

UNIVERSITY OF BIRMINGHAM

Research at Birmingham

Spring photosynthetic onset and net CO₂ uptake in Alaska triggered by landscape thawing

Parazoo, Nicholas; Arneth, Almut; Pugh, Thomas; Smith, Benjamin; Steiner, Nicholas; Luus, Kristina; Commane, Roisin; Benmergui, Josh; Stofferahn, Eric; Liu, Junjie; Rödenbeck, Christian; Kawa, Randy; Euskirchen, Eugenie; Zona, Donatella; Arndt, Kyle; Oechel, Walt; Miller, Charles

DOI:

[10.1111/gcb.14283](https://doi.org/10.1111/gcb.14283)

Document Version

Peer reviewed version

Citation for published version (Harvard):

Parazoo, N, Arneth, A, Pugh, T, Smith, B, Steiner, N, Luus, K, Commane, R, Benmergui, J, Stofferahn, E, Liu, J, Rödenbeck, C, Kawa, R, Euskirchen, E, Zona, D, Arndt, K, Oechel, W & Miller, C 2018, 'Spring photosynthetic onset and net CO₂ uptake in Alaska triggered by landscape thawing' *Global Change Biology*. <https://doi.org/10.1111/gcb.14283>

[Link to publication on Research at Birmingham portal](#)

Publisher Rights Statement:

Checked for eligibility: 02/05/2018

This is the peer reviewed version of the following article: Parazoo, N. C., Arneth, A., Pugh, T. A., Smith, B., Steiner, N., Luus, K., Commane, R., Benmergui, J., Stofferahn, E., Liu, J., Rödenbeck, C., Kawa, R., Euskirchen, E., Zona, D., Arndt, K., Oechel, W. and Miller, C. (2018), Spring photosynthetic onset and net CO₂ uptake in Alaska triggered by landscape thawing. *Glob Change Biol.*, which has been published in final form at doi:10.1111/gcb.14283. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

Spring photosynthetic onset and net CO₂ uptake in Alaska triggered by landscape thawing

Nicholas Parazoo¹, Almut Arneth², Thomas Pugh^{3,4}, Ben Smith⁵, Nicholas Steiner⁶, Kristina Luus⁷, Roisin Commane⁸, Josh Benmergui⁸, Eric Stofferahn⁹, Junjie Liu¹, Christian Rödenbeck¹⁰, Randy Kawa¹¹, Eugenie Euskirchen¹², Donatella Zona¹³, Kyle Arndt¹³, Walt Oechel¹³, Charles Miller¹

Jet Propulsion Laboratory, California Institute of Technology¹

Institute of Meteorology and Climate Research (IMK-IFU), Karlsruhe Institute of Technology,
Garmisch-Partenkirchen, Germany²

School of Geography, Earth and Environmental Sciences, University of Birmingham, UK.³

Birmingham Institute of Forest Research, University of Birmingham, U.K.⁴

Department of Physical Geography and Ecosystem Science, Lund University⁵

Department of Earth and Atmospheric Sciences, The City College of New York⁶

Centre for Applied Data Analytics, Dublin, Ireland⁷

Department of Earth and Planetary Sciences, Harvard University⁸

Conservation Science Partners, Truckee, CA⁹

Max Plank Institute for Biogeochemistry¹⁰

NASA Goddard Space Flight Center¹¹

Institute of Arctic Biology, University of Alaska Fairbanks¹²

Biology Department, San Diego State University¹³

Prepared for Global Change Biology

31 **Abstract**

32 The springtime transition to regional-scale onset of photosynthesis and net ecosystem carbon
33 uptake in boreal and tundra ecosystems is linked to the soil freeze-thaw state. We present
34 evidence from diagnostic and inversion models constrained by satellite fluorescence and airborne
35 CO₂ from 2012-2014 indicating the timing and magnitude of spring carbon uptake in Alaska
36 correlates with landscape thaw and ecoregion. Landscape thaw in boreal forests typically occurs
37 in late April (DOY 111±7) with a 29±6 day lag until photosynthetic onset. North Slope tundra
38 thaws 3 weeks later (DOY 133±5) but experiences only a 20±5 day lag until photosynthetic
39 onset. These time lag differences reflect efficient cold season adaptation in tundra shrub, and the
40 longer dehardening period for boreal evergreens. Despite the short transition from thaw to
41 photosynthetic onset in tundra, synchrony of tundra respiration with snowmelt and landscape
42 thaw delays the transition from net carbon loss (at photosynthetic onset) to net uptake by 13±7
43 days, thus reducing the tundra net carbon uptake period. Two global CO₂ inversions using a
44 CASA-GFED model prior estimate earlier northern high latitude net carbon uptake compared to
45 our regional inversion, which we attribute to (1) early photosynthetic onset model prior bias, (2)
46 inverse method (scaling factor + optimization window), and (3) sparsity of available Alaskan
47 CO₂ observations. Another global inversion with zero prior estimates the same timing for net
48 carbon uptake as the regional model but smaller seasonal amplitude. Analysis of Alaskan eddy
49 covariance observations confirms regional scale findings for tundra, but indicates that
50 photosynthesis and net carbon uptake occur up to 1 month earlier in evergreens than captured by
51 models or CO₂ inversions, with better correlation to above-freezing air temperature than date of
52 primary thaw. Further collection and analysis of boreal evergreen species over multiple years and
53 at additional sub-Arctic flux towers is critically needed.

54

55 **Introduction**

56 The future trajectory of the Arctic Boreal Zone as a net carbon (C) sink or source is of global
57 importance due to vast quantities of C stored in permafrost (Hugelius et al., 2014). Climate
58 warming threatens to thaw and release permafrost C back to the atmosphere as the greenhouse
59 gases carbon dioxide (CO₂) and methane, creating a positive feedback and promoting further
60 global warming (Hinzman et al., 2013). At the same time, warming can lead to higher
61 productivity (Natali et al., 2012), creating temporary C sinks via increased above-ground
62 biomass and delayed decomposition, offsetting potential C losses. The remainder of this paper
63 focuses on C in the form of CO₂.

64 The balance of net ecosystem C gain and loss processes is strongly modulated by land surface
65 freeze/thaw dynamics, the timing and duration of seasonal soil thawing (defined as the transition
66 from frozen to unfrozen soil water state), vegetation growing season, and surface moisture
67 supply (Kim et al., 2014; Yi et al., 2014). In spring, plant productivity (denoted as gross primary
68 production, or GPP) is hindered by cold temperatures and lack of liquid water in frozen soils and
69 snow cover. Climate warming promotes earlier landscape thawing (Goulden, 1998), reduced
70 spring snow cover duration (Lawrence & Slater, 2010), earlier budburst (Badeck et al., 2004),
71 and longer growing seasons (Barichivich et al., 2013). These processes lead to higher GPP
72 through simultaneous warming, CO₂ fertilization, and increased woody biomass (Bhatt et al.,
73 2010; Elmendorf et al., 2012; McGuire et al., 2012). Earlier spring snow melt and thawing also
74 expose the land surface to increasing solar absorption resulting in a longer decomposition season,
75 active layer deepening, an extended zero curtain period and talik formation, which can stimulate
76 terrestrial ecosystem respiration (TER) through enhanced soil warming and water drainage
77 (Lawrence et al., 2008; Romanovsky & Osterkamp, 2000).

78 The impacts of changes in growing season length on annual C balance are not well modeled
79 (Schaefer et al., 2012). In particular, Earth System Models used in IPCC climate assessments
80 predict photosynthetic growing season onsets that are systematically early on local (Peng et al.,
81 2015) to regional scales (Commane et al., 2017a). In turn, GPP biases propagate through the
82 model and affect the timing and magnitude of estimated net biosphere production (NBP) (Wang
83 et al., 2012), representing the balance of GPP and TER (NBP = GPP – TER). Because climate
84 change at high latitudes promotes earlier and longer growing seasons (Barichivich et al., 2013;

85 Kim et al., 2012), while the photoperiod remains fixed, models with early spring bias in the
86 current climate are likely to under-estimate the photosynthetic response to future warming.
87 Consequently, errors in the simulation of growing season onset and duration provide a plausible
88 explanation for the tendency of Earth System Models to underestimate peak growing season C
89 uptake in response to climate warming (Graven et al., 2013).

90 It is well known that changes in spring GPP onset in cold northern latitudes corresponds closely
91 with changes in the date of soil thaw when liquid water becomes available (Troeng and Linder,
92 1982; Black et al., 2000; Goulden, 1998; Jarvis & Linder, 2000). In evergreen needleleaf forests
93 (denoted evergreens), assimilated C initially accumulates as starch following soil thaw, and then
94 is used to grow new foliage, branches, and stem during the growing season peak (Bergh et al.,
95 1998). GPP onset can occur several weeks prior to changes in biomass in conifers (Ottander et
96 al., 1995; Soukupova et al., 2008; Richardson et al., 2011), but the spring dehardening period,
97 during which plants undergo the biochemical changes needed for green-up, can slow recovery
98 from winter dormancy (Ensminger et al., 2008). Land surface models that do not account for
99 effects of frozen soils or recovery of photosynthetic capacity in spring and summer overestimate
100 GPP gain by up to 10% across the entire permafrost domain (Jafarov & Schaefer, 2016) and up
101 to 40% in boreal forests (Bergh et al., 1998). However, the relationship between spring GPP
102 onset and soil freeze/thaw is complicated by confounding air temperature and snow cover
103 effects, which can lead to GPP onset while soils are frozen (Esminger et al., 2004; Arneth et al.,
104 2006; Jonsson et al., 2010; Gonsamo et al., 2012; Walther et al., 2016; Pulliainen et al., 2017).

105 Tundra ecosystems in the far northern Alaskan and Siberian Arctic also show a pattern of
106 increased GPP and NBP in spring with warming and earlier soil thaw and snowmelt (Griffis et
107 al., 2000; Harazono et al., 2003; Arneth et al., 2006; Lafleur et al., 2007; Ueyama et al., 2013).
108 The length of time from soil thaw to onset of GPP and net C uptake (date when ecosystem shifts
109 from net C source to net sink), however, varies under different environmental conditions and
110 vegetation types. Simultaneous increases in soil respiration (i.e., TER) with GPP following thaw
111 and snowmelt can delay daily net C uptake by 5-23 days depending on ambient temperature
112 (Oberbauer et al., 1998; Lafleur et al., 2007). Ecosystem type and fraction of evergreen vs
113 deciduous species is also important. Multi-year observations from a cluster of flux towers on the
114 Alaskan North Slope show much stronger correlation of thaw date with heath and wet sedge

115 tundra than with tussock tundra (Euskirchen et al., 2017). Likewise, evergreen mosses and
116 lichens transition to net uptake within one week of snowmelt, while deciduous shrubs show a
117 slower transition of 1-3 weeks (Lafleur et al., 2007). Direct observations of *Sphagnum* (moss)
118 along the northern coast of Alaska, near Barrow, show very weak levels of initial photosynthesis
119 following snowmelt due to photoinhibition as a stress response to high radiation levels, causing
120 a delay in net C uptake of ~3 weeks (Zona et al., 2011). The exact timing of spring GPP onset
121 and transition to net C uptake in Arctic tundra and in boreal ecosystems is thus not well
122 established at regional scale, in part due to sparse and variable results from field measurements,
123 but also because reliable indicators of GPP onset are limited.

124 Solar induced chlorophyll fluorescence (SIF) measures a direct outcome of foliar light absorption
125 by chlorophyll and provides an important seasonal GPP proxy (Frankenberg et al., 2011; Parazoo
126 et al., 2014). Recent satellite SIF estimates have been used to accurately represent the timing of
127 spring GPP onset and the duration of growing season C uptake in Alaskan ecosystems (Walther
128 et al., 2016; Jeong et al., 2017; Luus et al., 2017; Commane et al., 2017a). In particular, Luus et
129 al. (2017) show greenup and budburst to occur 1-2 weeks prior to SIF based GPP onset in
130 northern high latitude deciduous tundra ecosystems. Moreover, leaf level SIF measurements
131 show close correspondence to photochemical reflectance index and chlorophyll carotenoid index
132 optical indices during spring photosynthetic activation (from gas exchange measurements) in
133 boreal evergreens, reflecting a reversal of non-photochemical quenching and leaf pigments in
134 spring with changes in chloroplast functioning during cold dehardening (Wong & Gamon, 2015;
135 Springer et al., 2017). Especially in evergreens, SIF remote sensing has potential to provide a
136 powerful measure of the reactivation of photosynthesis in spring at large spatial scales, which is
137 otherwise invisible and difficult to assess with reflectance-based optical indices (Wong and
138 Gamon, 2015; Walther et al., 2016).

139 Analysis of SIF-GPP relationships in Alaska has shed light on the effects of plant structural vs
140 functional phenology changes on seasonal C fluxes across key Arctic biomes, and helped
141 quantify Alaskan C balance (Commane et al., 2017a), but have not yet clarified links between
142 plant phenology and environmental effects in driving seasonal onset of GPP and net C uptake.
143 As such, our quantitative and mechanistic understanding of links between environmental forcing,
144 phenology response, and plant C uptake across tundra and boreal ecosystems requires further

145 refining, and improved estimates of the timing of thaw, GPP, and net C uptake at regional-scale.
146 Here, we establish empirical relationships between spring thaw, GPP onset, and net C uptake at
147 regional scale as derived from established GPP and NBP estimates constrained by satellite
148 fluorescence and airborne CO₂ observations in Alaska (Luus et al., 2017; Commane et al.,
149 2017a). We also analyze regional estimates against eddy covariance observations at boreal and
150 tundra sites in interior and North Slope Alaska. By quantifying these relationships, we seek to
151 determine the extent to which landscape thaw controls the timing of GPP and net C uptake onset
152 in northern ecosystems, and understand the ecosystem dependencies and physiological
153 mechanism behind the timing and time lag of thaw and C fluxes.

154

155 **Materials and Methods**

156 *Freeze/Thaw State Determination*

157 Daily 10-km resolution maps of the bulk freeze/thaw state of the Alaskan land surface were
158 determined for 2012-2014 using passive microwave observations from the Advanced Microwave
159 Scanning Radiometer-EOS (AMSR-E) and the Special Sensor Microwave Imager/Sounder
160 (SSMIS-F17). The freeze/thaw mapping algorithm is based on wavelet analysis, which uses a
161 time-series singularity classifier to identify the timing of freeze/thaw and snowmelt transitions
162 (Steiner & Tedesco, 2014; Steiner et al., 2015; 2017). A brightness temperature gradient ($K - K_a$
163 Bands), sensitive to transitions between frozen and liquid state of water caused by contrasts in
164 the bulk landscape complex dielectric constant, is used to determine freeze/thaw status (Zhang &
165 Armstrong, 2001). Peak diurnal difference brightness temperatures determine snowmelt status
166 (Ramage & Isacks, 2002). Here, freeze/thaw state represents the transition of Alaskan landscapes
167 from frozen to unfrozen conditions, and does not distinguish between landscape components
168 (soil, vegetation, and snow).

169

170 *Regional GPP and NBP Flux Estimates*

171 Regional GPP is taken from the Polar Vegetation Photosynthesis and Respiration Model
172 (PVPRM) (Luus & Lin, 2015a). PVPRM is a functional representation of ecosystem C fluxes
173 parameterized using eddy covariance data for seven arctic and boreal vegetation types; it is
174 applied regionally and temporally using monthly GOME-2 SIF and North American Regional

175 Reanalysis (NARR) meteorology to obtain three hourly GPP, TER, and NBP at $1/6^\circ$ latitude x
176 $1/4^\circ$ longitude in Alaska. Phenology is driven by SIF from the Global Ozone Monitoring
177 Experiment (GOME-2) satellite (Joiner et al., 2014; Luus et al., 2017). GOME-2 SIF at 740 nm
178 is derived using a statistically based retrieval, which optimizes model parameters for atmospheric
179 absorption, surface reflectance, and fluorescence radiance using empirical principal component
180 analysis, to enhance retrieval precision and reduce noise. Cloud screening is applied such that
181 only pixels with cloud fraction less than 40% are retained, removing primarily heavily clouded
182 (overcast) pixels within the 40x80 km GOME-2 footprint. The main effect of the remaining
183 clouds is a shielding effect, which masks a fraction of the observed scene (80% of surface
184 observed for 40% cloud cover and cloud optical thickness up to 10) but does not alter the
185 spectral signature of fluorescence (Joiner et al., 2012; 2014). To alleviate reduced signal-to-noise
186 soundings for low sun angles over snow and other high albedo surfaces in northern high latitude
187 spring, GOME-2 SIF values are additionally screened for solar zenith angles less than 60° and
188 cloud fractions below 20%, aggregated monthly and separately calculated for each vegetation
189 class, then weighted according to component vegetation fractions at each PVPRM pixel (Luus et
190 al., 2017). We refer to SIF driven GPP as PVPRM-SIF GPP. We also compare monthly
191 constrained PVPRM-SIF GPP to 5-day mean SIF (same screening criteria) to assess the impact
192 of monthly aggregation on seasonal transitions.

193 PVPRM NBP in Alaska is further optimized using atmospheric CO_2 vertical profiles obtained in
194 the lower atmosphere across Alaska during the Carbon in the Arctic Reservoirs Vulnerability
195 Experiment (CARVE) (Chang et al., 2014; Commane et al., 2017a). Profiles were acquired from
196 Apr-Nov during CARVE campaigns from 2012–2014, and converted to mass-weighted, column-
197 mean CO_2 mole fraction in the atmospheric residual layer. The NBP optimization approach uses
198 the CARVE Polar Weather Research and Forecasting—Stochastic Time-Inverted Lagrangian
199 Transport (PWRf-STILT) framework (Henderson et al., 2015) to calculate the influence
200 function of land surface fluxes on CARVE profiles. Modeled partial column CO_2 enhancements
201 are obtained by convolving the land surface influence functions with NBP priors from PVPRM,
202 which were aggregated to $0.5^\circ \times 0.5^\circ$ for the CO_2 inversion. For each 2-wk measurement period,
203 additive corrections are made to PVPRM NBP that minimized the differences between modeled
204 and observed column CO_2 enhancements, providing spatially explicit, data-constrained NBP for
205 Alaska for each interval. Initial and final campaign dates varied each year, starting/ending on

206 May 27 / Sep 26 in 2012, April 2 / Oct 26 in 2013, and May 23 / Nov 9 in 2014, with a mean
207 start and end dates on day of year (DOY) 127 and 293. We consider optimized NBP as most
208 valid between mid-May and mid-October, although we note that CO₂ fluxes in Jan-Mar compare
209 well to near surface CO₂ observations at CRV and BRW towers as determined from STILT
210 footprints (Commane et al., 2017a). Additive flux corrections are linearly interpolated between
211 aircraft measurement periods and use PVPRM prior flux for late winter when CARVE flights are
212 not available (Dec-Mar) to obtain regional NBP for Alaska (daily, 0.5°x0.5°). CARVE NBP
213 estimates are denoted as CARVE-Opt (Commane et al., 2017b;
214 <https://doi.org/10.3334/ORNLDAAC/1389>).

215 Commane et al. (2017a) account for uncertainties in observations, background, transport, and the
216 model prior in CARVE-Opt using restricted maximum likelihood estimation, then generate
217 10,000 realizations of the additive flux correction. The standard deviation produces regionally
218 aggregated errors of ~0.25 gC m⁻² d⁻¹ in spring and 0.50 gC m⁻² d⁻¹ in summer, which translates to
219 a net C uptake onset error of 5-10 days on average (cf Fig. 3, Luus et al., 2017 and Fig. 1,
220 Commane et al., 2017a). We do not explicitly account for these uncertainties in our analysis, but
221 consider this timing error in our qualitative analysis of Alaskan net C uptake onset.

222 We provide an indirectly optimized estimate of TER as the difference between PVPRM-SIF GPP
223 and CARVE-Opt NBP, replacing the unconstrained estimate provided by PVPRM. Given that
224 PVPRM-SIF and CARVE-Opt are directly constrained by observations, we consider TER the
225 more uncertain term in this analysis. Since NBP is a small number that balances larger GPP and
226 TER components, small errors in NBP and GPP could lead to large compensating errors in TER.
227 To reduce these compensating errors, we apply a constraint on the signs of TER and GPP to
228 ensure the estimated TER is physically realistic (Bloom & Williams, 2015), and estimate TER
229 as:

$$230 \text{ TER} = \text{NBP} * a + \text{GPP} * b$$

231 where *a* and *b* reflect a range of possible scale factors based on estimated NBP and GPP
232 normally distributed uncertainties of 50% (1-sigma range of 0.5 – 1.5 for *a* and *b*). We then
233 sample 1000 samples of TER vectors, and reject unphysical values (TER < 0).

234 We analyze CARVE-Opt NBP against an ensemble of 3 global inverse estimates constrained
235 against satellite or surface CO₂ observations: (1) NASA Carbon Monitoring System Flux (CMS-

236 Flux) estimation and attribution strategy (Liu et al., 2014, 2017; Ott et al., 2015) constrained by
237 column CO₂ from the Greenhouse gases Observing SATellite (GOSAT) using the v7.3 ACOS
238 retrieval algorithm; (2) CarbonTracker 2016 (CT2016) (Peters et al., 2007, with updates
239 documented at <http://carbontracker.noaa.gov>) constrained by 124 datasets from a global network
240 of tower, aircraft, and shipboard surface *in situ* CO₂ observations; and (3) Jena CarboScope
241 s04_v4.1 (Jena4.1) (update of Rödenbeck et al, 2003, 2005), constrained by surface observations
242 at 59 sites. All inverse estimates are analyzed for the period 2012-2014.

243 We also analyze simulated GPP and NBP from the CASA-GFED3 model (van der Werf et al.,
244 2010), which is run at 0.5°x0.5° monthly resolution and scaled to 3-hour and 1°x1.25° for CO₂
245 modeling studies (<https://nacp-files.nacarbon.org/nacp-kawa-01/>). Biomass burning and fuel
246 wood C emissions were estimated by the model on daily and monthly time step. These
247 calculations are driven by analyzed meteorological data (MERRA) from the Goddard Modeling
248 and Assimilation Office from 2003-2016.

249

250 ***Flux Tower Site Description***

251 Data for this study were collected from eight eddy covariance towers across four sites on the
252 North Slope and in Interior Alaska (Fig. 1). Brief site descriptions, including location, years
253 analyzed, and references, are provided in Table 1. Tundra sites consist of five total towers at
254 three sites in the North Slope of Alaska, including one tower each at Atkasuk (ATQ) and Ivotuk
255 (IVO) and three towers at Imnavait Creek Watershed (IMN). Boreal sites include three towers at
256 the Bonanza Creek Experimental Forest (BON) in Interior Alaska. NBP measurements were
257 collected at each of the eight eddy covariance towers for at least one year during the period
258 2012-2014, and partitioned into GPP and TER components using the relation between NBP
259 during the nighttime ($PAR < 50 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) and air temperature (Euskirchen et al., 2017;
260 Reichstein et al., 2005). An additional technique using daytime light partitioning at ATQ and
261 IVO (Lasslop et al., 2010) is analyzed for comparison. All NBP and GPP estimates are processed
262 as half-hourly means, then gap-filled and averaged daily. The data processing methodologies for
263 BON and IMN are described in Euskirchen et al. (2014) and Euskirchen et al. (2017),
264 respectively, and for ATQ and IVO in Goodrich et al. (2016). For each location, we sample

265 PVPRM-SIF GPP and CARVE-Opt NBP only for years with available eddy covariance data
266 from 2012-2014 (see [Table 1](#)).

267 BON is our most southerly site, consisting of three stations in the boreal peatland lowlands of the
268 Tanana Flats of interior Alaska within 0.5 km of each other (Euskirchen et al., 2014). These sites
269 are ~30 km southeast of Fairbanks and vary in the presence and stability of permafrost. They
270 include a black spruce ecosystem with cold soils and permafrost (BON-Spr), a collapse scar bog
271 representing recent permafrost thaw (BON-Bog), and a rich fen lacking permafrost (BON-Fen).
272 BON-Spr is dominated by mature black spruce trees (*Picea mariana*, ~100 years old), with an
273 understory consisting of shrubs, mosses, grasses, and lichens, and sits on an intact peat plateau
274 that rises ~130 cm from the surrounding landscape. BON-Bog is a circular depression that
275 formed through thermokarst, and contains active thaw margins with significant dieback of *Picea*
276 *mariana*. BON-Fen is composed of grasses, sedges, and forbs. The sites are in close proximity
277 (<0.5 km), and thus co-located within a single grid box of CARVE-Opt and PVPRM-SIF.

278 IMN is located in the northern foothills of the Brooks Range in northern Alaska (Euskirchen et
279 al., 2017). The watershed is underlain by continuous permafrost, with predominant soils
280 containing 15–20 cm of organic peat underlain by silt and glacial till. The mean annual air
281 temperature (MAT) from 1988–2007 was -7.4°C and the mean annual precipitation was 318 mm,
282 with about 40% occurring as rain and 60% as snow. The landscape is treeless, located
283 approximately 100 km north from latitudinal treeline. IMN includes three stations across three
284 unique tundra sites, including heath (IMN-Hth), moist acidic tussock (IMN-Tus), and wet sedge
285 (IMN-Sed). These sites are also in close proximity (<0.5 km) and therefore share the same grid
286 box.

287 IVO is located ~300 km to the south of the Arctic Ocean at the foothills of the Brooks Range,
288 with a MAT and summer precipitation of -8.9°C and 210 mm from 2003-2008. IVO vegetation
289 is dominated by tussock-sedge, dwarf-shrub, and moss tundra, and represents the dominant
290 vegetation type in Alaska (Zona et al., 2016). Tussock tundra on flat ground consists of 57% *E.*
291 *vaginatum* tussocks, 42% inter-tussock vegetation (dominated by *Sphagnum* moss) and 1%
292 moss-dominated hollows (Davidson et al., 2016). The most northerly site, ATQ, is ~100 km
293 south of the Arctic Ocean. MAT and summer precipitation in ATQ are -10.8°C and 100 mm,
294 respectively, for the 1999 to 2006 period. ATQ vegetation is dominated by tundra sedges,

295 grasses, mosses, and some dwarf shrubs <40 cm tall. Tussock tundra on dry ridges and plateaus
296 comprised 21% *Eriophorum vaginatum* tussocks and 79% inter-tussock areas, which are
297 dominated by moss and evergreen dwarf shrubs (Davidson et al., 2016). ATQ has landcover
298 typical of arctic wetlands (Zona et al., 2016).

299 *Analysis*

300 We analyze the period 2012-2014 in Alaska (58°N-72°N, 140°W-170°W) due to availability of
301 CARVE-Opt data. All regional freeze/thaw, GPP and NBP datasets are aggregated to 0.5°x0.5°,
302 then averaged across years to provide a three-year climatology. This study focuses on
303 climatological spatial patterns over this period, rather than year-specific patterns or interannual
304 variability, to provide a first assessment of thaw-C uptake patterns over Alaska. We define
305 seasonal onset dates for snowmelt, thaw, GPP and net C uptake for each grid point in the
306 climatological mean. We acknowledge our short three year period provides a small sample of
307 northern high latitude springs, but captures a range of variability including an average spring in
308 2012, cool and late spring in 2013, and warm and early spring in 2014 (Davidson et al., 2016;
309 Euskirchen et al, 2014; Cox et al., 2017; Commane et al., 2017a).

310 Primary spring thaw is defined as the first DOY when a 14-day running filter contains at least 13
311 days when the land surface was classified as thawed. This high threshold (13 of 14 days, or 93%)
312 discriminates against early ‘false thaws’ and extended diurnal thaw-refreeze cycles that
313 characterize the Alaskan spring. Previous work (Kim et al., 2012) demonstrates that even an 80%
314 threshold is insufficiently stringent and defines a growing season start date that is too early.
315 Snow-melt date is identified as a one-time switch indicating wet snow with sensitivity to melt-
316 refreeze cycles minimized. We analyze freeze/thaw date as the primary switch for GPP onset, but
317 provide a brief analysis of snow-melt to provide context for spring respiration. We define the
318 GPP onset date as the mean DOY when GPP is between 10-20% of GPP_{max} for that year,
319 accounting for observation noise and range of transition dates from slow to rapid spring recovery
320 in tundra and boreal ecosystems. We define the net C uptake start as the first DOY when $NBP >$
321 $0 \text{ gC m}^{-2} \text{ d}^{-1}$.

322 We analyze only grid points with average elevation < 1300 m (no alpine vegetation) and less
323 than 60 days of reported thaw or snow-melt status from January 1 to spring thaw date as
324 identified above. This filter isolates data with smooth seasonal transition between frozen and

325 thawed conditions and clearly demarcated frozen winter soils from thawed summer soils. Results
326 are analyzed separately for individual land cover types from Environmental Protection Agency
327 Level 2 and 3 North America ecoregion maps (Fig. 1; [https://www.epa.gov/eco-](https://www.epa.gov/eco-research/ecoregions)
328 [research/ecoregions](https://www.epa.gov/eco-research/ecoregions)), with high elevation pixels masked out in white. The primary land cover
329 types analyzed are tundra and boreal, which are sub-divided into the following geographical sub-
330 regions: Tundra Southwest (includes Seward Peninsula, Subarctic Coastal Plains, and Bristol
331 Bay-Nashugak Lowlands), Tundra North Slope (Arctic Coastal Plain and Arctic Foothills),
332 Tundra Brooks (includes Brooks Range), Boreal Interior in central Alaska (Interior Forested
333 Lowlands, Uplands, and Bottomlands), and Boreal Mountains in southeast Alaska (Interior
334 Highlands and Ogilvie Mountains).

335 **Results**

336 *Flux Tower Evaluation*

337 Observationally constrained estimates of seasonal GPP and NBP (PVPRM-SIF and CARVE-
338 Opt, respectively) are sampled at and compared to eddy covariance towers (for years with
339 available eddy covariance data, Table 1) for individual sites in Fig. S1 and S2, using native
340 optimized grids (PVPRM-SIF: $1/6^\circ \times 1/4^\circ$; CARVE-Opt: $0.5^\circ \times 0.5^\circ$). PVPRM-SIF and eddy
341 covariance GPP show high consistency of seasonal amplitude, including decreasing amplitude
342 moving north from southern boreal (BON) to northern tundra (IMN, IVO). The high spatial
343 resolution of PVPRM-SIF resolves spatial gradients across diverse landscapes including low
344 GPP (relative to surrounding pixels) at BON and relatively high GPP at IMN (Fig. S3). PVPRM-
345 SIF overestimates growing season GPP at the northern most site (ATQ, Fig. S1H) by a factor of
346 2-3 depending on partitioning technique (larger error using daytime partitioning at IVO and
347 ATQ). We note a possible calibration bias at ATQ linked to PVPRM model parameter
348 calibration against 2005 ATQ data (Luus et al., 2015; evidence supporting this claim provided in
349 Discussion). We find consistency in the seasonal phase, including timing of GPP onset, at all
350 tundra sites (IMN, IVO, and ATQ), but delayed GPP onset in the lowland boreal landscapes at
351 the BON towers (Fig. S1 A-C). At the BON towers and especially BON-Spr, eddy covariance
352 GPP onset occurs ~ 1 month earlier than estimated by PVPRM-SIF or implied by GOME-2 SIF
353 retrievals sampled at each site.

354 CARVE-Opt NBP is less consistent with eddy covariance data (Fig. S2). Seasonal amplitude is
355 overestimated at BON boreal sites, underestimated at IMN and IVO tundra sites, and
356 overestimated at ATQ tundra. Reduced agreement of CARVE-Opt NBP (relative to GPP) is
357 attributed to spatial aggregation errors, due to regriding of PVPRM NBP from its native grid
358 ($1/6^\circ \times 1/4^\circ$) to the coarser $0.5^\circ \times 0.5^\circ$ grid used as the CARVE-Opt prior. The effect is seen clearly
359 in maps of PVPRM NBP at native and aggregated resolutions (Fig. S4 and S5, respectively).
360 Finer scale structure is ultimately smoothed out in CARVE-Opt NBP (Fig. S6). As such,
361 sampling NBP at the native resolution produces higher agreement with tower data than prior and
362 optimized NBP at coarser resolution (Fig. S2).

363 Across-site averages of GPP and NBP for combined tundra (IMN, IVO, ATQ) and boreal (BON)
364 sites are shown in Fig. 2. Here, PVPRM-SIF GPP and CARVE-Opt NBP are sampled at the eddy
365 covariance tower. Spatial averaging improves the NBP comparison at all sites, but especially at
366 IVO and IMN, which exhibit strong gradients of increasing NBP to the south. Estimates of the
367 onset date for GPP and net C uptake are within range of eddy covariance observations at tundra
368 sites, but one month late at BON. Tundra GPP onset is identical (DOY 155), while CARVE-Opt
369 net C uptake is only 6 days late (DOY 170 vs 164) despite a larger net C source through late
370 spring. Boreal GPP onset is 32 days late (DOY 136 vs 104) and net C uptake 25 days late (DOY
371 153 vs 128). GOME2-SIF shows earlier recovery than PVPRM-SIF, but the initial onset is still
372 later than in eddy covariance data. Thaw onset (from AMSR-E and SSM/I) occurs on average on
373 DOY 102 at BON and DOY 130 at tundra sites.

374 Overall, flux towers and observationally constrained estimates show consistent patterns of C flux
375 onset when averaged across boreal and tundra locations. This includes earlier onset of GPP and
376 net C uptake at our boreal location, and lag times of ~ 4 weeks between thaw and GPP onset at
377 tundra locations. We also find consistent time lags between onset of GPP and net C uptake, with
378 shorter lags in tundra (15 vs 9 days for observationally constrained and eddy covariance
379 estimates, respectively) and longer lags for boreal (17 vs 24 days).

380 Focusing on the relative time lag between thaw and GPP onset shows very different patterns in
381 boreal vs tundra; PVPRM-SIF shows similar time lags in boreal and tundra locations (~ 33 days),
382 whereas flux towers show no lag in boreal forests but a 33 day lag in tundra. These discrepancies
383 are attributed primarily to late GPP onset bias in PVPRM-SIF in boreal forests, which is linked

384 to late morning GOME-2 SIF snapshots and thus unresolved diurnal photosynthetic signals in
385 evergreens (e.g., Fig. S7). We elaborate on these discrepancies in the Discussion. Regional
386 patterns of thaw and onset of GPP and net C uptake are examined in more detail below.

387 *Regional Analysis*

388 In contrast to eddy covariance data, regional analysis indicates a systematic pattern of reduced
389 time until GPP onset for later thaw dates. Fig. 3a-c shows spatial gradients of spring onset dates
390 for thaw, GPP, and net C uptake. Mean onset dates for boreal and tundra regions are summarized
391 in Table 2. The spatial pattern is characterized by early thaw, GPP onset, and net C uptake in
392 boreal forests (DOY 111 ± 7 , 141 ± 5 , 145 ± 10 days in the 2012-2014 average, respectively), and
393 delayed onset in tundra (DOY 127 ± 10 , 151 ± 5 , 163 ± 10 days, respectively), consistent with
394 warmer southern boreal climate and cooler northern tundra climate. Uncertainty is estimated here
395 as sample uncertainties (standard deviation), with random errors in CARVE-Opt (~ 5 days) added
396 to net C uptake date using sum of errors. Sub-regional variability is negligible in boreal forests,
397 which is clumped in the interior and southeast, and strongly latitude dependent in tundra, which
398 ranges from southwest to northern Alaska. In tundra, thaw (DOY 119 ± 15 , 126 ± 5 , 133 ± 5), GPP
399 onset (DOY 146 ± 6 , 150 ± 3 , 153 ± 3), and net C uptake (DOY 159 ± 11 , 161 ± 8 , 168 ± 9) become
400 later moving north from Tundra Southwest, Brooks, and North Slope sub-regions.

401 While thaw and GPP onset dates are later in tundra compared to boreal regions, the lag time
402 between thaw and GPP onset (Fig. 3d) decreases slightly across the same regions. Lag times
403 range from 40 days in the southern mountains (Alaska Range and Alaska Peninsula Mountains)
404 to ~ 10 days along the west and north coast (Seward Peninsula and Arctic Coastal Plain), and
405 correspond to average lag times of 29 ± 6 days in boreal regions and 23 ± 7 days in tundra. We also
406 find a high correlation between thaw and GPP onset ($R^2 = 0.69$; p-value < 0.001) with slope less
407 than one ($\text{DOY}_{\text{thaw}} = 0.5 * \text{DOY}_{\text{GPP}} + 79.5$, where DOY_{thaw} and DOY_{GPP} denote dates of thaw and
408 GPP onset) and consistency across ecoregions (Fig. 4a). Seasonal change in incident shortwave
409 radiation (derived from NCEP2 downwelling shortwave), which increases later in spring moving
410 north, is consistent with the spatial pattern of GPP onset, but shows weaker grid scale correlation
411 with GPP onset compared to thaw onset. We test this by regressing GPP onset against two
412 shortwave onset metrics: (1) shortwave at the time of thaw onset, and (2) onset date of shortwave
413 (10-20% of its annual peak). This analysis yields $R^2 = 0.30$ and 0.31 , respectively, representing

414 weak correlations compared to thaw onset ($R^2 = 0.69$). Furthermore, high latitude tundra receives
415 higher radiation levels at thaw onset than forests to the south; on average, incident radiation
416 along the North Slope exceeds Boreal Interior values by 20% (290 ± 25 vs $241 \pm 26 \text{ Wm}^{-2}$) due to
417 later tundra thaw onset (DOY = 133 vs 110). The convergence of soil thawing and seasonal
418 phenology with latitude suggest that tundra ecosystems are well adapted to take advantage of this
419 extra light within 2-4 weeks of thaw onset (more detail on physiological mechanisms in
420 Discussion).

421 The magnitude of spring GPP and NBP also decrease with later thaw date, but their relationship
422 to each other is ecosystem dependent (Fig. 4b-d). We analyze GPP sensitivity during the one
423 month period from May 15 to June 15, following earliest ecosystem mean GPP onset (DOY 136
424 in Boreal Interior). May 15 also roughly corresponds to the mean date of first CARVE CO_2
425 observations (DOY 128), ensuring that CARVE-Opt NBP results are consistent with available
426 spring observations. Mean spring GPP decreases at a rate of $-0.8 \pm 0.03 \text{ gC m}^{-2}$ for every 2 weeks
427 of delayed thaw ($R^2=0.44$). All ecosystems exhibit similar relationships, but the sensitivity of
428 reduced GPP to delayed thaw date is three times stronger on average in boreal forests (e.g., -
429 $0.9 \pm 0.09 \text{ gC m}^{-2} \text{ d}^{-1}$ per 2 weeks) than in tundra (e.g., $-0.3 \pm 0.04 \text{ gC m}^{-2} \text{ d}^{-1}$ per 2 weeks). Spring
430 NBP also decreases with later thaw ($-0.5 \pm 0.02 \text{ gC m}^{-2} \text{ d}^{-1}$, Fig. 4c), but shows higher consistency
431 (within a factor of 2 difference) across ecosystems (tundra = $-0.2 \pm 0.06 \text{ gC m}^{-2} \text{ d}^{-1}$; boreal = $-0.4 \pm$
432 $0.04 \text{ gC m}^{-2} \text{ d}^{-1}$). As such, the sensitivities of GPP and NBP to thaw in tundra are of similar
433 magnitude while sensitivities for boreal forest are 2-3 times weaker for NBP than GPP. The
434 relationship between spring GPP and NBP for tundra and boreal ecosystems is summarized in
435 Fig. 4d. Overall, NBP increases at half the rate of GPP ($y=-0.5x+0.5$), but with higher overall
436 sensitivity in tundra (-0.7 ± 0.09) than boreal (-0.35 ± 0.02), and reduced sensitivity for lower GPP
437 (tundra= -0.6 ± 0.1 ; boreal= -0.5 ± 0.1).

438 The reduced sensitivity of NBP to GPP in boreal points to TER onset as a key factor also driven
439 by thawing, and which offsets the initial spring GPP. Aggregated plots of TER (Fig. 5a) show an
440 initial increase between snowmelt and landscape thaw (DOY 100 ± 10 and 111 ± 7 , respectively),
441 ~4 weeks prior to GPP onset (DOY 141 ± 5). The transition from onset of GPP to net C uptake
442 (DOY 145 ± 10) is short throughout boreal forests (Fig. 3f), but the C uptake rate is initially slow
443 ($-1.2 \text{ gC m}^{-2} \text{ month}^{-1}$) due to synchronous increases in GPP and TER following GPP onset. C

444 uptake accelerates in early June as respiration levels off with substrate depletion and GPP fully
445 recovers from winter.

446 Regional mean onset dates for boreal GPP (DOY 141 ± 5) and net C uptake (DOY 145 ± 10) are
447 early, and corresponding lag time (4 ± 7 das) short, compared to eddy covariance observations at
448 BOR (DOY 104 and 128, and 24 day lag, respectively). However, the lag time is highly variable
449 at regional scale (± 7 days). Further, the lag time sampled at the tower (17 days) corresponds
450 more closely with eddy covariance data (20 days). This suggests that the dynamics driving net C
451 uptake onset are not well captured by CARVE-Opt at BOR and potentially other boreal
452 locations, due to sparse airborne CO_2 coverage before mid-May and coarse spatial resolution of
453 CARVE-Opt. Enhanced airborne sampling in after mid-May leads to improved representation of
454 the transition from GPP to net C uptake onset.

455 Respiration offsets an even larger fraction of spring GPP in tundra (Fig. 5b) due to early
456 respiration in mid-April (similar timing to boreal) and delayed GPP onset (10 days later than
457 boreal). The timing of TER onset corresponds closer to the mean onset date of snowmelt (DOY
458 112 ± 12) than landscape thaw (DOY 127 ± 10), consistent with onset of subnivean respiration. The
459 GPP delay also causes a slight phase shift between GPP and TER seasonal cycles, increasing the
460 transition time from onset of GPP (151 ± 5) to net C uptake (163 ± 10 days) by a factor of 3
461 compared to boreal (13 ± 7 days). Longer transition times are found throughout western and North
462 Slope tundra, with longest times just north of the Brooks Range (Fig. 3f). Consequently, the
463 transition time from thaw to net C uptake is delayed in tundra by 37 ± 9 days (Fig. 3e), similar to
464 the boreal transition (34 ± 9 days), but leads to a 50% higher NBP following the transition to net C
465 uptake ($-1.8 \text{ gC m}^{-2} \text{ month}^{-1}$). Regional mean C flux onset dates and lag times in tundra are
466 consistent and within the uncertainty of eddy covariance data analyzed in this study.

467 *Analysis Against Other CO_2 Inversion Systems*

468 Our reported spring C uptake patterns are specific to CARVE-Opt, which represents an estimate
469 of Alaskan regional-scale dynamics complementary to global inversions due to the closer
470 proximity of airborne CO_2 measurements to regional flux and the higher resolution of
471 atmospheric transport. Using CARVE-Opt as a benchmark, we compare the timing and depth of
472 spring C uptake to global inverse estimates derived from near-surface CO_2 observations from

473 CT2016 and Jena4.1 (Fig. 5 c-d), which are reported daily, and satellite column data from
474 CMSb7.3 (Fig. 5 e-f), which is reported monthly (15th of month).

475 In boreal forests, global and regional inversions show general agreement of earlier and greater
476 uptake compared to tundra. The inversions also show remarkable agreement in spring net C
477 uptake onset and transition back to net source in fall. Global inversions do not show a boreal
478 respiration pulse as seen in CARVE-Opt in mid-May in the three year average, although Jena4.1
479 does reflect this in individual years. Likewise, the presence of this pulse in CARVE-Opt is
480 predicted by PVPRM in all years but only confirmed by CARVE airborne observations in 2013.
481 The pulse is not detected in eddy covariance data at BON-Spr or BON-Bog, but is observed at
482 BON-Fen (Fig. S2). Thus, the repeatability of this pulse over multiple years and at regional scale
483 is unclear.

484 Jena4.1 estimates a smaller rate and depth of uptake in the early growing season compared to
485 CARVE-Opt and CT2016. The smooth transition from March to July aligns well with BON-Spr
486 but not with BON-Fen or BON-Bog. The small seasonal amplitude in Jena4.1 is likely related to
487 the model prior which, in contrast to both CARVE-Opt and the other global inversions, uses a
488 constant zero prior in place of a modeled prior.

489 The relative seasonal patterns across inversions are similar for tundra, but here we give more
490 weight to CARVE-Opt due to the high agreement in phase and amplitude with eddy covariance
491 data (Fig. 2d). CMSb7.3 and CT2016 capture the depth and rate of spring uptake. The sustained
492 tundra efflux from late April to early June is absent from all methods. The true magnitude of the
493 spring tundra source likely falls somewhere between CARVE-Opt ($\sim 0.5 \text{ gC m}^{-2} \text{ d}^{-1}$) and surface
494 inversions ($< 0.1 \text{ gC m}^{-2} \text{ d}^{-1}$) as suggested by eddy covariance data ($\sim 0.25 \text{ gC m}^{-2} \text{ d}^{-1}$), although
495 we note a stronger pulse at the representative tundra site of IVO (Fig. S2g), which peaks at 0.5
496 $\text{gC m}^{-2} \text{ d}^{-1}$ in mid June. Nevertheless, CT2016 and Jena4.1 capture the delayed timing of spring
497 uptake in tundra. In contrast, CMSb7.3 has a pronounced early spring bias in tundra of ~ 3 weeks.

498 We investigate the CMSb7.3 spring bias in more detail by comparing posterior and prior NBP.
499 Prior NBP is prescribed from CASA-GFED3, shown in Fig. 5e,f. Seasonal NBP amplitude in
500 CMSb7.3 is much improved compared CASA-GFED3. However, the timing of the spring and
501 fall transitions are generally fixed relative to CASA-GFED3, which is early compared to
502 CARVE-Opt in spring. In contrast, CT2016 shows a shift in both the seasonal amplitude and

503 phase relative to its prior, CASA-GFED4.1. Although CASA-GFED4.1 also has an early bias,
504 CT2016 forces a delay in net C uptake onset in boreal and tundra regions in closer agreement
505 with CARVE-Opt across the range of fossil fuel, ocean, and biosphere priors in the CT2016
506 ensemble. The inversion does not have substantial impact on the seasonal amplitude or duration
507 of drawdown following peak uptake, which is underestimated compared to CARVE-Opt. An
508 explanation of spring timing difference across inverse methods is provided in the Discussion.

509 Finally, we examine the source of the early spring bias in CASA-GFED. Previous analyses of
510 CASA in lower latitude boreal forests characterized GPP as generally well represented in
511 satellite constrained diagnostic models, and that differential phasing of TER with respect to GPP
512 is needed to accurately estimate NBP timing surrounding the growing season peak
513 (Messerschmidt et al., 2013). Our analysis of cold northern boreal and tundra ecosystems
514 suggests the opposite: The timing of spring TER onset is well represented in CASA-GFED,
515 while GPP onset is systematically early in boreal and tundra regions (Fig. 6). In tundra in
516 particular, CASA-GFED predicts an early initial GPP increase in late April, followed by a larger
517 secondary jump in late May which increases more rapidly than suggested by PVPRM-SIF. The
518 timing is exacerbated by use of monthly mean normalized difference vegetation index and
519 APAR in CASA, causing GPP to increase more instantaneously than a monthly interpolated
520 change.

521

522 **Discussion**

523 *Spring Photosynthetic Recovery in Alaska Tundra and Boreal Forests*

524 Our results indicate that the timing and magnitude of spring C fluxes in Alaska are correlated
525 with landscape thaw and ecoregion. Tundra ecosystems thaw on average 2 weeks later than
526 boreal forests, and require less time to transition to GPP onset. This pattern of later thaw and
527 reduced lag time in tundra (23 ± 7 days) compared to boreal forests (29 ± 6 days) is consistent with
528 eddy covariance data for eastern Canada and Sweden (Kim et al., 2012). The short time lag in
529 Alaskan tundra, and especially North Slope tundra (20 ± 5 days), is consistent with data in
530 Siberian tundra showing rapid physiological response to warming and snowmelt, a plausible
531 adaptation of high latitude tundra ecosystems to the short growing season (Arneeth et al., 2006).

532 Interior boreal forests, on the other hand, have been found to require at least an extra week to
533 reach 10-20% capacity due to pigment adjustments (e.g., Ottander et al., 1995).

534 In Alaskan tundra, PVPRM-SIF indicates a weak physiological response for the first two weeks
535 after thaw onset followed by a more rapid response, with 15% of peak annual GPP attained after
536 three weeks and peak GPP after eight weeks. Low initial GPP, especially in northern Alaska, is
537 attributed to high radiation exposure with later thaw; incident radiation along the North Slope
538 and Brooks Range exceeds Boreal Interior values by 20% and represents a larger percentage of
539 peak annual radiation (82% vs 67%). This apparent light stress, and subsequent rapid recovery, is
540 supported by evidence from *Sphagnum* moss near Barrow, Alaska, which show low levels of
541 photosynthesis early in the season due to photoinhibition, then development of subsurface moss
542 layers and structural protection from high radiation later in the season, enabling increased
543 photosynthetic capacity with reduced risk of light damage (Zona et al., 2011). High nitrogen (N)
544 availability early in the growing season, driven by decreases in microbial biomass and release of
545 N during snowmelt, provides further stimulus to photosynthesis under snow and following
546 snowmelt (Brooks et al., 1998; Starr and Oberbaur, 2003; Larsen et al., 2007). The convergence
547 of soil thawing and seasonal phenology with latitude thus appears to reflect the efficient
548 adaptation of high latitude shrubby ecosystems to cold, high light, and nutrient rich environments
549 and the need to maximize the number of growing days and soil liquid water availability during
550 the short thaw season.

551 These same factors (warm temperatures and high N availability at thaw onset) also stimulate
552 decomposition of soil organic carbon by microbes, leading to simultaneous increases in soil
553 respiration (Oberbaur et al., 1998; Lafleur et al., 2007). Further, competition for N by plants and
554 microbes leads to a crash ~1 month following snow melt, such that tundra plants become N
555 limited (Larsen et al., 2007). These studies are consistent with our finding of delayed time from
556 GPP onset to net C uptake, roughly 2 weeks (14 ± 8 days) in the Tundra North Slope.

557 Although we estimate a longer time lag in boreal forests on average, we note the difference from
558 tundra is within the statistical uncertainty, thus permitting cases where time lag is reversed and
559 shorter in boreal forests. Evidence from mire (tundra) and pine (boreal) sites in Siberia sharing
560 similar climate indicate a shorter time lag in the pine forest, which exhibits a rapid physiological
561 response to above zero temperature even when there is snow on the ground (Arneeth et al., 2006;

562 Eukskirchen et al., 2014). Needleleaf trees such as black spruce at Bonanza Creek show a
563 negative lag (GPP reaches ~15% of peak prior to thaw) triggered by early warming (Fig. S7),
564 with the first non-zero GPP values occurring in the afternoon (12–3 pm), prior to onset of
565 primary thaw, on days with above freezing afternoon air temperature and near or below freezing
566 morning temperature (9am–12pm). This early photosynthesis, at least in evergreens, represents a
567 physiological adaptation to stress when sufficient radiation is already available and absorbed by
568 green needles, and small amounts of plant available liquid water in soils can be transported
569 through xylem in conifers and evaporated through leaf stomata as a cooling mechanism (Ishida et
570 al., 2001). These results suggest that sunlight, air temperature, and xylem flow may be better
571 predictors of photosynthetic onset in evergreens than date of primary thaw. However, we note
572 that weak levels of photosynthesis have been observed during transient freeze/thaw cycles during
573 the spring zero curtain preceding primary thaw (Tanja et al., 2003). Diurnal freeze/thaw data
574 may therefore offer a useful indicator of initial photosynthesis, provided that the resolution is
575 fine enough ($< 10 \text{ km}^2$) to distinguish between vegetation and soil landscape components.

576

577 *Limitations and Uncertainties for SIF and CO₂ Observations*

578 In evaluating PVPRM-SIF and CARVE-Opt C flux patterns against eddy covariance data, we
579 find good representation of tundra C flux seasonality and earlier GPP onset in boreal forests, but
580 a potential late onset bias in the timing of spring onset of GPP and net C uptake in boreal forests.
581 We analyze temperature forcing for a cold bias in PVPRM, which might lead to late GPP onset,
582 but find good agreement to observed temperature at Bonanza Creek (Fig. S9). The following
583 limitations in our use of satellite SIF for constraining spring onset of evergreen photosynthesis
584 provides a more likely explanation: (1) GOME-2 overpass time, (2) assumed SIF-GPP linearity,
585 and (3) monthly aggregation.

586 First and foremost, we note that the GOME-2 SIF late morning overpass in Alaska (~11:30 am)
587 hinders observation of early season peak daytime photosynthesis in high latitude evergreens,
588 which can occur even if morning or daily mean temperatures are below freezing (as discussed
589 above), or under transitional (AM frozen, PM thawed) thaw events (Kim et al., 2012). The
590 switch from negative to positive SIF signals at Bonanza Creek occurs following a significant rise
591 in morning temperature of 3-5°C above freezing and near primary thaw (Fig. S7). As such,

592 PVPRM-SIF is unlikely to capture early GPP onset in boreal evergreen forests when constrained
593 solely by spaceborne spectrometers with morning overpasses. Instruments with midday overpass,
594 such as TROPOMI and OCO-2 (e.g., Guanter et al., 2015), are better suited to capture daytime
595 signals, but inadequate by themselves to detect transitional thaw events, and thus cannot
596 represent true daily mean SIF. OCO-2 also lacks the temporal resolution (16 day repeat cycles)
597 to resolve the spring transition (e.g., Sun et al., 2018). Ideally, a harmonized product combining
598 spatially resolved, polar orbiting instruments with morning (GOME-2, SCIAMACHY) and
599 midday (TROPOMI, OCO-2) is needed.

600 It is important to note, however, that SIF is not as well correlated with photosynthesis during the
601 early growing season when leaf level photochemistry precedes increasing SIF emissions
602 (Springer et al., 2017). In evergreens, the SIF-GPP relation changes seasonally with changes in
603 non-photochemical quenching (NPQ) and shifts in carotenoid pigments during transition seasons
604 (Ottander et al., 1995). Increasing pigmentation in fall functions to shed more absorbed energy as
605 NPQ than SIF over winter months (Ottander et al., 1995, Demmig-Adams and Adams, 1996;
606 Porcar-Castell, 2011; Muller et al., 2001) and in early spring with increasing exposure to harmful
607 radiation (Arneth et al., 2006). Increases in absorbed light and temperature in spring during the
608 cold de-hardening period cause relative declines in carotenoid pigments and increases in
609 chlorophyll concentrations, leading to increasing photosynthetic activity, reduced NPQ, and
610 increased dissipation of absorbed light as SIF (Wong and Gamon, 2015; Springer et al., 2017).
611 The increase in SIF and GPP in evergreens is gradual due to the gradually changing pigment
612 ratios of carotenoids and chlorophyll (Wong and Gamon, 2015). Although a recent analysis of
613 GOME-2 SIF has supported a temperature triggered early onset mechanism at pan-Arctic scale
614 (Walther et al., 2016), our results suggest that true onset may occur several weeks earlier. We
615 thus recommend the use of additional remote sensing indices such as chlorophyll carotenoid
616 index (CCI) and photochemical reflectance index (PRI) with midday and morning SIF to
617 interpret the full dynamical range of photosynthesis during spring onset (Springer et al., 2017).

618 This research has also demonstrated that our method to aggregate GOME-2 SIF retrievals by
619 month and biome class, with linear interpolation between values (Luus et al., 2017), is
620 inadequate to resolve spring transitions at high latitudes. Analysis of 5-day mean SIF retrievals,
621 for example, suggest earlier photosynthetic recovery at BON than in the regional average of

622 Alaskan evergreens (Fig. 2a). Future efforts to reduce these errors and interpret patterns of thaw
623 vs C flux onset requires at a minimum non-linear interpolation methods for monthly SIF, and
624 ideally more spatiotemporal explicit application of satellite SIF data in light use efficiency
625 models. More sustained early season, spatially intensive sampling of airborne CO₂ (Parazoo et
626 al., 2016) and longer-term eddy covariance fluxes and from additional sites in high northern
627 boreal forests is also needed.

628 SIF based GPP onset biases in forests feed into NBP calculations and contribute to errors in
629 seasonal amplitude and timing. NBP optimization by CARVE CO₂ observations alleviate most
630 errors at regional scale, but a few remaining grid scale errors persist at tundra and boreal
631 locations. These are attributed to four key factors. First, as discussed above, is the high spatial
632 variability and biome dependence of net C uptake onset. This has an especially large impact on
633 NBP at tundra sites (IMN, IVO) located along the border of Brooks and North Slope sub-
634 regions. Second is the small sample size of boreal forest sites, represented only by BON-Spr.
635 BON-Spr is also unique in its sudden shift in summer NBP magnitude during the two years of
636 overlap with CARVE-Opt, switching from a large summer sink from 2010-2012 to a small or
637 neutral summer sink from 2013-2016 (Fig. S8). We suspect the reduced summer sink is related
638 to a local respiration source from underlying permafrost and thermokarst near the tower, which is
639 undetected by CARVE flights. Third is the lack of consistent airborne CO₂ flights from early
640 April through late May during the eddy covariance NBP transition. Thus our NBP estimate
641 during this period relies on PVPRM, which estimates a delayed net C uptake onset following late
642 GPP onset. Fourth is the relatively short three year record. Significant natural year-to-year
643 variability in the onset of thaw, phenology, and gross/net C uptake at ecosystem and regional
644 scale is common in Alaska (e.g., Kim et al., 2012; Commane et al, 2017a), and makes it difficult
645 to examine climatological spatial patterns over short records. Although the focus of this research
646 is regional scale and thus limited by data availability, we note that ongoing measurements of
647 satellite SIF and airborne CO₂ from the recent NASA Arctic-Boreal Vulnerability Experiment
648 (ABoVE, <https://above.nasa.gov>) will provide a longer period of record to analyze interannual
649 variability.

650

651 *Limitations and Uncertainties for Eddy Covariance Observations*

652 We also note the factor of 2-3 overestimation of GPP at ATQ by PVPRM-SIF. This error is
653 attributed to two factors: (1) a calibration/validation inconsistency, with PRVPM parameters
654 calibrated using year-round 2005 ATQ data but validated against 2014 ATQ data, and (2)
655 representativeness of eddy covariance. The first factor would cause a high bias only if GPP and
656 NBP in 2005 were higher than 2014 data shown here. Although 2005 data is not available for
657 comparison, we can infer the tendency of GPP in 2005 vs 2014 using a very simple model of
658 GPP as a function of thawing degree days (TDD), estimated as the sum of the mean daily
659 temperature above 0°C and for which we have site level data available from 2005-2014. This
660 model assumes higher peak GPP for larger TDD. We find a TDD of 650 days in 2005 and 563
661 days in 2014, indicating higher productivity in 2005. Previous work using chamber data shows
662 higher GPP in 2013 than in 2014 at ATQ (Davidson et al., 2016), consistent with higher TDD
663 (720 days). These findings indicate higher GPP in 2005, which supports a calibration bias at
664 ATQ and argues for an updated calibration of PVPRM using the longer record of data at existing
665 eddy covariance towers (Luus et al., 2015) and inclusion of new tundra and boreal towers
666 (<http://ameriflux.lbl.gov/data/>).

667 With regard to the second factor (representativeness), eddy covariance is the most direct
668 measurement of ecosystem fluxes available, however, several uncertainties should be considered
669 in the interpretation of our results: (1) The tower footprint ($\sim 10^0$ km²) is large compared to
670 individual tree canopies (< 5 m), making it a challenge to disentangle contributions from
671 different vegetation types and C sources in heterogeneous Alaskan landscapes. For example,
672 moss contributions to total NBP range from 25% to 60% in mixed tundra landscapes (Zona et al.,
673 2011) such as seen at Ivotuk (tussock-sedge, dwarf-shrub, and moss tundra) and Atqasuk (sedge,
674 grass, mosses, and dwarf sedge). At the BON cluster, nearby thermokarst permafrost emissions
675 have a substantial influence of C fluxes observed at BON-Spr (Fig. S8); (2) The tower footprint
676 is much smaller compared to footprints for PVPRM-SIF ($\sim 10^2$ km²), CARVE-OPT ($\sim 10^3$ km²),
677 and aggregated SIF soundings ($\sim 10^4$ km²). Although some effort is made to capture sub-grid
678 variability by combining tower clusters (e.g., IMN, BON) and similar ecosystems (e.g., Fig. 2),
679 and by examining sensitivity to spatial resolution (e.g., Fig. S1), we caution that spatial
680 representativeness issues remain in the flux tower – model comparisons. Airborne eddy
681 covariance surveys provide a viable option to increase footprint size toward regional scale
682 (Wolfe et al., 2017); (3) Flux partitioning of eddy covariance NEE into GPP and TER also

683 carries large uncertainties and can yield very different results depending on method (e.g., Fig.
684 S1). This uncertainty in itself may explained the large time lags between thaw and GPP observed
685 at Bonanza Creek. More work is needed to understand the sensitivity of nighttime vs daytime
686 partitioning techniques in Alaska and impact on GPP seasonal onset/offset and amplitude, in
687 particular as a function of length of day, and to compare flux partitioning algorithms to measured
688 respiration form dark chambers across the Arctic.

689

690 *Implications for Top-Down and Bottom-Up Estimates of Net Carbon Exchange*

691 Our results also indicate similar time lags from thaw to net C uptake onset in tundra and boreal
692 (~5 weeks), such that net C uptake occurs later in tundra, with exact timing depending on
693 vegetation type (wet sedge, heath, tussock) (Fig. S2). Delayed tundra uptake is captured in global
694 inverse models, but with net C uptake onset too early in spring and too shallow in summer.
695 Further assessment of CMSb73, which has the most severe spring timing bias, indicates a link to
696 early net C uptake onset in the CASA-GFED prior, and exacerbated by estimation of monthly
697 scale factors for net exchange and limited seasonal coverage of satellite observations. Since
698 CMSb7.3 and CT2016 share a similar prior in CASA-GFED, we can identify three additional
699 factors contributing to difference in spring timing across inverse methods: (1) observation
700 source, (2) optimization method, indicating the application of scale factor correction to model
701 priors, and (3) optimization window, representing the length of time in which scale factors are
702 estimated in the optimization procedure.

703 Regarding the first factor (observation source), CT2016 assimilates *in situ* data, which have
704 continuous year-round coverage, whereas CMSb7.3 assimilates satellite observations derived
705 from reflected sunlight, which have seasonal dependent coverage over high latitudes. As such,
706 the correction to fluxes occurring during polar winter and during snow cover in spring is minimal
707 in CMSb7.3, especially for North Slope and Brooks tundra. However, the enhanced spatial
708 coverage of GOSAT in summer provides a boost in peak summer uptake compared to CASA-
709 GFED. Combining high latitude flask, airborne, and satellite observations into a consistent
710 global inversion framework will improve seasonal and spatial constraints, and retain the
711 advantage of dense satellite observational coverage in summer.

712 Regarding the second factor (optimization method), Jena4.1 has no prior flux information and
713 thus does not apply scale factor correction. This flexible approach produces an accurate
714 representation of the seasonal transition in spring and fall, but with a trade-off in seasonal
715 amplitude. CT2016 and CMSb7.3 optimize scale factors for NBP at regional and grid-scale,
716 respectively, as corrections to prior fluxes, and thus are more strongly weighted by prior
717 information. This less flexible approach produces more accurate representation of seasonal
718 amplitude, but leads to errors in the seasonal transition timing, which is strongly weighted by
719 prior information under reduced observational coverage.

720 Regarding the third factor (optimization window), CMSb7.3 uses a monthly window; CT2016
721 uses a weekly (8 day) window. We propose that the smaller 8 day window allows more
722 flexibility for data assimilation to adjust the spring transition date, which greatly affects the
723 interpretation of seasonal C uptake dynamics. Alternative inverse methods which estimate
724 scaling factors for gross fluxes (Deng et al., 2016) or persistent grid scale biases (Lokupitiya et
725 al., 2008; Parazoo et al., 2012) permit a shift in seasonal NBP phase relative to prior information.

726 Early C uptake bias in CASA-GFED is consistent with CMIP5 model estimates of seasonal NBP
727 in Alaska, which predict spring net C uptake onset to occur by an average of 18 days earlier than
728 estimated by CARVE-Opt, with 7 of 10 models showing early bias exceeding 15 days, and three
729 models showing a bias exceeding one month (Commane et al., 2017a). In attributing the early C
730 uptake bias, our analysis of GPP and TER fluxes in CASA-GFED indicates an accurate
731 representation of the timing of TER in spring consistent with subnivean respiration, which is
732 simulated in CASA-GFED as a function of soil moisture and temperature (Potter et al., 2013)
733 and in PVPRM as a function of soil temperature (Luus & Lin, 2015b). Our results therefore
734 suggest early GPP onset as the primary culprit in tundra ecosystems. Satellite constrained light
735 use efficiency models that prescribe green biomass using reflectance based vegetation indices
736 typically predict earlier GPP onset and larger spring C uptake in cold climate ecosystems
737 compared to the same models constrained by SIF (Luus et al., 2017; Commane et al., 2017a).
738 Prognostic and diagnostic models used in CMIP5, IPCC, and NACP reports also have a well-
739 known early spring GPP bias (Peng et al., 2015), especially for temperatures below freezing
740 (Schaefer et al., 2012). It is critical for these models to account for survival adaptation under
741 repeated exposure to frost, cold, and frozen soils, which limits root uptake of water and stomatal

742 conductance (Strand and Öquist, 1985; Waring and Winner, 1996; Bergh et al., 1998), and
743 allows cold adapted plants to avoid spring frost damage after budburst (Jeong et al., 2012, 2013)
744 and high radiation following snowmelt inhibiting photosynthetic C uptake (Zona et al., 2011),
745 thus delaying or reducing initial GPP. Other factors such as incorrect prescription of plant
746 functional type also have important effects. Some models such as LPJ-GUESS simulates herbs
747 (grasses) as a proxy for tundra vegetation which in reality may consist largely of shrubs. Grasses
748 have a low growing degree day sum threshold for leaf onset and high light use efficiency which
749 may explain early GPP onset in tundra in Earth System Models. The same issue also applies to
750 conifers and diffuse-porous broadleaves, to which most boreal zone broadleaves belong. Our
751 regional and site-level results support low levels of photosynthesis in tundra initially following
752 snowmelt and leaf-out, as well as longer time lag of ~3 weeks for full phenological recovery.

753

754 *Outlook*

755 Climate models disagree on the trajectory of C balance in northern terrestrial ecosystems under
756 future warming. The advance of spring C uptake observed over the past several decades in these
757 ecosystems is a key climate change metric, but subject to high uncertainty in ecosystem model
758 simulations, which systematically predict early growing season onset. Our results point to
759 landscape thawing as a key driver of seasonal C cycle dynamics in cold northern ecosystems, and
760 a likely factor contributing to early spring C flux biases reported in ecosystem models used in
761 IPCC climate assessment reports for projections of future climate. Failure to account for cold
762 season soil and biochemical processes will lead to biased model and empirical-based estimates of
763 pan-Arctic C sinks which produce too strong of biogenic uptake. This would affect estimates of
764 the timing and magnitude of the permafrost C feedback. Next steps are to quantify sensitivity of
765 (1) spring thaw to meteorological inputs and soil physical processes, and (2) GPP onset to
766 biological processes such as dehardening, xylem flow, and budburst.

767 **Acknowledgements**

768 We thank the two Anonymous Reviewers for comments/suggestions that significantly improved
769 this paper. CarbonTracker CT2016 results provided by NOAA ESRL, Boulder, Colorado, USA
770 from the website at <http://carbontracker.noaa.gov>. Some of the research described in this paper
771 was performed for CARVE, an Earth Ventures (EV-1) investigation, under contract with NASA.

772 Funding for the Imnavait flux towers is provided by the National Science Foundation Arctic
773 Observation Network program (Grant 1503912), and for the boreal flux towers by the US
774 Geological Survey Climate Research and Development Program. A portion of this research was
775 carried out at the Jet Propulsion Laboratory, California Institute of Technology, under contract
776 with NASA. D Zona is supported by the Office of Polar Programs of the National Science
777 Foundation (NSF) (award number 1702797), by the National Aeronautics and Space
778 Administration, and by the ABoVE (NNX15AT74A; NNX16AF94A) Program, and by European
779 Union's Horizon 2020 research and innovation program under grant agreement (No. 727890) ©
780 2017. All rights reserved

781

782 **References**

- 783 Arneth, A., Lloyd, J., Shibistova, O., Sogachev, A., and Kolle, O.: Spring in the boreal
 784 environment: Observations on pre- and post-melt energy and co2 fluxes in two central
 785 siberian ecosystems, *Boreal Environment Research*, 11, 311-328, 2006
- 786 Badeck, F.W., Bondeau, A., Bottcher, K., Doktor, D., Lucht, W., Schaber, J., Sitch, S., 2004.
 787 Responses of spring phenology to climate change. *New Phytol.* 162, 295–309.
- 788 Barichivich, J., Briffa, K. R., Myneni, R. B., Osborn, T. J., Melvin, T. M., Ciais, P., ... Tucker,
 789 C. (2013a). Large-scale variations in the vegetation growing season and annual cycle of
 790 atmospheric CO₂ at high northern latitudes from 1950 to 2011. *Global Change Biology*,
 791 19(10), 3167–3183. <https://doi.org/10.1111/gcb.12283>
- 792 Bergh, J., McMurtrie, R. E., & Linder, S. (1998). Climatic factors controlling the productivity of
 793 Norway spruce: A model-based analysis. *Forest Ecology and Management*, 110(1–3), 127–
 794 139. [https://doi.org/Doi 10.1016/S0378-1127\(98\)00280-1](https://doi.org/Doi 10.1016/S0378-1127(98)00280-1)
- 795 Bhatt, U. S., Walker, D. A., Raynolds, M. K., Comiso, J. C., Epstein, H. E., Jia, G., ... Webber,
 796 P. J. (2010). Circumpolar Arctic tundra vegetation change is linked to sea ice decline. *Earth*
 797 *Interactions*, 14(8). <https://doi.org/10.1175/2010EI315.1>
- 798 Black, T. A., Chen, W. J., Barr, A. G., Arain, M. A., Chen, Z., Nesic, Z., ... Yang, P. C. (2000).
 799 Increased carbon sequestration by a Boreal deciduous forest in years with a warm spring.
 800 *Geophysical Research Letters*, 27(9), 1271–1274. <https://doi.org/10.1029/1999GL011234>
- 801 Bloom, A. A., & Williams, M. (2015). Constraining ecosystem carbon dynamics in a data-
 802 limited world: Integrating ecological “common sense” in a model-data fusion framework.
 803 *Biogeosciences*, 12(5), 1299–1315. <https://doi.org/10.5194/bg-12-1299-2015>
- 804 Brooks, P. D., Williams, M. W., and Schmidt, S. K., 1998: Inorganic nitrogen and microbial
 805 biomass dynamics before and during spring snow-melt. *Biogeochemistry*, 43: 1–15.
- 806 Chang, R. Y.-W., Miller, C. E., Dinardo, S. J., Karion, A., Sweeney, C., Daube, B. C., ... Wofsy,
 807 S. C. (2014). Methane emissions from Alaska in 2012 from CARVE airborne observations.
 808 *Proceedings of the National Academy of Sciences of the United States of America*,
 809 (September 2012), 2–7. <https://doi.org/10.1073/pnas.1412953111>
- 810 Commane, R., Lindaas, J., Benmergui, J., Luus, K. A., Chang, R. Y.-W., Daube, B. C., ...
 811 Wofsy, S. C. (2017a). Carbon dioxide sources from Alaska driven by increasing early
 812 winter respiration from Arctic tundra. *Proceedings of the National Academy of Sciences of*
 813 *the United States of America*, 114(21). <https://doi.org/10.1073/pnas.1618567114>
- 814 Commane, R., J. Benmergui, J.O.W. Lindaas, S. Miller, K.A. Luus, R.Y-W. Chang, B.C. Daube,
 815 S. Euskirchen, J. Henderson, A. Karion, J.B. Miller, N.C. Parazoo, J.T. Randerson, C.
 816 Sweeney, P. Tans, K. Thoning, S. Veraverbeke, C.E. Miller, and S.C. Wofsy. 2017b.
 817 CARVE: Net Ecosystem CO₂ Exchange and Regional Carbon Budgets for Alaska, 2012
 818 2014. ORNL DAAC, Oak Ridge, Tennessee, USA,
 819 <https://doi.org/10.3334/ORNLDAAC/1389>.
- 820 Damm, A., Elbers, J., Erler, A., Gioli, B., Hamdi, K., Hutjes, R., ... Moersch, A. (2010). Remote
 821 sensing of sun-induced fluorescence to improve modeling of diurnal courses of gross
 822 primary production (GPP). *Global Change Biology*, 16(1), 171–186.
- 823 Davidson, S. J., Sloan, V. L., Phoenix, G. K., Wagner, R., Fisher, J. P., Oechel, W. C., & Zona,
 824 D. (2016). Vegetation Type Dominates the Spatial Variability in CH₄ Emissions Across
 825 Multiple Arctic Tundra Landscapes. *Ecosystems*, 19(6), 1116–1132.
 826 <https://doi.org/10.1007/s10021-016-9991-0>

827 Demmig-Adams, B.; Adams, W.W. The role of xanthophyll cycle carotenoids in the protection of
828 photosynthesis. *Trends Plant Sci.* 1996, 1, 21–26.

829 Deng, F., D. B. A. Jones, C. W. O’Dell, R. Nassar, and N. C. Parazoo (2016), Combining
830 GOSAT XCO₂ observations over land and ocean to improve regional CO₂ flux estimates, *J.*
831 *Geophys. Res. Atmos.*, 121, 1896–1913, doi:10.1002/2015JD024157.

832 Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N.,
833 Cooper, E. J., ... Wipf, S. (2012). Plot-scale evidence of tundra vegetation change and links
834 to recent summer warming. *Nature Climate Change*, 2(6), 453–457.
835 <https://doi.org/10.1038/nclimate1465>

836 Ensminger, I., Sveshnikov, D., Campbell, D. A., Funk, C., Jansson, S., Lloyd, J., ... Öquist, G.
837 (2004). Intermittent low temperatures constrain spring recovery of photosynthesis in boreal
838 Scots pine forests. *Global Change Biology*, 10(6), 995–1008.
839 <https://doi.org/10.1111/j.1365-2486.2004.00781.x>

840 Euskirchen, E. S., Bret-Harte, M. S., Shaver, G. R., Edgar, C. W., & Romanovsky, V. E. (2017).
841 Long-Term Release of Carbon Dioxide from Arctic Tundra Ecosystems in Alaska.
842 *Ecosystems*, 20(5), 960–974. <https://doi.org/10.1007/s10021-016-0085-9>

843 Euskirchen, E. S., Edgar, C. W., Turetsky, M. R., Waldrop, M. P., & Harden, J. W. (2014).
844 Differential response of carbon fluxes to climate in three peatland ecosystems that vary in
845 the presence and stability of permafrost. *Journal of Geophysical Research G: Biogeosciences*,
846 119(8), 1576–1595. <https://doi.org/10.1002/2014JG002683>

847 Fleischer, K., Wårlind, D., Van Der Molen, M. K., Rebel, K. T., Arneth, A., Erisman, J. W., ...
848 Dolman, A. J. (2015). Low historical nitrogen deposition effect on carbon sequestration in
849 the boreal zone. *Journal of Geophysical Research G: Biogeosciences*, 120(12), 2542–2561.
850 <https://doi.org/10.1002/2015JG002988>

851 Ensminger I, Schmidt L, Lloyd J (2008) Soil temperature and intermittent frost modulate the rate
852 of recovery of photosynthesis in Scots pine under simulated spring conditions. *New*
853 *Phytologist*, 177, 428–442.

854 Fisher, J. B. and co-authors (2014) Carbon cycle uncertainty in the Alaskan Arctic.
855 *Biogeoscience*, 11, 4271-4288.

856 Frankenberg, C., Fisher, J. B., Worden, J., Badgley, G., Saatchi, S. S., Lee, J. E., ... Yokota, T.
857 (2011). New global observations of the terrestrial carbon cycle from GOSAT: Patterns of
858 plant fluorescence with gross primary productivity. *Geophysical Research Letters*, 38(17),
859 1–22. <https://doi.org/10.1029/2011GL048738>

860 Gonsamo A, Chen JM, Price DT, Kurz WA, Wu C (2012) Land surface phenology from optical
861 satellite measurement and CO₂ eddy covariance technique. *Journal of Geophysical*
862 *Research: Biogeosciences*, 117, doi: 10.1029/2012JG002070.

863 Goodrich, J. P., Oechel, W. C., Gioli, B., Moreaux, V., Murphy, P. C., Burba, G., & Zona, D.
864 (2016). Impact of different eddy covariance sensors, site set-up, and maintenance on the
865 annual balance of CO₂ and CH₄ in the harsh Arctic environment. *Agricultural and Forest*
866 *Meteorology*, 228–229, 239–251. <https://doi.org/10.1016/j.agrformet.2016.07.008>

867 Goulden, M. L. (1998). Sensitivity of Boreal Forest Carbon Balance to Soil Thaw. *Science*,
868 279(5348), 214–217. <https://doi.org/10.1126/science.279.5348.214>

869 Graven, H. D., Keeling, R. F., Piper, S. C., Patra, P. K., Stephens, B. B., Wofsy, S. C., ... Bent,
870 J. D. (2013). Enhanced seasonal exchange of CO₂ by northern ecosystems since 1960.
871 *Science (New York, N.Y.)*, 341(September), 1085–9.
872 <https://doi.org/10.1126/science.1239207>.

873 Griffis TJ, Rouse WR, Waddington JM (2000) Interannual variability of net ecosystem
874 CO₂ exchange at a subarctic fen. *Global Biogeochemical Cycles*, **14**, 1109–1121.

875 Guanter, L., Aben, I., Tol, P. et al. (2015) Potential of the TROPospheric Monitoring Instrument
876 (TROPOMI) onboard the Sentinel-5 Precursor for the monitoring of terrestrial chlorophyll
877 fluorescence, *Atmos. Meas. Tech.*, **8**, 1337-1352.

878 Harazono Y, Mano M, Miyata A, Zulueta RC, Oechel WC (2003) Inter-annual carbon dioxide
879 uptake at a wet sedge tundra ecosystem in the Arctic. *Tellus*, **55B**, 215–231.

880 Henderson, J. M., Eluszkiewicz, J., Mountain, M. E., Nehrkorn, T., Chang, R. Y. W., Karion, A.,
881 ... Miller, C. E. (2015). Atmospheric transport simulations in support of the Carbon in
882 Arctic Reservoirs Vulnerability Experiment (CARVE). *Atmospheric Chemistry and*
883 *Physics*, **15**(8), 4093–4116. <https://doi.org/10.5194/acp-15-4093-2015>

884 Hinzman, L. D., Deal, C. J., Mcguire, A. D., Mernild, S. H., Polyakov, I. V., & Walsh, J. E.
885 (2013). Trajectory of the Arctic as an integrated system. *Ecological Applications*, **23**(8),
886 1837–1868. <https://doi.org/10.1890/11-1498.1>

887 Hugelius G, Strauss J, Zubrzycki S et al. (2014) Estimated stocks of circumpolar permafrost
888 carbon with quantified uncertainty ranges and identified data gaps. *Biogeosciences*, **11**,
889 6573-6593.

890 Jafarov, E., & Schaefer, K. (2016). The importance of a surface organic layer in simulating
891 permafrost thermal and carbon dynamics. *Cryosphere*, **10**(1), 465–475.
892 <https://doi.org/10.5194/tc-10-465-2016>

893 Jarvis, P., & Linder, S. (2000). Constraints to growth of boreal forests. *Nature*, **405**(6789), 904–
894 905. [https://doi.org/10.1002/\(SICI\)1097-0177\(199909\)216:1<1::AID-DVDY1>3.0.CO;2-T](https://doi.org/10.1002/(SICI)1097-0177(199909)216:1<1::AID-DVDY1>3.0.CO;2-T)

895 Jeong, S. J., Schimel, D., Frankenberg, C., Drewry, D. T., Fisher, J. B., Verma, M., ... Joiner, J.
896 (2017). Application of satellite solar-induced chlorophyll fluorescence to understanding
897 large-scale variations in vegetation phenology and function over northern high latitude
898 forests. *Remote Sensing of Environment*. <https://doi.org/10.1016/j.rse.2016.11.021>

899 Jeong, S., Medvigy, D., Shevliakova, E., & Malyshev, S. (2012). Uncertainties in terrestrial
900 carbon budgets related to spring phenology, **117**(March), 1–17.
901 <https://doi.org/10.1029/2011JG001868>

902 Jeong, S., Medvigy, D., Shevliakova, E., & Malyshev, S. (2013). Predicting changes in
903 temperate forest budburst using continental-scale observations and models, **40**(December
904 2012), 1–6. <https://doi.org/10.1029/2012GL054431>

905 Joiner, J., Yoshida, Y, Vasilkov, A.P., Schaefer, K., Jung, M. (2014). The seasonal cycle of
906 satellite chlorophyll fluorescence observations and its relationship to vegetation phenology
907 and ecosystem atmosphere carbon exchange, *Remote Sens. Environ.*, **152**, 375-391.

908 Jonsson AM, Eklundh L, Hellström M, B€arring L, J€onsson P (2010) Annual changes in
909 MODIS vegetation indices of Swedish coniferous forests in relation to snow dynamics and
910 tree phenology. *Remote Sensing of Environment*, **114**, 2719–2730.

911 Kim, Y., Kimball, J. S., Zhang, K., Didan, K., Velicogna, I., & McDonald, K. C. (2014).
912 Attribution of divergent northern vegetation growth responses to lengthening non-frozen
913 seasons using satellite optical-NIR and microwave remote sensing. *International Journal of*
914 *Remote Sensing*, **35**(10), 3700–3721. <https://doi.org/10.1080/01431161.2014.915595>

915 Kim, Y., Kimball, J. S., Zhang, K., & McDonald, K. C. (2012). Satellite detection of increasing
916 Northern Hemisphere non-frozen seasons from 1979 to 2008: Implications for regional
917 vegetation growth. *Remote Sensing of Environment*, **121**, 472–487.
918 <https://doi.org/10.1016/j.rse.2012.02.014>

- 919 Lafleur, P. M., and E. R. Humphreys. 2007. Spring warming and carbon dioxide exchange over
920 low Arctic tundra in central Canada. *Global Change Biology* 14:740–756.
- 921 Lasslop, G., Reichstein, M., Papale, D., Richardson, A., Arneeth, A., Barr, A., ... Wohlfahrt, G.
922 (2010). Separation of net ecosystem exchange into assimilation and respiration using a light
923 response curve approach: Critical issues and global evaluation. *Global Change Biology*,
924 16(1), 187–208. <https://doi.org/10.1111/j.1365-2486.2009.02041.x>
- 925 Lawrence, D. M., & Slater, A. G. (2010). The contribution of snow condition trends to future
926 ground climate. *Climate Dynamics*, 34(7), 969–981. <https://doi.org/10.1007/s00382-009-0537-4>
- 927
928 Lawrence, D. M., Slater, A. G., Romanovsky, V. E., & Nicolsky, D. J. (2008). Sensitivity of a
929 model projection of near-surface permafrost degradation to soil column depth and
930 representation of soil organic matter. *Journal of Geophysical Research: Earth Surface*,
931 113(2). <https://doi.org/10.1029/2007JF000883>
- 932 Lawrence, D. M., Slater, A. G., & Swenson, S. C. (2012). Simulation of present-day and future
933 permafrost and seasonally frozen ground conditions in CCSM4. *Journal of Climate*, 25(7),
934 2207–2225. <https://doi.org/10.1175/JCLI-D-11-00334.1>
- 935 Lead, C., Oleson, K. W., Lawrence, D. M., Authors, L., Bonan, G. B., Drewniak, B., ... Yang,
936 Z.-L. (2013). Technical Description of version 4.5 of the Community Land Model (CLM).
937 Retrieved from <http://library.ucar.edu/research/publish-technote>
- 938 Liu, J., Bowman, K. W., Lee, M., Henze, D. K., Bousserrez, N., Brix, H., ... Nassar, R. (2014).
939 Carbon monitoring system flux estimation and attribution: Impact of ACOS-GOSAT XCO2
940 sampling on the inference of terrestrial biospheric sources and sinks. *Tellus, Series B:
941 Chemical and Physical Meteorology*, 66(1), 1–18. <https://doi.org/10.3402/tellusb.v66.22486>
- 942 Liu, J., Bowman, K. W., Schimel, D. S., Parazoo, N. C., Jiang, Z., Lee, M., ... Eldering, A.
943 (2017). Contrasting carbon cycle responses of the tropical continents to the 2015–2016 El
944 Niño. *Science*, 358(6360). <https://doi.org/10.1126/science.aam5690>
- 945 Lokupitiya, R. S., Zupanski, D., Denning, A. S., Kawa, S. R., Gurney, K. R., and Zupanski, M.
946 (2008) Estimation of global CO2 fluxes at regional scale using the maximum likelihood
947 ensemble filter, *J. Geophys. Res.*, 113, D20110, doi:10.1029/2007JD009679.
- 948 Luus, K. A., & Lin, J. C. (2015a). The Polar Vegetation Photosynthesis and Respiration Model:
949 A parsimonious, satellite-data-driven model of high-latitude CO2 exchange. *Geoscientific
950 Model Development*, 8(8), 2655–2674. <https://doi.org/10.5194/gmd-8-2655-2015>
- 951 Luus, K. A., & Lin, J. C. (2015b). The Polar Vegetation Photosynthesis and Respiration Model:
952 A parsimonious, satellite-data-driven model of high-latitude CO2 exchange. *Geoscientific
953 Model Development*. <https://doi.org/10.5194/gmd-8-2655-2015>
- 954 McGuire, A. D., Christensen, T. R., Hayes, D., Heroult, A., Euskirchen, E., Kimball, J. S., ... Yi,
955 Y. (2012). An assessment of the carbon balance of Arctic tundra: Comparisons among
956 observations, process models, and atmospheric inversions. *Biogeosciences*, 9(8), 3185–
957 3204. <https://doi.org/10.5194/bg-9-3185-2012>
- 958 Messerschmidt, J., Parazoo, N., Wunch, D., Deutscher, N. M., Roehl, C., Warneke, T., &
959 Wennberg, P. O. (2013). Evaluation of seasonal atmosphere-biosphere exchange
960 estimations with TCCON measurements. *Atmospheric Chemistry and Physics*, 13(10),
961 5103–5115.
- 962 Müller, P.; Li, X.P.; Niyogi, K.K. Non-photochemical quenching. A response to excess light
963 energy. *Plant Physiol.* 2001, 125, 1558–1566.
- 964 Natali, S. M., Schuur, E. A. G., & Rubin, R. L. (2012). Increased plant productivity in Alaskan

965 tundra as a result of experimental warming of soil and permafrost. *Journal of Ecology*,
966 *100*(2), 488–498. <https://doi.org/10.1111/j.1365-2745.2011.01925.x>

967 Oberbaur, S.F., G. Starr, E. W. Pop. 1998. Effects of extended growing season and soil warming
968 on carbon dioxide and methane exchange of tussock tundra in Alaska

969 Ottander C, Campbell D, € Oquist G (1995) Seasonal changes in photosystem II organization
970 and pigment composition in *Pinus sylvestris*. *Planta*, 197, 176–183.

971 Parazoo, N. C., A. S. Denning, S. R. Kawa, S. Pawson, and R. Lokupitiya (2012) CO₂ flux
972 estimation errors associated with moist atmospheric processes. *Atmos. Chem. Phys.*, 12,
973 6405-6416.

974 Parazoo, N. C., Commane, R., Wofsy, S. C., Koven, C. D., Sweeney, C., Lawrence, D. M., ...
975 Miller, C. E. (2016). Detecting regional patterns of changing CO₂ flux in Alaska.
976 *Proceedings of the National Academy of Sciences of the United States of America*, 113(28).
977 <https://doi.org/10.1073/pnas.1601085113>

978 Peng, S., Ciais, P., Chevallier, F., Peylin, P., Cadule, P., Sitch, S., ... Zhao, H. (2015).
979 Benchmarking the seasonal cycle of CO₂ fluxes simulated by terrestrial ecosystem models.
980 *Global Biogeochemical Cycles*, 29, 46-64, <https://doi.org/10.1002/2014GB004931>

981 Peters, W., Jacobson, A. R., Sweeney, C., Andrews, A. E., Conway, T. J., Masarie, K., ... Tans,
982 P. P. (2007). An atmospheric perspective on North American carbon dioxide exchange :
983 CarbonTracker, (8).

984 Porcar-Castell, A. A high-resolution portrait of the annual dynamics of photochemical and non-
985 photochemical quenching in needles of *Pinus sylvestris*. *Physiol. Plant.* 2011, 143, 139–153.

986 Pulliainen, J. and co-authors (2017) Early snowmelt significantly enhances boreal springtime
987 carbon uptake, *Proceedings of the National Academy of Science*, 114, 42, 11081-11086.

988 Ramage, J.M., B.L. Isacks. 2002. Determination of melt-onset and refreeze timing on southeast
989 Alaskan icefields using SSM/I diurnal amplitude variations. *Annals of*
990 *Glaciology* 34(1):391-398, <https://doi.org/10.3189/172756402781817761>

991 Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., ... Valentini, R.
992 (2005). On the separation of net ecosystem exchange into assimilation and ecosystem
993 respiration: Review and improved algorithm. *Global Change Biology*, 11(9), 1424–1439.
994 <https://doi.org/10.1111/j.1365-2486.2005.001002.x>

995 Richardson AD, Braswell BH, Hollinger DY, Jenkins JP, Ollinger SV (2011) Near-surface
996 remote sensing of spatial and temporal variation in canopy phenology. *Ecological*
997 *Applications*, 19, 1417–1428.

998 Romanovsky, V. E., & Osterkamp, T. E. (2000). Effects of unfrozen water on heat and mass
999 transport processes in the active layer and permafrost. *Permafrost and Periglacial*
1000 *Processes*, 11(3), 219–239.

1001 Schaefer, K., & Jafarov, E. (2016). A parameterization of respiration in frozen soils based on
1002 substrate availability. *Biogeosciences*, 13(7), 1991–2001. [https://doi.org/10.5194/bg-13-](https://doi.org/10.5194/bg-13-1991-2016)
1003 [1991-2016](https://doi.org/10.5194/bg-13-1991-2016)

1004 Schaefer, K., Schwalm, C. R., Williams, C., Arain, M. A., Barr, A., Chen, J. M., ... Zhou, X.
1005 (2012). A model-data comparison of gross primary productivity: Results from the north
1006 American carbon program site synthesis. *Journal of Geophysical Research: Biogeosciences*,
1007 *117*(3), 1–15. <https://doi.org/10.1029/2012JG001960>

1008 Soukupova J, Csefalvay L, Urban O, Kosvancova M, Marek M, Rascher U, Nedbal L (2008)
1009 Annual variation of the steady-state chlorophyll fluorescence emission of evergreen plants
1010 in temperate zone. *Functional Plant Biology*, 35, 63–76.

1011 Springer, K. R., R. Wang, J. A. Gamon (2017) Parallel Seasonal Patterns of Photosynthesis,
 1012 Fluorescence, and Reflectance Indices in Boreal Trees, *Remote Sens.* 9, 691,
 1013 doi:10.3390/rs9070691

1014 Starr, G., and Oberbauer, S., 2003: Photosynthesis of arctic evergreens under snow: implications
 1015 for tundra ecosystem carbon balance. *Ecology*, 84: 1415–1420.

1016 Steiner, N., & Tedesco, M. (2014). A wavelet melt detection algorithm applied to enhanced-
 1017 resolution scatterometer data over Antarctica (2000-2009). *The Cryosphere*, 8(1), 25,
 1018 <https://doi.org/10.5194/tc-8-25-2014>,

1019 Steiner, N. and McDonald, K.C. and Dinardo, S.J. and Miller, C.E. (2015) Snowmelt and
 1020 Surface Freeze/Thaw Timings over Alaska derived from Passive Microwave Observations
 1021 using a Wavelet Classifier, AGU Fall Meeting Abstracts

1022 Steiner N., McDonald K.C., and Miller C. (2017a) Snowmelt and Freeze/Thaw Mapping of
 1023 Boreal and Arctic Alaska using Wavelet Analysis *IEEE Transactions on Geoscience and*
 1024 *Remote Sensing*, In-Prep.

1025 Steiner, N., K.C. McDonald, and C.E. Miller. 2017b. CARVE: Daily Thaw State of Boreal and
 1026 Arctic Alaska from AMSR-E and SSM/I, 2003-2014. ORNL DAAC, Oak Ridge,
 1027 Tennessee, USA. <https://doi.org/10.3334/ORNLDAAC/1383>

1028 Strand, M., and G. Öquist (1985), Inhibition of photosynthesis by freezing temperatures and high
 1029 light levels in cold-acclimated seedlings of Scots pine (*Pinus sylvestris*): I. Effects on the
 1030 light-limited and light-saturated rates of CO₂ assimilation, *Physiol. Plant.*, 64, 425–430,
 1031 doi:10.1111/j.1399-3054.1985.tb08517.x.

1032 Sun, Y., C. Frankenberg, M. Jung, J. Joiner, L. Guanter, P. Köhler, T. Magney (2018) Overview
 1033 of solar-induced fluorescence (SIF) from the Orbiting Carbon Observatory-2: Retrieval,
 1034 cross-mission comparison, and global monitoring for GPP, *Remote Sensing of*
 1035 *Environment*, <https://doi.org/10.1016/j.rse.2018.02.016>.

1036 Tanja S, Berninger F, Vesala T et al. (2003) Air temperature triggers the recovery of evergreen
 1037 boreal forest photosynthesis in spring. *Global Change Biology*, 9, 1410–1426.

1038 Ueyama M, Iwata H, Harazono Y, Euskirchen ES, Oechel WC, Zona D (2013) Growing season
 1039 and spatial variations of carbon fluxes of Arctic and boreal ecosystems in Alaska (USA).
 1040 *Ecological Applications*, 23, 1798-1816.

1041 Walther, S., Voigt, M., Thum, T., Gonsamo, A., Zhang, Y., Köhler, P., ... Guanter, L. (2016).
 1042 Satellite chlorophyll fluorescence measurements reveal large-scale decoupling of
 1043 photosynthesis and greenness dynamics in boreal evergreen forests. *Global Change*
 1044 *Biology*, 22(9), 2979–2996. <https://doi.org/10.1111/gcb.13200>

1045 Walther, S., Voigt, M., Thum, T., Gonsamo, A., Zhang, Y., Köhler, P., ... Guanter, L. (2016).
 1046 Satellite chlorophyll fluorescence measurements reveal large-scale decoupling of
 1047 photosynthesis and greenness dynamics in boreal evergreen forests. *Global Change*
 1048 *Biology*. <https://doi.org/10.1111/gcb.13200>

1049 Waring, R. H., and W. E. Winner (1996), Constraints on terrestrial primary production along the
 1050 Pacific Coast of North and South America, in *High Latitude Rain Forests and Associated*
 1051 *Ecosystems of the West Coast of the Americas: Climate, Hydrology, Ecology, and*
 1052 *Conservation*, edited by R. G. Lawford, P. Alaback, and E. R. Fuentes, pp. 89–102,
 1053 Springer-Verlag, New York, doi:10.1007/978-1-4612-3970-3_6.

1054 Wolfe, G. M., Kawa, S. R., Hanisco, T. F., Hannun, R. A., Newman, P. A., Swanson, A., Bailey,
 1055 S., Barrick, J., Thornhill, K. L., Diskin, G., DiGangi, J., Nowak, J. B., Sorenson, C., Bland,
 1056 G., Yungel, J. K., and Swenson, C. A.: The NASA Carbon Airborne Flux Experiment

1057 (CARAFE): Instrumentation and Methodology, Atmos. Meas. Tech. Discuss.,
1058 <https://doi.org/10.5194/amt-2017-398>, in review, 2017.

1059 Wong, C. Y. S., & Gamon, J. A. (2015). The photochemical reflectance index provides an
1060 optical indicator of spring photosynthetic activation in evergreen conifers. *New Phytologist*,
1061 *206*(1), 196–208. <https://doi.org/10.1111/nph.13251>

1062 Yi, S., Wischnewski, K., Langer, M., Muster, S., & Boike, J. (2014). Freeze/thaw processes in
1063 complex permafrost landscapes of northern Siberia simulated using the TEM ecosystem
1064 model: Impact of thermokarst ponds and lakes. *Geoscientific Model Development*, *7*(4),
1065 1671–1689. <https://doi.org/10.5194/gmd-7-1671-2014>

1066 Zhang, T., & Armstrong, R. L. (2001). Soil freeze/thaw cycles over snow-free land detected by
1067 passive microwave remote sensing. *Geophysical Research Letters*, *28*(5), 763-
1068 766, <https://doi.org/10.1029/2000gl011952>

1069 Zhang, K., Kimball, J. S., Kim, Y., & McDonald, K. C. (2011). Changing freeze-thaw seasons in
1070 northern high latitudes and associated influences on evapotranspiration. *Hydrological*
1071 *Processes*, *25*(26), 4142–4151. <https://doi.org/10.1002/hyp.8350>

1072 Zona, D., Oechel, W. C., Richards, J. H., Hastings, S., Kopetz, I., Ikawa, H., & Oberbauer, S.
1073 (2011). Light-stress avoidance mechanisms in a Sphagnum-dominated wet coastal Arctic
1074 tundra ecosystem in Alaska. *Ecology*, *92*(3), 633–644. <https://doi.org/10.1890/10-0822.1>

1075 Zona, D., Beniamigo, G., Commane, R. et al. (2016). Cold season emissions dominate the Arctic
1076 tundra methane budget. *PNAS*, *133*(1), 40-45.

1077

1078

1079

1080 **Tables**

1081

1082 **Table 1.** Site Characteristics of Eddy Covariance Flux Towers for Alaska.

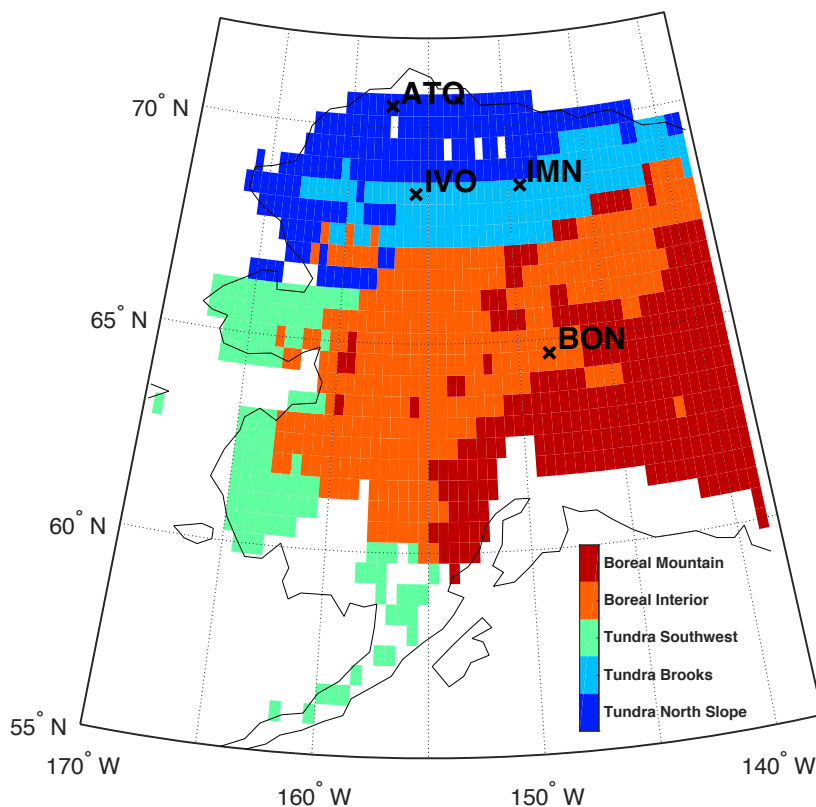
Site Name/ID	Ecosystem / Station ID	Region	Latitude, Longitude	Elevation	Site Years Analyzed	Reference
Bonanza Creek Experimental Forest (BON)	Black Spruce Forest (BON-Spr)	Interior Alaska	64.696°N, 148.323°W	100 m	2012-2013	Euskirchen et al., 2014
	Thermokarst Collapse Scar Bog (BON-Bog)	Interior Alaska	64.695°N, 148.321°W	100 m	2012-2013	Euskirchen et al., 2014
	Rich Fen (BON-Fen)	Interior Alaska	64.703°N, 148.313°W	100 m	2012-2013	Euskirchen et al., 2014
Imnavait Creek Watershed (IMN)	Wet Sedge Tundra (IMN-Sed)	North Slope Alaska	68.606°N, 149.311°W	920 m	2012-2014	Euskirchen et al., 2017
	Moist Acidic Tussock Tundra (IMN-Tus)	North Slope Alaska	68.606°N, 149.304°W	930 m	2012-2014	Euskirchen et al., 2017
	Heath Tundra (IMN-Hth)	North Slope Alaska	68.607°N, 149.296°W	940 m	2012-2014	Euskirchen et al., 2017
Ivotuk (IVO)	Tundra dominated by tussock-sedge, dwarf-shrub, moss	North Slope Alaska	68.486°N, 155.750°W	543 m	2014	Goodrich et al., 2016; Zona et al., 2016
Atqasuk (ATQ)	Tundra dominated by sedge, grass, dwarf shrub	North Slope Alaska	70.469°N, 157.409°W	24 m	2014	Goodrich et al., 2016; Zona et al., 2016

1083

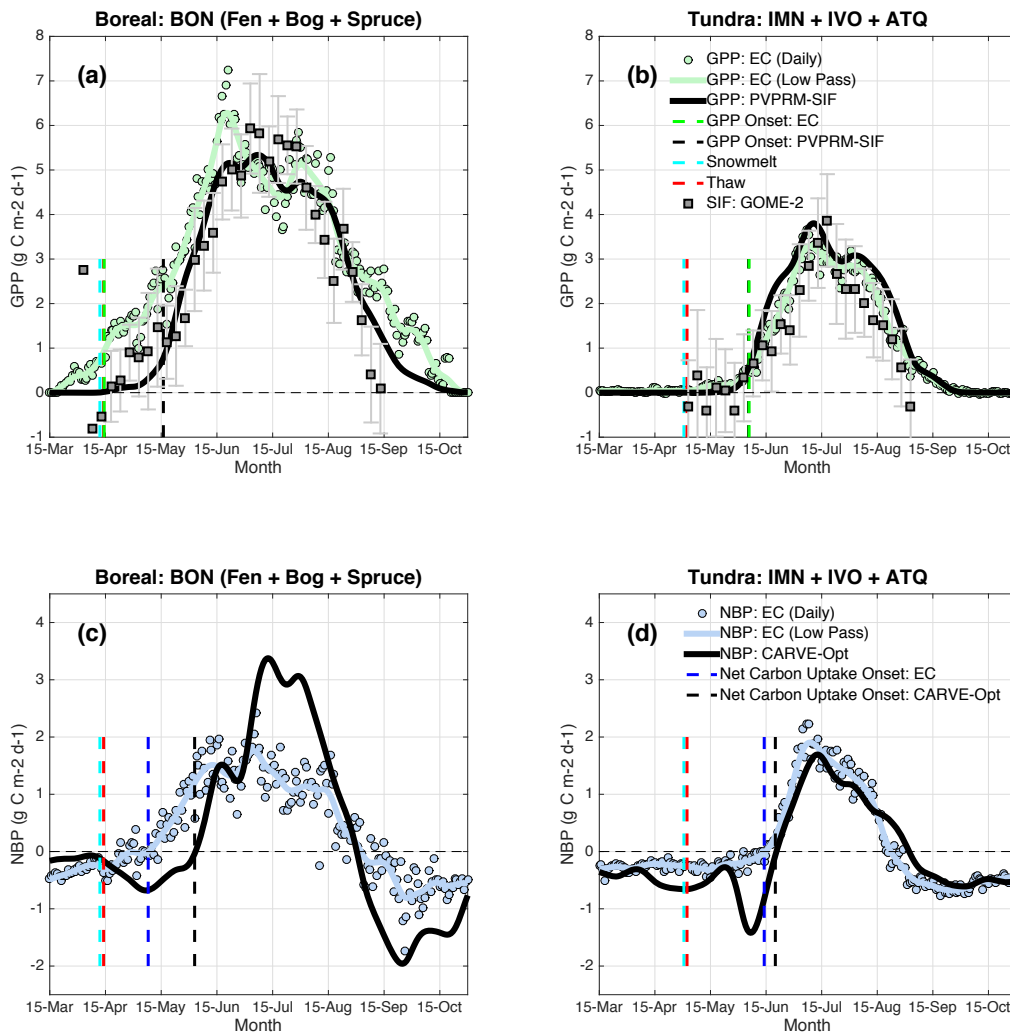
1084

1085 **Table 2:** Mean (\pm SD) [Min Max] dates (DOY) for regional estimates of spring snow melt,
1086 landscape thaw, GPP onset, C sink onset and mean time lags (days) between thaw and GPP onset
1087 and between thaw and C sink onset. Results are shown at eddy covariance (eddy covariance)
1088 towers (eddy covariance observations shown in parentheses), EPA Level II and III ecoregions
1089 (rows 3-7), and for combined tundra and boreal ecoregions (rows 8-9).

Region	Snow-Melt Date (DOY)	Thaw Date (DOY)	GPP Onset Date (DOY)	C Sink Onset Date (DOY)	Thaw-GPP Lag (Days)	Thaw-C Sink Lag (Days)	GPP – C Sink Lag (Days)
Tundra: IMN-ATQ- IVO	121	122	155 (155)	170 (164)	33 (33)	48 (42)	15 (9)
Boreal: BON	102	104	136 (104)	153 (128)	32 (0)	49 (24)	17 (24)
Tundra North Slope	117 \pm 12; [84.2 153]	133 \pm 5; [118 148]	154 \pm 3; [144 160]	167 \pm 9; [147 182]	20 \pm 5; [9 31]	36 \pm 10; [16 50]	14 \pm 8; [2 27]
Tundra Brooks	112 \pm 8; [94 127]	126 \pm 5; [113 132]	150 \pm 3; [142 156]	161 \pm 8; [139 180]	24 \pm 4; [17 33]	35 \pm 7; [16 50]	11 \pm 6; [-3 25]
Tundra Southwest	103 \pm 12; [77 131]	119 \pm 15; [85 135]	146 \pm 5; [137 164]	159 \pm 11; [139 178]	26 \pm 11; [7 57]	41 \pm 10; [13 76]	13 \pm 8; [-3 36]
Boreal Interior	98 \pm 8; [78 121]	110 \pm 7; [96 129]	139 \pm 3; [135 149]	144 \pm 7; [137 175]	29 \pm 5; [16 42]	34 \pm 6; [16 61]	5 \pm 5; [-2 30]
Boreal Mountain	102 \pm 11 [66 136]	112 \pm 7; [89 152]	142 \pm 5; [135 177]	146 \pm 12; [133 188]	30 \pm 6; [-2 67]	34 \pm 11; [5 82]	4 \pm 9; [-17 38]
Tundra: North Slope + Brooks + Southwest	112 \pm 12; [77 153]	127 \pm 10; [85 148]	151 \pm 5; [137 164]	163 \pm 10; [139 182]	23 \pm 7; [7 57]	37 \pm 9; [13 76]	13 \pm 7; [-3 36]
Boreal: Interior + Mountain	100 \pm 10; [66 136]	111 \pm 7; [89 152]	141 \pm 5; [135 177]	145 \pm 10; [133 188]	29 \pm 6; [-2 67]	34 \pm 9; [5 82]	4 \pm 7; [-17 38]



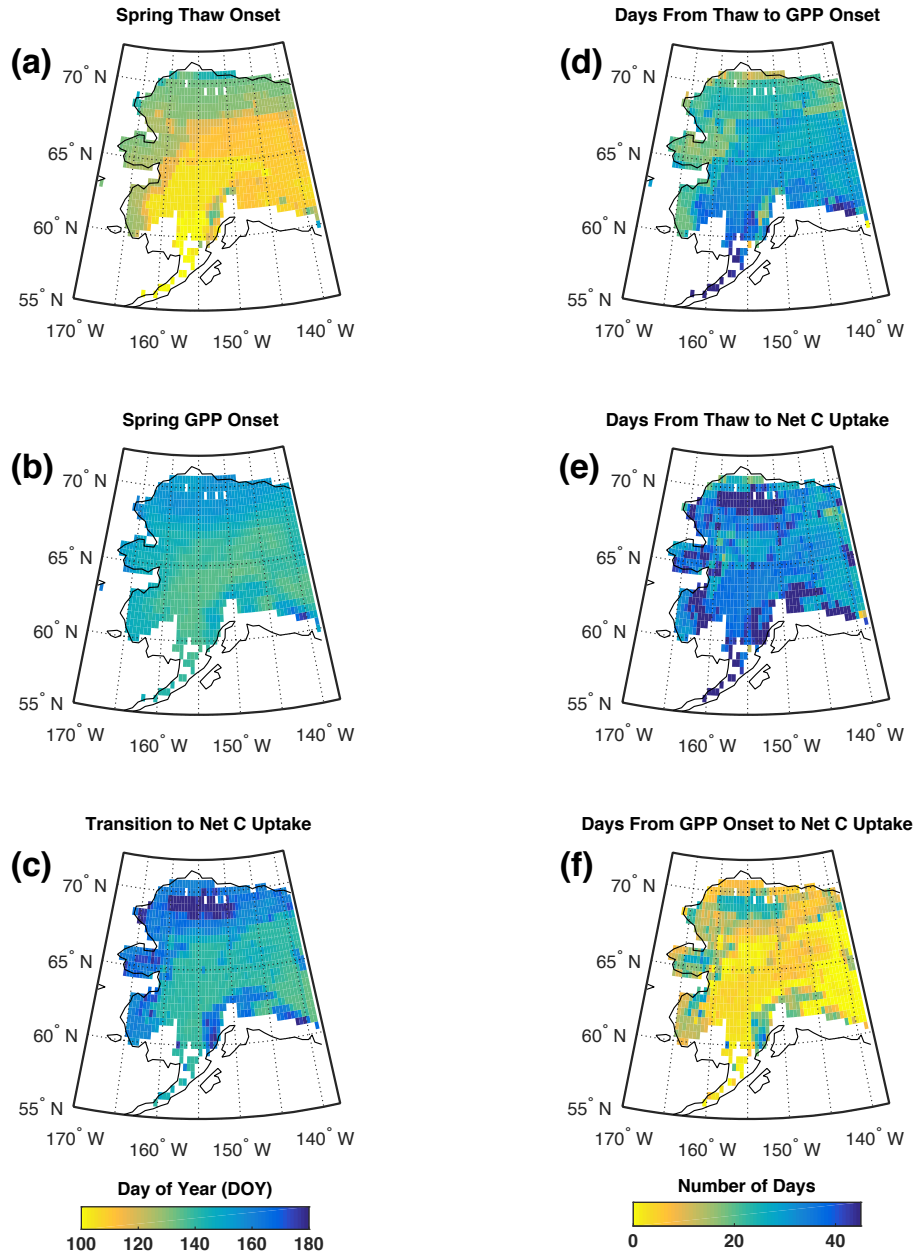
1091
 1092 **Fig. 1:** Map showing spatial pattern of vegetation and location of flux towers. Vegetation is
 1093 derived from US EPA Level 2 ecoregion maps for boreal (reds) and tundra (blue). Tower sites
 1094 include: Bonanza Creek (BNZ: 64.70°N, 148.32°W), Innavait (IMN: 68.62°N, 149.30°W),
 1095 Ivotuk (IVO: 68.48°N, 155.75°W), and Atqasuk (ATQ: 70.47°N, 157.40°W). IMN and BON sites
 1096 each include three additional eddy covariance stations (see Table 1).



1097

1098 **Fig. 2:** Evaluation of observationally constrained estimates of seasonal gross primary production
 1099 (PVPRM-SIF GPP, a-b) and net biome production (CARVE-Opt NBP, c-d) against tower eddy
 1100 covariance data in interior and northern Alaska, averaged from 2012-2014. Daily averages
 1101 (symbols) and low pass filters (lines) are shown for flux towers (green = GPP, blue = NBP), and
 1102 low pass butterworth filters (order 2, cutoff frequency = 0.1) for PVPRM-SIF (solid black, top)
 1103 and CARVE-Opt (solid black, bottom). Boreal fluxes are averaged over the cluster of Spruce,
 1104 Fen, and Bog sites at Bonanza Creek Experimental Forest (BON, 3 sites total). Tundra fluxes are
 1105 averaged over the cluster of Hedge, Sedge, and Tussock sites at IMN and individual sites at IVO
 1106 and ATQ (five sites total). CARVE-Opt and PVPRM-SIF are sampled at towers only for years

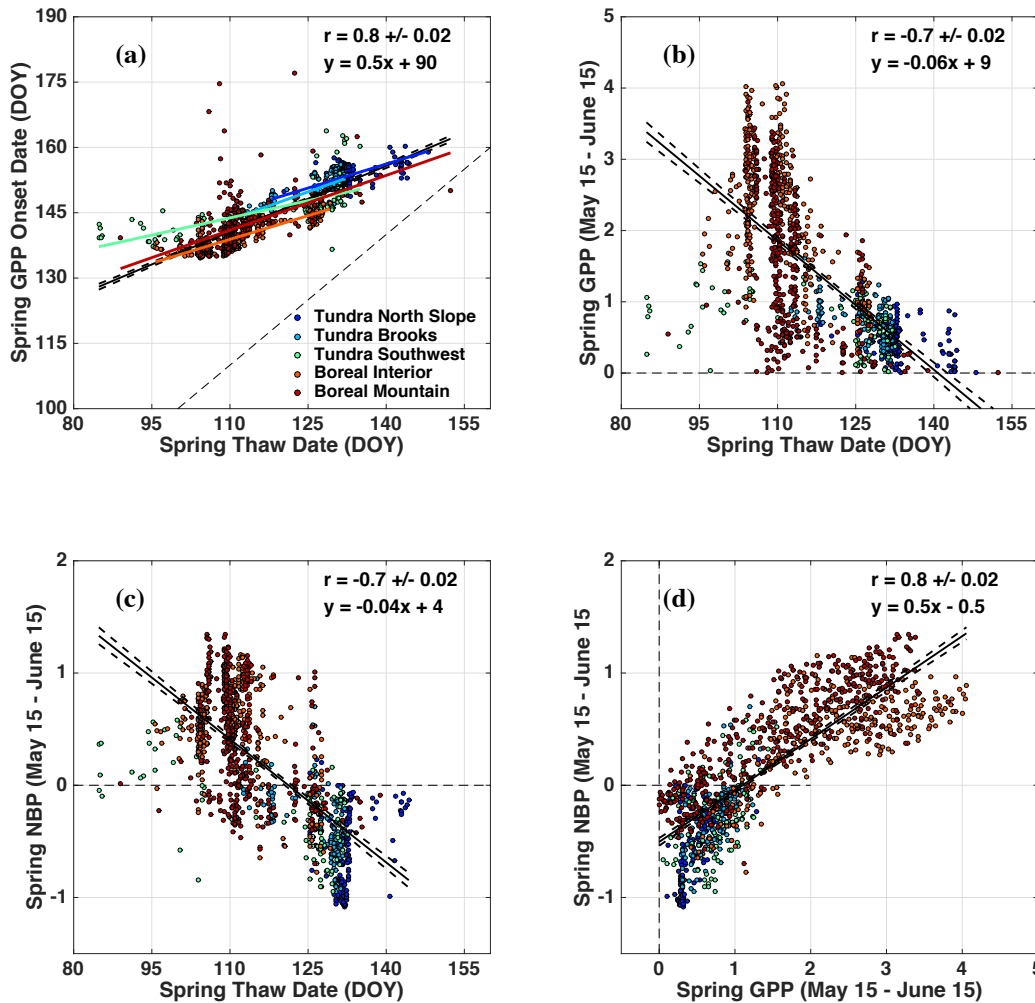
1107 when growing season eddy covariance data is available, which differs between sites (see Table
1108 1). Onset dates for snowmelt, thaw, GPP, and net carbon uptake shown in vertical dashed lines.
1109 5-day mean retrievals of GOME-2 solar induced fluorescence (SIF) and standard error sampled
1110 in a 2° x 2° grid box surrounding eddy covariance tower and normalized by PVPRM-SIF are
1111 shown in grey in A-B. Thaw, GPP, and net C sink onset dates are provided in Table 2. Positive
1112 NBP values denote net sink of atmospheric CO₂. Seasonal C flux dynamics are well represented
1113 by observationally constrained estimates in tundra, but show delayed spring onset compared to
1114 the black spruce forest.



1115

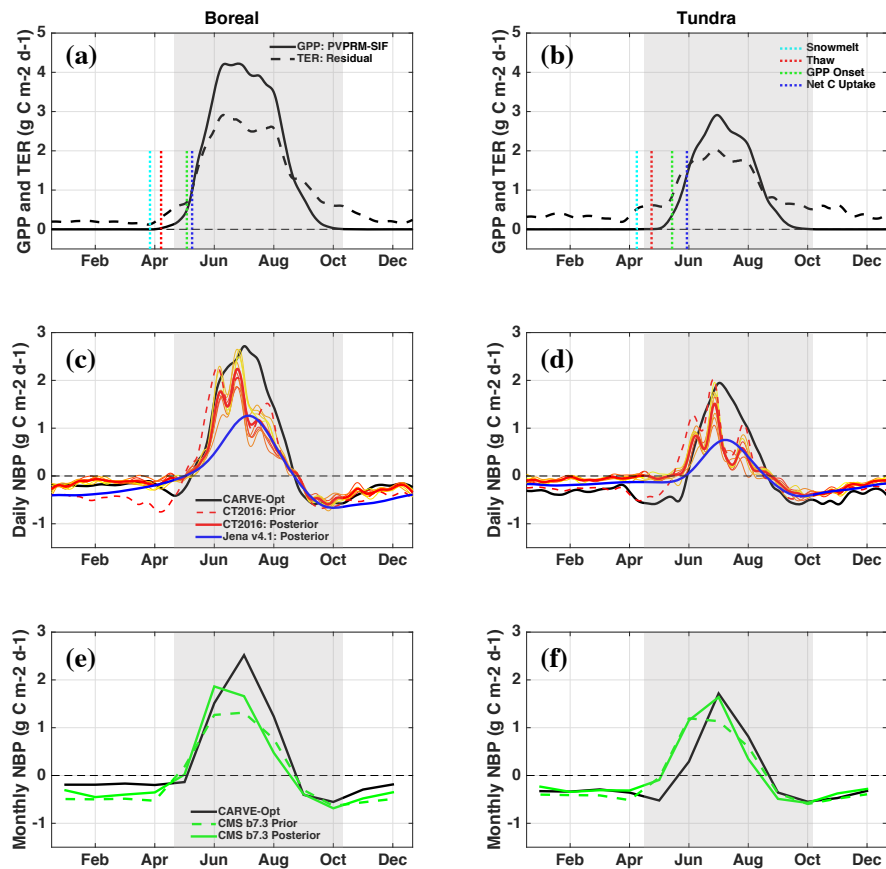
1116 **Fig. 3:** Maps showing spatial patterns of spring onset dates for landscape thaw, GPP, and net C
 1117 uptake at regional scale for Alaska. (A) Spring thaw date, representing the transition of the
 1118 landscape from frozen to thawed conditions, is derived from AMSR-E and SSM/I. (B) Spring
 1119 GPP onset, representing the date when ecosystem GPP reaches 10% of the growing season peak,
 1120 is derived from PVPRM-SIF. (C) Net C uptake, representing the spring transition from net C
 1121 source in winter to net C sink in summer, is derived from CARVE-Opt, a regional flux inversion

1122 for Alaska constrained by airborne CO₂ profiles. Number of days between thaw and GPP onset
 1123 (D), thaw and net C uptake (E), and GPP onset to net C uptake (F) are estimated as the difference
 1124 between maps in A-C. Values in A-C are plotted as day of year (DOY). This shows similar
 1125 spatial patterns of the timing of spring thaw and GPP onset, and a decrease in the number of days
 1126 from thaw to spring onset moving from south to north along the boreal-tundra gradient.



1127
 1128 Fig. 4: Relationship between spring CO₂ flux and landscape thaw. Scatter plots show regressions
 1129 of (A) Spring GPP onset date vs thaw date, (B) Mean spring GPP from May 15 – June 15 vs
 1130 thaw date, (C) Mean spring NBP from May 15 – June 15 vs thaw date, and (D) mean spring NBP
 1131 vs GPP (g C m⁻² d⁻¹). Positive NBP denotes net C uptake by plants. Colors denote the 5

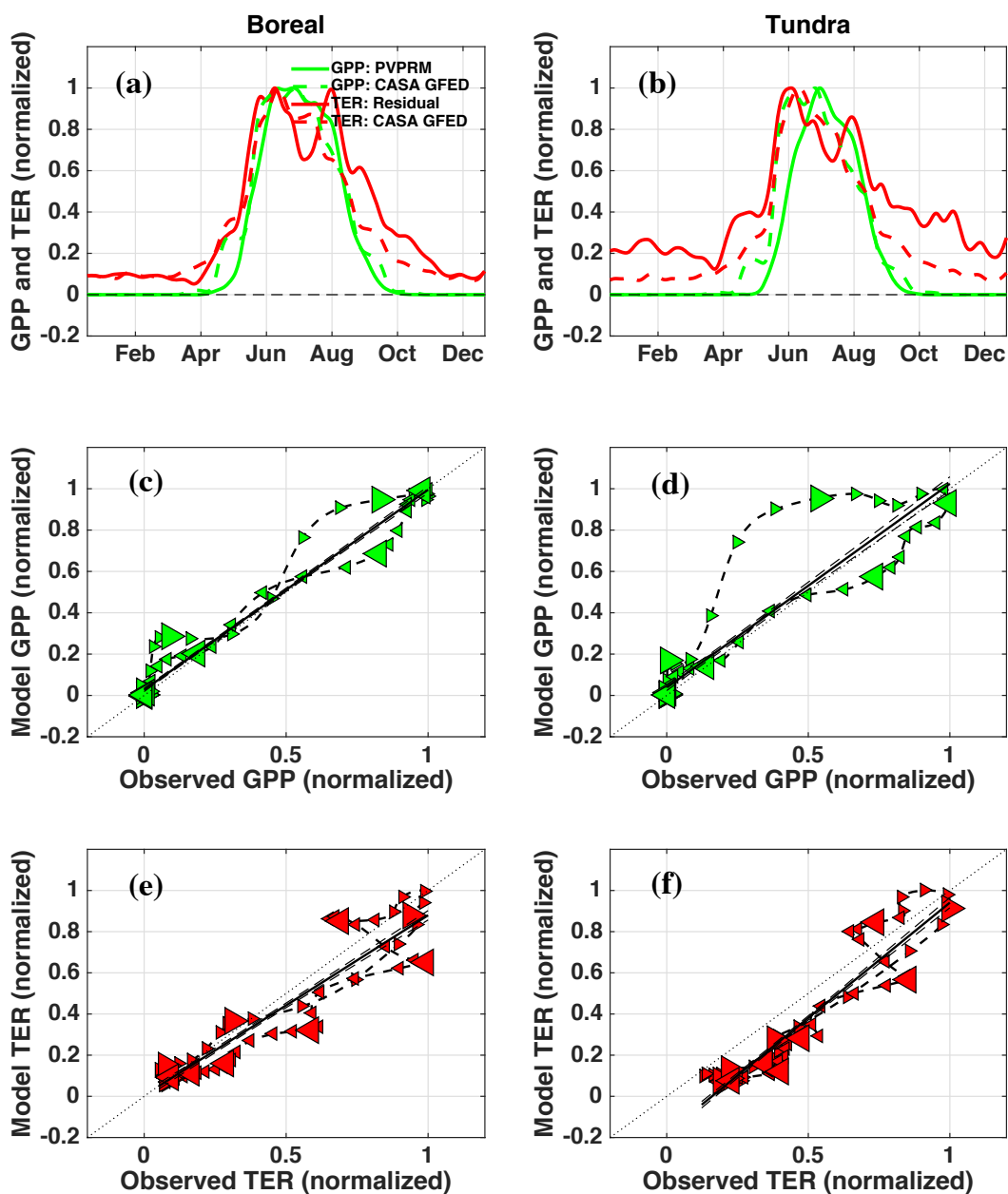
1132 ecoregions of interest. Regression lines are plotted for each ecoregion in A. Regression statistics
 1133 are reported for all points combined in each sub-panel. We note several emergent patterns: (1)
 1134 the relationship between dates of spring GPP onset and landscape thaw are consistent across
 1135 ecoregions, (2) the magnitude of GPP is more sensitive to thaw date in boreal than tundra, (3)
 1136 NBP magnitude is equally sensitive to thaw date in boreal and tundra, and (4) NBP is more
 1137 sensitive to GPP change, and hence thaw date, in tundra.



1138
 1139 **Fig. 5:** Seasonal GPP and NBP patterns for boreal and tundra ecoregions. (A-B) Seasonal GPP
 1140 (solid) from PVPRM-SIF and terrestrial ecosystem respiration (TER, dashed) from the residual
 1141 of CARVE-Opt NBP and PVPRM-SIF GPP. (C-D) Seasonal NBP derived from daily averages
 1142 of CARVE-Opt (black), CT2016 ensemble (red), and Jena v4.1 (blue) posterior fluxes and
 1143 CT2016 prior fluxes (red dashed). (E-F) Seasonal NBP (positive denotes net sink) derived from
 1144 monthly averages of CARVE-Opt (black) and CMS b7.3 posterior (green solid) and prior (green

1145 dashed) fluxes. Results for boreal ecoregions shown in the left column, and tundra in the right
1146 column. X-axis labels represent middle of month. Shaded area shows valid range of
1147 climatological CARVE-Opt NBP for the period 2012-2014, representing CARVE campaign start
1148 and end dates (May 7 and Oct 20 on average). Vertical dashed lines denote mean date of snow-
1149 melt (cyan), landscape thaw (red), GPP onset (green), and net C uptake (blue) for each
1150 ecoregion. CT2016 and Jena v4.1 are global inverse estimates derived from near-surface CO₂
1151 observations. CMS b7.3 is derived from satellite column integrated CO₂. CT2016 results are
1152 shown for 8 ensemble runs driven by different combination of fossil fuel, ocean, and biosphere
1153 priors. The results show variable patterns of the amplitude and timing of seasonal CO₂ exchange
1154 for each ecoregion and inversion method.

1155



1156

1157 **Fig. 6:** Errors in predicted seasonal GPP and TER. (A-B) Seasonal time series of daily optimized
 1158 (solid) and simulated (dashed) GPP (green) and TER (red). (C-D) Regression of simulated and
 1159 optimized GPP. (E-F) Regression of simulated and optimized TER. Optimized GPP is taken
 1160 from PVPRM-SIF and TER as the residual of CARVE-Opt NBP and PVPRM-SIF GPP. Values
 1161 are reported every 5 days, with large symbols denoting mid-month. Model fluxes are taken from

1162 CASA GFED3. The results show a positive bias in spring GPP in boreal and tundra ecosystems,
1163 driven by early GPP onset, which leads to an early transition from net C source to sink compared
1164 to CARVE-Opt.

1165

1166

1167