

1 **Title:**

2 An increasing Arctic-Boreal CO<sub>2</sub> sink despite strong regional sources

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81

82 **Abstract (151 words)**

83

84 The Arctic-Boreal Zone (ABZ) is rapidly warming, impacting its large soil carbon stocks. We use  
85 a new compilation of terrestrial ecosystem CO<sub>2</sub> fluxes, geospatial datasets and random forest  
86 models to show that although the ABZ was an increasing terrestrial CO<sub>2</sub> sink from 2001 to 2020  
87 (mean ± standard deviation in net ecosystem exchange: -548 ± 140 Tg C yr<sup>-1</sup>; trend: -14 Tg C  
88 yr<sup>-1</sup>, p<0.001), more than 30% of the region was a net CO<sub>2</sub> source. Tundra regions may have  
89 already started to function on average as CO<sub>2</sub> sources, demonstrating a critical shift in carbon  
90 dynamics. After factoring in fire emissions, the increasing ABZ sink was no longer statistically  
91 significant (budget: -319 ± 140 Tg C yr<sup>-1</sup>; trend: -9 Tg C yr<sup>-1</sup>), with the permafrost region  
92 becoming CO<sub>2</sub> neutral (budget: -24 ± 123 Tg C yr<sup>-1</sup>; trend: -3 Tg C yr<sup>-1</sup>), underscoring the  
93 importance of fire in this region.

94

95 **Main text (3159 words)**

96

97 Estimating terrestrial net ecosystem CO<sub>2</sub> exchange (NEE) of the Arctic-Boreal Zone (ABZ)  
98 poses a significant challenge<sup>1-4</sup> due to their complex functions<sup>4-6</sup> and a limited network of field  
99 measurements<sup>7,8</sup>. As a result, models show a wide range of CO<sub>2</sub> budgets, from substantial net  
100 atmospheric sinks (-1,800 Tg C yr<sup>-1</sup>) to moderate atmospheric sources (600 Tg C yr<sup>-1</sup>)<sup>1,4,5,9,10</sup>, a  
101 concerning discrepancy as northern permafrost soils hold nearly half of global soil organic  
102 carbon stocks<sup>11</sup>. The release of this soil carbon to the atmosphere as CO<sub>2</sub> could significantly  
103 exacerbate climate change<sup>12</sup>. Thus, there is an urgent need to improve CO<sub>2</sub> budget estimates  
104 across the ABZ.

105

106 The rapid climate change of the ABZ makes this discrepancy even more critical<sup>13</sup>. Increasing  
107 air and soil temperatures in both summer and non-summer seasons are causing changes in the  
108 CO<sub>2</sub> budget that remain poorly understood<sup>9</sup>. Furthermore, it is not known how the widespread  
109 but spatially heterogeneous increase in vegetation productivity and greening<sup>14,15</sup> impacts the  
110 annual CO<sub>2</sub> balance although links to enhanced CO<sub>2</sub> sinks during the spring-summer period  
111 have been found<sup>16,17</sup>. Some of the enhanced uptake might be offset by CO<sub>2</sub> losses associated  
112 with vegetation dieback ('browning'), and the escalating frequency and intensity of disturbances  
113 such as abrupt permafrost thaw (e.g., thermokarst), drought and fires, further complicating the  
114 understanding of ABZ carbon dynamics and climate feedbacks<sup>18-20</sup>.

115

116 Current evidence on recent ABZ CO<sub>2</sub> budget trends and their main drivers is limited to few in-  
117 situ data-driven synthesis and modeling studies without a regional perspective on where and  
118 why CO<sub>2</sub> budgets are changing<sup>1,5,9,10</sup>. These studies have focused primarily on ecosystem CO<sub>2</sub>  
119 fluxes (i.e., not incorporating fire emissions), coarse annual or seasonal CO<sub>2</sub> fluxes (i.e.,  
120 overlooking the intra-annual dynamics), and spatial patterns in CO<sub>2</sub> fluxes with data from only  
121 one to two decades. Most importantly, earlier studies have not extended into the 2020s, a  
122 period of time where warming has further accelerated and more fires have occurred<sup>21</sup>. Thus, we  
123 lack a comprehensive understanding of the regional and seasonal patterns in recent ecosystem  
124 CO<sub>2</sub> fluxes, including fire emissions, and their multidecadal trends, and the links to changing  
125 environmental conditions across the ABZ.

126

127 Here, we address this knowledge gap using the most comprehensive site-level ABZ CO<sub>2</sub> flux  
128 dataset to-date—including monthly terrestrial photosynthesis (gross primary production; GPP),  
129 ecosystem respiration (R<sub>eco</sub>), and NEE data from 200 terrestrial eddy covariance and flux  
130 chamber sites (4,897 site-months). This dataset is at least four times larger than in earlier  
131 upscaling efforts and covers a longer time period with data extending to 2020. The same  
132 dataset was previously used to analyze in-situ CO<sub>2</sub> flux trends in permafrost versus non-  
133 permafrost regions, with the conclusion that the annual net uptake is increasing in the non-  
134 permafrost region but not in the permafrost region<sup>22</sup>. Here we extend that study from the site  
135 level to the full ABZ region by combining flux observations with meteorological, remote sensing,  
136 and soil data, together with random forest models to estimate CO<sub>2</sub> budgets across the ABZ. We  
137 do this upscaling over two periods, 2001-2020 (1-km resolution) and 1990-2016 (8-km  
138 resolution); results in the main text are based on the 1-km models unless stated otherwise. We

139 then assess regional and seasonal patterns and trends in ABZ ecosystem CO<sub>2</sub> fluxes and their  
140 environmental drivers. We also integrate annual fire emissions from 2002 to 2020<sup>23</sup> to provide  
141 near-complete terrestrial CO<sub>2</sub> budget estimates (referred as NEE + fire).

142

## 143 **Results**

144

### 145 **CO<sub>2</sub> budgets across the ABZ**

146

147 Using machine learning models that had a high predictive performance (up to two times higher  
148 cross-validated R<sup>2</sup> compared to earlier efforts<sup>5,9</sup>), we find that from 2001-2020 circumpolar  
149 tundra was on average CO<sub>2</sub> neutral without accounting for fire emissions (in-situ NEE:  $-4 \pm 44$  g  
150 C m<sup>-2</sup> yr<sup>-1</sup>; upscaled NEE:  $7 \pm 3$  g C m<sup>-2</sup> yr<sup>-1</sup>; upscaled budget  $45 \pm 53$  Tg C yr<sup>-1</sup>; mean  $\pm$   
151 standard deviation; Table 1). In contrast, the boreal was a strong sink (in-situ NEE:  $-41 \pm 82$  g C  
152 m<sup>-2</sup> yr<sup>-1</sup>; upscaled NEE:  $-43 \pm 7$  g C m<sup>-2</sup> yr<sup>-1</sup>; upscaled budget  $-593 \pm 101$  Tg C yr<sup>-1</sup>). Including  
153 fire emissions (on average 237 Tg C yr<sup>-1</sup><sup>23</sup>, i.e., 2% of R<sub>eco</sub> and 43% of the ABZ net CO<sub>2</sub> uptake  
154 budget) changed the budget to  $-383 \pm 101$  Tg C yr<sup>-1</sup> in the boreal and to  $64 \pm 53$  Tg C yr<sup>-1</sup> in the  
155 tundra. With fire emissions included, the permafrost region turned into CO<sub>2</sub> neutral (NEE:  $-249 \pm$   
156  $123$  Tg C yr<sup>-1</sup>, NEE + fire:  $-24 \pm 123$  Tg C yr<sup>-1</sup>).

157

158 Although the entire ABZ domain was a terrestrial CO<sub>2</sub> sink across all years during 2001-2020  
159 with an average NEE of  $-548 \pm 140$  Tg C yr<sup>-1</sup>, our upscaling of NEE revealed a large areal  
160 fraction of annual ecosystem CO<sub>2</sub> sources across the domain (34% of the total region, Fig. 1).  
161 For the permafrost domain, the fraction of annual CO<sub>2</sub> sources was even higher (41% of the  
162 region). This large fraction is also seen in our in-situ CO<sub>2</sub> flux database, with 30% of sites being  
163 CO<sub>2</sub> sources (NEE between 0-142 g C m<sup>-2</sup> yr<sup>-1</sup>). These CO<sub>2</sub> source sites were mostly in Alaska  
164 (44%), but also in northern Europe (25%), Canada (19%), and Siberia (13%). One key factor  
165 driving CO<sub>2</sub> sources is the long and persistent non-summer season (September-May) emissions  
166 in the tundra that, on average, exceed the short summer (June-August) net CO<sub>2</sub> uptake (Table  
167 1). In the boreal, longer summers with strong uptake still dominate over non-summer emissions.

168

### 169 **Model performance and comparison**

170

171 We observed moderate correlation of our upscaled NEE results with an ensemble of  
172 atmospheric inversions<sup>24</sup> across space (Pearson's correlation 0.5,  $p < 0.001$ ), but the correlation  
173 between the temporal trends was weaker (Pearson's correlation 0.2,  $p < 0.001$ ) (Fig. 1).  
174 However, the ensemble net uptake budgets from the inversions, as well as from a global  
175 machine-learning based upscaling product (FLUXCOM<sup>25</sup>) were 1.5 to 3 times higher than our  
176 upscaled budgets (Supplementary Section 5). Moreover, the global Coupled Model  
177 Intercomparison Project Phase 6 (CMIP6) process model ensemble<sup>26</sup> had barely any annual  
178 CO<sub>2</sub> sources across the ABZ, indicating that the process models may not accurately simulate  
179 CO<sub>2</sub> source situations (Fig. 1), especially given the prevalence of site-level sources. The cross-  
180 validated predictive performances of our random forest models for GPP, R<sub>eco</sub>, and NEE showed  
181 high correlations between observed and predicted fluxes (R<sup>2</sup> varied from 0.5 to 0.78 and root  
182 mean square error from 19.4 to 37.3 g C m<sup>-2</sup> month<sup>-1</sup>; Supplementary Fig. 1-3), but upscaling

183 uncertainties remain. For example, areas with the most extensive strong sink or source  
 184 estimates rarely had in-situ data and were thus largely extrapolated (e.g., sources in central  
 185 Siberia, or sinks in southern Siberia, Supplementary Fig. 4). These areas also had the highest  
 186 uncertainties in our analysis (approximately twice as large uncertainties as in the more densely  
 187 measured areas; Supplementary Fig. 5).

188

189 *Table 1. Mean gross primary productivity (GPP), ecosystem respiration ( $R_{eco}$ ), and net*  
 190 *ecosystem exchange (NEE) fluxes and budgets over 2001-2020, and NEE + fire budgets from*  
 191 *2002-2020. Uncertainties are standard deviations across sites or pixels (for the mean fluxes) or*  
 192 *across bootstrapped budget estimates. Positive numbers for NEE indicate net CO<sub>2</sub> loss to the*  
 193 *atmosphere and negative numbers indicate net CO<sub>2</sub> uptake by the ecosystem. Mismatches in*  
 194 *the site-level versus upscaled CO<sub>2</sub> fluxes are likely related to sites being biased to certain*  
 195 *regions and years while upscaled summaries should provide more representative regional*  
 196 *estimates but are influenced by model performance. Mismatches in the NEE vs. GPP- $R_{eco}$*   
 197 *estimates are related to different numbers of sites and observations being available for the*  
 198 *different fluxes. Supplementary Table 1 shows the budgets for different vegetation types and*  
 199 *regions.*

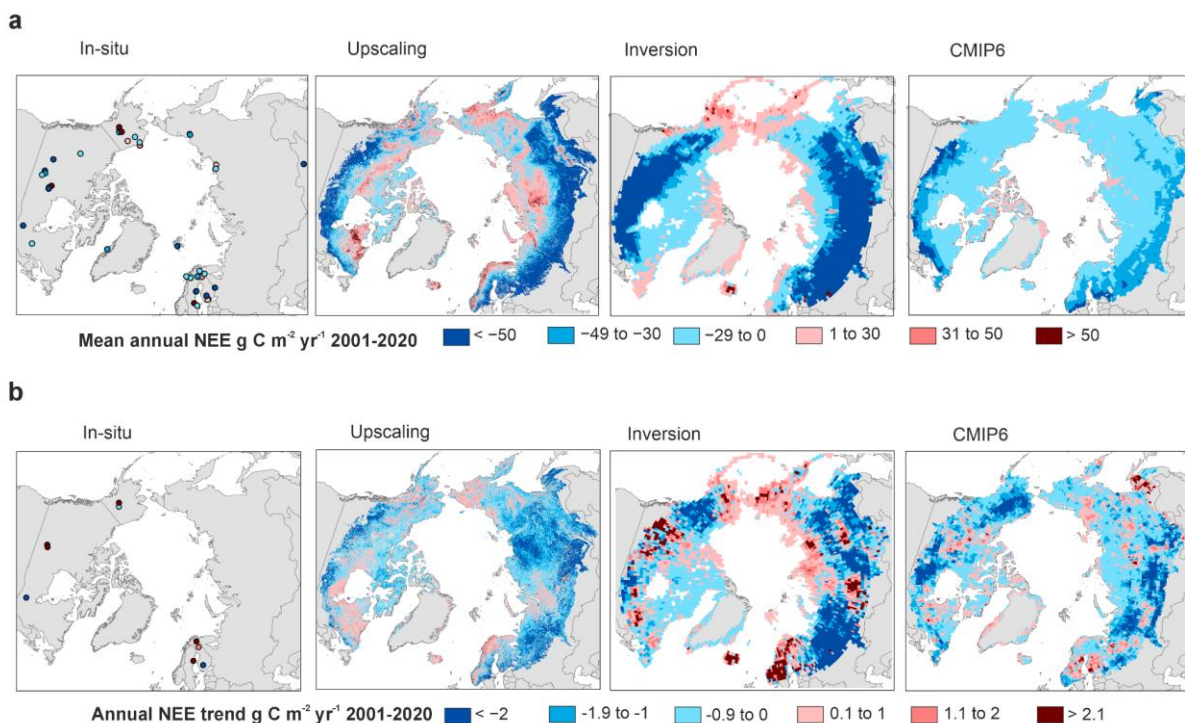
200

Class	In-situ average			Upscaled per-area average			Average regional budget			The proportion of summer net uptake budget of non-summer net emissions	Average regional budget with fire	Area (x 10 <sup>6</sup> km <sup>2</sup> )
Flux and unit	NEE g C m <sup>-2</sup> yr <sup>-1</sup>	GPP g C m <sup>-2</sup> yr <sup>-1</sup>	$R_{eco}$ g C m <sup>-2</sup> yr <sup>-1</sup>	NEE g C m <sup>-2</sup> yr <sup>-1</sup>	GPP g C m <sup>-2</sup> yr <sup>-1</sup>	$R_{eco}$ g C m <sup>-2</sup> yr <sup>-1</sup>	NEE Tg C yr <sup>-1</sup>	GPP Tg C yr <sup>-1</sup>	$R_{eco}$ Tg C yr <sup>-1</sup>	%	NEE + fire Tg C yr <sup>-1</sup>	
Arctic-Boreal Zone	-32 (± 76)	617 (± 396)	587 (± 385)	-26 (± 5)	482 (± 20)	460 (± 15)	-548 (± 140)	9970 (± 144)	9525 (± 90)	1.4	-319	20.79
Tundra	-4 (± 44)	302 (± 124)	311 (± 133)	7 (± 3)	300 (± 14)	306 (± 12)	45 (± 53)	2049 (± 49)	2090 (± 33)	0.9	64	6.8
Boreal	-41 (± 82)	705 (± 402)	664 (± 398)	-43 (± 7)	572 (± 24)	537 (± 17)	-593 (± 101)	7920 (± 106)	7435 (± 74)	1.6	-383	13.9
Permafrost region	-21 (± 62)	459 (± 197)	447 (± 172)	-15 (± 5)	416 (± 20)	405 (± 16)	-249 (± 123)	6918 (± 109)	6719 (± 69)	1.2	-24	16.6

201

202





203

204 *Figure 1. Maps showing the mean annual terrestrial NEE (a) and its trends (b) based on site-*  
 205 *level data, our upscaling, atmospheric inversion ensemble, and CMIP6 process model*  
 206 *ensemble. In-situ trends in b are based on sites that have >7 years of data. Supplementary Fig.*  
 207 *5c shows the significance of the trends. While the average upscaled NEE values can go up to*  
 208 *116 g C m<sup>-2</sup> yr<sup>-1</sup>, most of the values are below 60 g C m<sup>-2</sup> yr<sup>-1</sup>. While the NEE values of the*  
 209 *inversions can go down to -1636 g C m<sup>-2</sup> yr<sup>-1</sup>, most of the values are higher than -200 g C m<sup>-2</sup> yr*  
 210 *<sup>-1</sup>, similar to upscaling and CMIP6 model outputs.*

211

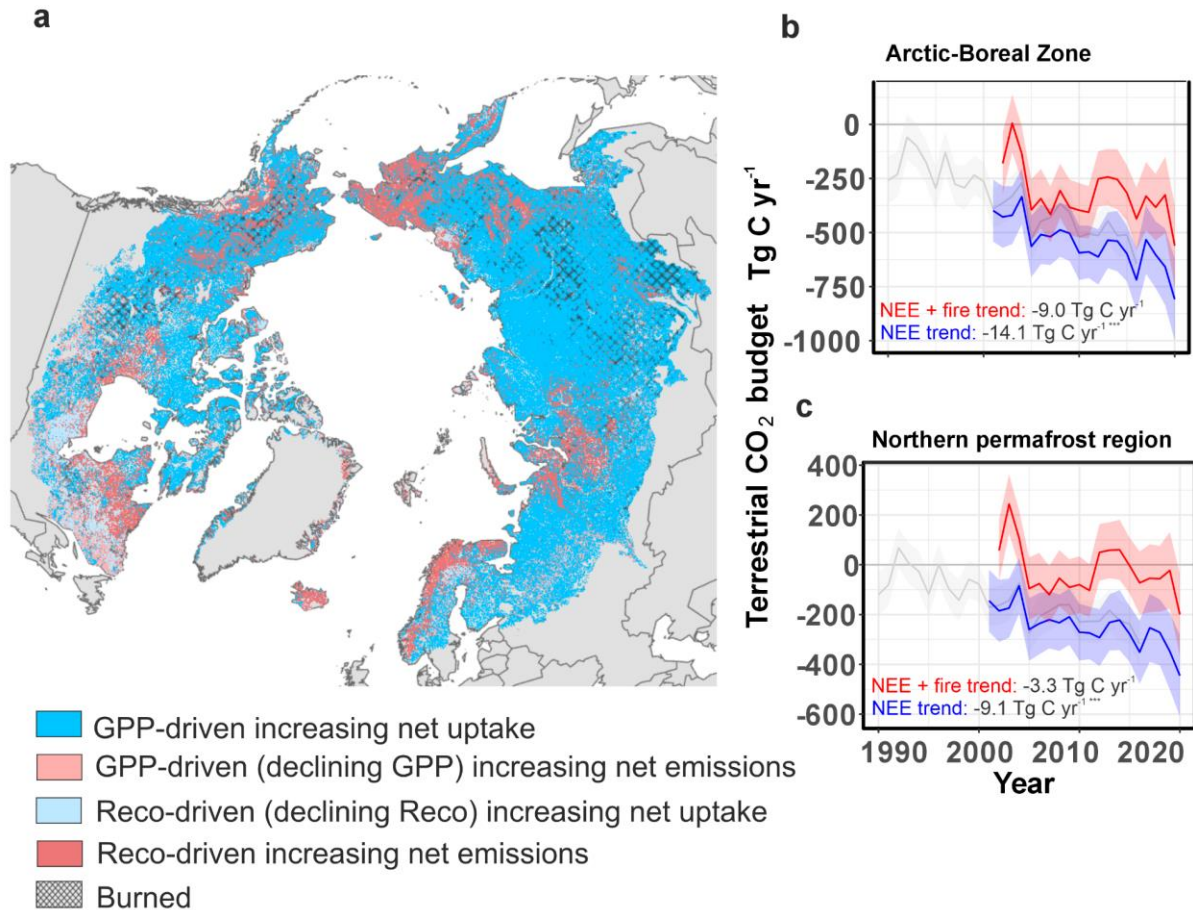
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### 213 **Temporal trends in upscaled ABZ CO<sub>2</sub> budgets**

214

215 The ABZ has been an increasing terrestrial CO<sub>2</sub> sink based on NEE alone from 2001 to 2020  
 216 (temporal trend: -14 Tg C yr<sup>-1</sup>, p<0.001) (Fig. 2). However, the increasing sink strength was no  
 217 longer statistically significant when fire emissions were added to NEE (average NEE + fire  
 218 budget trend -9 Tg C yr<sup>-1</sup> over 2002-2020). In the permafrost region, the NEE + fire trend was  
 219 only 3.3 Tg C yr<sup>-1</sup>. Nevertheless, based on our NEE upscaling, 23% of the region increased  
 220 (p<0.05) net CO<sub>2</sub> uptake from 2001 to 2020 (Fig. 1). Most of the increasing net sink activity was  
 221 driven by an increase in GPP, especially in Siberia (Fig. 2). Some of the trends were also  
 222 related to a declining R<sub>eco</sub>, likely associated with disturbed ecosystems (e.g., forest fires,  
 223 harvesting) with high R<sub>eco</sub> during the first post-disturbance years now recovering<sup>27</sup>. However,  
 224 evidence for the increasing overall net uptake trend from the in-situ data is limited due to the low  
 225 number of long-term sites (>7 years of year-round measurements; 9 sites) out of which only one

226 site showed a statistically significant trend (increasing uptake at a boreal forest site in Finland).  
227 Some of the relationships in our model are likely thus influenced by spatial differences across  
228 the sites rather than temporal and truly causal patterns, creating some uncertainty in upscaled  
229 trends<sup>28</sup>. However, the model reproduces temporal patterns at individual sites well (see  
230 Supplementary Fig. 6), and our upscaled trends are similar to a recent in-situ time-series  
231 analysis<sup>22</sup> and somewhat similar to those estimated from the inversion ensemble (Fig. 1),  
232 providing confidence in our trend results.  
233



234  
235 *Figure 2. An overlay analysis of NEE, GPP,  $R_{eco}$  trend maps identifying how trends in GPP and*  
236  *$R_{eco}$  relate to trends in NEE over 2001-2020 (includes significant and non-significant trends),*  
237 *showing also pixels that burned during 2002-2020 (a). Terrestrial  $CO_2$  budgets for 1-km (blue;*  
238 *2001-2020) and 8-km (grey; 1990-2016) NEE, and 1-km NEE + fire emissions (red; 2002-2020)*  
239 *across the ABZ (b) and permafrost region (c). Trends are shown for the 2002-2020 (NEE + fire)*  
240 *and 2001-2020 (NEE) periods. Uncertainties are standard deviations in bootstrapped estimates.*  
241 *Stars in the trend values depict the significance of the trend (\*= $p < 0.05$ , \*\*= $p < 0.01$ ,*  
242 *\*\*\*= $p < 0.001$ ).*  
243

244 Parts of the ABZ also show increasing annual net  $CO_2$  emissions over time (Fig. 1). Such trends  
245 have been observed at six long-term sites (2 to 17 g C m<sup>-2</sup> yr<sup>-1</sup>,  $p > 0.05$ ), and in 2% of the  
246 upscaled region ( $p < 0.05$ ) from 2001 to 2020. Most of the increasing net emission trends were

247 driven by an increase in  $R_{\text{eco}}$  instead of a decline in GPP (Fig. 2). Regions experiencing  
248 increased net  $\text{CO}_2$  emissions in upscaling were found especially in (i) northern Europe and  
249 Canada (dominated by evergreen needleleaf forests with mild and moderately wet climates), (ii)  
250 parts of central Alaska and northern Siberia (sparse boreal ecosystems and graminoid tundra  
251 with permafrost and high soil carbon stocks), and (iii) Hudson Bay and Siberian lowlands  
252 (wetlands with some permafrost and high soil organic carbon stocks). Some sites in Alaska  
253 have increasing net emissions of  $\text{CO}_2$  due to permafrost thaw<sup>18,29</sup>, but it is unclear if similar  
254 changes are occurring in other regions with increasing net  $\text{CO}_2$  emissions.

255  
256 We calculated an overall 25% increase in seasonal amplitude of  $\text{CO}_2$  fluxes from the upscaled  
257 NEE time series from 2001 to 2020 across the ABZ, on par with earlier atmospheric and  
258 modeling studies<sup>30,31</sup>. Both increasing summer uptake and non-summer season emissions—the  
259 key dynamics driving increasing annual sinks and sources—were evident in the tundra and  
260 boreal biomes (Fig. 3). However, over the 2001-2020 period, the increasing uptake (GPP)  
261 during summer months dominated over increasing net emissions ( $R_{\text{eco}}$ ) during non-summer  
262 months across most of the domain. On average across both biomes, net uptake increased the  
263 most during July (an average upscaled increase of  $-5 \text{ g C m}^{-2} \text{ month}^{-1}$  in the boreal and  $-3 \text{ g C}$   
264  $\text{m}^{-2} \text{ month}^{-1}$  in the tundra in 2011-2020 compared to 2001-2010), and increasing net emissions  
265 were occurring throughout the entire non-summer season, with no clear peaks ( $0.1\text{-}0.9 \text{ g C m}^{-2}$   
266  $\text{month}^{-1}$ ). Although increases in early growing season (May-June) uptake were evident, late  
267 growing season (September) trends were absent or minimal (Fig. 3).

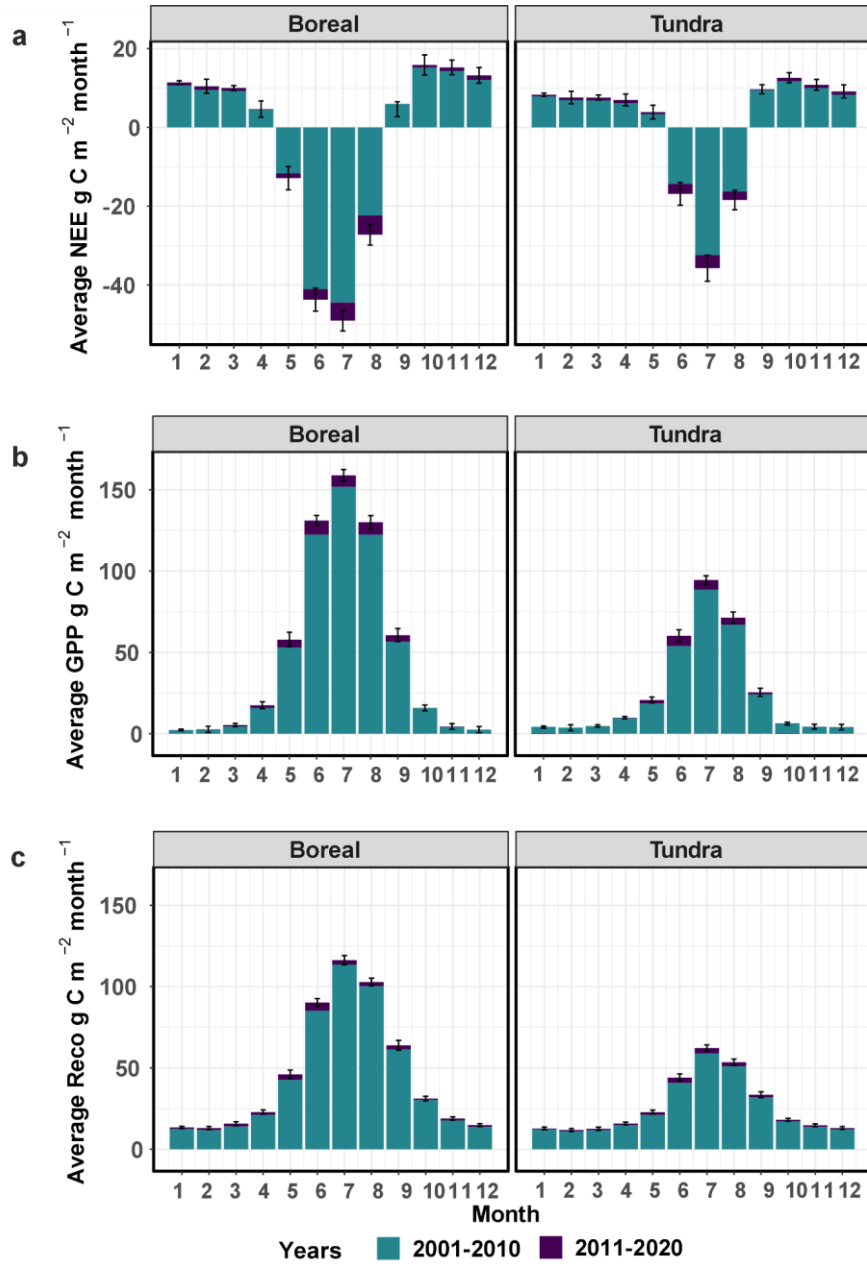
## 268 269 **Drivers of ABZ $\text{CO}_2$ fluxes**

270  
271 There are several environmental conditions driving  $\text{CO}_2$  budgets across the ABZ. Our variable  
272 importance analysis showed  $\text{CO}_2$  fluxes, and thus the overall increasing sink strength, are  
273 explained by dynamic variables of air or surface temperatures, solar radiation, the Normalized  
274 Difference Vegetation Index (NDVI), and partially also by soil temperature, snow cover, and the  
275 vapor pressure deficit (Supplementary Fig. 8-10). Other less important dynamic variables were  
276 vegetation cover and atmospheric  $\text{CO}_2$  concentration. Volumetric soil water content was not  
277 important in our models, likely due to the large uncertainties and coarse spatial resolution in the  
278 gridded product, although in-situ studies have shown drier soils to be linked to larger net  $\text{CO}_2$   
279 emissions and wetter soils to enhanced plant growth due to the lack of water limitation<sup>32</sup>. Static  
280 variables (primarily vegetation type, soil carbon stock, soil pH) were also important in explaining  
281 spatial differences.

282  
283 The most important dynamic variables had a positive overall effect on net uptake, GPP, and  
284  $R_{\text{eco}}$  (Supplementary Fig. 8-10), however, these relationships are more nuanced in reality. In  
285 fact, the recent permafrost in-situ trend analysis of  $\text{CO}_2$  fluxes using the same database  
286 suggests that the  $\text{CO}_2$  flux response to warmer temperatures ranges from positive to negative,  
287 depending on the availability of water and nutrients at the site<sup>22</sup>. Consequently, strong warming  
288 or greening trends did not always translate into increasing net  $\text{CO}_2$  sinks in our upscaling  
289 (Supplementary Fig. 11). For example, while 49% of the region experienced greening (June-  
290 August average NDVI; based on MODIS NDVI,  $p < 0.05$ ), only 12% of those greening pixels



291 showed an annual increasing net CO<sub>2</sub> uptake trend, and 29% an increasing June-August net  
292 uptake.  
293



294

295 *Figure 3. Average upscaled monthly NEE, GPP, and  $R_{eco}$  in boreal and tundra biomes during*  
296 *the past two decades. Negative NEE values represent net uptake and positive net release. Error*  
297 *bars represent standard deviations across bootstrapped estimates and are only shown for the*  
298 *2011-2020 period but are similar for the 2001-2010 period. Note that NEE was  $1.4 \text{ g C m}^{-2}$*   
299 *month<sup>-1</sup> lower in September 2011-2020 compared to 2001-2020 in the boreal biome, but this is*  
300 *not shown in the figure. For a similar figure made based on the in-situ data, see Supplementary*  
301 *Fig. 7.*

302

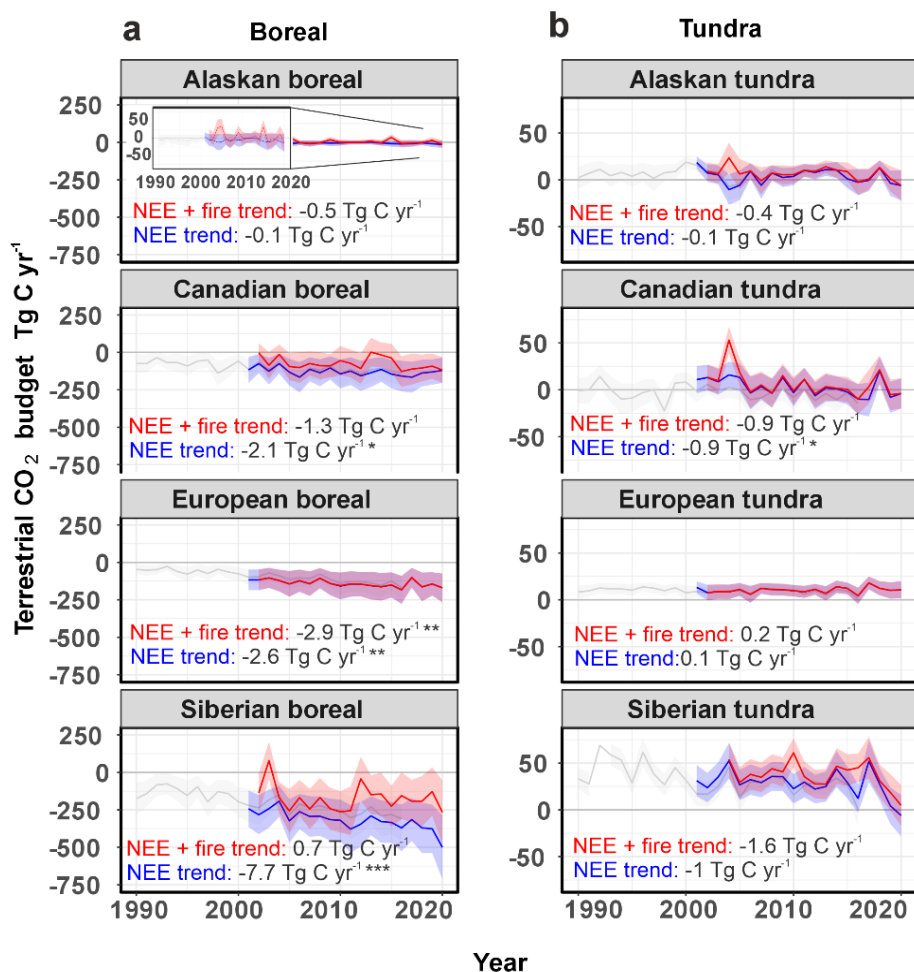
### 303 **Continental and regional patterns in CO<sub>2</sub> budgets and their trends**

304

305 Our upscaling showed clear continental patterns in NEE budgets and trends (Fig. 4), with the  
306 boreal biome primarily driving the budget and trend differences between the continents<sup>1,33</sup>. The  
307 increasing net uptake trend was more pronounced in Eurasia ( $-11 \text{ Tg C yr}^{-1}$ ,  $p < 0.001$ ) compared  
308 to North America ( $-3 \text{ Tg C yr}^{-1}$ ,  $p < 0.05$ ), which corresponds with the smaller area, weaker  
309 warming, declining snow cover and greening trends in North America (Supplementary Fig. 12-  
310 14). We found statistically significant declining summer soil moisture trends in Siberian boreal  
311 (Supplementary Fig. 15), but this did not translate into stronger net emissions. When fire  
312 emissions were added, continental differences were less pronounced due to the much larger  
313 and more rapidly increasing CO<sub>2</sub> emissions from Siberian fires (on average 160 compared to 76  
314 Tg C yr<sup>-1</sup> in North America; Supplementary Fig. 16). Fire emissions even reversed some NEE  
315 trends: the strong increasing sink in Siberia became a source when fire emissions were  
316 included (trend:  $+0.7 \text{ Tg C yr}^{-1}$ ;  $p > 0.05$ ). However, Siberian ecosystems have the largest  
317 uncertainty for both the upscaled fluxes and inversion-based estimates due to lack of in situ  
318 observations, making it challenging to accurately determine the magnitude of continental  
319 differences (Fig. 4, Supplementary Fig. 17).

320

321 Alaska is an important contributor in the weaker North American CO<sub>2</sub> sink. Based on our  
322 analysis, Alaska as a whole was consistently CO<sub>2</sub> neutral or a source over 2002-2020 (NEE +  
323 fire emissions), both in the boreal (budget  $+5 \text{ Tg C yr}^{-1}$ ) and tundra (budget  $+7 \text{ Tg C yr}^{-1}$ ). Alaska  
324 has a relatively high density of observations, making this result more certain compared to other  
325 regions. Alaska is therefore different from the other ABZ regions where boreal regions still  
326 remain on average CO<sub>2</sub> sinks. Potential reasons for the Alaskan CO<sub>2</sub> source include Alaska  
327 having the most rapidly warming autumns and declining autumn snow cover, which has high  
328 inter-annual variability (Supplementary Fig. 14 and 18). Further, field measurements suggest  
329 that many of the observed changes in Alaskan ecosystems can be attributed to permafrost thaw  
330<sup>18,29</sup>—a phenomenon that has accelerated significantly in response to Alaska's pronounced  
331 warming trend since the 1950s<sup>34</sup>. However, we were unable to incorporate permafrost thaw into  
332 our models as high-resolution geospatial data from 1990 to 2020 were not available. The  
333 question of whether analogous trends will manifest in other regions across the northern  
334 permafrost region remains an important research priority.



335

336 *Figure 4. Terrestrial CO<sub>2</sub> budgets for NEE and NEE + fire in key regions and biomes across the*  
 337 *boreal (a) and tundra (b). Terrestrial CO<sub>2</sub> budgets are shown for 1-km (blue; 2001-2020) and 8-*  
 338 *km (grey; 1990-2016) NEE, and 1-km NEE + fire emissions (red; 2002-2020). Trends are shown*  
 339 *for the 2002-2020 (NEE + fire) and 2001-2020 (NEE) periods. The inset in Alaskan boreal in (a)*  
 340 *shows the time series with a narrower y axis compared to the main figure to better detect*  
 341 *interannual variability. Uncertainties are standard deviations in bootstrapped estimates. Stars in*  
 342 *the trend values depict the significance of the trend (\*=  $p < 0.05$ , \*\*= $p < 0.01$ , \*\*\*= $p < 0.001$ ). Fire*  
 343 *emissions alone are shown in Supplementary Fig. 16.*

344

345

## 346 Discussion

347

348 Our results show that the ABZ was on average an increasing terrestrial CO<sub>2</sub> sink (GPP is  
 349 increasing more than R<sub>eco</sub> + fire), indicating that the region still creates an important negative  
 350 feedback to global warming. However, our study also suggests some positive feedbacks to  
 351 climate change that have been more regional and of shorter duration in recent decades. We

352 show that the presence of annual sources was large as indicated by several site-level and  
353 regional studies <sup>35,36</sup>, and even larger with fire emissions included <sup>37</sup>. There were also extreme  
354 years when fire emissions exceeded annual net CO<sub>2</sub> uptake (e.g., 2003 in Siberian boreal, 2012  
355 in Canadian boreal, and several years in the permafrost region; Fig. 2). Moreover, while  
356 summer net uptake increase still dominates over non-summer CO<sub>2</sub> emissions, net CO<sub>2</sub> uptake  
357 is increasing only in the early and peak growing season (May-August in the boreal and June-  
358 August in the tundra) and not in the late growing season (September), because GPP does not  
359 increase later in the season due to plant physiological limitations, and drier and warmer  
360 conditions cause enhanced R<sub>eco</sub> instead <sup>38-43</sup>. A better understanding of how soil moisture and  
361 hydrology have been and will be changing, and the impact of these changes on CO<sub>2</sub> fluxes is  
362 critical for more accurate ABZ CO<sub>2</sub> budgets.

363  
364 In the tundra, our findings reveal a noteworthy shift in carbon dynamics. While the tundra region  
365 has been a carbon sink for millennia <sup>44</sup>, our results suggest that many tundra regions may now  
366 have started to function as CO<sub>2</sub> sources. This transition from an ecosystem CO<sub>2</sub> sink to a CO<sub>2</sub>  
367 source may have begun prior to 1990 <sup>45</sup>, yet the precise timing of this transformation remains  
368 uncertain. The main drivers of this pattern may be related to warming-induced permafrost thaw,  
369 the drying of soils, or vegetation shifts <sup>46-48</sup> but remain unresolved. Tundra regions are also  
370 progressing towards conditions where average annual soil (0-7 cm) temperatures are above  
371 freezing, resulting in more soil organic material being susceptible to decomposition  
372 (Supplementary Fig. 12). Overall, the primary reason behind the annual CO<sub>2</sub> emissions from  
373 tundra ecosystems is the limited duration of the high net CO<sub>2</sub> uptake period, and the substantial  
374 non-summer season net emissions. However, we observed lower in-situ and upscaled October-  
375 April season NEE fluxes and budgets compared to Natali et al. (2019) throughout the entire  
376 period (Supplementary Fig. 19; <sup>49</sup>).

377  
378 Our results demonstrate the need to further study Siberian CO<sub>2</sub> flux trends. Our upscaling  
379 indicated that some of the strongest net sources and sinks, and strongest increasing sink trends  
380 occur in the Siberian boreal. Increasing sink trends in Siberian tundra were also the strongest  
381 across tundra regions. The Siberian sink trend might be explained by strong greening trends <sup>50</sup>,  
382 earlier growing season starts and increasing carbon uptake due to declining spring snow cover  
383 (Supplementary Fig. 14), increases in tree growth and distribution <sup>51,52</sup>, rapid recovery of  
384 ecosystems after fire <sup>53</sup>, and high cover of larch forests that can rapidly take up CO<sub>2</sub>  
385 (Supplementary Table 1)<sup>8,54</sup>. However, the large inversion model spread, sparse measurement  
386 network, and our upscaling uncertainties indicate that it remains challenging to conclude the  
387 magnitude of the Siberian CO<sub>2</sub> balance <sup>2</sup>. This is a significant problem given that Siberia stores  
388 more than half of the permafrost region's C stocks and is now warming more rapidly than other  
389 ABZ regions.

390  
391 In summary, our study reveals distinct spatial and temporal patterns in CO<sub>2</sub> budgets across the  
392 ABZ and underscores the importance of three decades' worth of data. Relatively robust spatial  
393 patterns can be seen, such as the Alaskan CO<sub>2</sub> sources and southern Eurasian boreal sinks  
394 while the temporal trends remain more uncertain. While CO<sub>2</sub> fluxes can be relatively well  
395 modeled using machine learning and existing gridded datasets, gaps persist, such as the



396 incomplete characterization of thermokarst and harvesting disturbances and their links to  
397 ecosystem CO<sub>2</sub> fluxes, and the lack of accurate predictors describing soil moisture <sup>1</sup>. Sustaining  
398 long-term sites is crucial to accurately track trends in ABZ CO<sub>2</sub> balance, while establishing new  
399 year-round sites in data-poor areas like Siberia and the Canadian Arctic is vital to fill knowledge  
400 gaps and enhance our understanding of carbon dynamics <sup>55</sup>.

401

## 402 **Online Methods**

403

### 404 **In-situ data overview**

405

406 We used a recently compiled dataset of in-situ Arctic-boreal terrestrial ecosystem CO<sub>2</sub> flux  
407 measurements (ABCflux, led by Virkkala et al. 2021 <sup>8</sup>) within the ABZ (Supplementary Methods  
408 Section 1). The synthesized data were cumulative fluxes of gross NEE, GPP, and R<sub>eco</sub>  
409 aggregated at the monthly timescale (3,968 to 4,897 site-months depending on the flux). In  
410 addition to eddy covariance data, we included fluxes estimated with the chamber method to  
411 increase data coverage especially during the growing season. The dataset included metadata  
412 out of which we used the site coordinate, biome, flux measurement method, and disturbance  
413 history information in the analysis. For further details on the dataset, see Virkkala et al. (2021) <sup>8</sup>  
414 and a description of additional data processing and screening in the Supplementary Methods  
415 Section 2. Note that our study does not include lateral transport of carbon which was recently  
416 summarized to be 93 Tg C yr<sup>-1</sup> in a roughly similar region (i.e., 17 % of the net uptake budget  
417 calculated in this study) <sup>56</sup>.

418

419 This dataset is more comprehensive than the ones used in earlier upscaling studies as it  
420 represents monthly fluxes from the entire year if available, while Virkkala et al. (2021) focused  
421 on coarse seasonal or annual fluxes <sup>5</sup>, Natali et al. (2019) on monthly winter fluxes <sup>9</sup>, and Mu et  
422 al. (2023) a more limited temporal period (2013-2017) <sup>57</sup>. Furthermore, we included more data  
423 from recent years (805 monthly observations from 2015-2020 compared to 32 and 95 fluxes in  
424 Virkkala et al. 2021 and Natali et al. 2019, respectively), and the sample size in our models was  
425 4 to 25 times larger here compared to the earlier upscaling efforts.

426

### 427 **Geospatial data**

428

429 We used data from geospatial products as predictor variables to upscale fluxes. Our models  
430 had the following predictors: month, incident solar radiation, vapor pressure deficit, atmospheric  
431 CO<sub>2</sub> concentration, vegetation type, snow cover (the fraction covered by snow), soil temperature  
432 (0-7 cm), soil moisture (0-7 cm), NDVI (MODIS- or AVHRR-based), land surface temperature  
433 (or air temperature; MODIS- or ERA5 Land-based), compound topographic index (i.e.,  
434 topographic wetness index), continuous vegetation fields describing percent non-tree vegetation  
435 and non-vegetated fraction and percent tree cover (MODIS- or AVHRR-based), soil pH (0-5  
436 cm), soil organic carbon stock in 0-2 meters, and permafrost probability. In our analysis, NDVI  
437 was the primary predictor describing disturbances, with declines in NDVI being related to  
438 disturbances <sup>5</sup>. Data were in daily, weekly, monthly, annual, and static format (i.e., no temporal  
439 changes such as in the compound topographic index). If data were of higher temporal resolution

440 than monthly, they were aggregated to monthly time steps. Gaps in MODIS and AVHRR NDVI  
441 time series were filled to produce a continuous time series. Data were re-projected to North Pole  
442 Lambert Azimuthal Equal Area Projection at 1 and 8 km spatial resolution and extracted at the  
443 flux sites. See Supplementary Section 3 for further descriptions and data sources.

444

445 We used the Global Fire Emissions Database (GFED) 500-m fire product<sup>23</sup> to calculate fire  
446 emissions. The product is based on a global fire emissions model with a spatial resolution of  
447 500 m using MODIS data. The model was developed using an updated field measurement  
448 synthesis database of fuel load and consumption which included improvements, for example, in  
449 boreal soil carbon combustion. The higher resolution of the 500-m model compared to earlier  
450 coarser models improved the detection of small-scale fires and understanding of landscape  
451 heterogeneity, and reduced the scale mismatch in comparing field measurements to model grid  
452 cells. However, some small fires might still be undetected by this model, leading to potential  
453 underestimations in carbon emissions in this product.

454

### 455 **Machine learning modeling**

456 We used random forest models to upscale GPP,  $R_{eco}$ , and NEE to the ABZ from 1990 to 2020,  
457 the period with in-situ flux measurements. Two sets of predictive models were developed: (i)  
458 models using primarily predictors with a spatial resolution  $\leq 1$  km from 2001 to 2020 (i.e., the  
459 MODIS era) at 1-km spatial resolution (hereafter 1-km models;), and (ii) models using coarser-  
460 resolution predictors from the AVHRR GIMMS era (1990-2016;) from 1990 to 2016 at 8-km  
461 spatial resolution (hereafter 8-km models) (Supplementary Table 3). Each model included all  
462 available monthly fluxes from the entire year, i.e. no separate models for individual months or  
463 seasons were developed, as this approach resulted in the best predictive performance. All  
464 models included 17 predictors, but the sample sizes were variable depending on the amount of  
465 data available for each flux and time period; NEE models had the highest amount of model  
466 training data compared to GPP and  $R_{eco}$  models. For the 1-km model, coarsest predictors were  
467 at 9-km resolution but most important predictors were at 1 to 4-km resolution. For the 8-km  
468 model, the coarsest predictor resolution was 9 km, and the most important variables had a  
469 resolution of 1 to 9 km.

470

471 Model parameter tuning was performed based on leave-one-site out cross validation (CV) to  
472 achieve minimum predictive error. The models were run using the “caret” package in R version  
473 4.2<sup>58</sup>. We assessed the predictive performance of the final models using the (1)  $R^2$ , (2) root  
474 mean square error (RMSE), (3) mean absolute error (MAE), and (4) mean bias error (MBE)  
475 between predicted and observed values using the CV data. Larger RMSE and MAE values  
476 indicate larger errors, and positive MBE values indicate overestimation. The predictive  
477 performance of our models was good or high, ranging from 0.55 to 0.78 for  $R^2$  and 19.4 to 37.3  
478  $\text{g C m}^{-2} \text{ month}^{-1}$  for RMSE, but was occasionally limited (Supplementary Fig. 1-3), mostly due to  
479 1) our model not being able to identify landscape heterogeneity with nearby sites showing large  
480 differences in  $\text{CO}_2$  fluxes (e.g., a forest and wetland site), and 2) our model not capturing inter-  
481 annual variability at individual sites, both of which are likely attributed to the coarse, uncertain,  
482 and missing predictors characterizing such conditions (e.g., soil moisture, disturbances).

483

484 We evaluated the uncertainty of predictions by creating 20 bootstrapped model training datasets  
485 (with replacement; same sample size as in the original model training data) and using those to  
486 develop 20 individual models and predictions. Out of the 20 predictions, we calculated the  
487 standard deviation to represent prediction uncertainty. The uncertainty ranges in NEE + fire  
488 budgets only represent NEE uncertainties. We further assessed the area of extrapolation of the  
489 models, and the influence of the flux measurement method and disturbance history information  
490 on flux predictions by training models with different subsets. Further details of the uncertainty  
491 analyses can be found in the Supplementary Methods Section 4.

492

### 493 **Spatial upscaling of fluxes**

494

495 We upscaled fluxes across the Arctic-boreal terrestrial area  $\geq 49^\circ \text{N}$ <sup>59</sup>, which comprises 20.69  
496  $\times 10^6 \text{ km}^2$  of land (excluding glaciers and ice sheets; Fig. 1) with lake and glacier areas  
497 removed. The models were applied at a monthly time step from 2001 to 2020 for the 1-km  
498 models and from 1990 to 2016 for the 8-km models.

499

500 We analyzed the upscaled flux maps as well as environmental predictor rasters for temporal  
501 trends using the nonparametric Mann–Kendall test using the “zyp” package<sup>60,61</sup> with pre-  
502 whitening (Zhang method<sup>62</sup>) to remove autocorrelation. We report the significance of Kendall’s  
503 correlation coefficient (the strength of the time-series) and the Theil–Sen slope to describe  
504 trends over time. Finally, we calculated zonal statistics of average annual, seasonal, and  
505 monthly fluxes and trends across key regions (Siberia defined as all land east from the Ural  
506 mountains, including a small portion of Mongolia; the rest of Eurasia, including Greenland are  
507 grouped within the European classes), biomes (tundra and boreal)<sup>59</sup>, permafrost region<sup>63</sup>, and  
508 vegetation types<sup>8</sup>.

509

### 510 **Comparison to process models and atmospheric inversions**

511

512 We compared our estimates with the CMIP6 process models<sup>26</sup>, atmospheric inversions used in  
513 the Global Carbon Project's Global Carbon Budget 2022<sup>64</sup>, and a global upscaling product  
514 FLUXCOM<sup>25</sup>. We included a subset of CMIP6 process models (13 in total) that had soil thermal  
515 processes at several depths to assure they had some information about the freeze-thaw  
516 patterns in the permafrost region. We included inversions with data from the whole 2001-2020  
517 period (i.e., included five inversions and excluded four). Fire CO<sub>2</sub> emissions<sup>23</sup> were subtracted  
518 from the inversions. CMIP6 process model and FLUXCOM outputs were only available for the  
519 2001-2014 and 2000-2013 period, respectively. The final model outputs used here represent  
520 terrestrial NEE (GPP- $R_{\text{eco}}$ ) in a similar way across the models except for inversions that also  
521 include vertical CO<sub>2</sub> fluxes from water bodies.

522

### 523 **Acknowledgements**

524

525 This work was supported by funding from the Gordon and Betty Moore Foundation (grant  
526 #8414) and funding catalyzed by the TED Audacious Project (Permafrost Pathways). We  
527 additionally acknowledge the funding from the NASA Arctic-Boreal Vulnerability Experiment and

528 Carbon Cycle Science programs (NNX17AE13G), NSF PLR Arctic System Science Research  
529 Networking Activities (RNA, Grant#1931333), Minderoo Foundation, KAKENHI(19H05668), The  
530 Danish National Research Foundation (CENPERM DNR100), EU HORIZON GreenFeedBack,  
531 grant agreement No. 101056921, Danish Arctic Climate support through Greenland Ecosystem  
532 Monitoring and ICOS grants, Natural Sciences and Engineering Research Council, the  
533 Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's  
534 Excellence Strategy – EXC 2037 'CLICCS - Climate, Climatic Change, and Society' – Project  
535 Number: 390683824, NASA Grant/Cooperative Agreement Number: NNX17AD69A, The  
536 Research Council of Norway (BioGov, project nr. 323945), ERC synergy project Q-Arctic (grant  
537 agreement no. 951288), the Copernicus Atmosphere Monitoring Service, implemented by  
538 ECMWF on behalf of the European Commission (Grant: CAMS2 55), the Environment  
539 Research and Technology Development Fund of the Environmental Restoration and  
540 Conservation Agency of Japan (JPMEERF21S20810), ArCSII(JPMXD142031886), Financial  
541 support from the Swedish Research Council (VR) and consortium partners to ICOS Sweden  
542 (grants 2015–06020 and 2019–00205) and SITES (grant 2017–00635), VR grant 2019-04676  
543 and 2018-03966, ArcticNet and NSERC, NOAA Cooperative Agreement NA16SEC4810008,  
544 Research Council of Finland (NPERM project nrs 341349, 330840, 349503 ICOS-FIRI), ICOS-  
545 FI via University of Helsinki funding, the EU Horizon Europe (GreenFeedback nr. 101056921  
546 and LiweFor nr. 101079192), NRF-2021M1A5A1065425 (KOPRI-PN23011), NRF-  
547 2021M1A5A1065679, NRF-2021R111A1A01053870, the Dutch Research Council (NWO)  
548 (project number VI.Vidi.213.143), and The Natural Environment Research Council through the  
549 National Centre for Earth Observation (NE/R000115/1). Part of the research was carried out at  
550 the Jet Propulsion Laboratory, California Institute of Technology, under a contract with the  
551 National Aeronautics and Space Administration (80NM0018D0004). Part of the inverse  
552 analyses were performed on the supercomputer systems at the National Institute for  
553 Environmental Studies and Meteorological Research Institutes (NEC SX-Aurora TSUBASA and  
554 FUJITSU PRIMERGY CX2550M5) and at the HPC cluster Aether at the University of Bremen,  
555 financed by DFG within the scope of the Excellence Initiative (Germany).

556

## 557 **Data availability**

558

559 In-situ data used here can be accessed from ORNL DAAC <sup>65</sup>. Environmental predictors and  
560 links to the datasets are: TerraClimate (<https://www.climatologylab.org/terraclimate.html>), ERA5  
561 Land (<https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land?tab=overview>),  
562 MODIS land surface temperature MOD11A2v006  
563 (<https://lpdaac.usgs.gov/products/mod11a2v006/>), Barrow CO<sub>2</sub> concentrations  
564 (doi:10.15138/yaf1-bk21), ESA CCI land cover (<https://www.esa-landcover-cci.org/>), CAVM  
565 vegetation type (<https://geobotany.uaf.edu/>), MODIS NDVI MOD13A1v006  
566 (<https://lpdaac.usgs.gov/products/mod13a1v006/>), GIMMS3g NDVI  
567 (<https://climatedataguide.ucar.edu/climate-data/ndvi-normalized-difference-vegetation-index-3rd-generation-nasagfsc-gimms>), MOD44B continuous vegetation fields  
568 ([https://developers.google.com/earth-engine/datasets/catalog/MODIS\\_006\\_MOD44B](https://developers.google.com/earth-engine/datasets/catalog/MODIS_006_MOD44B)),  
569 MEaSUREs Vegetation Continuous Fields (<https://lpdaac.usgs.gov/products/vcf5kyrv001/>), ESA  
570 CCI permafrost probability (<https://doi.pangaea.de/10.1594/PANGAEA.888600>), SoilGrids  
571



572 (<https://files.isric.org/soilgrids/former/2017-03-10/data/>), MERIT DEM topographic indices  
573 (<https://doi.pangaea.de/10.1594/PANGAEA.899135>) (for more details see Supplementary Table  
574 3). CMIP6 process model outputs can be accessed at <https://aims2.llnl.gov/search/cmip6/>, and  
575 Global Carbon Budget inversion outputs at <https://meta.icos->  
576 [cp.eu/objects/GahdRITjT22GGmq\\_GCi4o\\_wy](https://meta.icos-cp.eu/objects/GahdRITjT22GGmq_GCi4o_wy) (for more details see Supplementary Table 6).  
577 The 1-km and 8-km upscaled rasters of NEE, GPP, and  $R_{eco}$  together with their uncertainties will  
578 be published via ORNL DAAC upon publication.

579

#### 580 **Code availability**

581 The main analysis codes can be found in the Supplement.

582

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