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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

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

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4	Spring photosynthetic onset and net CO ₂ uptake in Alaska triggered by landscape thawing
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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 CO₂ observations. Another global inversion with zero prior estimates the same timing for net 47 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.

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 (CO_2) 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 CO_2 .

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).

The impacts of changes in growing season length on annual C balance are not well modeled (Schaefer et al., 2012). In particular, Earth System Models used in IPCC climate assessments predict photosynthetic growing season onsets that are systematically early on local (Peng et al., 2015) to regional scales (Commane et al., 2017a). In turn, GPP biases propagate through the model and affect the timing and magnitude of estimated net biosphere production (NBP) (Wang et al., 2012), representing the balance of GPP and TER (NBP = GPP – TER). Because climate change at high latitudes promotes earlier and longer growing seasons (Barichivich et al., 2013; Kim et al., 2012), while the photoperiod remains fixed, models with early spring bias in the current climate are likely to under-estimate the photosynthetic response to future warming. Consequently, errors in the simulation of growing season onset and duration provide a plausible explanation for the tendency of Earth System Models to underestimate peak growing season C 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 (Oberbaur 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 photoininhibition 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).

Analysis of SIF-GPP relationships in Alaska has shed light on the effects of plant structural vs functional phenology changes on seasonal C fluxes across key Arctic biomes, and helped quantify Alaskan C balance (Commane et al., 2017a), but have not yet clarified links between plant phenology and environmental effects in driving seasonal onset of GPP and net C uptake. As such, our quantitative and mechanistic understanding of links between environmental forcing, 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 time-series singularity classifier to identify the timing of freeze/thaw and snowmelt transitions 161 162 (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 dialectric 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° latitude x 176 ¹/₄° 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 (overcast) pixels within the 40x80 km GOME-2 footprint. The main effect of the remaining 182 183 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 CO₂ 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 CO₂ enhancements 201 are obtained by convolving the land surface influence functions with NBP priors from PVPRM, 202 which were aggregated to $0.5^{\circ} \ge 0.5^{\circ}$ for the CO₂ 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 CO₂ 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).

Commane et al. (2017a) account for uncertainties in observations, background, transport, and the model prior in CARVE-Opt using restricted maximum likelihood estimation, then generate 10,000 realizations of the additive flux correction. The standard deviation produces regionally 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 a net C uptake onset error of 5-10 days on average (cf Fig. 3, Luus et al., 2017 and Fig. 1, Commane et al., 2017a). We do not explicitly account for these uncertainties in our analysis, but 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 TER = NBP*a + GPP*b

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

We analyze CARVE-Opt NBP against an ensemble of 3 global inverse estimates constrained against satellite or surface CO₂ observations: (1) NASA Carbon Monitoring System Flux (CMS- Flux) estimation and attribution strategy (Liu et al., 2014, 2017; Ott et al., 2015) constrained by column CO₂ from the Greenhouse gases Observing SATellite (GOSAT) using the v7.3 ACOS retrieval algorithm; (2) CarbonTracker 2016 (CT2016) (Peters et al., 2007, with updates documented at http://carbontracker.noaa.gov) constrained by 124 datasets from a global network of tower, aircraft, and shipboard surface *in situ* CO₂ observations; and (3) Jena CarboScope s04_v4.1 (Jena4.1) (update of Rödenbeck et al, 2003, 2005), constrained by surface observations at 59 sites. All inverse estimates are analyzed for the period 2012-2014.

We also analyze simulated GPP and NBP from the CASA-GFED3 model (van der Werf et al., 244 2010), which is run at $0.5^{\circ}x0.5^{\circ}$ monthly resolution and scaled to 3-hour and $1^{\circ}x1.25^{\circ}$ 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 Atqasuk (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 during the nighttime (PAR < 50 umol $m^{-2} s^{-1}$) and air temperature (Euskirchen et al., 2017; 259 260 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 $0.5^{\circ}x0.5^{\circ}$, 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 > $0 \text{ gC m}^{-2} \text{ d}^{-1}$. 321

We analyze only grid points with average elevation < 1300 m (no alpine vegetation) and less than 60 days of reported thaw or snow-melt status from January 1 to spring thaw date as 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-328 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°x1/4°; CARVE-Opt: 0.5°x0.5°). 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 regridding of PVPRM NBP from its native grid 358 $(1/6^{\circ}x1/4^{\circ})$ to the coarser 0.5°x0.5° 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 NPB 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.

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

Focusing on the relative time lag between thaw and GPP onset shows very different patterns in boreal vs tundra; PVPRM-SIF shows similar time lags in boreal and tundra locations (~33 days), whereas flux towers show no lag in boreal forests but a 33 day lag in tundra. These discrepancies are attributed primarily to late GPP onset bias in PVPRM-SIF in boreal forests, which is linked to late morning GOME-2 SIF snapshots and thus unresolved diurnal photosynthetic signals in
 evergreens (e.g., Fig. S7). We elaborate on these discrepancies in the Discussion. Regional
 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 find a high correlation between thaw and GPP onset ($R^2 = 0.69$; p-value < 0.001) with slope less 406 than one $(DOY_{thaw} = 0.5*DOY_{GPP} + 79.5)$, where DOY_{thaw} and DOY_{GPP} denote dates of thaw and 407 408 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 (10-20% of its annual peak). This analysis yields $R^2 = 0.30$ and 0.31, respectively, representing 413

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±26 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 CO₂ 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±0.03 gC m⁻² for every 2 weeks of delayed thaw ($R^2=0.44$). All ecosystems exhibit similar relationships, but the sensitivity of 427 428 reduced GPP to delayed thaw date is three times stronger on average in boreal forests (e.g., -429 0.9 ± 0.09 gC m⁻² d⁻¹ per 2 weeks) than in tundra (e.g., -0.3\pm0.04 gC m⁻² d⁻¹ per 2 weeks). Spring 430 NBP also decreases with later thaw (-0.5 \pm 0.02 gC m⁻² d⁻¹, Fig. 4c), but shows higher consistency 431 (within a factor of 2 difference) across ecosystems (tundra = -0.2 ± 0.06 gC m⁻² d⁻¹; boreal = $-0.4\pm$ 0.04 g C m⁻² d⁻¹). As such, the sensitivities of GPP and NBP to thaw in tundra are of similar 432 magnitude while sensitivities for boreal forest are 2-3 times weaker for NBP than GPP. The 433 434 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 $(tundra=-0.6\pm0.1; boreal=-0.5\pm0.1).$

The reduced sensitivity of NBP to GPP in boreal points to TER onset as a key factor also driven by thawing, and which offsets the initial spring GPP. Aggregated plots of TER (Fig. 5a) show an initial increase between snowmelt and landscape thaw (DOY 100±10 and 111±7, respectively), ~4 weeks prior to GPP onset (DOY 141±5). The transition from onset of GPP to net C uptake (DOY 145±10) is short throughout boreal forests (Fig. 3f), but the C uptake rate is initially slow (-1.2 gC m⁻² 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 fully445 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 $(4\pm7 \text{ das})$ 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 CO₂ 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 that to net C uptake is delayed in tundra by 37 ± 9 days (Fig. 3e), similar to 464 the boreal transition $(34\pm9 \text{ days})$, but leads to a 50% higher NBP following the transition to net C uptake (-1.8 gC m⁻² month⁻¹). Regional mean C flux onset dates and lag times in tundra are 465 466 consistent and within the uncertainty of eddy covariance data analyzed in this study.

467 Analysis Against Other CO₂ 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.

Jena4.1 estimates a smaller rate and depth of uptake in the early growing season compared to CARVE-Opt and CT2016. The smooth transition from March to July aligns well with BON-Spr but not with BON-Fen or BON-Bog. The small seasonal amplitude in Jena4.1 is likely related to the model prior which, in contrast to both CARVE-Opt and the other global inversions, uses a 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 spring tundra source likely falls somewhere between CARVE-Opt (~0.5 gC m⁻² d⁻¹) and surface 493 inversions (< 0.1 gC m⁻² d⁻¹) as suggested by eddy covariance data (~0.25 gC m⁻² d⁻¹), although 494 495 we note a stronger pulse at the representative tundra site of IVO (Fig. S2g), which peaks at 0.5 gC m⁻² d⁻¹ in mid June. Nevertheless, CT2016 and Jena4.1 capture the delayed timing of spring 496 497 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 $(23\pm7 \text{ days})$ compared to boreal forests $(29\pm6 \text{ days})$ 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 (Arneth et al., 2006).

Interior boreal forests, on the other hand, have been found to require at least an extra week toreach 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.

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

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

This research has also demonstrated that our method to aggregate GOME-2 SIF retrievals by month and biome class, with linear interpolation between values (Luus et al., 2017), is inadequate to resolve spring transitions at high latitudes. Analysis of 5-day mean SIF retrievals, for example, suggest earlier photosynthetic recovery at BON than in the regional average of Alaskan evergreens (Fig. 2a). Future efforts to reduce these errors and interpret patterns of thaw vs C flux onset requires at a minimum non-linear interpolation methods for monthly SIF, and ideally more spatiotemporal explicit application of satellite SIF data in light use efficiency models. More sustained early season, spatially intensive sampling of airborne CO_2 (Parazoo et al., 2016) and longer-term eddy covariance fluxes and from additional sites in high northern 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 measurement of ecosystem fluxes available, however, several uncertainties should be considered 668 in the interpretation of our results: (1) The tower footprint ($\sim 10^{0}$ km²) is large compared to 669 670 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), and aggregated SIF soundings ($\sim 10^4$ km²). Although some effort is made to capture sub-grid 677 678 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 $(\sim 5 \text{ weeks})$, 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 orrection. 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.

Regarding the third factor (optimization window), CMSb7.3 uses a monthly window; CT2016 uses a weekly (8 day) window. We propose that the smaller 8 day window allows more flexibility for data assimilation to adjust the spring transition date, which greatly affects the interpretation of seasonal C uptake dynamics. Alternative inverse methods which estimate scaling factors for gross fluxes (Deng et al., 2016) or persistent grid scale biases (Lokupitiya et 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

We thank the two Anonymous Reviewers for comments/suggestions that significantly improved
this paper. CarbonTracker CT2016 results provided by NOAA ESRL, Boulder, Colorado, USA
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

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1080 1081 1082 Tables

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
	Black Spruce Forest (BON-Spr)	Interior Alaska	64.696°N, 148.323°W	100 m	2012-2013	Euskirchen et al., 2014
Bonanza Creek Experimental Forest (BON)	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
	Wet Sedge Tundra (IMN-Sed)	North Slope Alaska	68.606°N, 149.311°W	920 m	2012-2014	Euskirchen et al., 2017
Imnavait Creek Watershed (IMN)	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

Table 2: Mean (\pm SD) [Min Max] dates (DOY) for regional estimates of spring snow melt,1086landscape thaw, GPP onset, C sink onset and mean time lags (days) between thaw and GPP onset1087and between thaw and C sink onset. Results are shown at eddy covariance (eddy covariance)1088towers (eddy covariance observations shown in parentheses), EPA Level II and III ecoregions1089(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	117 ± 12;	$133 \pm 5;$	$154 \pm 3;$	167 ± 9;	$20 \pm 5;$	$36 \pm 10;$	14 ± 8;
North Slope	[84.2 153]	[118 148]	[144 160]	[147 182]	[9 31]	[16 50]	[2 27]
Tundra	112 ± 8;	$126 \pm 5;$	$150 \pm 3;$	161 ± 8;	24 ± 4;	35 ± 7;	11 ± 6;
Brooks	[94 127]	[113 132]	[142 156]	[139 180]	[17 33]	[16 50]	[-3 25]
Tundra	103 ± 12;	119 ± 15;	$146 \pm 5;$	$159 \pm 11;$	26 ± 11;	$41 \pm 10;$	$13 \pm 8;$
Southwest	[77 131]	[85 135]	[137 164]	[139 178]	[7 57]	[13 76]	[-3 36]
Boreal	98 ± 8;	110 ± 7;	139 ± 3;	144 ± 7;	$29 \pm 5;$	34 ± 6;	5 ± 5;
Interior	[78 121]	[96 129]	[135 149]	[137 175]	[16 42]	[16 61]	[-2 30]
Boreal	102 ± 11	112 ± 7;	142 ± 5;	$146 \pm 12;$	$30 \pm 6;$	34 ± 11;	4 ± 9;
Mountain	[66 136]	[89 152]	[135 177]	[133 188]	[-2 67]	[5 82]	[-17 38]
Tundra: North Slope + Brooks + Southwest	112 ± 12; [77 153]	127 ± 10; [85 148]	151 ± 5; [137 164]	163 ± 10; [139 182]	23 ± 7; [7 57]	37 ± 9; [13 76]	13 ± 7; [-3 36]
Boreal: Interior + Mountain	100 ± 10; [66 136]	111 ± 7; [89 152]	141 ± 5; [135 177]	$145 \pm 10;$ [133 188]	$29 \pm 6;$ [-2 67]	34 ± 9; [5 82]	4 ± 7; [-17 38]

1090 Figures



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Fig. 1: Map showing spatial pattern of vegetation and location of flux towers. Vegetation is derived from US EPA Level 2 ecoregion maps for boreal (reds) and tundra (blue). Tower sites include: Bonanza Creek (BNZ: 64.70°N, 148.32°W), Imnavait (IMN: 68.62°N, 149.30°W), 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).





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 low pass butterworth filters (order 2, cutoff frequency = 0.1) for PVPRM-SIF (solid black, top) 1102 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.



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

for Alaska constrained by airborne CO_2 profiles. Number of days between thaw and GPP onset (D), thaw and net C uptake (E), and GPP onset to net C uptake (F) are estimated as the difference between maps in A-C. Values in A-C are plotted as day of year (DOY). This shows similar spatial patterns of the timing of spring thaw and GPP onset, and a decrease in the number of days from thaw to spring onset moving from south to north along the boreal-tundra gradient.



Fig. 4: Relationship between spring CO_2 flux and landscape thaw. Scatter plots show regressions of (A) Spring GPP onset date vs thaw date, (B) Mean spring GPP from May 15 – June 15 vs thaw date, (C) Mean spring NBP from May 15 – June 15 vs thaw date, and (D) mean spring NBP vs GPP (g C m-2 d-1). Positive NBP denotes net C uptake by plants. Colors denote the 5

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



Fig. 5: Seasonal GPP and NBP patterns for boreal and tundra ecoregions. (A-B) Seasonal GPP (solid) from PVPRM-SIF and terrestrial ecosystem respiration (TER, dashed) from the residual of CARVE-Opt NBP and PVPRM-SIF GPP. (C-D) Seasonal NBP derived from daily averages of CARVE-Opt (black), CT2016 ensemble (red), and Jena v4.1 (blue) posterior fluxes and CT2016 prior fluxes (red dashed). (E-F) Seasonal NBP (positive denotes net sink) derived from 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 observations. CMS b7.3 is derived from satellite column integrated CO2. CT2016 results are 1151 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.





Fig. 6: Errors in predicted seasonal GPP and TER. (A-B) Seasonal time series of daily optimized (solid) and simulated (dashed) GPP (green) and TER (red). (C-D) Regression of simulated and optimized GPP. (E-F) Regression of simulated and optimized TER. Optimized GPP is taken from PVPRM-SIF and TER as the residual of CARVE-Opt NBP and PVPRM-SIF GPP. Values 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.