

Large loss of CO₂ in winter observed across pan-arctic permafrost region

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102

103 Elevated warming in the Arctic, which has been amplified during the winter¹⁻³,
104 greatly enhances microbial decomposition of soil organic matter and release of carbon
105 dioxide (CO₂) from soils⁴. However, the amount of CO₂ released in winter is highly
106 uncertain and has not been well represented by ecosystem models or by empirically-based
107 estimates^{5,6}. Here we synthesize regional *in situ* observations of CO₂ flux from arctic and
108 boreal soils to assess current and future winter carbon losses from the pan-arctic domain.
109 We estimate a contemporary loss of 1662 Tg C yr⁻¹ from the permafrost region during the
110 winter season (October through April). This loss is greater than the average growing
111 season carbon uptake for this region estimated from process models (-1032 Tg C yr⁻¹).
112 Extending model predictions to warmer conditions in 2100 indicates that winter CO₂
113 emissions will increase 17% under a moderate mitigation scenario—Representative
114 Concentration Pathway (RCP) 4.5—and 41% under business-as-usual emissions
115 scenario—RCP 8.5. Our results provide a new baseline for winter CO₂ emissions from
116 northern terrestrial regions and show enhanced soil CO₂ loss due to winter warming may
117 offset growing season carbon uptake under future climatic conditions.

120 Air and soil temperatures in the Arctic are increasing rapidly, with the most severe
121 climate amplification occurring in autumn and winter^{1,2}. Although warmer soils decompose
122 more quickly, thus releasing more CO₂ into the atmosphere, microbial respiration is known to
123 occur even under extremely cold winter conditions (e.g., down to ~ -20°C) in the presence of
124 unfrozen microsites that can persist at sub-zero soil temperatures⁷. This production and release
125 of CO₂ in winter is expected to increase substantially as soils continue to warm and thaw under a
126 warming climate^{4,8}.

127 However, it remains highly uncertain how much CO₂ is currently emitted from the
128 permafrost region during winter⁹ and to what magnitude these emissions might increase in the
129 future^{8,10}. Many ecosystem models are not well adapted to characterize respiration from high
130 latitude soils⁵ and may greatly underestimate present and future winter CO₂ emissions⁶. Given
131 the limitations in current models, lack of satellite and airborne CO₂ data for the Arctic during
132 winter¹¹, and gaps in spatial coverage of Arctic air monitoring networks¹², *in situ* CO₂ flux
133 observations provide the most direct insight into the state of winter CO₂ emissions across the
134 northern permafrost domain.

135 Studies of winter respiration indicate that the amount of CO₂ released during cold periods
136 depends greatly on vegetation type¹³, availability of labile carbon substrates^{14,15,16}, non-frozen
137 soil moisture^{4,7,15,17,18}, microbial community composition and function¹⁹, and snow depth^{15, 20, 21}.
138 However, knowledge of the influence of these drivers on the rates and patterns of winter CO₂
139 flux on a regional scale remains limited^{6, 9}.

140 Here we present a new compilation of *in situ* CO₂ winter flux data for the northern
141 permafrost domain (Fig. 1, Supplementary Information (SI) Table 1) to examine the drivers and
142 magnitude of winter respiration in the Arctic. We define the winter period as October through

143 April—months when the landscape is generally covered by snow and photosynthesis is
144 negligible^{22,23}. The dataset represents more than 100 high latitude sites and comprises more than
145 1,000 aggregated monthly fluxes. We examined patterns and processes driving winter CO₂
146 emissions and scaled fluxes to the permafrost domain using a boosted regression tree (BRT)
147 machine learning model based on hypothesized drivers of winter CO₂ flux. Environmental and
148 ecological drivers (e.g., vegetation type and productivity, soil moisture, and soil temperature)
149 obtained from satellite remote sensing and reanalysis data were used to estimate regional winter
150 CO₂ emissions for contemporary (2003-2017) climatic conditions. We estimated winter fluxes
151 through 2100 using meteorological and carbon cycle drivers from ensembles of Earth System
152 Model (ESM) outputs for RCP 4.5 and RCP 8.5²⁴.

153 Soil temperature had the strongest influence on winter CO₂ emissions, with fluxes
154 measured at soil temperatures down to -20°C (Fig. 2a), in line with results from lab incubations
155 (Fig. 2b), demonstrating that microbial respiration can occur in unfrozen microsites that persist at
156 sub-zero bulk soil temperatures¹⁸. Diffusion of stored CO₂ produced during the non-frozen
157 season may have driven some of the emissions measured in winter, but the magnitude of this
158 contribution is unclear. Winter CO₂ emissions increased by a factor of 2.9 (95% CI = 2.1, 4.2)
159 per 10°C soil temperature increase (i.e., Q10) for *in situ* fluxes and by a factor of 8.5 (CI= 5.0,
160 14.5) for CO₂ release from low temperature lab incubations. Differences between *in situ* and lab
161 Q10s may reflect site-level differences in environmental drivers other than temperature (*in situ*
162 and lab sites were not fully overlapping) or variation in the depth of *in situ* CO₂ production—
163 which can occur throughout the soil profile—relative to the depth of recorded temperature,
164 which tended to be closer to the soil surface (~ 10 cm).

165 Air and soil temperatures had the strongest influence on winter flux with a combined
166 relative influence (RI) of 32%. Vegetation type (15% RI), leaf area index (LAI, 11%), tree cover
167 (TC; 10%), and previous summer's gross primary productivity (GPP; 8.5%) also influenced
168 winter CO₂ emissions (SI Fig. 1). Along with warmer air and soil temperatures in winter and
169 corresponding increases in CO₂ loss, summer GPP has also been increasing across the Arctic²⁵.
170 The positive relationship between GPP and winter CO₂ emissions suggests that increased CO₂
171 uptake during the growing season may be offset, in part, by winter CO₂ emissions.

172 Another important driver of winter respiration was unfrozen water content, which is a
173 function of soil temperature and texture, as finer textured soils contain more unfrozen water than
174 coarse soils for a given sub-zero temperature²⁶. Indirect measurements of unfrozen water
175 availability confirm its importance: soils with low sand and high clay content, which tend to have
176 greater unfrozen microsites, were characterized by higher CO₂ flux rates. While snow cover is a
177 key driver of winter flux through its impact on ground temperature²⁷, remote sensing estimates of
178 snow cover were not significant predictors in the model; this may be a result of high uncertainty
179 in regional snow products or because snow depth and density, which are difficult to determine
180 from space using currently available satellite technology²⁸, have a greater influence on ground
181 temperatures than snow presence alone.

182 Using our model to assess winter flux for the terrestrial permafrost domain, we estimate
183 approximately 1662 Tg C winter⁻¹ released under current climatic conditions (2003-2017), with a
184 corresponding uncertainty of 813 Tg (SI Methods). There were no detected temporal trends in
185 winter CO₂ flux during this 15-year period ($p > 0.1$), which largely reflects the lack of a
186 significant arctic-wide trend in the reanalysis winter air or soil temperature data used as model
187 inputs ($p > 0.1$). Although we did not observe region-wide trends during the past 15 years,

188 atmospheric CO₂ enhancements for Alaska⁸ and site-level studies from Alaskan tundra^{29,30}
189 showed recent increases in winter emissions, which are already shifting some tundra regions
190 from an annual carbon sink to a source.

191 Our flux estimates are twofold higher than a previous estimate derived from *in situ*
192 measurements reported in the Regional Carbon Cycle Assessment and Processes (RECCAP)
193 tundra and northern boreal domain¹⁰, which was based on a much smaller dataset (< 20 site-years
194 for winter data). The RECCAP study reported fluxes of 24 - 41 g C m⁻² winter⁻¹ from *in situ* data,
195 compared to 64 g C m⁻² winter⁻¹ estimated here for the RECCAP region and 98 g C m⁻² winter⁻¹
196 for the full permafrost domain (SI Fig. 2). Our estimate of winter flux agrees more closely with
197 the RECCAP atmospheric inversion estimate (27-81 g C m⁻² winter⁻¹), providing some closure
198 between bottom-up and top-down assessments^{6,12}.

199 We then compared our permafrost region flux estimates to winter net ecosystem
200 exchange (NEE) outputs from five process-based terrestrial models and from FluxCom, a global
201 machine-learning NEE product³¹. Our winter CO₂ flux estimate was generally higher than
202 estimates from these models, which ranged from 377 Tg C winter⁻¹ for FluxCom and from 503 to
203 1301 Tg C for the process models (mean: 1008 Tg C winter⁻¹; SI Fig. 3). Similar variation in
204 carbon budget estimates from terrestrial models has been reported elsewhere for high latitude
205 regions⁵ and reflects considerable differences in model parameterization of soil temperature,
206 unfrozen water, and substrate effects on CO₂ production under winter conditions. Some process-
207 based models may underestimate winter CO₂ emissions simply by erroneously shutting down
208 respiration at sub-zero soil temperatures³² or because they are unable to capture small-scale
209 processes that influence winter flux, such as talik formation and shrub-snow interactions that are
210 more likely to be captured by *in situ* measurements.

211 Combining growing season (-687 to -1647 Tg C season⁻¹) and winter NEE derived from
212 these process models results in an estimated annual NEE of -351 to 514 Tg C yr⁻¹ (-555 for
213 FluxCom; SI Table 2). Because our winter emissions estimate was higher than the process
214 models, we expect that annual CO₂ losses may also be higher. For example, if we account for
215 growing season NEE using the process model estimates, this would yield an average annual CO₂
216 emission of 646 Tg C yr⁻¹ (range of 15 to 975) from the permafrost region, based on our estimate
217 of winter CO₂ flux.

218 Our assessment of future winter emissions—obtained by forcing the BRT model with
219 environmental conditions from CMIP5 ESM outputs²—showed significant increases in winter
220 CO₂ emissions under both climate scenarios ($p < 0.001$, Fig. 3); however, emissions were
221 substantially lower with climate mitigation in RCP 4.5 than with RCP 8.5. Compared to current
222 winter emissions (2003-2017), there was a 17% projected increase in winter CO₂ flux under RCP
223 4.5 by 2100 (to 1950 Tg C yr⁻¹) and a 41% increase under RCP 8.5 by 2100 (to 2345 Tg C yr⁻¹)
224 (Fig. 4).

225 The present-day continuous permafrost zone experienced the strongest positive trend in
226 winter CO₂ emissions under both climate scenarios ($p < 0.001$); however, accounting for
227 differences in area, the largest rate of change occurred across the discontinuous zone (SI Table 3)
228 where soils have warmed rapidly and permafrost has diminished in recent years³³. The
229 differences in projected changes in winter CO₂ emission among permafrost zones may reflect the
230 influence of latitudinal variation in environmental and ecological variables, including tree cover,
231 dominant vegetation, and soil organic matter content and composition³⁴.

232 Increased projected winter CO₂ emissions from our data-driven BRT model were largely
233 driven by changes in soil and air temperatures, which both increased by 0.04°C yr⁻¹ under RCP

234 4.5, and increased by $0.08^{\circ}\text{C yr}^{-1}$ for soil and $0.1^{\circ}\text{C yr}^{-1}$ for air under RCP 8.5 (SI Fig. 4).
235 Vegetation leaf area and GPP, both of which were positively related to winter CO_2 flux, also
236 significantly increased through 2100.

237 From 2018 to 2100, we estimated a cumulative winter flux of 150 Pg C for RCP 4.5 and
238 162 Pg C for RCP 8.5. This represents an additional 15 Pg C for RCP 4.5 and 27 Pg C for RCP
239 8.5 emitted as a result of climate change, when compared to the estimated 135 Pg of C that
240 would be emitted through 2100 if current (2003-2017) climatic conditions remained constant.
241 These losses are comparable to 70% of the current permafrost-region near-surface (0-30cm) soil
242 carbon pool³⁵. These projected increases are substantially lower than projections from CMIP5
243 ESMs, in which winter CO_2 emissions from ecosystem respiration for the permafrost region
244 ($1753 \pm 1066 \text{ Pg C yr}^{-1}$ for 2003-2005) were projected to increase in 2100 by 37% and 86%
245 under RCP 4.5 ($2482 \pm 1403 \text{ Pg C yr}^{-1}$) and 8.5 ($3473 \pm 1731 \text{ Pg C yr}^{-1}$), respectively (Fig. 4).
246 Our data-driven BRT model may provide more conservative estimates because current *in situ*
247 observations may not adequately reflect future environmental responses to substantially warmer
248 winter conditions. However, it is also possible that the ESMs are missing stabilizing drivers and
249 mechanisms that might provide negative feedbacks to winter CO_2 emissions. Hence, we stress
250 the importance of addressing current uncertainties in process-model estimates of both growing
251 season and winter CO_2 exchange. Given the data limitations during the winter, there is a
252 particular need for long-term monitoring of winter CO_2 exchange in permafrost regions to
253 provide key insights into processes that may enhance or mitigate change. As most of the CMIP5
254 models do not currently include a permafrost component, these data are critical for improving
255 pan-arctic carbon cycle simulations.

256 Some of the projected winter CO₂ emissions could be offset by plant carbon uptake,
257 which is expected to increase as plants respond favorably to warming and CO₂ fertilization^{36,37}.
258 In addition, our modeled results do not explicitly account for CO₂ uptake during the shoulder
259 seasons (early and late winter period, e.g., October and April), which can occur, even under the
260 snowpack^{22,23,38} and which may increase with climate warming²². Our model projections also did
261 not incorporate all changes expected under future climates, such as changes in permafrost
262 distribution, delayed seasonal freeze-up, increased fire frequency, changes in snow cover and
263 distribution, and landscape-level hydrologic changes (e.g., lake drainage).

264 The CO₂ emissions reported here are only part of the winter carbon budget, which also
265 includes significant CH₄ emissions from land^{17,39} and CO₂ and CH₄ emissions from inland
266 waters⁴⁰. Recent data-derived estimates of high-latitude terrestrial winter CH₄ emissions range
267 from 1.6 Tg C yr⁻¹ (land area > 60°N)³⁹ to 9 Tg C yr⁻¹ for arctic tundra¹⁷. Similar to winter CO₂
268 emissions, process models significantly underestimated the fraction of annual CH₄ emissions
269 released during the winter³⁹.

270 To reduce uncertainty in estimates of current and future emissions, we recommend
271 increased spatial and temporal coverage and coordination and standardization of *in situ* winter
272 measurements, improvements to regional snow density products, and development of remote
273 sensing active sensors that can detect high resolution (< 20 km) changes in atmospheric CO₂
274 concentrations during periods of low to no light, which is a key constraint on efforts to monitor
275 changes in permafrost region carbon cycling. Current rates of winter CO₂ emissions may be
276 offsetting CO₂ uptake by vegetation across the permafrost region. Pan-arctic winter CO₂
277 emissions will likely increase in the near future if Arctic temperatures continue to rise; however,

278 this positive feedback on global climate can be mitigated with a reduction of global
279 anthropogenic greenhouse gas emissions.

280 **Methods**

281 Data overview

282 We compiled a dataset of *in situ* winter season (Oct-April) CO₂ emissions and potential
283 driving variables from sites within the northern permafrost zone⁴¹. The synthesized dataset
284 included 66 published studies and 21 unpublished studies (SI Table 1) conducted at 104 sites
285 (*i.e.*, sample areas with unique geographic coordinates) and in 152 sampling locations (*i.e.*,
286 different locations within a site as distinguished by vegetation type, landscape position, *etc.*).
287 Sites spanned boreal and tundra landcover classes (SI Fig. 5, SI Table 4) in continuous
288 permafrost (n=69), discontinuous (n=24), and isolated/sporadic (n=11) permafrost zones (Fig. 1).
289 Data were aggregated at the monthly level; however, the number of measurements per month
290 varied among studies. The dataset included more than 1,000 site-month flux measurements. We
291 also extracted CO₂ data from incubations of permafrost-region soils (SI Table 5) to compare their
292 temperature response functions (Q10) with Q10 derived from the synthesized *in situ* flux data.
293 Further details of data extraction and Q10 calculations can be found in the Supplementary
294 Methods.

295
296 Data extraction, geospatial data

297 We extracted data from regional gridded geospatial products including climatological
298 data, soil temperature and moisture, snow water equivalent, soil carbon stocks and texture,
299 permafrost status, vegetation cover, proxies of vegetation growth and productivity (*e.g.*,
300 enhanced vegetation index, EVI; leaf area index, LAI; gross primary productivity, GPP). See
301 Supplementary Methods for further description and data sources. All geospatial data were re-

302 gridded to the National Snow and Ice Data Center Equal Area Scalable Earth (EASE) 2.0
303 format⁴² at a 25-km spatial resolution prior to the CO₂ flux upscaling and simulations.

304 Boosted regression tree analysis

305
306 We used boosted regression tree analysis (BRT) to model drivers of winter CO₂
307 emissions and to upscale emissions to the pan-arctic region under current and future climate
308 scenarios. The BRT model was fit in R⁴³ using 'gbm' package version 2.1.1⁴⁴, and using code
309 adapted from⁴⁵. The BRT model was fitted with the following metaparameters: Gaussian error
310 distribution, bag-fraction (*i.e.*, proportion of data used in each iteration) of 0.5, learning rate
311 (contribution of each tree to the final model) of 0.005, and a tree complexity (maximum level of
312 interactions) of two. We used 10-fold cross-validation (CV) to determine the optimal number of
313 trees to achieve minimum predictive error and to fit the final model to the data.

314 We used geospatial data as explanatory variables in our BRT model (See Supplementary
315 Methods for full description of input data). We removed highly correlated variables from the
316 models (Spearman $\rho = 0.7$), retaining the variable within each functional category (*e.g.*, air
317 temperature) that had the highest correlation with winter flux. We further reduced the model by
318 removing variables in reverse order of their relative influence, until further removal resulted in a
319 2% average increase in predictive deviance. We compared this model with one in which we
320 included site level *in situ* data as explanatory variables. We used the geospatial model because it
321 allowed us to upscale results and because the percent deviance (SI Table 6) and driving variables
322 (SI Fig. 1) were similar between models.

323 We assessed BRT model performance using: 1. The correlation between predicted and
324 observed values using the CV data (*i.e.*, data withheld from model fitting), hereafter referred to

325 as the CV correlation, and; 2. deviance explained by the model over the evaluation dataset (*i.e.*,
326 CV data), calculated as: % deviance = (CV null deviance - CV residual deviance)/CV null
327 deviance *100. Further details of the BRT models can be found in the Supplementary Methods.

328 We obtained an estimate of model uncertainty by first obtaining the average internal root
329 mean squared error (RMSE; 0.21 g C m⁻² d⁻¹) for the ensemble of boosted regression trees. We
330 then made the assumption that this error applied equally to all grid cell areas within the domain.
331 Scaling this error to the full domain (16.95 × 10⁶ km²) and by the total number of days for the
332 winter (October through April) period provided us with a winter flux error of 813 Tg C.

333

334 Spatial and temporal domain for mapping

335 We scaled the modeled flux data to the northern permafrost land area $\geq 49^\circ \text{N}^{41}$, which
336 comprises 16.95 × 10⁶ km² of tundra and boreal lands (excludes glaciers, ice sheets, and barren
337 lands; Fig. 1) with lake area removed. We defined the winter period as the months of October
338 through April. Because the climate within this timeframe varies substantially across the
339 permafrost zone, this month-based definition, while temporally consistent, may include some
340 areas that are influenced by climate that would fall outside expected winter temperature ranges.
341 Therefore, in a separate approach (presented in the Supplementary Method), we defined winter
342 based on soil temperature, but we did not find substantial differences in regional flux budgets
343 when using the two approaches (temperature-defined winter flux was ~ 5% higher, 1,743 Tg C,
344 than when using the month-based winter period).

345

346 Spatial upscaling of fluxes

347 The BRT model was applied at a monthly time step from 2003 through 2017. For each
348 month, the map predictions were applied to a raster stack of input predictors using the R 'dismo'
349 package⁴⁶ for interface with the 'gbm' package and the 'raster' v2.6-7 predict function for
350 geospatial model applications. A n.tree (# of trees) of 1,000 was selected for each model run.
351 Output monthly mean estimates of daily CO₂ flux (g CO₂-C m⁻² d⁻¹) were generated for each 25-
352 km grid cell. Total pan-arctic CO₂ flux was obtained on a monthly basis by first calculating the
353 terrestrial area for each grid cell by subtracting lake fractions (MODIS satellite product
354 MOD44W) from each grid cell area. The fluxes were then scaled according to days per month
355 and terrestrial area to obtain per grid cell totals.

356 We analyzed the pan-arctic flux data for annual temporal trends using the nonparametric
357 Mann-Kendall test, which was run in the R 'zyp' package⁴⁷ with pre-whitening (Yue and Pilon
358 method) to remove autocorrelation. We report Kendall's correlation coefficient, τ , to describe the
359 strength of the time-series and Theil-Sen slope to describe trends over time.

360

361 Comparison of BRT estimates with process-based models

362 We compared our regional winter flux estimates to: 1) outputs from five process-based
363 terrestrial models estimated for the northern permafrost domain: National Center for
364 Atmospheric Research (NCAR) Community Land Model (CLM) versions 4.5 and 5; Lund-
365 Potsdam-Jena Dynamic Global Vegetation Model (LPJ-DGVM), Wald Schnee und Landschaft
366 version (LPJ-wsl); CARbon DAta MOdel FraMework (CARDAMOM); and the NASA SMAP
367 Level 4 Carbon (L4C) Version 3 product; 2) estimates for the northern permafrost domain
368 derived from FluxCom, a global gridded machine-learning net ecosystem exchange (NEE)
369 product; and 3) four process-based terrestrial models and eight atmospheric inversion models

370 from the high latitude model intercomparison for the Regional Carbon Cycle Assessment and
371 Processes (RECCAP) tundra and northern boreal domain¹⁰. See Supplementary Methods for
372 further description of these models.

373

374 Projected CO₂ flux

375 Inputs for the BRT model of future scenarios of winter CO₂ flux were obtained from
376 ensembles of Earth System Model (ESM) outputs from the Fifth Coupled Model
377 Intercomparison Project (CMIP5) for RCP 4.5 and 8.5². Inputs included: 1) Annual GPP; 2)
378 mean annual summer LAI (July & August); 3) mean summer soil moisture (June, July, August);
379 4) mean monthly soil moisture; 5) mean monthly near-surface (2 m) air temperature; and 6)
380 mean monthly soil temperature (layer 1) (SI Table 7). Ensemble mean RCP 4.5 and 8.5 predictor
381 fields were bias-corrected using the delta, or perturbation method⁴⁸, based on historic ESM
382 outputs and observed historical data and re-projected to EASE2 25 km grids.

383 In addition to the 0.21 g C m⁻² d⁻¹ error obtained based on the BRT model RMSE, we
384 used the outcome from bootstrapped BRT model simulations to estimate additional, inherit
385 prediction variability in the machine learning outcomes for current and future CO₂ emissions⁴⁹
386 (see Supplementary Information).

387 For the CMIP5 RCP 4.5 and 8.5 simulations of respiration, we used an r1i1p1 ensemble
388 mean from 15 models (see Supplementary Information).

389 **Data Availability:** Data are archived and freely available at the ORNL Distributed Active
390 Archive Center (DAAC). The synthesis dataset will be available at
391 <https://doi.org/10.3334/ORNLDAAC/1692>. Monthly carbon flux maps (25 km, October-April,
392 2003-2018; 2018-2100 for RCP 4.5 and RCP 8.5) will be available at
393 <https://doi.org/10.3334/ORNLDAAC/1683>.

394
395 **Supplementary Information** includes Supplementary Methods, Supplementary Tables 1-8, and
396 Supplementary Figures 1-6.

397
398 Correspondence and requests for materials should be addressed to S.M.N.

399
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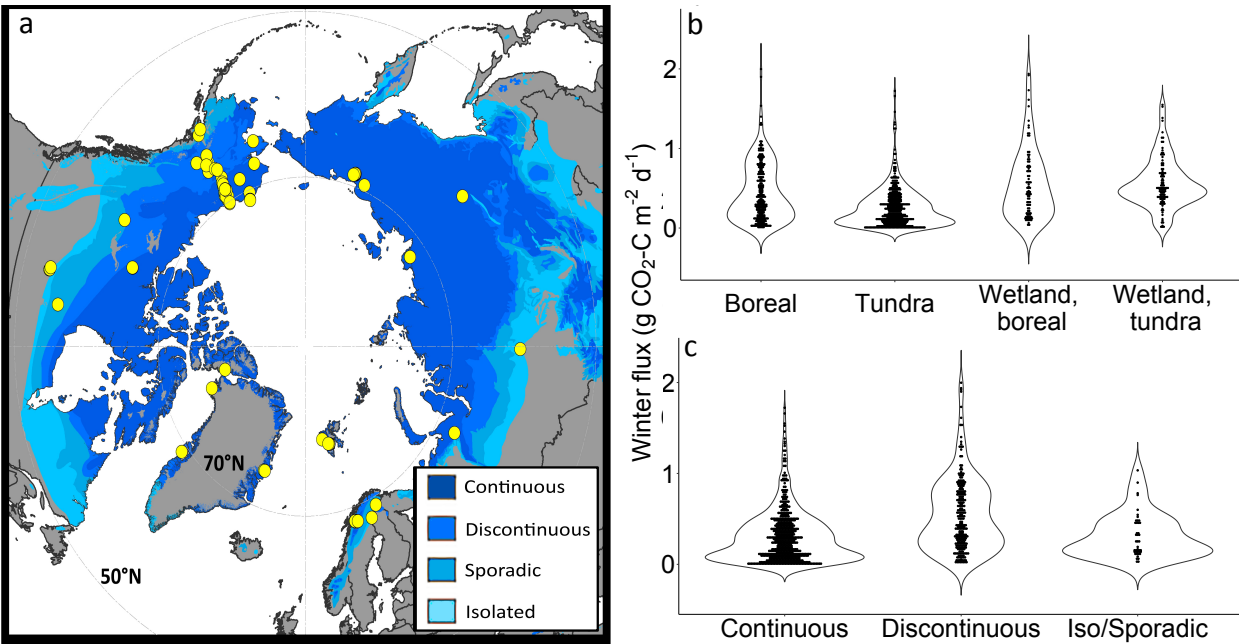
405
406
407 **Author contributions:** S.M.N., J.D.W., and B.M.R conceived the work. B.W.A., G.C., C.T.C.,
408 H.G., E.E.J., M.M.L., S.M.L., M.L., A.M., C.M., S.M.N., F.R., B.M.R., K.S., A.S., C.C.T.,
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411 R.M., J.M., A.M., S.M.N., W.C.O., F.W.P., N.P., W.Q., D.R., T.S., N.M.S., E.A.G.S, P.R.S.,

412 O.S., P.F.S., M.P.W., C.W., and D.Z. provided unpublished or raw data. L.B., A.A.B., J.D.,
413 J.S.K., Z.L., N.M., A.D.M., B.P., and Z.Z. provided modeled data/results. S.M.L., C.M., S.M.N.,
414 S.P., and J.D.W. prepared tables and figures. G.C., H.G., M.J.L., M.M.L., S.M.L., S.M.N., S.P.,
415 B.M.R., P.F.S., and J.D.W. performed statistical analyses, including BRT modeling. S.P.,
416 B.M.R., and J.W. led the BRT upscaling or projection analyses. All authors contributed to data
417 interpretation and preparation of manuscript text.

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422 **Fig. 1. Distribution of *in situ* data included in this winter CO₂ flux synthesis.** (a) Locations of

423 *in situ* winter CO₂ flux data (yellow circles) in this synthesis included (b) upland and wetland

424 sites in boreal and tundra biomes located (c) within the northern permafrost region⁴¹. Violin plots

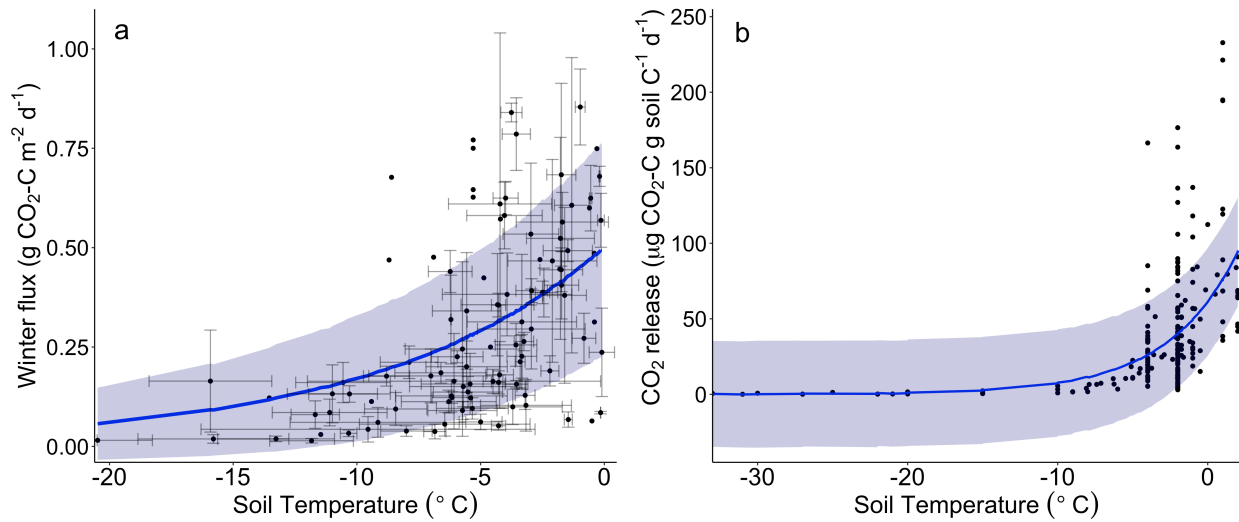
425 (b,c) depict magnitude and distribution density (width; dots are monthly aggregated data) of *in*

426 *situ* data used in our machine-learning model.

427

428

429



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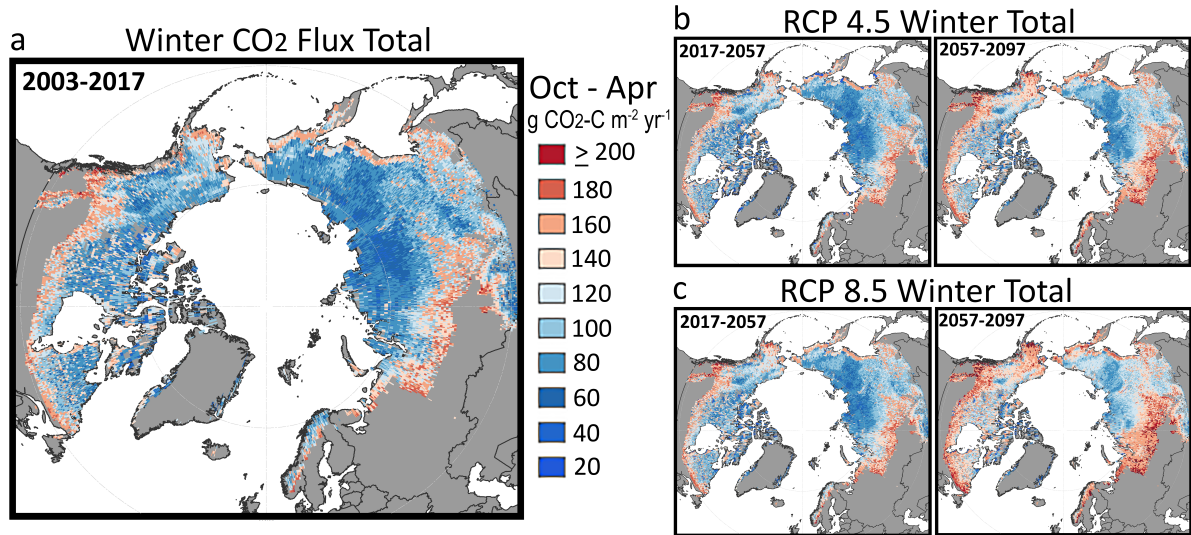
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Fig. 2. Effect of soil temperature on CO₂ release from soils. (a) Relationships between *in situ* soil temperature (~ 10 cm average depth) and CO₂ fluxes and (b) temperature and CO₂ released from lab incubations. Shading represents the standard deviation of an exponential model, which, for *in situ* fluxes, was fit to mean CO₂ flux from each sample location (symbols shown with standard error). Note that the different soil temperature scales between panels reflect data ranges.



436

437 **Fig. 3. Pan-Arctic winter CO₂ emissions under current and future climate scenarios. (a)**

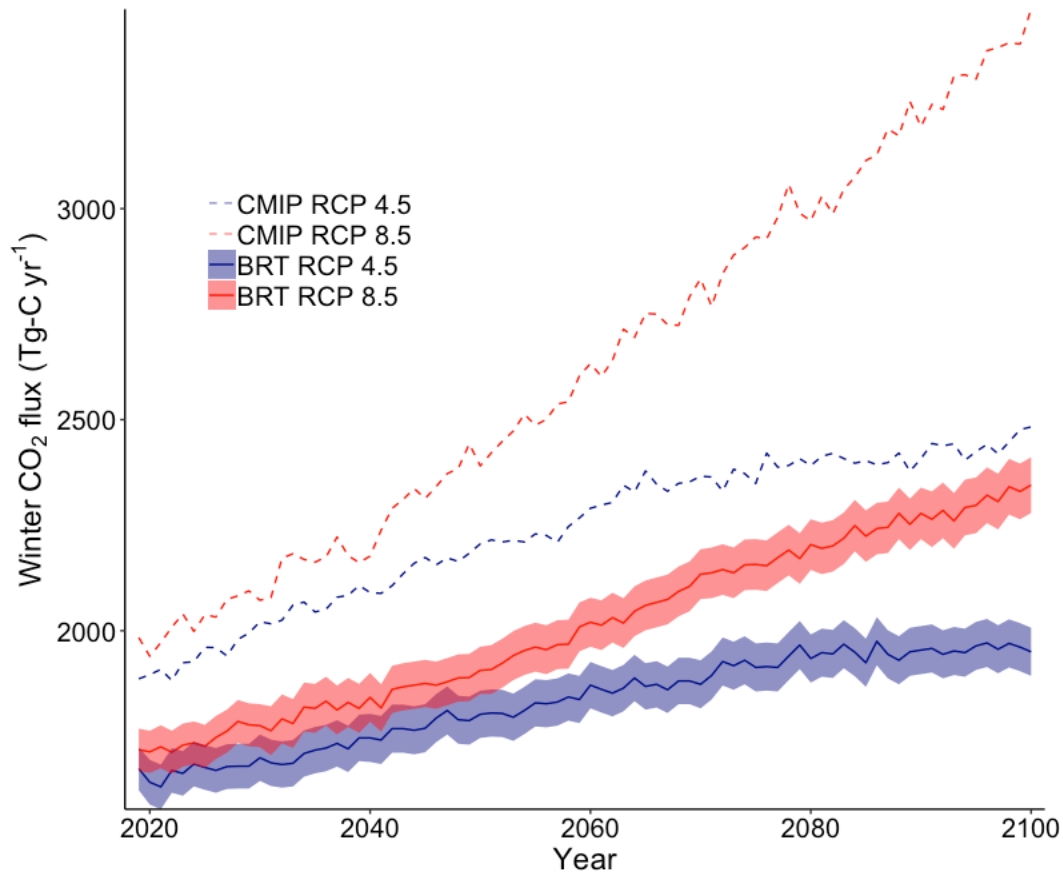
438 Average annual winter (October - April) CO₂ emissions estimated for the permafrost region for

439 the baseline years 2003-2017. Cumulative winter CO₂ fluxes under (b) RCP 4.5 and (c) RCP 8.5

440 scenarios over an 80-year period (2017-2057 and 2057-2097). Fluxes are reported on an annual

441 basis (g CO₂-C m⁻² yr⁻¹).

442



444

445

Fig. 4. Projected annual CO₂ emissions during the winter for the northern permafrost

446

region. Solid lines represent BRT modeled results through 2100 under RCP 4.5 (red solid line)

447

and RCP 8.5 (blue solid line), with bootstrapped 95% confidence intervals indicated by shading.

448

For reference, CMIP5 ensemble respiration for RCP 4.5 and 8.5 are also shown (dashed lines).

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450

References

- 452 1 Huang, J. Recently amplified arctic warming has contributed to a continual global
453 warming trend. *Nat. Clim. Change* **7**, 875-879 (2017).
- 454 2 Koenigk, T. et. al. Arctic climate change in 21st century CMIP5 simulations with EC-
455 Earth. *Clim. Dyn.* **40**, 2719-2743 (2013).
- 456 3 Cohen, J., Screen, J.A., Furtado, J.C., Barlow, M., et al. Recent Arctic amplification and
457 extreme mid-latitude weather. *Nature Geosci.* **7**, 627-637 (2014).
- 458 4 Schadel, C., Bader, M.K-F., Schuur, E.A.G., Biasi, C., Bracho, R. et al. Potential carbon
459 emissions dominated by carbon dioxide from thawed permafrost soils. *Nat. Clim. Change*
460 **6**, 950-953 (2016).
- 461 5 Fisher, J. B. et. al. Carbon cycle uncertainty in the Alaskan Arctic. *Biogeosciences* **11**,
462 4271-4288 (2014).
- 463 6 Commane, R., Lindaas, J., Benmergui, J., Luus, K.A., et al. Carbon dioxide sources from
464 Alaska driven by increasing early winter respiration from Arctic tundra. *Proc. Natl. Acad.*
465 *Sci.* **114**, 5361-5366 (2017).
- 466 7 Elberling, B., Brandt, K.K. Uncoupling of microbial CO₂ production and release in
467 frozen soil and its implications for field studies of arctic C cycling. *Soil Biol.*
468 *Biogeochem.* **35**, 263-272 (2003).
- 469 8 Schuur, E. A. G., McGuire, A.D., Schadel, C., Grosse, G., et al. Climate change and the
470 permafrost carbon feedback. *Nature* **520**, 171-179 (2015).
- 471 9 Belshe, E. F., Schuur, E.A.G., Bolker, B.M. Tundra ecosystems observed to be CO₂
472 sources due to differential amplification of the carbon cycle. *Ecology Lett.* **16**, 1307-1315
473 (2013).
- 474 10 McGuire, A. D. et. al. An assessment of the carbon balance of Arctic tundra:
475 Comparisons among observations, process models, and atmospheric inversions.
476 *Biogeosciences* **9**, 3185–3204 (2012).
- 477 11 Schimel, D., Pavlick, R., Fisher, J.B., Asner, G.P. et al. Observing terrestrial ecosystems
478 and the carbon cycle from space. *Glob.Change Biol.* **21**, 1762-1776 (2014).
- 479 12 Parazoo, N., Commane, R., Wofsy, S.C., Koven, C.D. Detecting regional patterns of
480 changing CO₂ flux in Alaska. *Proc. Natl. Acad. Sci.* **113**, 7733-7738 (2016).
- 481 13 Grogan, P. Cold season respiration across a Low Arctic landscape: The influence of
482 vegetation type, snow depth, and interannual climatic variation. *Arctic, Antarct. Alp. Res.*
483 **44**, 446–456 (2012).
- 484 14 Michaelson, G. J., Ping, C.L. Soil organic carbon and CO₂ respiration at subzero
485 temperature in soils of Arctic Alaska. *J.G.R. Atmos.* **108** (2005).
- 486 15 Rogers, M. C., Sullivan, P.F., Welker, J.M. Evidence of nonlinearity in the response of
487 net ecosystem CO₂ exchange to increasing levels of winter snow depth in the high Arctic
488 of Northwestern Greenland. *Arct. Antarct. Alpine Res.* **43**, 95-106 (2011).
- 489 16 Wang, T., Ciais, P., Piao, S.L., Otle, C., et al. Controls on winter ecosystem respiration
490 in temperate and boreal ecosystems. *Biogeosciences* **8**, 2009-2025 (2011).
- 491 17 Zona, D., Gioli, B., Commane, R., Lindaas, J., et al. Cold season emissions dominate the
492 Arctic tundra methane budget. *Proc. Natl. Acad. Sci.* **113**, 40-45 (2016).
- 493 18 Schaefer, K. J., et al. A parameterization of respiration in frozen soils based on substrate
494 availability. *Biogeosciences* **13**, 1991–2001 (2016).

- 495 19 Monson, R., Lipson, D., Burns, S.P., Turnipseed, A.A., et al. Winter forest soil
496 respiration controlled by climate and microbial community composition. *Nature* **439**,
497 711-714 (2006).
- 498 20 Welker, J. M., Fahnestock, J.T., Jones, M.H. Annual CO₂ flux in dry and moist arctic
499 tundra: field responses to increases in summer temperatures and winter snow depth. .
500 *Clim. Chan* **44**, 139-150 (2000).
- 501 21 Natali, S. M., Schuur, E.A.G., Trucco, C., Hicks Pries, C.E., et al. Effects of experimental
502 warming of air, soil and permafrost on carbon balance in Alaskan tundra. *Glob. Chan.*
503 *Biol.* **17**, 1394-1407 (2011).
- 504 22 Webb, E. E., et. al. Increased wintertime CO₂ loss as a result of sustained tundra
505 warming. *Biogeosciences* **121**, 1-17 (2016).
- 506 23 Christiansen, C. T., Schmidt, N. M. & Michelsen, A. High Arctic dry heath CO₂
507 exchange during the early cold season. *Ecosystems* **15**, 1083-1092 (2012).
- 508 24 Knutti, R., Masson, D. & Gettelman, A. Climate model genealogy: Generation CMIP5
509 and how we got there. *Geophys. Res. Lett.* **40**, 1194–1199 (2013).
- 510 25 Forkel, M., et. al. Enhanced seasonal CO₂ exchange caused by amplified plant
511 productivity in northern ecosystems. *Science* **351**, 696-699 (2016).
- 512 26 Tucker, C. Reduction of air- and liquid water-filled soil pore space with freezing explains
513 high temperature sensitivity of soil respiration below 0 degrees C. *Soil Biol. Biochem.* **78**,
514 90–96 (2014).
- 515 27 Huang, Y., Jiang, J., Ma, S., Ricciuto, D., Hanson, P.J., Luo, Y. Soil thermal dynamics,
516 snow cover, and frozen depth under five temperature treatments in an ombrotrophic bog:
517 constrained forecast with data assimilation. *J.G.R. Biogeosci.* **122**, 2046-2063 (2017).
- 518 28 Witze, A. Snow-sensing fleet to unlock water’s icy secrets. *Nature* **7**, 1, doi:doi:
519 10.1038/532017a (2016).
- 520 29 Natali, S. M., Schuur, E.A.G., Mauritz, M., Schade, J.D., et al. Permafrost thaw and soil
521 moisture driving CO₂ and CH₄ release from upland tundra. *J.G.R. Biogeosci.* **120**, 525-
522 537 (2015).
- 523 30 Euskirchen, E. S., Bret-Harte, M. S., Shaver, G. R., Edgar, C. W., Romanovsky, V. E.
524 Long-term release of carbon dioxide from arctic tundra ecosystems in Alaska. .
525 *Ecosystems* **20**, 960–974 (2017).
- 526 31 Tramontana, G., et. al. Predicting carbon dioxide and energy fluxes across global
527 FLUXNET sites with regression algorithms. *Biogeosciences* **13**, 4291–4313 (2016).
- 528 32 Koven, C. D., et. al. Permafrost carbon-climate feedbacks accelerate global warming.
529 *Proc. Natl. Acad. Sci.* **108**, 14769–14774 (2011).
- 530 33 Slater, A. G., & Lawrence, D.M. Diagnosing present and future permafrost from climate
531 models. . *J. Climate* **26**, 5608-5623 (2013).
- 532 34 Vanhala, P., K. Karhu, M. Tuomi, K. Bjorklof, H. Fritze, J. Liski. Temperature sensitivity
533 of soil organic matter decomposition in southern and northern areas of the boreal forest
534 zone. *Soil Biol. Biochem.* **40**, 1758-1764 (2008).
- 535 35 Hugelius, G. e. a. Estimated stocks of circumpolar permafrost carbon with quantified
536 uncertainty ranges and identified data gaps. . *Biogeosciences* **11**, 6573–6593 (2014).
- 537 36 McGuire, A. D., et. al. Dependence of the evolution of carbon dynamics in the northern
538 permafrost region on the trajectory of climate change. *Proc. Natl. Acad. Sci.*,
539 doi:doi:10.1073/pnas.1719903115 (2018).

- 540 37 Qian, H., Joseph, R., Zeng, N. Enhanced terrestrial carbon uptake in the Northern High
541 Latitudes in the 21st century from the Coupled Carbon Climate Model Intercomparison
542 Project model projections. *Glob. Chan. Biol.* **16**, 641-656, doi:10.1111/j.1365-
543 2486.2009.01989.x.
- 544 38 Starr, G. O., et. al. Photosynthesis of Arctic evergreens under snow: Implications for
545 tundra ecosystem carbon balance. *Ecology* **84**, 1415-1420 (2003).
- 546 39 Treat, C. C., Bloom, A. A. & Marushchak, M. E. Nongrowing season methane
547 emissions—a significant component of annual emissions across northern ecosystems. .
548 *Glob. Chang. Biol.* **24**, 3331–3343 (2018).
- 549

550 **Methods References**

- 551
- 552 40 Walter Anthony, K., et. al. 21st-century modeled permafrost carbon emissions
553 accelerated by abrupt thaw beneath lakes. *Nat. Commun.* **9** (2018).
- 554 41 Brown, J., Ferrians, O., Heginbottom, J. & Melnikov, E. Circum-Arctic map of
555 permafrost and ground-ice conditions, version 2. (2002).
- 556 42 Brodzik, M. J., Billingsley, B., Haran, T., Raup, B. & Savoie, M. H. EASE-Grid 2.0:
557 Incremental but significant improvements for Earth-gridded data sets. *ISPRS Int. J. Geo-*
558 *Information* **1**, 32-45 (2012).
- 559 43 Team., R. C. R: A language and environment for statistical computing. (2016).
- 560 44 Ridgeway, G. Generalized Boosted Models: A guide to the gbm package. 1-12 (2007).
- 561 45 Elith, J., Leathwick, J. R. & Hastie, T. A working guide to boosted regression trees. *J.*
562 *Anim. Ecol.*, 802-813 (2008).
- 563 46 Hijmans, R. J., Phillips, S., Leathwick, J. & Elith, J. . R “dismo” package. (2017).
- 564 47 Bronaugh, D. W. R “zyp” trends package. (2017).
- 565 48 Rogers, B. M., et. al. Impacts of climate change on fire regimes and carbon stocks of the
566 U.S. Pacific Northwest. *J. Geophys. Res. Biogeosciences* **116** (2011).
- 567 49 Leathwick, J. R., Elith, J., Francis, M. P., Hastie, T. & Taylor, P. Variation in demersal
568 fish species richness in the oceans surrounding New Zealand: An analysis using boosted
569 regression trees. *Mar. Ecol. Prog. Ser.* **321**, 267–281 (2006).
- 570