄ m⁻² y⁻¹, Table S1). The majority of
309 measurements were made in the boreal region in nearly every ecosystem class (Fig. 2c).

310 Permafrost presence and dominant vegetation cover were also correlated with annual
311 CH₄ emissions. Permafrost-free sites were larger CH₄ sources annually, emitting 2.5 times
312 more CH₄ than sites with permafrost (6.9 vs. 2.7 g CH₄ m⁻² y⁻¹; Fig. 4a). In permafrost sites,
313 the relationship between active layer thickness and annual CH₄ flux was significant and
314 positive (Fig. S4; Chi² = 25, d.f.=1, P<0.0001). In permafrost-free sites, *Cyperacae*-
315 dominated sites had larger annual CH₄ emissions (23.7 ± 2.2 g CH₄ m⁻² y⁻¹) than shrub-
316 dominated sites (9.9 ± 1.1 g CH₄ m⁻² y⁻¹) and tree-dominated sites (4.5 ± 2.1 g CH₄ m⁻² y⁻¹);
317 trends were similar in sites with permafrost but fluxes were 50-95% smaller (Fig. S3). The
318 relationship between water table depth and annual CH₄ flux was positive and significant but
319 explained little variance (Fig. S2).

320

321 *Modeled and measured non-growing season fractions and flux magnitude*

322 At mid-latitudes (40° to 60° N), the model ensemble means predicted a lower non-growing
323 season CH₄ contribution to the annual emissions relative to the measured CH₄ fluxes. The
324 median non-growing season fraction from the measured data between 40° - 60°N was 16.0%

325 (95% CI: 11.0 – 23.0%) of annual fluxes, substantially higher than the median from the
326 combined model ensembles (Fig. 5a). For mid-latitudes in WetCHARTs, the modeled median
327 non-growing season fraction was 4.7% (4.2-5.2%) and in WETCHIMP, it was 10.0% (6.2-
328 17.0%) (Fig. 5a). The median total non-growing season emissions for the mid-latitude region
329 between 40-60°N was 0.9 ± 0.2 Tg CH₄ y⁻¹ in WetCHARTs and WETCHIMP combined
330 (Fig. 6a; Table S2).

331 At northern latitudes (60° to 90° N), the two model ensembles performed better in
332 representing the timing of the annual CH₄ emissions. The median non-growing season
333 fraction in WetCHARTs was 15.8% (14.6-17.2%), while in WETCHIMP it was 22.9% (16.7
334 – 38.5%; Fig. 5b). The median non-growing season fraction from the measured data was
335 intermediate: 17.0% (16.0-23.3%) of annual fluxes (Fig. 5b). The median total non-growing
336 season emissions for the high-latitude region between 60-90° N was 1.0 ± 0.2 Tg CH₄ y⁻¹ for
337 WetCHARTs and WETCHIMP combined (Fig. 6b; Table S2).

338 Across both mid-latitudes (40° to 60° N) and northern latitudes (60° to 90° N),
339 WetCHARTs and WETCHIMP model ensembles exhibited significant correlations between
340 total non-growing season CH₄ fluxes and non-growing season fractions ($r = 0.63 - 0.85$, P
341 ≤ 0.02 ; Fig. 5a and 6b). We utilized the emergent relationship between modeled non-growing
342 season fractions and fluxes to place a measurement-informed constraint on total CH₄
343 emissions from mid- and high-latitudes. For both spatial domains, we identified the model
344 runs from the WetCHARTs and WETCHIMP model ensembles that fell within the 95%
345 confidence intervals of the median measured non-growing season fraction (Fig. 6). Using this
346 data-constraint, the resulting non-growing season flux from WETCHIMP and WetCHARTs
347 was 4.5 ± 1.0 Tg CH₄ y⁻¹ for wetlands in the region between 40 – 60° N, four times larger
348 relative to the unconstrained emissions estimates (Fig. 6a; Table S2). For wetlands in the
349 region between 60-90° N, the total data-constrained non-growing season emissions were 1.6

350 $\pm 0.6 \text{ Tg CH}_4 \text{ y}^{-1}$, 60% higher than the non-growing season emissions without the constraint.
351 Based on the data-constrained model results, annual wetland emissions for 40-60° N
352 amounted to $28.7 \pm 4.7 \text{ Tg CH}_4 \text{ y}^{-1}$, in contrast to $23.0 \pm 2.0 \text{ Tg CH}_4 \text{ y}^{-1}$ in unconstrained
353 model ensemble (Fig. S5a; Table S2). The annual wetland emission for >60° N amounted to
354 $8.7 \pm 2.8 \text{ Tg CH}_4 \text{ y}^{-1}$ in contrast to $6.8 \pm 0.7 \text{ Tg CH}_4 \text{ y}^{-1}$ in the unconstrained model ensemble
355 (Fig. S5b; Table S2). The observational constraint increased estimates of total annual wetland
356 CH_4 emissions across all biomes > 40° N by 25%, from $29.8 \pm 2.7 \text{ Tg CH}_4 \text{ y}^{-1}$ to 37.4 ± 7.2
357 $\text{Tg CH}_4 \text{ y}^{-1}$ (Table S2). This was due to higher estimated emissions during both the growing
358 season (40% of increase) and non-growing season (60% of increase).

359

360 **Discussion**

361 *The role of non-growing season emissions in annual CH_4 flux*

362 This first attempt to synthesize the non-growing season emissions from pristine ecosystems
363 of the northern hemisphere clearly shows that they are an important and non-zero component
364 of annual emissions across all regions and ecosystem classifications (Fig. 3). Our results
365 based on 131 measurements from 48 sites across the tundra, boreal, and temperate regions,
366 generally agree with both of the conflicting observations that non-growing season emissions
367 were and were not a large component of the annual budget (Alm *et al.*, 1999, Dise, 1992,
368 Mastepanov *et al.*, 2008, Mastepanov *et al.*, 2013, Melloh & Crill, 1996, Zona *et al.*, 2016)
369 by showing a substantial range in the non-growing season fraction among sites (Fig. 3c,d).
370 The relative importance of the non-growing season emissions to annual budgets is largely
371 driven by the magnitude of growing season emissions (Fig. S1), which vary more greatly in
372 magnitude than non-growing season emissions (Fig. 3a,b, Table S3). Non-growing season
373 emissions were generally larger from wet sites than dry sites, while the non-growing season
374 fraction showed opposite trends (Fig. 3a,c). Nevertheless, non-growing season CH_4 fluxes

375 were large enough that they cannot be discounted in measurements of annual emissions,
376 especially in drier sites (Fig. 3).

377 On average, process-based models significantly underestimated the non-growing
378 season fraction, especially in temperate and boreal regions (Fig. 5a). As a result, total non-
379 growing season wetland emissions for 40-90° N from WETCHIMP and WetCHARTs were
380 more than three times larger when the model results were constrained using the data (Fig. 6).
381 The biased representation of non-growing season CH₄ emissions in process-based models and
382 in atmospheric inversion frameworks can have a significant impact on continental-scale CH₄
383 budget estimates (Fig. 6; Thonat *et al.*, 2017, Xu *et al.*, 2016a) and lead to substantial biases
384 in estimates of the role of wetland CH₄ carbon-climate feedbacks.

385 There is mounting evidence from atmospheric CH₄ concentration data of significant
386 terrestrial emissions outside of the growing season (Karion *et al.*, 2016, Miller *et al.*, 2016,
387 Sweeney *et al.*, 2016), but the magnitude of the flux is uncertain based on results from
388 inversion and process-based models. Process-based models may curtail CH₄ production and
389 emission too early relative to the time of soil freezing (Miller *et al.*, 2016), thus resulting in a
390 seasonal emissions bias. Still, our unconstrained model estimates of non-growing season
391 emissions from >60° N (1.0 Tg CH₄ y⁻¹) were significantly smaller than the 12 ± 5 Tg CH₄ y⁻¹
392 recently estimated for arctic tundra wetlands and uplands (Zona *et al.*, 2016), and even with
393 the data constraint, the non-growing season emissions from wetlands were only 1.6 ± 0.6 Tg
394 CH₄ y⁻¹ (Fig. 6b). Upland areas, not included to this model-data comparison, may or may not
395 be an additional, significant CH₄ sources during the non-growing season (Lohila *et al.*, 2016,
396 Zona *et al.*, 2016) since their fluxes were small but variable (0.0 ± 0.2 g CH₄ m⁻²; Fig. 3a).
397 Additionally, episodic CH₄ emissions, previously reported to occur, e.g., during soil freezing
398 (Mastepanov *et al.*, 2008, Pirk *et al.*, 2015) as well as during the growing season, may have
399 been missed in some studies due to low measurement frequency and are not well represented

400 in process models. The differences between the models and the data (Figs. 5, 6) demonstrate
401 the need to further investigate which process representations and parameterizations lead to
402 modeled emission estimates that are in agreement with measured data.

403

404 *Processes controlling non-growing season and annual emissions.*

405 While the environmental and substrate controls favorable for high emissions during
406 the growing season extend to the non-growing season, the processes responsible for non-
407 growing season emissions seem to vary across the landscape. Non-growing season emissions
408 in wetlands followed similar patterns to annual and growing season emissions and were
409 related to moisture, temperature, and dominant vegetation (Fig. 2a,b, 3a,b, S2), as expected
410 based on previous studies (Blodau, 2002, Bubier, 1995, Olefeldt *et al.*, 2013). The highest
411 non-growing season and annual emissions were from wet sites rather than dry sites (Fig. 3a,
412 S2), from *Cyperaceae*-dominated sites without permafrost rather than sites with little
413 vegetation, trees, and/or permafrost (Fig. S3a). Permafrost-free sites had 2.5 times larger CH₄
414 fluxes annually and four times larger fluxes during the non-growing season than their
415 permafrost counterparts (Fig. 4a), a larger difference than previously observed in daily
416 emissions during the growing season (Olefeldt *et al.*, 2013). This trend likely resulted from a
417 tight coupling between soil temperatures and potential CH₄ production (Moore & Dalva,
418 1997, Treat *et al.*, 2015). . Furthermore, in sites with permafrost, annual fluxes were larger
419 from sites with deeper active layers (Fig. S4) where warmer soils also result in a larger
420 thawed soil volume, and with additional substrate available for decomposition (Levy *et al.*,
421 2012). These results suggest increased CH₄ emissions in future warmer climate from
422 permafrost regions as soil temperatures warm and active layers deepen.

423 The relatively high non-growing season fraction in tundra as opposed to boreal and
424 temperate ecosystems (e.g. Table 1, Fig. S1) may result from an interaction between soil

425 temperature, vegetation, and substrate availability that potentially affect both rates of CH₄
426 production and oxidation. For example, several sub-arctic sites in discontinuous permafrost
427 that were classified both as tundra (Stordalen, Seida) and boreal (Vaisjeaggi), had a relatively
428 high non-growing season fraction (Bäckstrand *et al.*, 2010, Jackowicz-Korczyński *et al.*,
429 2010, Marushchak *et al.*, 2016, Nykänen *et al.*, 2003). These sites all have elevated
430 permafrost bog surfaces, peat plateaus and palsas, where CH₄ emissions were very small
431 (<0.1 g CH₄ m⁻² y⁻¹), and adjacent low-lying, permafrost-free fens, which are hot spots of
432 CH₄ emission in the heterogeneous landscape. Both the elevated peat plateaus and the low-
433 lying fens had a high non-growing season fraction, ranging from 30% to 100% of annual
434 emissions. However, the high non-growing season is likely the result of different processes in
435 the drier and wetter sites. In the low-lying wetlands, snowpacks are often thicker than
436 surrounding uplands and peat plateaus due to wind redistribution of snow to the low-lying
437 areas where fens are found (Heikkinen *et al.*, 2002), resulting in warmer soil temperatures
438 throughout the year to a greater depth in the soil, reflected in deeper active layers and/or the
439 absence of permafrost (Blanc-Betes *et al.*, 2016). With persistent anaerobic conditions
440 provided by ice cover near the surface, little variation in the water table during the winter,
441 and temperatures often above 0° C, CH₄ production continues during the winter-time, albeit at
442 slower rates (Juottonen *et al.*, 2008, Melloh & Crill, 1996, Treat *et al.*, 2015). Additionally,
443 the low-lying fens are also often more productive (Bäckstrand *et al.*, 2010, Marushchak *et al.*,
444 2013), and may also receive substrate inputs (DOC) via lateral flow from elevated areas,
445 potentially increasing substrate available for CH₄ production. This points to the importance of
446 warmer temperatures deeper in the peat profile for non-growing season CH₄ production,
447 which can be facilitated by factors such as thick snow-pack or sufficiently deep peat that
448 result in warmer (thawed) peat at depth while surface peats may be colder or frozen, and may
449 occur at a broader geographic range of sites.

450 The non-growing season fraction showed an opposite wetness trend than the flux
451 magnitude: It was twice as large in dry upland soils as in wetlands (Fig. 3a,c). The high
452 contribution of non-growing season emissions in uplands is in accordance with findings from
453 several upland arctic tundra sites in Alaska (Zona *et al.*, 2016). In upland soils, wintertime
454 methanogenesis may be promoted by low oxygen diffusion into the frozen soil resulting in
455 anaerobic conditions and substrate enrichment of the liquid water phase in partly frozen soil
456 (Teepe *et al.*, 2001). However, inhibition of CH₄ oxidation through oxygen limitation and
457 colder surface soil temperatures could be an even more important reason for the high
458 contribution of wintertime CH₄ emissions in upland soils, including mineral soils, peat
459 plateaus, and permafrost bogs, that commonly show net uptake of atmospheric CH₄ during
460 the growing season (Fig. 2b, 3c; Marushchak *et al.*, 2016, Nykänen *et al.*, 2003, Zona *et al.*,
461 2016). Importantly, the wintertime emissions can turn upland soils that are summertime CH₄
462 sinks to net CH₄ sources annually, which occurred in at least four sites in this study (Lohila *et*
463 *al.*, 2016, Ullah & Moore, 2011). Detailed, process-level studies are needed to show the
464 contribution of CH₄ production vs. oxidation to the seasonality of CH₄ dynamics in upland or
465 dry soils.

466 Storage and subsequent release of CH₄ during the non-growing season, which can be
467 seen as decoupling of CH₄ production and emission, is important in some permafrost tundra
468 sites (FechnerLevy & Hemond, 1996, Pirk *et al.*, 2015). Our synthesis data implies that the
469 storage and subsequent release of previously produced CH₄ during the non-growing season
470 can be related to the presence of permafrost and differences in vegetation type (Comas *et al.*,
471 2008, Parsekian *et al.*, 2011). As a rule, the non-growing season fraction of CH₄ emissions
472 was higher in permafrost sites than in sites without permafrost (Fig. 4b). The presence of
473 permafrost likely limited the size of the soil gas reservoir and, as the volume of ice increased
474 as the soil water froze, CH₄ was pushed out (Pirk *et al.*, 2015), leading to a higher fraction of

475 non-growing season emissions in permafrost soils although the flux magnitude was still small
476 (Fig. 4b). However, in *Cyperacae* dominated sites, permafrost had no effect on the non-
477 growing season fraction (Fig. S3b). Efficient plant transport by *Cyperacae* reduces the lag
478 time between CH₄ production and emission to the atmosphere, thus reducing the role of
479 storage within the peat (King *et al.*, 1998, Parsekian *et al.*, 2011, Strom *et al.*, 2003).

480

481 *Spatial and temporal variability in CH₄ emissions*

482 As hypothesized, the predictability of CH₄ emissions improved with longer time-scales.
483 Considering annual time scales instead of daily time scales reduced the variability of CH₄
484 fluxes within wetland classes from 57-290% (Olefeldt *et al.*, 2013) to 56 – 130% in this
485 study. Furthermore, the variability in CH₄ flux was reduced at the annual time scale (median
486 = 34%, range = 2 to 290%) compared with the cumulative growing season (median = 45%,
487 range = 2 to 450%), indicating that storage and transport played a significant role in the
488 decoupling of CH₄ production and emission across all sites. This significant decoupling has
489 implications for both modeling and measurements. For modeling, using daily CH₄ flux
490 measurements during the growing season to calibrate or validate process-based models may
491 result in an underestimation of the net annual CH₄ flux due storage in the peat structure.
492 Future measurements need to focus on processes, including CH₄ production, oxidation, and
493 transport pathways throughout the year, rather than simply on measuring the net CH₄ flux at
494 the peat surface.

495 In addition to the known temporal and spatial variability, measurement-associated
496 errors and data gaps may also contribute to the variance in annual CH₄ emissions (e.g. Fig.
497 2a,b) and need to be considered when planning measurements outside of the non-growing
498 season. Static chambers were most commonly used for measurements during both the
499 growing season (734/853 measurements) and during the non-growing season (99/131

500 measurements). Static chambers have a number of drawbacks, including potentially
501 overestimating annual fluxes when diurnal temperature variations are high (Friborg *et al.*,
502 1997, Yao *et al.*, 2009), which can be common during the shoulder seasons and in some
503 continental and drier sites (Mikkela *et al.*, 1995, Yao *et al.*, 2009). Static chambers also can
504 miss ebullition fluxes. Additionally, the calculation of CH₄ fluxes based on a linear increase
505 in concentration in chambers can underestimate the magnitude of CH₄ fluxes by ~30%
506 (Pihlatie *et al.*, 2013). Automated chamber setups have higher temporal resolution, which
507 improves both the flux response to temperature and can better capture ebullition fluxes
508 (Goodrich *et al.*, 2011) but are more expensive to set up and maintain and can generally cover
509 smaller spatial region than manual static chambers. Eddy covariance methods can be
510 preferable for winter measurements due to the harsh winter conditions but frequently result in
511 low coverage of data with acceptable quality despite high frequency measurements.
512 Methodological advancements in eddy covariance, including developing methods for the
513 continuous measurement of CH₄, are improving the reliability of measurements during the
514 non-growing season (Goodrich *et al.*, 2016). Currently, there were too few measurements to
515 assess whether there were systematic differences between measurement techniques during the
516 non-growing season. While increasing precision in methane flux measurements helps to
517 reduce uncertainty of northern wetland methane emissions, factors like uncertainty in wetland
518 area may still hamper accurate flux estimates and must also be addressed (e.g. Bloom *et al.*,
519 2017, Melton *et al.*, 2013).

520 Upland sites present a particular challenge to measuring annual CH₄ flux. First, there
521 are relatively few measurements of annual CH₄ flux in upland ecosystems (Fig. 2c),
522 especially ones that explicitly differentiate the role of non-growing season emissions.
523 Therefore, due to the low number of samples and high variability of emissions (Fig. 2a, b),
524 magnitude of non-growing season fluxes should be treated with caution. Furthermore, many

525 estimates in upland ecosystems (and some treed wetlands) are based only on measurements
526 from the soil surface, rather than above the tree canopy, and thus may be missing CH₄
527 released through trees (Machacova *et al.*, 2016). Additionally, year-round measurements of
528 CH₄ flux in uplands are not common (Fig. 2c) but wet periods in forests can result in net
529 annual CH₄ emissions rather than uptake (Lohila *et al.*, 2016, Ullah & Moore, 2011).

530

531 *Moving high latitude methane budgets forward*

532 Nearly 25 years ago, Bartlett and Harriss (1993) used all available CH₄ flux data and
533 wetland maps from Matthews and Fung (1987) to estimate that wetlands north of 45° emitted
534 34 Tg CH₄ y⁻¹ with an additional 4 Tg CH₄ y⁻¹ from upland tundra soils. Using data-
535 constrained process-based models based on significantly more annual CH₄ flux
536 measurements (Fig. 2c), we arrived at a similar answer (37 ± 7 Tg CH₄ y⁻¹) for wetland
537 emissions north of 40° (Table S2), which is also in good agreement with inverse modeling
538 estimates of wetland CH₄ flux of 39 Tg CH₄ y⁻¹ from natural emissions sources north of 30°
539 (Saunois *et al.*, 2016). In the 25 years since Bartlett and Harriss (1993), process-based
540 studies have provided key insights into the role of environmental conditions (e.g. Blodau,
541 2002, and references therein, Olefeldt *et al.*, 2013), substrate (Hodgkins *et al.*, 2014, Strom *et*
542 *al.*, 2003), microbes (McCalley *et al.*, 2014), transport pathways (Christensen *et al.*, 2003,
543 FechnerLevy & Hemond, 1996, King *et al.*, 1998), and storage (Comas *et al.*, 2008,
544 Parsekian *et al.*, 2011, Pirk *et al.*, 2015) in net ecosystem CH₄ flux, which are represented
545 with varying degrees of success in process-based models (Xu *et al.*, 2016b). The relatively
546 small number of model runs falling within the non-growing season fraction observational
547 constraint (15-33%, Fig. 6, Table S2) indicate that there is still significant room for
548 improvement in the representation of CH₄ flux in process-based models.

549 Although most models underestimate growing season emissions, further efforts are
550 required to attribute the model mismatch to specific model parameterizations or process
551 representations. The range of model mismatches is partially independent of model process
552 complexity, since the WetCHARTs model structure is relatively simple (in contrast to the
553 range of WetCHIMP models). Both WetCHARTs and WetCHIMP model ensembles have
554 similar success in accurately replicating the non-growing season fraction observational
555 constraint (Fig. 6, Table S3), suggesting parameter uncertainty alone is a prominent source of
556 error. For example, many of the WetCHARTS models within the observational data-
557 constraint (Fig. 6) exhibited a low anaerobic CH₄:CO₂ temperature sensitivity (Fig. S6),
558 although other constraints on the WetCHARTs ensemble parameterizations did not exhibit
559 any clear tendencies. Aside from these trends, we anticipate that accurate representation of
560 non-growing season processes, such as "zero-curtain" period emissions (Miller *et al.*, 2016,
561 Zona *et al.*, 2016) and ebullition processes (Mastepanov *et al.*, 2008, Pirk *et al.*, 2015) are
562 likely to have a substantial impact on the timing of and magnitude of modeled CH₄ emissions
563 at high latitudes, while uncertainties in the competing influences of winter-time temperature
564 and wetland extent controls likely play a significant role on non-growing wetland CH₄
565 emissions at lower latitudes (Bloom *et al.*, 2017). Ultimately, further investigation on the
566 mismatch between the spatial components of modeled and observed non-growing season CH₄
567 fluxes - particularly with respect to climate forcing and wetland type - are essential to
568 reconcile observed and model representations of wetland CH₄ processes. However, simply
569 improving the representation of CH₄ processes might not be sufficient to improve modeled
570 CH₄ flux; substantial improvements to the representation of soil temperature may also be
571 required due to the several-fold differences between permafrost- and permafrost-free
572 wetlands that must be captured in order to accurately represent CH₄ flux (Fig. 4).

573 The lack of empirical understanding about the processes involved in non-growing
574 season CH₄ flux directly hinders efforts to model non-growing season flux. In the future,
575 detailed process studies should be conducted to gain not only a better understanding of the
576 role of different mechanisms controlling the CH₄ emissions outside of the growing season,
577 but also the quantitative representation of these processes. An increased use of laser
578 instruments for year-round, high-frequency measurements should further clarify the role of
579 episodic CH₄ emissions during freeze-up, winter thaw events (e.g. Mastepanov *et al.*, 2008),
580 and the growing season, and should be combined with continuous measurements of peat
581 temperatures throughout the profile as well as measurements of porewater CH₄
582 concentrations as an indicator of CH₄ production. These efforts should be coordinated
583 between measurement and modeling approaches in order to improve the bottom-up estimates
584 of CH₄ flux. Additionally, future CH₄ flux measurements should focus on understudied
585 ecosystems, such as shallow water wetlands, marshes, and uplands, and measure regularly
586 throughout the year. This is particularly important in order to detect changing magnitude and
587 seasonality of CH₄ fluxes due to climate change against the background interannual
588 variability in CH₄ flux (Miller *et al.*, 2016, Sweeney *et al.*, 2016), and important for
589 understanding global emission trends of this important greenhouse gas.

590

591

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602

603

604 **References**

- 605 Alm J, Saarnio S, Nykanen H, Silvola J, Martikainen PJ (1999) Winter CO₂, CH₄ and N₂O
 606 fluxes on some natural and drained boreal peatlands. *Biogeochemistry*, **44**, 163-
 607 186.
- 608 Bartlett KB, Harriss RC (1993) Review and Assessment of Methane Emissions from
 609 Wetlands. *Chemosphere*, **26**, 261-320.
- 610 Bates D (2010) *lme4: Mixed-effects modeling with R*. pp Page, Madison, WI, Springer.
- 611 Bates D, Maechler M, Bolker B, Walker S (2014) *lme4: Linear mixed-effects models*
 612 *using Eigen and S4*. pp Page.
- 613 Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models
 614 Using *lme4*. 2015, **67**, 48.
- 615 Blanc-Betes E, Welker JM, Sturchio NC, Chanton JP, Gonzalez-Meler MA (2016) Winter
 616 precipitation and snow accumulation drive the methane sink or source strength
 617 of Arctic tussock tundra. *Global Change Biology*, **22**, 2818-2833.
- 618 Blodau C (2002) Carbon cycling in peatlands- A review of processes and controls.
 619 *Environmental Reviews*, **10**, 111-134.
- 620 Bloom AA, Bowman KW, Lee M *et al.* (2017) A global wetland methane emissions and
 621 uncertainty dataset for atmospheric chemical transport models (WetCHARTs
 622 version 1.0). *Geosci. Model Dev.*, **10**, 2141-2156.
- 623 Bridgham SD, Megonigal JP, Keller JK, Bliss NB, Trettin C (2006) The carbon balance of
 624 North American wetlands. *Wetlands*, **26**, 889-916.
- 625 Bubier JL (1995) The Relationship of Vegetation to Methane Emission and
 626 Hydrochemical Gradients in Northern Peatlands. *Journal of Ecology*, **83**, 403-420.
- 627 Bäckstrand K, Crill PM, Jackowicz-Korczyński M, Mastepanov M, Christensen TR,
 628 Bastviken D (2010) Annual carbon gas budget for a subarctic peatland, Northern
 629 Sweden. *Biogeosciences*, **7**, 95-108.
- 630 Christensen TR, Panikov N, Mastepanov M *et al.* (2003) Biotic controls on CO₂ and CH₄
 631 exchange in wetlands - a closed environment study. *Biogeochemistry*, **64**, 337-
 632 354.
- 633 Comas X, Slater L, Reeve A (2008) Seasonal geophysical monitoring of biogenic gases in
 634 a northern peatland: Implications for temporal and spatial variability in free
 635 phase gas production rates. *Journal of Geophysical Research: Biogeosciences*,
 636 **113**, n/a-n/a.
- 637 Dise NB (1992) Winter Fluxes of Methane from Minnesota Peatlands. *Biogeochemistry*,
 638 **17**, 71-83.

- 639 Fechnerlevy EJ, Hemond HF (1996) Trapped methane volume and potential effects on
640 methane ebullition in a northern peatland. *Limnology and Oceanography*, **41**,
641 1375-1383.
- 642 Friborg T, Christensen TR, Sogaard H (1997) Rapid response of greenhouse gas
643 emission to early spring thaw in a subarctic mire as shown by
644 micrometeorological techniques. *Geophysical Research Letters*, **24**, 3061-3064.
- 645 Goodrich JP, Oechel WC, Gioli B, Moreaux V, Murphy PC, Burba G, Zona D (2016) Impact
646 of different eddy covariance sensors, site set-up, and maintenance on the annual
647 balance of CO₂ and CH₄ in the harsh Arctic environment. *Agricultural and Forest
648 Meteorology*, **228-229**, 239-251.
- 649 Goodrich JP, Varner RK, Froelking S, Duncan BN, Crill PM (2011) High frequency
650 measurements of methane ebullition over a growing season at a temperate
651 peatland site. *Geophys. Res. Lett.*
- 652 Group NWW (1988) Wetlands of Canada. Ecological land classification series, no. 24.
653 Sustainable Development Branch, Environment Canada, Ottawa, Ontario, and
654 Polyscience Publications Inc., Montreal, Quebec, **452**.
- 655 Heikkinen JEP, Maljanen M, Aurela M, Hargreaves KJ, Martikainen PJ (2002) Carbon
656 dioxide and methane dynamics in a sub-Arctic peatland in northern Finland.
657 *Polar Research*, **21**, 49-62.
- 658 Hodgkins SB, Tfaily MM, Mccalley CK *et al.* (2014) Changes in peat chemistry associated
659 with permafrost thaw increase greenhouse gas production. *Proceedings of the
660 National Academy of Sciences*, **111**, 5819-5824.
- 661 Jackowicz-Korczyński M, Christensen TR, Bäckstrand K, Crill P, Friborg T, Mastepanov
662 M, Ström L (2010) Annual cycle of methane emission from a subarctic peatland.
663 *Journal of Geophysical Research: Biogeosciences*, **115**, n/a-n/a.
- 664 Juottonen H, Tuittila E-S, Juutinen S, Fritze H, Yrjälä K (2008) Seasonality of rDNA-and
665 rRNA-derived archaeal communities and methanogenic potential in a boreal
666 mire. *The ISME journal*, **2**, 1157-1168.
- 667 Karion A, Sweeney C, Miller JB *et al.* (2016) Investigating Alaskan methane and carbon
668 dioxide fluxes using measurements from the CARVE tower. *Atmospheric
669 Chemistry and Physics*, **16**, 5383-5398.
- 670 King JY, Reeburgh WS, Regli SK (1998) Methane emission and transport by arctic sedges
671 in Alaska: Results of a vegetation removal experiment. *Journal of Geophysical
672 Research-Atmospheres*, **103**, 29083-29092.
- 673 Kirschke S, Bousquet P, Ciais P *et al.* (2013) Three decades of global methane sources
674 and sinks. *Nature Geosci*, **6**, 813-823.
- 675 Levy PE, Burden A, Cooper MDA *et al.* (2012) Methane emissions from soils: synthesis
676 and analysis of a large UK data set. *Global Change Biology*, **18**, 1657-1669.
- 677 Lohila A, Aalto T, Aurela M *et al.* (2016) Large contribution of boreal upland forest soils
678 to a catchment-scale CH₄ balance in a wet year. *Geophysical Research Letters*,
679 **43**, 2946-2953.
- 680 Machacova K, Bäck J, Vanhatalo A *et al.* (2016) *Pinus sylvestris* as a missing source of
681 nitrous oxide and methane in boreal forest. *Scientific Reports*, **6**, 23410.
- 682 Marushchak ME, Friborg T, Biasi C *et al.* (2016) Methane dynamics in the subarctic
683 tundra: combining stable isotope analyses, plot- and ecosystem-scale flux
684 measurements. *Biogeosciences*, **13**, 597-608.
- 685 Marushchak ME, Kiepe I, Biasi C *et al.* (2013) Carbon dioxide balance of subarctic tundra
686 from plot to regional scales. *Biogeosciences*, **10**, 437-452.

- 687 Mastepanov M, Sigsgaard C, Dlugokencky EJ, Houweling S, Strom L, Tamstorf MP,
688 Christensen TR (2008) Large tundra methane burst during onset of freezing.
689 Nature, **456**, 628-U658.
- 690 Mastepanov M, Sigsgaard C, Tagesson T, Ström L, Tamstorf MP, Lund M, Christensen TR
691 (2013) Revisiting factors controlling methane emissions from high-Arctic tundra.
692 Biogeosciences, **10**, 5139-5158.
- 693 Matthews E, Fung I (1987) Methane emission from natural wetlands: Global
694 distribution, area, and environmental characteristics of sources. Global
695 Biogeochemical Cycles, **1**, 61-86.
- 696 Mccalley CK, Woodcroft BJ, Hodgkins SB *et al.* (2014) Methane dynamics regulated by
697 microbial community response to permafrost thaw. Nature, **514**, 478-481.
- 698 Mcguire AD, Christensen TR, Hayes D *et al.* (2012) An assessment of the carbon balance
699 of Arctic tundra: comparisons among observations, process models, and
700 atmospheric inversions. Biogeosciences, **9**, 3185-3204.
- 701 Melloh RA, Crill PM (1996) Winter methane dynamics in a temperate peatland. Global
702 Biogeochemical Cycles, **10**, 247-254.
- 703 Melton JR, Wania R, Hodson EL *et al.* (2013) Present state of global wetland extent and
704 wetland methane modelling: conclusions from a model inter-comparison project
705 (WETCHIMP). Biogeosciences, **10**, 753-788.
- 706 Mikkela C, Sundh I, Svensson BH, Nilsson M (1995) Diurnal variation in methane
707 emission in relation to the water table, soil temperature, climate and vegetation
708 cover in a Swedish acid mire. Biogeochemistry, **28**, 93-114.
- 709 Miller SM, Miller CE, Commane R *et al.* (2016) A multiyear estimate of methane fluxes in
710 Alaska from CARVE atmospheric observations. Global Biogeochemical Cycles, **30**,
711 1441-1453.
- 712 Moore TR, Dalva M (1997) Methane and carbon dioxide exchange potentials of peat
713 soils in aerobic and anaerobic laboratory incubations. Soil Biology &
714 Biochemistry, **29**, 1157-1164.
- 715 Moore TR, Roulet NT (1993) Methane Flux - Water-Table Relations in Northern
716 Wetlands. Geophysical Research Letters, **20**, 587-590.
- 717 Myhre G, Shindell D, Bréon F-M *et al.* (2013) Anthropogenic and Natural Radiative
718 Forcing. In: *Climate Change 2013: The Physical Science Basis. Contributions of*
719 *Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on*
720 *Climate Change.* . (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK,
721 Boschung J, Nauels A, Xia Y, Bex V, Midgley PM) pp Page. Cambridge, United
722 Kingdom and New York, NY, USA, Cambridge University Press.
- 723 Nisbet EG, Dlugokencky EJ, Bousquet P (2014) Methane on the Rise—Again. Science,
724 **343**, 493-495.
- 725 Nykänen H, Heikkinen JEP, Pirinen L, Tiilikainen K, Martikainen PJ (2003) Annual CO₂
726 exchange and CH₄ fluxes on a subarctic peat mire during climatically different
727 years. Global Biogeochemical Cycles, **17**, n/a-n/a.
- 728 Olefeldt D, Turetsky MR, Crill PM, Mcguire AD (2013) Environmental and physical
729 controls on northern terrestrial methane emissions across permafrost zones.
730 Global Change Biology, **19**, 589-603.
- 731 Olson DM, Dinerstein E, Wikramanayake ED *et al.* (2001) Terrestrial Ecoregions of the
732 World: A New Map of Life on Earth: A new global map of terrestrial ecoregions
733 provides an innovative tool for conserving biodiversity. Bioscience, **51**, 933-938.

- 734 Parsekian AD, Comas X, Slater L, Glaser PH (2011) Geophysical evidence for the lateral
735 distribution of free phase gas at the peat basin scale in a large northern peatland.
736 Journal of Geophysical Research: Biogeosciences, **116**, n/a-n/a.
- 737 Pihlatie MK, Christiansen JR, Aaltonen H *et al.* (2013) Comparison of static chambers to
738 measure CH₄ emissions from soils. Agricultural and Forest Meteorology, **171**,
739 124-136.
- 740 Pirk N, Santos T, Gustafson C *et al.* (2015) Methane emission bursts from permafrost
741 environments during autumn freeze-in: New insights from ground-penetrating
742 radar. Geophysical Research Letters, **42**, 6732-6738.
- 743 Saunio M, Bousquet P, Poulter B *et al.* (2016) The global methane budget 2000–2012.
744 Earth Syst. Sci. Data, **8**, 697-751.
- 745 Segarra K, Schubotz F, Samarkin V, Yoshinaga M, Hinrichs K, Joye S (2015) High rates of
746 anaerobic methane oxidation in freshwater wetlands reduce potential
747 atmospheric methane emissions. Nature Communications, **6**, 7477.
- 748 Strom L, Ekberg A, Mastepanov M, Christensen TR (2003) The effect of vascular plants
749 on carbon turnover and methane emissions from a tundra wetland. Global
750 Change Biology, **9**, 1185-1192.
- 751 Sweeney C, Dlugokencky E, Miller CE *et al.* (2016) No significant increase in long-term
752 CH₄ emissions on North Slope of Alaska despite significant increase in air
753 temperature. Geophysical Research Letters, **43**, 6604-6611.
- 754 Team RDC (2008) R: A language and environment for statistical computing. pp Page,
755 Vienna, Austria, R Foundation for Statistical Computing.
- 756 Teepe R, Brumme R, Beese F (2001) Nitrous oxide emissions from soil during freezing
757 and thawing periods. Soil Biology and Biochemistry, **33**, 1269-1275.
- 758 Thonat T, Saunio M, Bousquet P *et al.* (2017) Detectability of Arctic methane sources at
759 six sites performing continuous atmospheric measurements. Atmos. Chem. Phys.,
760 **17**, 8371-8394.
- 761 Treat CC, Bubier JL, Varner RK, Crill PM (2007) Timescale dependence of environmental
762 and plant-mediated controls on CH₄ flux in a temperate fen. Journal of
763 Geophysical Research-Biogeosciences, **112**, G01014.
- 764 Treat CC, Natali SM, Ernakovich J *et al.* (2015) A pan-Arctic synthesis of CH₄ and CO₂
765 production from anoxic soil incubations. Global Change Biology, **21**, 2787-2803.
- 766 Turetsky MR, Kotowska A, Bubier J *et al.* (2014) A synthesis of methane emissions from
767 71 northern, temperate, and subtropical wetlands. Global Change Biology, **20**,
768 2183-2197.
- 769 Ullah S, Moore TR (2011) Biogeochemical controls on methane, nitrous oxide, and
770 carbon dioxide fluxes from deciduous forest soils in eastern Canada. Journal of
771 Geophysical Research: Biogeosciences, **116**, n/a-n/a.
- 772 Whiting GJ, Chanton JP (1993) Primary Production Control of Methane Emission from
773 Wetlands. Nature, **364**, 794-795.
- 774 Xu X, Riley WJ, Koven CD *et al.* (2016a) A multi-scale comparison of modeled and
775 observed seasonal methane emissions in northern wetlands. Biogeosciences, **13**,
776 5043-5056.
- 777 Xu X, Yuan F, Hanson PJ *et al.* (2016b) Reviews and syntheses: Four decades of modeling
778 methane cycling in terrestrial ecosystems. Biogeosciences, **13**, 3735-3755.
- 779 Yao Z, Zheng X, Xie B *et al.* (2009) Comparison of manual and automated chambers for
780 field measurements of N₂O, CH₄, CO₂ fluxes from cultivated land. Atmospheric
781 Environment, **43**, 1888-1896.

782 Zona D, Gioli B, Commane R *et al.* (2016) Cold season emissions dominate the Arctic
783 tundra methane budget. *Proceedings of the National Academy of Sciences*, **113**,
784 40-45.
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786

787 **Table 1.** Relationship between cumulative growing season CH₄ flux (g CH₄ m⁻²) and
 788 annual growing season flux (g CH₄ m⁻²) from sites that were measured throughout
 789 the year using linear mixed effects modeling. The relationship differed significantly
 790 among biomes in wetlands and between sites with and without permafrost in
 791 uplands. Parentheses indicate standard error. Models were tested against a null
 792 model including additive effects of cumulative growing season and biome (wetlands)
 793 or permafrost presence/absence (uplands).

Class	Slope	Intercept	n
<i>Wetlands</i>			
Temperate	1.054 (± 0.018)	1.654 (± 0.775)	25
Boreal/Taiga	1.017 (± 0.028)	2.680 (± 0.468)	67
Tundra	1.486 (± 0.060)	0.178 (± 0.850)	25
	Chi ² =21.8, d.f.=4	P=0.0002	
<i>Uplands</i>			
No permafrost	0.816 ± 0.304	-0.346 ± 0.171	2
Permafrost	2.443 ± 0.431	-0.016 ± 0.036	6
	Chi ² =18.4, d.f.=2	P< 0.0001	

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797 **Fig. 1.** Map of sites with annual CH₄ flux measurements (pink circles), sites with annual flux
 798 estimates based on the relationship of total growing season CH₄ flux and annual CH₄ flux
 799 (blue squares, Table 1), and sites where original authors modeled annual fluxes (green
 800 triangles). Borders of biomes/ecoregions used in the study are delineated (Olson *et al.*, 2001).
 801 Additional sites (n=18) are not shown due to missing coordinates.

802
 803 **Fig. 2.** (a) Measured non-growing season CH₄ emissions, (b) measured, modeled and
 804 estimated annual CH₄ emissions, and (c) number of measurements among wetland categories
 805 and uplands for temperate, boreal/taiga, and tundra regions. Boxes represent 25th, 75th
 806 percentile of data, line represents median, whiskers denote 10th and 90th percentile of data.
 807 Note differing y-axis scales. Annual CH₄ fluxes include measured, modeled, and estimated
 808 fluxes (Methods, Table 1). (c) Total number of site x year measurements, including annual
 809 fluxes estimated from growing season measurements only (solid, n=853) plus sites measured
 810 during the non-growing season (shaded, n=131).

811
 812 **Fig. 3.** The measured non-growing season CH₄ emissions (top) and non-growing season
 813 fraction of annual emissions among ecosystem classes and biomes. (a) Non-growing season
 814 CH₄ fluxes differed significantly among ecosystem classes (Chi²=46, d.f.=5, *P*<0.0001); (b)
 815 Non-growing season CH₄ fluxes did not differ significantly among biomes (Chi²=0.9, d.f.=2,
 816 *P*=0.63); (c) non-growing season fraction differed significantly among ecosystem classes
 817 (Chi²=18.0, d.f.=5, *P*=0.003), and (b) biomes (Chi² = 11, d.f. = 2, *P*=0.005). Letters indicate
 818 significant differences (α =0.05) among the groups.

819
 820 **Fig. 4.** Differences between sites with and without permafrost in (a) measured growing
 821 season, estimated non-growing season (Chi²=19, d.f. = 1, *P*<0.0001), and estimated annual
 822 CH₄ fluxes (Chi²=34, d.f. = 1, *P*<0.0001); and (b) measured non-growing season fraction
 823 (Chi²=13, d.f. = 1, *P*=0.0003).

824
 825 **Fig. 5.** The cumulative distribution function of observations of the non-growing season
 826 fraction (non-growing season CH₄ flux/annual CH₄ flux, %) for wetlands in the regions of (a)
 827 40 – 60° N and (b) 60 – 90° N. Points represent the cumulative data distribution of the non-
 828 growing season fraction for the model ensembles (WetCHART, WETCHIMP) and measured
 829 datasets (Wetland data, blue). Vertical lines and boxes represent the median and the 95%
 830 confidence intervals around the median for each dataset.

831
 832 **Fig. 6.** The non-growing season fraction and the total non-growing season flux from the two
 833 model ensembles for (a) 40° - 60° N and (b) north of 60° N. The model ensembles are
 834 wetCHARTs (open circles; n=324) and wetCHIMP (orange diamonds; n=6). Each point
 835 represents wetland CH₄ emissions from a single process model. The gold point represents the
 836 unconstrained median among all models (Model est). The blue point represents the median of
 837 data-constrained model results (Data-const) after selecting the model results that fell within
 838 the 95% confidence intervals of the measured median non-growing season fraction (Fig. 5),
 839 indicated by the gray box. Upland tundra areas may constitute an additional source (Fig.
 840 2a)(Zona *et al.*, 2016); this estimate is strictly from wetland areas (Methods).

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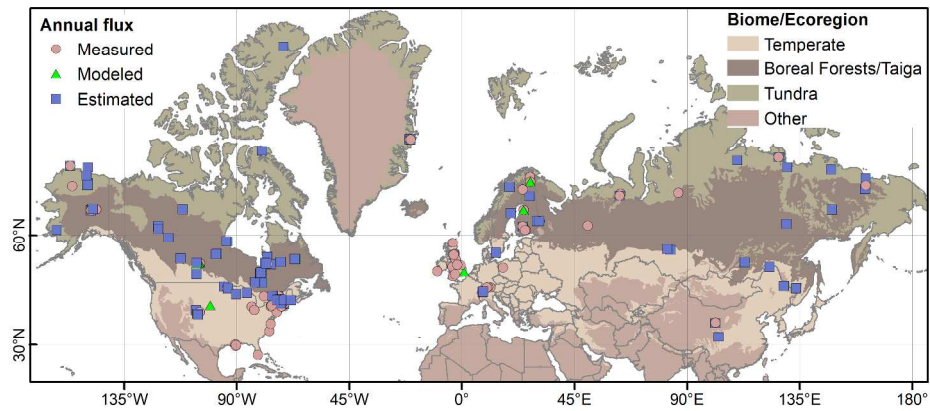
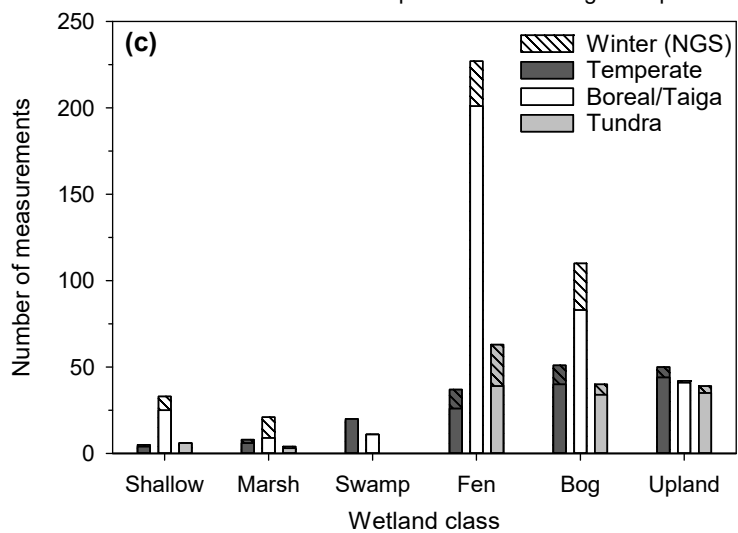
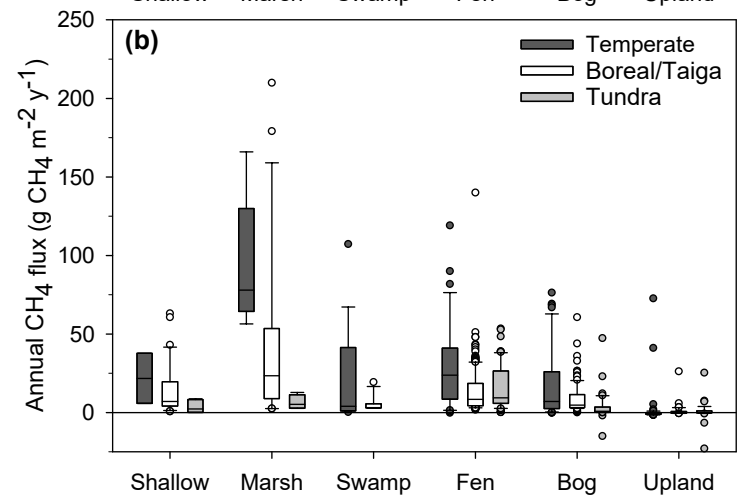
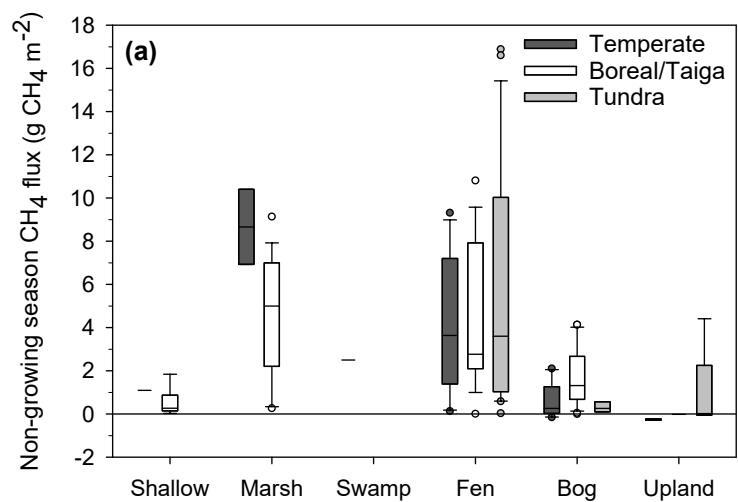


Figure 1. Map of sites with annual CH₄ flux measurements (pink circles), sites with annual flux estimates based on the relationship of total growing season CH₄ flux and annual CH₄ flux (blue squares, Table 1), and sites where original authors modeled annual fluxes (green triangles). Borders of biomes/ecoregions used in the study are delineated (Olson et al., 2001). Additional sites (n=18) are not shown due to missing coordinates.



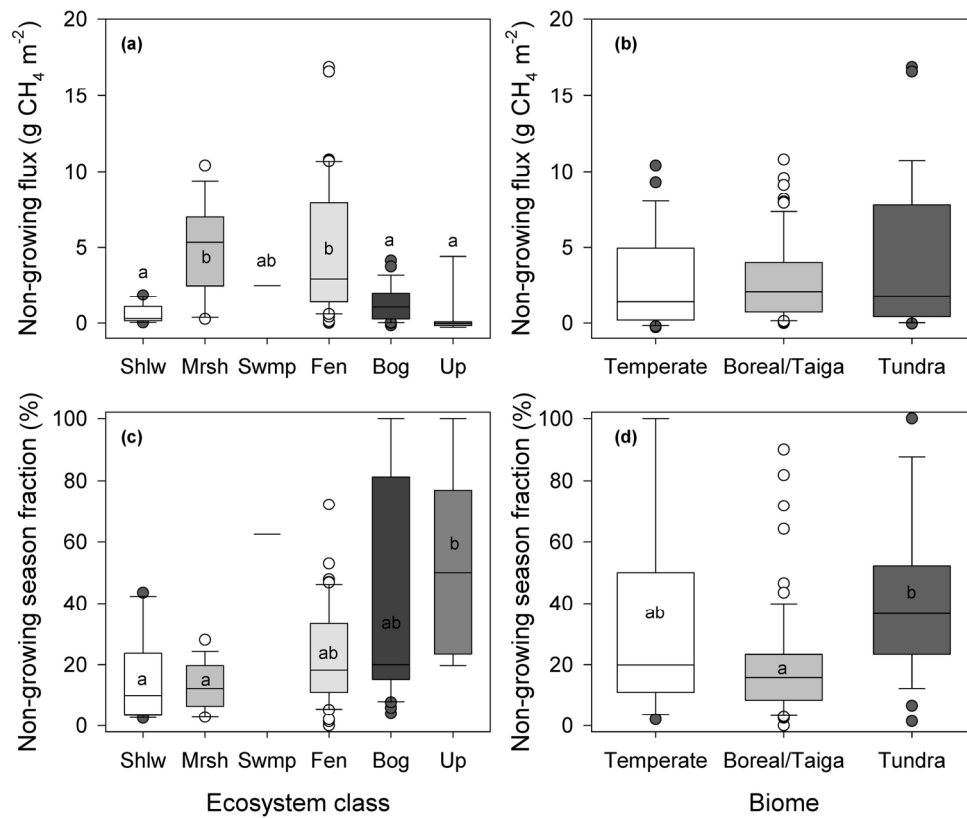
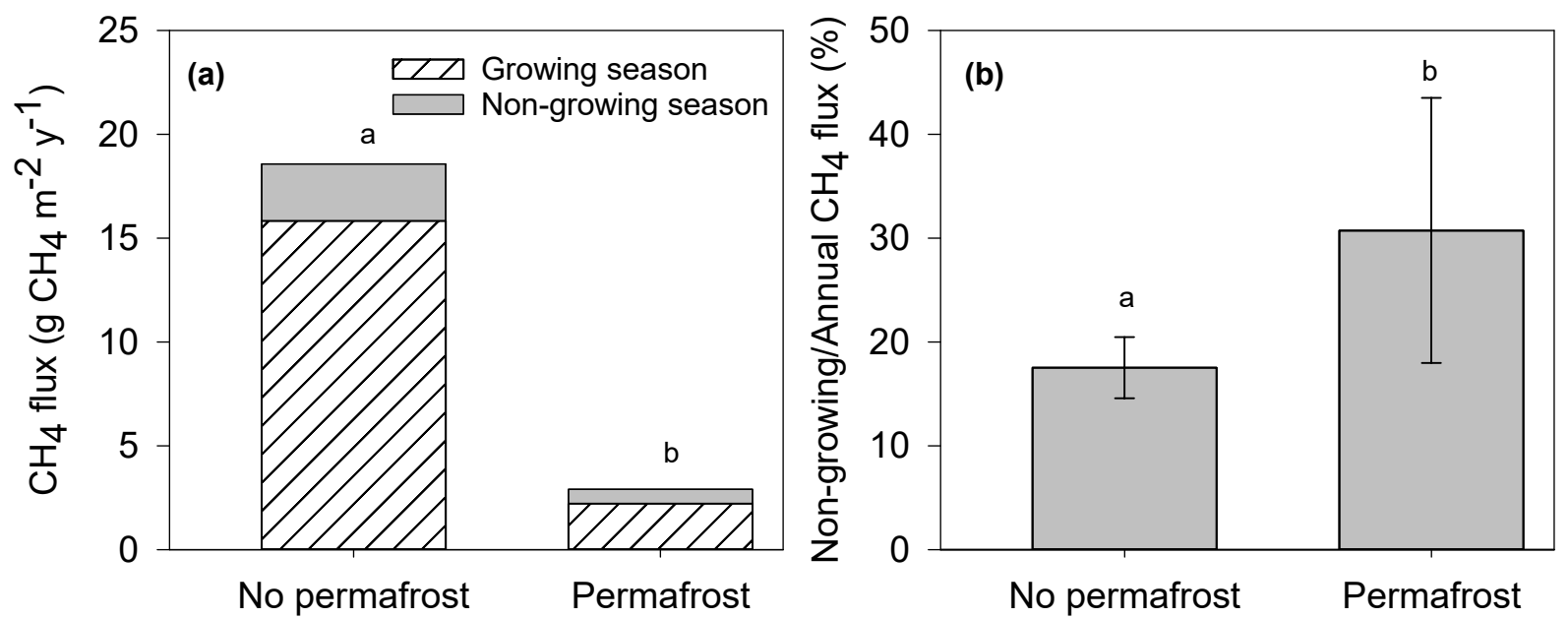


Figure 3. The measured non-growing season CH₄ emissions (top) and non-growing season fraction of annual emissions among ecosystem classes and biomes. (a) Non-growing season CH₄ fluxes differed significantly among ecosystem classes ($\text{Chi}^2=46$, d.f.=5, $P<0.0001$); (b) Non-growing season CH₄ fluxes did not differ significantly among biomes ($\text{Chi}^2=0.9$, d.f.=2, $P=0.63$); (c) non-growing season fraction differed significantly among ecosystem classes ($\text{Chi}^2=18.0$, d.f.=5, $P=0.003$), and (d) biomes ($\text{Chi}^2 = 11$, d.f. = 2, $P=0.005$). Letters indicate significant differences ($\alpha=0.05$) among the groups.

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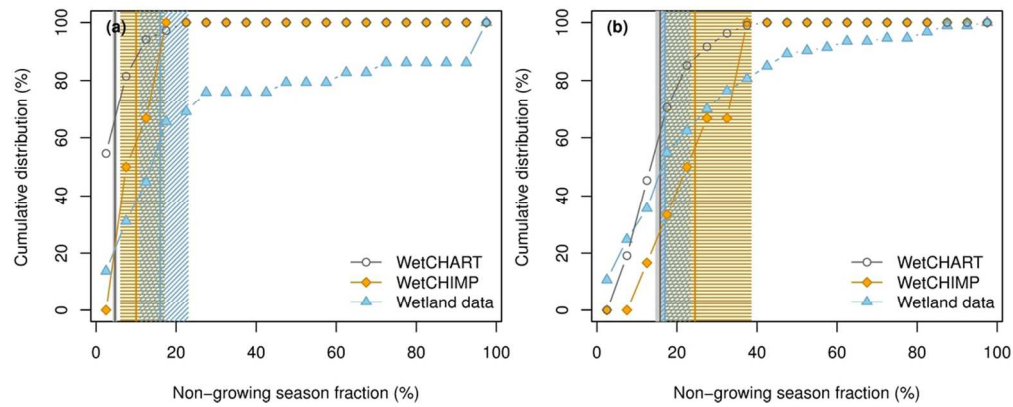


Fig. 5. The cumulative distribution function of observations of the non-growing season fraction (non-growing season CH₄ flux/annual CH₄ flux, %) for wetlands in the regions of (a) 40 – 60° N and (b) 60 – 90° N.

Points represent the cumulative data distribution of the non-growing season fraction for the model ensembles (WetCHART, WETCHIMP) and measured datasets (Wetland data, blue). Vertical lines and boxes represent the median and the 95% confidence intervals around the median for each dataset.

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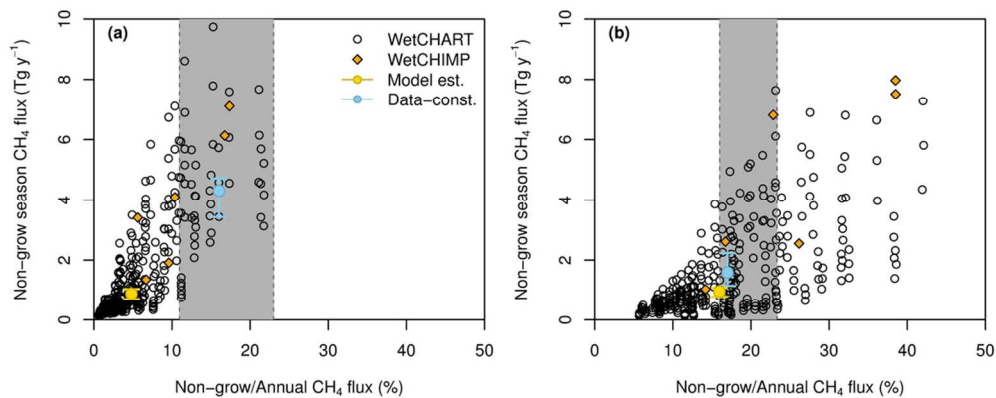


Figure 6. The non-growing season fraction and the total non-growing season flux from the two model ensembles for (a) 40° - 60° N and (b) north of 60° N. The model ensembles are wetCHARTs (open circles; n=324) and wetCHIMP (orange diamonds; n=6). Each point represents wetland CH₄ emissions from a single process model. The gold point represents the unconstrained median among all models (Model est). The blue point represents the median of data-constrained model results (Data-const) after selecting the model results that fell within the 95% confidence intervals of the measured median non-growing season fraction (Fig. 5), indicated by the gray box. Upland tundra areas may constitute an additional source (Fig. 2a)(Zona et al., 2016); this estimate is strictly from wetland areas (Methods).

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