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1 Primary Research Article

2 **Satellite chlorophyll fluorescence measurements**
3 **reveal large-scale decoupling of photosynthesis and**
4 **greenness dynamics in boreal evergreen forests**
5 **SIF tracks photosynthesis in ENF**

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22 **Key words:** *Phenology, photosynthesis, satellite sun-induced chlorophyll fluorescence,*
23 *vegetation greenness index, model GPP, spring recovery, boreal evergreen forests, light-use-*
24 *efficiency*

25 **Abstract**

26 Mid-to-high latitude forests play an important role in the terrestrial carbon cycle, but the
27 representation of photosynthesis in boreal forests by current modelling and observational
28 methods is still challenging. In particular the applicability of existing satellite-based proxies
29 of greenness to indicate photosynthetic activity is hindered by small annual changes in green
30 biomass of the often evergreen tree population and by the confounding effects of background
31 materials like snow. As an alternative, satellite measurements of sun-induced chlorophyll
32 fluorescence (SIF) can be used as a direct proxy of photosynthetic activity.

33 In this study, the start and end of the photosynthetically active season of the main boreal
34 forests are analysed using space-borne SIF measurements retrieved from the GOME-2
35 instrument and compared to that of green biomass, proxied by vegetation indices including
36 the Enhanced Vegetation Index (EVI) derived from MODIS data. We find that
37 photosynthesis and greenness show a similar seasonality in deciduous forests. In high-
38 latitude evergreen needleleaf forests, however, the length of the photosynthetically-active
39 period indicated by SIF is up to six weeks longer than the green biomass changing period
40 proxied by EVI, with SIF showing a start-of-season of approximately one month earlier than
41 EVI. On average, the photosynthetic spring recovery as signalled by SIF occurs as soon as air
42 temperatures exceed the freezing point (2-3 °C) and when the snow on the ground has not yet
43 completely melted. These findings are supported by model data of gross primary production
44 and a number of other studies which evaluated in-situ observations of CO₂ fluxes,
45 meteorology and the physiological state of the needles. Our results demonstrate the
46 sensitivity of space-based SIF measurements to light-use efficiency of boreal forests and their
47 potential for an unbiased detection of photosynthetic activity even under the challenging
48 conditions interposed by evergreen boreal ecosystems.

49 **Introduction**

50 Mid-to-high latitude forests are a substantial contributor to carbon fluxes (e.g. Beer et al.,
51 2010), constitute a large carbon pool globally (Thurner et al., 2014) and are expected to react
52 in a very sensitive way to global warming (Lenton et al., 2008). Despite their important role
53 in the global carbon cycle, the modelling of the carbon fluxes between the atmosphere and
54 the land surface is still challenging. Simulations show a large spread in the predicted
55 magnitudes, often the timing is inaccurate and/or the models do not truly represent
56 interannual variability (Jung et al., 2011; Huntzinger et al., 2012; Keenan et al., 2012;
57 Richardson et al., 2012; Schaefer et al., 2012; Anav et al., 2015). Biases in the predicted
58 gross primary production (GPP, gross carbon flux from the atmosphere into the plants) in
59 early spring and late autumn make the simulations prone to errors in determining the
60 respective start and end of the season (Schaefer et al., 2012). Thus, knowledge of the
61 seasonality of photosynthesis of the terrestrial vegetation cover gained from spatially and
62 temporally extensive observations is highly relevant. This calls for a global, spatially
63 resolved technique to monitor carbon fluxes and ecosystem functioning, especially in the
64 arctic/boreal zone where in-situ observations are sparse and spatially biased (Schimel et al.,
65 2015).

66 Satellite observations of the surface reflectance are a widely used approach to
67 infer the amount of green biomass on Earth and the photosynthetic potential of the terrestrial
68 vegetation cover. Often this is done using vegetation indices (VIs), which are a combination
69 of reflectances in different spectral bands designed to enhance the sensitivity to green
70 vegetation (e.g. Huete et al., 2002). In vegetation with large seasonal greenness changes,
71 where leaf phenology and carbon uptake are strongly connected (Hadley et al., 2009),
72 reflectance based tracking of greenness provides good estimates of the seasonality of GPP

73 (Shen et al., 2014). However, greenness indices have a low sensitivity to short-term
74 variations in GPP (e.g. Yang et al., 2015). Another major drawback of surface reflectance
75 measurements is that they suffer from seasonally changing contamination by shadows, snow
76 and other canopy backgrounds, non-photosynthetically active plant materials and the
77 atmosphere. Although greenness indices have been proven useful to delineate potential GPP
78 for many biomes (e.g. Xiao et al., 2004), the limitations to indicate photosynthetic
79 activity become particularly evident in boreal evergreen needleleaf forests (ENF). Here
80 greenness changes cannot be well distinguished from the signals driven by the annual snow
81 cover (e.g. Delbart et al., 2005; Beck et al., 2006; Böttcher et al., 2014). More than half of the
82 annual change of greenness indices has been found to be caused by snow in many boreal
83 evergreen areas (Delbart et al., 2005; Jönsson et al., 2010). In contrast to deciduous
84 broadleaf forests (DBF), in ENF changes in biomass related to bud burst, shoot elongation,
85 needle growth and shedding are small and slow and in sparse forests influenced by the
86 understorey vegetation (Jönsson et al., 2010; Böttcher et al., 2014). Also, as opposed to
87 photosynthesis, greenness indices are not reduced down to zero in ENF in dormant periods,
88 hence they do not provide an unambiguous index on when actual photosynthesis starts or
89 ends. Ongoing efforts to exploit reflectance-based observations to indicate GPP seasonality
90 also in boreal ecosystems have lead to the development of improved vegetation indices with
91 lower sensitivity to snow and background changes and higher consistency in the relationship
92 to canopy development and GPP. Examples are the plant phenology index (Jin and Eklundh,
93 2014) or the phenology index (Gonsamo et al., 2012; D'Odorico et al., 2015).

94 Still, to monitor GPP in boreal evergreen areas, indicators of instantaneous
95 physiological function are needed. A promising example is the photochemical reflectance
96 index PRI (Gamon et al., 1992; Peñuelas et al., 1995) which has been shown to be related to

97 photoprotective mechanisms in a leaf and hence to photosynthetic light use efficiency Φ_p
98 (e.g. Gamon et al., 1992; Peñuelas et al., 1995; Gamon et al., 1997; Nichol et al., 2000;
99 Barton and North, 2001; Garbulsky et al., 2011; Wong and Gamon, 2014, 2015). However,
100 there does not yet exist a global PRI data set which can be applied at ecosystem level and
101 studies employing PRI have mostly been limited to the leaf and stand scale due to influences
102 of background material and understorey, illumination and viewing conditions, canopy
103 structure/LAI, nutrient status, atmospheric effects, very low temperatures and overlapping
104 physiological effects that confound the interpretation of PRI at different temporal and spatial
105 scales (Gamon et al., 1992, 1997; Nichol et al., 2000; Barton and North, 2001; Garbulsky et
106 al., 2011; Porcar-Castell et al., 2012; Wong and Gamon, 2014, 2015; Damm et al., 2015).

107

108 Complementarily to that, satellite measurements of sun-induced chlorophyll
109 fluorescence (SIF) offer the possibility to monitor actual photosynthetic activity. After the
110 first global retrievals of satellite-based SIF were accomplished in 2011 (Joiner et al., 2011;
111 Frankenberg et al., 2011), strong positive seasonal correlations between SIF retrieved from
112 GOSAT and GOME-2 and GPP from model simulations and flux-tower estimates have
113 empirically been found for different biomes (Frankenberg et al., 2011; Guanter et al., 2012;
114 Lee et al., 2013; Parazoo et al., 2013; Joiner et al., 2014). Yang et al. (2015) report on high
115 diurnal and seasonal correlations between satellite and ground-based SIF and tower GPP in
116 deciduous forests. Also, first initiatives to constrain model GPP with SIF brought remarkable
117 results in that the adapted GPP values and seasonalities are in closer agreement with flux
118 tower measurements (Guanter et al., 2014; Parazoo et al., 2014; Zhang et al., 2014). The
119 exact behaviour of the positive relationship between SIF and GPP varies with retrieval
120 wavelength, biome, canopy structure, temporal scale and stress level (e.g. Guanter et al.,

121 2012; Damm et al., 2015; Rossini et al., 2015).

122 Complex photosynthetic processes underlie the relationship between SIF and
123 GPP. In the light reactions of photosynthesis, energy from solar photons is absorbed by
124 pigments and transferred to reaction centres in so-called photosystems. A chain of reactions
125 and electron transport eventually leads to the storage of the energy in chemical compounds.
126 In the dark reactions, this energy is consumed in biochemical processes to fix carbon and
127 produce sugars (photochemical quenching, resulting in GPP; Jones and Vaughan, 2010).
128 What we approximate with surface reflectance measurements and VIs is the amount of
129 absorbed photosynthetically active radiation (APAR). However, due to both, intrinsic
130 limitations of the photosynthetic machinery and external stress factors, the APAR cannot
131 completely be used for carbon fixation. Excess energy is re-emitted from the leaf at longer
132 wavelengths, which is termed chlorophyll fluorescence, or dissipated as heat (non-
133 photochemical quenching, NPQ). Chlorophyll fluorescence can be evaluated as a proxy for
134 the activity of photosystems of type II and its electron transport rate (PSII, there exist also
135 photosystems of type I with a rather constant but non-negligible contribution to SIF, also
136 dependent on the wavelength of the retrieval; Maxwell and Johnson, 2000; Baker, 2008;
137 Rossini et al., 2015). The fluxes of SIF and GPP have been modelled and observed to be
138 positively correlated, albeit with variable strength in response to environmental conditions
139 and the activity of NPQ (van der Tol et al., 2009; Frankenberg et al., 2011; Guanter et al.,
140 2012; van der Tol et al., 2014; Damm et al., 2015).

141 In ENF, which are the focus of this work, Wong and Gamon (2015) find that
142 CO₂ exchange and the activity of PSII, or more precisely the electron transport away from it,
143 start to recover at similar times in spring (see the beginning of the positive slope in Fig. 4 in
144 Wong and Gamon, 2015). As SIF is a proxy for the PSII electron transport eventually leading

145 to GPP, we expect this positive seasonal relationship between SIF and GPP to hold at the
146 synoptic scale. As an example for ENF, Fig. 1 shows the time series of GPP over a
147 homogeneous spruce stand at the flux tower site Fyodorovskoye, Russia, in 8-day time
148 resolution and sampling together with the satellite observations of SIF from the GOME-2
149 instrument within a radius of 30 km of the tower site. They have very similar timing of
150 spring and autumn transitions and often even react in parallel on the short time scale of some
151 weeks. These are compelling examples that support the assumption that SIF provides an
152 unambiguous indication of photosynthetically active periods (Yang et al., 2015).

153

154 This study focuses on the seasonality of photosynthesis in mid-to-high latitude
155 forests. To further our understanding of the functioning of boreal forested ecosystems, even
156 under the challenging conditions in ENF, we complementarily use the information content of
157 greenness and satellite SIF. The obtained results are related with meteorological data sets to
158 identify the main environmental factors driving the photosynthetic activity of boreal
159 ecosystems, especially the evergreen ones, at synoptic scales.

160

161

162 **Method and data**

163 *Data*

164 All data sets are evaluated from January 2007 to December 2011. They are all averaged to a
165 0.5° grid and sampled every 8 days with an average over the 16-day period following a
166 sampling date.

167

168 Sun-induced chlorophyll fluorescence is retrieved from measurements of the

169 GOME-2 instrument onboard the MetOp-A satellite which crosses the equator close to 9.30
170 local solar time. The retrieval is done in a wavelength range between 720 and 758 nm and
171 measurements taken with an effective cloud fraction of $>50\%$ are discarded (Köhler et al.,
172 2015). The resulting daily SIF data with a native pixel size of approximately 40 by 80 km²
173 are gridded in 0.5° cell boxes and binned in 16-day intervals with a sampling every 8 days.
174 Please note, that with SIF we exclusively refer to satellite retrievals of the sun-induced
175 chlorophyll fluorescence flux, which is different from the fluorescence yield or efficiency
176 (Φ_f , fluorescence flux divided by APAR) and other related fluorescence parameters often
177 employed in in-situ studies with active measurement techniques.

178 The enhanced vegetation index EVI (Huete et al., 2002) and the normalized
179 difference vegetation index NDVI (Tucker, 1979) are calculated from NBAR surface
180 reflectance measurements from the MODIS instrument in a 0.05° spatial resolution
181 (MCD43C4, v005, combination of MODIS measurements onboard Terra and Aqua). NBAR
182 means reflectances are normalized to nadir from multi-angular, cloud-free, atmospherically
183 corrected measurements using the bidirectional reflectance distribution function for the solar
184 angle at local noon time
185 (http://landweb.nascom.nasa.gov/QA_WWW/forPage/C005_Change_BRDF.pdf). The
186 reflectances in the MCD43C4 product are a weighted average over 16 days ascribed
187 to the first day of a corresponding 16-day period. We calculate the VIs from the NBAR
188 reflectances instead of using the official MODIS vegetation index product in order to
189 minimize potential seasonal effects of the illumination geometry. The resulting time series
190 are filtered, in that only retrievals with up to 'moderate' quality (quality flag in the MODIS
191 files 0-best/75% or more with best full inversions, 1-good/75% or more with full inversions
192 and 2-mixed/75% or less full inversions and 25% or less fill values) are retained. As

193 reflectances are strongly affected by the occurrence of snow, a snow correction is necessary.
194 The snow flag provided by the MCD43C4 files indicates the percentage of sub-pixels that are
195 covered with snow (36 sub-pixels per $0.05^\circ \times 0.05^\circ$ box). Identification of snow is done via
196 different criteria (http://modis.gsfc.nasa.gov/data/atbd/atbd_mod10.pdf) using the normalized
197 difference snow index, band 1 and band 2 and the NDVI. This snow flag is used to identify
198 pixels containing snow (similar to Zhang et al., 2006), which are then removed from the data
199 sets. We tested for a stricter quality filtering using only retrievals with best and good quality
200 (flags 0 and 1) and for less strict criteria in the snow filter allowing 10% and 30% snow. The
201 results largely remain the same (section S1 of the supporting information).

202 As a complementary data source, the NDVI3g data stream has been
203 included in the analysis (<https://nex.nasa.gov/nex/projects/1349/>). It is a GIMMS AVHRR
204 time series improved for usage in high latitudes (compared to its predecessor) in native
205 0.0833° resolution with 15-day temporal resolution. It is a maximum value composite
206 (MVC) with unknown exact day of acquisition and no direct correction for bidirectional
207 reflectance effects (Guay et al., 2014). We assigned a value to the first day of a possible
208 acquisition period, i.e. days 1 and 16 of a month, as also in the MODIS files the values
209 correspond to the 16-day period starting at the indicated date. It has been quality filtered
210 using the flags provided in the data files. Values flagged 4, 6 or 7 (possibly containing snow
211 or missing) have been discarded. In contrast to all other data sets NDVI3g is evaluated at the
212 native 15-day resolution and bimonthly sampling.

213 Model data for GPP stem from an ensemble of statistical, remote sensing
214 (MODIS) data-driven models used to empirically upscale flux tower measurements to the
215 global scale (FLUXCOM, Jung et al. 2015, in prep.). These models employ machine-learning
216 techniques and have been shown to perform well in representing seasonal patterns (Jung et

217 al., 2011). The median of 18 ensemble members (nine different machine-learning techniques
218 and two different methods to partition flux tower measurements into GPP and respiration) is
219 taken as representative for GPP. These model GPP data have a native resolution of 0.083°
220 and 8 days.

221 Meteorological variables provided by the European Center for Medium-Range
222 Weather Forecasts (ECMWF) ERAInterim data set (Dee et al., 2011) are used to evaluate the
223 dependency and interaction of SIF, model GPP and the VIs with environmental conditions.
224 We use 2 m air temperature, soil temperature, soil water content and photosynthetically
225 active radiation arriving at the surface (PAR). ERAInterim data provide soil measures
226 (volumetric water content and temperature) in 4 layers: 0-0.07 m depth, 0.07-0.28 m, 0.28-
227 1.0 m and 1.0-2.89 m. Complete information on the forest conditions cannot be provided by a
228 single layer. This is because the sensitivity of the trees to soil temperature and available
229 water does not only depend on the vertical rooting distribution and depth but also on soil
230 composition and the resulting hydraulic conductivity (Plamboeck et al., 1999). In this
231 analysis, we chose the second layer between 7 and 28 cm depth. The uppermost layer will not
232 reliably indicate the available amount of water and temperature conditions to the trees as
233 their rooting will extend to greater depth. The lowest layer will be important for the forests
234 but it is weakly affected by meteorology and may contain the groundwater level and hence
235 we do not expect it to be a crucial factor in (inter-)annual phenology. We use the second
236 rather than the third layer to enlarge comparability of our results with in-situ ground
237 measurements which usually are taken in 2, 5, or 10 cm depth. Qualitatively the results do
238 only slightly change when the third layer is used as the timing of the annual peaks and
239 minima is shifted a little (not shown). PAR is produced as an accumulated variable over a
240 certain time range, hence the PAR values contain information on both the actual radiation

241 arriving at the surface and the day length. The data have a spatial resolution of 0.5°. The
242 native temporal resolution is 6 hours (or 12 hours for accumulated variables like radiation).

243 Identification of the forest area of interest is based on the IGBP
244 (International Geosphere-Biosphere Programme) classification scheme and the data
245 provided in the MODIS MCD12C1 v051 data file for 2009. We take 2009 as representative
246 for the whole period under investigation between 2007 and 2011. The IGBP data have a
247 spatial resolution of 0.05°. To aggregate them to 0.5°, we allocate the vegetation class to a
248 0.5° pixel where the majority of the underlying 0.05° subpixels belong to. To verify a certain
249 level of homogeneity in the vegetation cover type, we only use those grid boxes in the
250 evaluation where the frequency of subpixels belonging to a certain vegetation type is at least
251 75%. The threshold of 75% is chosen as a compromise between assuring high homogeneity
252 and at the same time retaining sufficient pixels for a meaningful analysis. This correction is
253 expected to influence and clarify the results as Klosterman et al. (2014) found larger biases in
254 some satellite derived transition dates in comparison to local observations for heterogeneous
255 pixels.

256 Further, we divide the forest areas classified by IGBP into ecoregions as they
257 are delineated by Olson et al. (2001, <http://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world>). Polygons are rasterized to 0.5° by again assigning the ecoregion
258 ecoregions-of-the-world). Polygons are rasterized to 0.5° by again assigning the ecoregion
259 with the largest cover fraction to a pixel.

260 Northern hemisphere forests are shown in Fig. 4a. The focus in this study is on
261 boreal forests, which we delineate as north of 50° N.

262

263 *Method*

264 White et al. (2009) compare different methods to determine key phenological dates of the

265 growing season from the same data set and report that methods vary widely in the determined
 266 date of phenological phases, their variability, retrieval ability and their ordinal ranking. Hird
 267 and McDermid (2009) find that function fitting outperforms other noise reduction
 268 techniques in preserving the original shape of the time series (at least applied to NDVI time
 269 series). We chose the function fitting method proposed by Gonsamo et al. (2013) as a means
 270 to objectively quantify phenology. Here, the term phenology is used as a synonym for the
 271 research on periodically recurring events in biological life cycles in general and not limited to
 272 the study of morphological developments of plants. The method consists in fitting a double
 273 sigmoidal function to a complete cycle of vegetation development via non-linear least
 274 squares (Gonsamo et al., 2013).

$$275 \quad t(x) = a_1 + \frac{a_2}{1 + \exp(-d_1(x - b_1))} - \frac{a_3}{1 + \exp(-d_2(x - b_2))} \quad (1)$$

276 Equation (1) has been adapted to our time series with a maximum of 2000 iterations and a
 277 minimum step size of 10^{-6} . If no convergence is achieved, up to ten additional fitting attempts
 278 with slightly changed first guesses for the fitting parameters are done. Additionally to the
 279 weighting applied in Gonsamo et al. (2013), relatively smooth periods of the time series are
 280 'rewarded'. The central point of a three-point running median is double-weighted if it is
 281 within $\pm 25\%$ of the median value. This is intended to deal with the relatively high noise level
 282 of SIF retrievals, especially in winter. The fitting procedure has been applied pixel-wise for
 283 all five years of data availability (2007-2011). As the analysis is limited to forests in middle
 284 and high latitudes, it is sufficient to carry out the fitting procedure year-wise as only one
 285 vegetation cycle will be completed in one year. Details on the performance of the fitting can
 286 be found in section S2 of the supporting information. To derive the starting point in time of
 287 phenological phases, Gonsamo et al. (2013) provide easy to apply formulae using the

288 coefficients of the fitted function. The characteristic phases employed here are

289 1. start of season (SOS) or onset:
$$SOS = b_1 - \frac{4.562}{2d_2}$$

290 2. end of the season (EOS) or dormancy in case of evergreens:
$$EOS = b_2 + \frac{4.562}{2d_2}$$

291 The equations for the transition dates have been analytically derived from the extrema of the
292 derivatives of the fitted functions and describe the curvature behaviour of the time series/fit.
293 That means that they represent times when vegetation starts to progress from one state to
294 another. Hence, the phenological markers inferred from the fitted double-sigmoidal function
295 have biophysical meaning, which is the main reason for choosing this approach. Other
296 possible methods to determine SOS and EOS might be unphysical. For example, the crossing
297 of fixed thresholds of the annual amplitude as a measure for start and end of season neglects
298 the fact that spring onset is generally a faster process than the rather gradual autumn
299 senescence (Stöckli et al., 2008; Elmore et al., 2012). Fisher et al. (2006) discuss the
300 short-comings of various other methods to quantify phenology and advocate the midpoint
301 instead of the start of increase/decrease as the most robust measures for SOS/EOS. As this
302 corresponds to the date of the most rapid growth/senescence and not to the absolute starting
303 and ending times we decided to apply the SOS/EOS measures above by Gonsamo et al.
304 (2013). Figure 2 shows a SIF time series together with the fitted function and the transition
305 dates inferred from it.

306 **Results**

307 *Mean annual cycle and phenological transition dates*

308

309 As a first step in the analysis, we spatially average the VIs, model GPP and SIF over DBF
310 (east coast of North America, see Fig. 4a) and ENF (whole northern hemisphere north of 50°

311 N) and compare the median of the five annual cycles in Fig. 3.

312 In Fig. 3a we see that in DBF the seasonality of the photosynthesis proxy SIF,
313 the model GPP data and the greenness index EVI are very similar. Sharply increasing values
314 are observed from the start of April followed by the annual maximum by the end of May. In
315 summer, between June and September, slightly declining photosynthetic activity and EVI are
316 observed, before a rapid autumn shut-down follows from September to November. This
317 decline of photosynthesis in summer has also been observed by several studies but its causes
318 are still discussed. Wilson et al. (2000) find decreasing photosynthetic capacity (the
319 maximum rate of carboxylation v_{cmax}) in summer and suggest that changing fractions of
320 nitrogen allocated to the photosynthesis enzyme rubisco might play a major role. Bauerle et
321 al. (2012) explain with the help of experiments that decreasing photosynthetic capacity in
322 summer might be regulated by photoperiod. Yang et al. (2014) report on a 'summer
323 greendown' of the canopy measured with cameras and MODIS images. EOS_{EVI} is indicated
324 slightly later than EOS_{SIF} and EOS_{GPP} (Fig. 3a). It has often been reported that greenness
325 indices have a late EOS because the signal is influenced by litter, senesced or dead plant
326 material that has not yet been abscised and NIR scattering at low illumination angles (e.g.
327 Hadley et al., 2009; Jones and Vaughan, 2010; Gonsamo et al., 2012). These effects are weak
328 here in the case of the EVI in comparison to the findings of other studies using the NDVI
329 (e.g. Hmimina et al., 2013). A high degree of variability is also observed in the time series of
330 SIF in summer (similar to Yang et al., 2015), which often parallels the behaviour of model
331 GPP. Further details on that are shown in Fig. S12 and discussed in the supporting
332 information in section S4.

333 The high similarity of SIF to model GPP and the EVI in DBF supports the
334 assumption that photosynthesis and greenness are highly correlated in time and that our

335 methodological framework combining different data sets is consistent. However, the
336 behaviour of the two NDVI data streams (Fig. 3a) in DBF is inconsistent in that both tend to
337 increase early, the MODIS NDVI only slightly, NDVI3g significantly. Also, both are
338 characterized by a long summer plateau (in contrast to the declining values in summer in
339 EVI, SIF and model GPP) and late autumn senescence. Similar observations hold for
340 deciduous needleleaf forests (DNF, Fig. S5 of the supporting information), albeit the lag
341 between the NDVIs and the other three data streams is apparently larger here. The summer
342 plateau can possibly be explained by the well-known saturation effects of the NDVI in high
343 biomass canopies which is not seen in the EVI. Different sensitivities to background changes
344 like wetness and stronger multiple NIR scattering in the canopy at low illumination angles
345 which results in higher NDVI might play a role in the lag between NDVI and EVI from
346 MODIS (e.g. Huete et al., 2002). Diverse behaviour of the two NDVI data sets might
347 originate from distinct compositing methods (averaging vs. maximum value composite) and
348 sensor characteristics between MODIS and AVHRR. The following analysis will mostly
349 focus on the EVI. This is because of the differences of the NDVI to the independent data sets
350 of SIF, model GPP and EVI observed in deciduous forests, where high correspondence
351 between GPP and greenness (Hadley et al., 2009; Shen et al., 2014) as well as low snow
352 influence are expected. Also the EVI can handle background changes better than the NDVI
353 (Huete et al., 2002) which might become evident in a lower noise level in the EVI. Note that
354 the VIs do not return to zero in winter.

355

356 When it comes to evergreen forests of the high northern latitudes in Fig. 3b,
357 the photosynthesis proxies satellite SIF and model GPP again show a very similar seasonal
358 cycle. Both start to indicate photosynthetic activity in late March, while the EVI does not

359 mark greenness changes before late April/beginning of May. This is the most striking
360 difference in this mean seasonal cycle. While in summer and autumn the time series are close
361 to each other, the EVI tends to cease to its annual minimum of about 0.2 approximately two
362 weeks earlier than SIF. The EVI is strongly affected by the quality and snow filtering
363 (section S1). Apparently there are still some artifacts in the data resulting in variability in
364 winter and early spring (dashed green line in Fig. 3b). Restricting the MODIS reflectance
365 data to only the ones flagged with good quality will not change the behaviour of this mean
366 seasonal cycle (not shown). The tendency towards a broader growing season observed in
367 deciduous forests of MODIS NDVI and NDVI3g is also present in ENF. NDVI shows a very
368 late autumn senescence and a spring increase much earlier than the EVI increase and at
369 similar times like the SIF and model GPP.

370

371 When identifying the SOS objectively with the approach described in the
372 Methods section, Fig. 4b shows that there is spatial variability in SOS_{SIF} related to latitude
373 and continentality. For example, the SOS in the cold east Siberian DNF and mixed forests in
374 May (DOY 128-144) is in sharp contrast to the relatively early SOS in the beginning of April
375 (DOY 80-96) in the rather temperate ENF in southwestern Canada at the same latitude.

376 In Figure 4c the difference in the commencement of photosynthetic activity
377 (SOS_{SIF}) and green-up (SOS_{EVI}) largely exceeds one month in ENF and partly (in northern
378 areas) also in mixed forests. In the southern parts of the mixed forests, where the fraction of
379 deciduous species is expected to be higher, the differences decrease until they are much
380 smaller in the range of ± 8 days in DBF and DNF. The last column in Table 1 makes clear
381 that spatially averaged there are no differences between SOS_{SIF} and SOS_{EVI} in DBF,
382 whereas they amount to approximately 30 days in the whole ENF north of 50° N averaged

383 over all five years.

384 At the EOS, the map (Fig. 4d) shows a slightly later EOS_{EVI} in the deciduous
385 forests. However, this amounts to only 5 days in DBF (see Table S1). At finer temporal and
386 spatial resolution, a lag between leaf phenology/greenness and GPP seasonality has been
387 observed (Shen et al., 2014; D'Odorico et al., 2015) both at the start and end of the growing
388 season in deciduous vegetation. Although the maps in Fig. 4c,d show a tendency of SIF
389 towards a narrower growing season than EVI in DBF and DNF, these effects cannot reliably
390 be resolved with the temporal and spatial resolution in this study (see also Table 1). In the
391 mixed forests in western Russia (Fig. 4d), the EVI shows a delayed EOS by 2-4 weeks. In
392 ENF and mixed forests in North America, Siberia and Fenno-Scandinavia, SIF indicates a
393 later EOS than EVI of two to three weeks, which is in line with what we see in Fig. 3b. It is
394 remarkable how clear the maps of the phenological dates are able to show the transition
395 between mixed forests and DNF, e.g. in eastern Siberia.

396 Comparing the length of the growing season (difference of EOS-SOS, Fig.
397 4e), the results indicate that the period of photosynthetic activity is five weeks and in
398 individual spots even longer than the 'green phase' identified from EVI in the ENF and
399 northern parts of the mixed forests. It is approximately two to three weeks shorter in the
400 southwestern parts of Russia. In the DBF, EVI indicates up to two weeks longer growing
401 season than SIF.

402 Comparing the phenological transition dates between EVI and model GPP
403 (Fig. S6a of the supporting information) the patterns in ENF are similar to those between SIF
404 and EVI, but they partly have larger amplitudes. The differences at SOS between the
405 photosynthesis proxies and NDVI mostly have the same sign as in the comparison to the EVI
406 (Fig. S6b,c of the supporting information), albeit it needs to be acknowledged that their

407 magnitude is much smaller. At the EOS the patterns observed between EVI and SIF/model
 408 GPP are mostly replicated by the NDVI.

409

410 Overall, these results show that in deciduous forests the seasonality shown by
 411 SIF, model GPP and EVI is very similar, with a slightly late EOS_{EVI} . In ENF, however, the
 412 growing season of greenness as indicated by the EVI is approximately five weeks shorter
 413 than the one of SIF and model GPP with a much later SOS_{EVI} (more than a month) and a
 414 slightly advanced EOS_{EVI} (about one to two weeks).

415

416

417 *Sensitivity of SIF to the light-use efficiency of boreal forests*

418

419 Following a production-efficiency model (Monteith, 1972), SIF and GPP can be
 420 approximated as the product of APAR and a yield-term describing the efficiency with which
 421 the absorbed light energy is quenched in the photochemical and fluorescence pathway (e.g.
 422 Guanter et al., 2014; Joiner et al., 2014).

423
$$GPP = APAR \Phi_p = f APAR PAR \Phi_p \square EVI \square PAR \Phi_p \tag{2}$$

424
$$SIF = APAR \Phi_f \square \epsilon_{esc} = f APAR PAR \Phi_f \square \epsilon_{esc} \square EVI \square PAR \Phi_f \square \epsilon_{esc} \tag{3}$$

425 fPAR is the fraction of the incident PAR that is absorbed and can be approximated by the
 426 EVI. ϵ_{esc} is a wavelength dependent structural factor describing the fractional escape of
 427 fluorescence from the canopy for differently organized canopies. The question arises whether
 428 APAR or Φ_f dominate the SIF signal. SIF is a good indicator for green APAR which might
 429 be very useful for ecosystems in which GPP is driven by canopy chlorophyll content. This
 430 may explain the good correlations found between SIF and GPP for crops where stress levels

431 are mostly low (Guanter et al., 2014). But this will not be sufficient for biomes subject to
432 sustained stress periods like the ENF. Comparison of the mean annual cycles of SIF, EVI and
433 EVI·PAR approximating APAR over ENF in Fig. 5 reveals major differences between them.
434 EVI·PAR clearly has a much advanced seasonal cycle compared to EVI with earlier spring
435 rise, peak and autumn decrease which is also much earlier than in the case of SIF. The fact
436 that SIF and EVI·PAR have distinct seasonal cycles suggests that SIF over ENF is not only
437 driven by APAR but does contain major information on Φ_f . Combination of Eq. 2 and 3
438 offers the chance to deduct knowledge on Φ_p and GPP. The relationship between Φ_p and Φ_f
439 changes gradually in response to stress and environmental conditions. They are positively
440 correlated under NPQ dominance (in high light, most of the day, in the enzyme-limited case)
441 and change the sign of their relationship when light becomes a limiting factor (e.g. van der
442 Tol et al., 2009; Damm et al., 2015). Boreal forests in spring are normally exposed to high
443 light conditions as will be shown in Fig. 6 and 7 suggesting a positive relationship between
444 Φ_p and Φ_f . This is an important finding, especially for the carbon cycle modelling
445 community.

446

447 *Environmental conditions and photosynthetic activity*

448

449 Having identified the main differences in the seasonal behaviour of SIF and EVI, we studied
450 under what environmental conditions the evergreen forests leave winter dormancy and
451 become photosynthetically active again and green up on the large scale.

452

453 As an example for the regional scale, we examine in more detail the ENF of
454 the ecoregion of the Fenno-Scandinavian and Russian taiga (ecoregion number 706 following

455 Olson et al., 2001). This corresponds quite accurately to the ENF in Scandinavia, Finland and
456 Russia up to 60° E (compare Fig. 4a). The time series in Fig. 6 confirm the late SOS_{EVI}
457 relative to SOS_{SIF} . Comparing SOS_{SIF} with SOS_{NDVI} , there is also a lag between the
458 commencement of photosynthesis and green-up, although their magnitudes are much smaller
459 than in case of the EVI. Noise in the NDVI in Fig. 6 is higher than for the EVI (despite the
460 snow filter applied to it) which is another reason why we focus our analysis rather on the
461 latter.

462 The meteorological time series in Fig. 6 show that at the time of SOS_{SIF} , PAR
463 is already at $0.7-0.8 \text{ MJ m}^{-2} \text{ 12h}^{-1}$ which corresponds to almost two thirds of the annual
464 PAR maximum in the Fenno-Scandinavian and Russian taiga. The snow flag is indicating
465 that between one and two thirds of the surface are already snow free and the soil water
466 content is reaching its annual maximum at SOS_{SIF} . Average soil temperatures in 7-28 cm
467 depth are close to 0 °C. Mean daily mean air temperatures range between 0 ° and 5 °C and
468 the average daily minimum temperatures (lower bound of gray shading) are just crossing the
469 freezing point when photosynthetic activity commences. Similar observations can be made in
470 North America in the central and mid-western shield forests, which is shown as another
471 example in the supporting information in Fig. S11. Here the time series also reveal short-term
472 parallel behaviour between SIF and model GPP, e.g. short drops during cold spells in spring
473 and summer.

474 The same meteorological variables have been averaged over the phenological
475 transition dates of all five years of SIF and EVI and their spatial distribution is displayed in
476 Fig. 7. The start of the active period indicated by SIF occurs at mean daily air and soil
477 temperatures between 0 ° and 5 °C in the mid-to-high latitude evergreen forests, and it
478 becomes progressively warmer the more mixed and/or deciduous the vegetation gets.

479 Average daily minimum temperatures are slightly negative, but average daily maximum air
480 temperatures are markedly above 0 °C at SOS_{SIF} (shown in section S3, Fig. S7). Between 30
481 and 70% of the surface in ENF is still snow covered, so photosynthetic recovery coincides
482 with the time of snow melt (except for the region south of the Canadian Muskwa-Slave-Lake
483 where the surface is mostly snow free). In the mixed and deciduous forests, SOS_{SIF} takes
484 place after complete snow melt. PAR is already higher than half the annual maximum at
485 SOS_{SIF}. Soil water content at the SOS is highest in the northern most areas for both SIF and
486 EVI and becomes progressively lower to the south of the investigation area (Fig. S7). For the
487 EVI, this meridional gradient is larger than for SIF, which becomes most apparent in the
488 mixed forests. The conditions are similar between SIF and model GPP and between EVI and
489 NDVI, respectively (Fig. S8). Their small differences are consistent with the slightly earlier
490 SOS of model GPP than SIF and NDVI than EVI.

491 In Table 1 the environmental conditions averaged over the SOS of all five
492 years in all ENF pixels north of 50° N confirm air temperatures between 1 and 3 °C, 72% of
493 the annual illumination maximum and between 37 and 59% (with high variability) ground
494 snow cover at the start of photosynthesis. At SOS_{EVI} air temperatures are at 9 °C and
495 illumination has reached 90% of its annual maximum. In DBF, SOS is marked at 13 °C and
496 about 80% of the annual illumination maximum for SIF, model GPP and EVI.

497

498 The differences in EOS between SIF and EVI in evergreen forests in Russia,
499 Finland and Scandinavia (Fig. 6) become slightly smaller than at the SOS and hence also the
500 meteorological conditions are closer to each other. The first snow is accumulating, average
501 daily mean air and soil temperatures are in the range of +5 °C (except 2009, both at 0 °C) and
502 illumination has already been reduced drastically. Only around 0.2 MJ m⁻² 12h⁻¹ (17% of

503 annual maximum) PAR reach the canopy at the approximate EOS.

504

505 The situation is similar in the evergreen forests in North America in Figures
506 S9 and S10. Table S1 confirms that averaged over all northern hemisphere ENF PAR is
507 everywhere between 15 and 19% of the annual maximum, at EOS_{EVI} still a bit higher than at
508 EOS_{SIF} . Average soil and air temperatures are again close to the freezing point (0-2 °C) at
509 EOS for both SIF and EVI, although in North America temperatures at EOS_{SIF} are slightly
510 lower than for EOS_{EVI} . No or very little snow has already fallen at this time of year
511 (maximum 28% in case of EOS_{SIF}). The conditions are again similar between EOS_{SIF} and
512 EOS_{GPP} and between EOS_{EVI} and EOS_{NDVI} respectively. Striking is an exceptionally early
513 EOS in case of NDVI north of the Great Lakes (Fig. S7).

514

515

516 **Discussion**

517 *Spring recovery in evergreen needleleaf forest*

518

519 The most important finding of this study is twofold: In the high latitude ENF, green-up lags
520 behind the commencement of photosynthesis as proxied by SIF by several weeks. Further,
521 the
522 seasonal behaviour of SIF is much more similar to model GPP than to APAR, which means
523 that SIF contains information on photosynthetic light-use-efficiency Φ_p in ENF. Both
524 findings are fully consistent with process understanding at the leaf and molecular scale and
525 supported by model GPP data (Fig. 3, 4 and 6, Table 1) on the synoptic scale and by flux
526 tower observations and dedicated studies at site-level.

527 Several small scale studies comparing CO₂-fluxes inferred from tower eddy-
528 covariance measurements with maximum photosynthetic light use efficiency Φ_p , satellite VIs
529 and various temperature measures confirm that physiological spring recovery commences
530 before any change in biomass or greenness (Ottander et al., 1995; Tanja et al., 2003; Louis et
531 al., 2005; Arneth et al., 2006; Soukupová et al., 2008; Richardson et al., 2011; Thum et al.,
532 2009; Jönsson et al., 2010; Melaas et al., 2013; Böttcher et al., 2014). We find the magnitude
533 of the temporal lag between green-up and the first signs of photosynthesis to be around one
534 month (Fig. 4, Table 1 and Fig. S6 in the supporting information). This is in accordance with
535 site-level studies, too, as net accumulation of chlorophyll and other pigments as well as bud
536 burst have been observed to occur approximately one month after the first photosynthetic
537 activities (Ottander et al., 1995; Soukupová et al., 2008; Richardson et al., 2011). Wong and
538 Gamon (2015) describe the spring recovery of a series of leaf-level physiological indicators
539 in coniferous species with sigmoidal functions similar to our approach. The approximation of
540 the measurements by logistic functions offers the chance to try to directly compare our SOS
541 on the large scale with the start of spring recovery of the several parameters in their Fig. 4 by
542 visually identifying SOS as the point with the highest curvature change rate/the start of
543 increase (Gonsamo et al., 2013). Please note that this differs in methodology from their
544 approach, which consists in using the half recovery time as SOS. The chlorophyll:carotenoid
545 pigment pool ratio in Fig. 4 in Wong and Gamon (2015) starts to recover several weeks after
546 the commencement of photosynthesis which supports the consistency of our result despite
547 the large gap between the spatial scales.

548 In the absence of observations at intermediate scales, comparisons between
549 measurements in a satellite footprint and pigments in a leaf can only be of hypothetical
550 nature. Still, we put our second major finding - the similarity between SIF and GPP - into the

551 context of a series of major changes of the chloroplast functioning between winter and
552 spring. In a state of acclimation to low temperatures in winter which inhibit enzymatic and
553 hence photosynthetic activity the trees need to keep a balance between the light energy
554 absorbed and the energy used in carbon fixation. Mechanisms aiming to reach this balance
555 include reduced absorption capacities as a result of lowered relative chlorophyll content
556 (Wong and Gamon, 2015) and effective thermal energy dissipation (NPQ; Ottander et al.,
557 1995; Öquist and Huner, 2003; Ensminger et al., 2004; Busch et al., 2007; Porcar-Castell,
558 2011; Porcar-Castell et al., 2014; Verhoeven, 2014). Xanthophyll and other carotenoid
559 pigments modulate the thermal energy dissipation by the PSII. Sustained conversion of
560 carotenoid pigments of the so-called xanthophyll cycle and increased relative carotenoid
561 pools lead to high NPQ levels at low temperatures (e.g. Porcar-Castell, 2011; Porcar-Castell
562 et al., 2012; Verhoeven, 2014; Wong and Gamon, 2014, 2015). Next to the pigment pool
563 sizes mentioned earlier the physiological indicators in the study by Wong and Gamon (2015)
564 include the reversible component of NPQ (in contrast to sustained, which is superposed on
565 the sustained form to allow higher flexibility for the plants; Ensminger et al., 2004; Porcar-
566 Castell, 2011), photosynthetic gas exchange, electron transport rate, photosynthetic light use
567 efficiency and PRI. Identifying again the SOS as the point in time when the values of the
568 several indicators start to increase, their Fig. 4 suggests a close timing of the recovery of the
569 reversible NPQ component, the activity of PSII (indicated by electron transport rate) and of
570 the photosynthetic gas exchange. So both, the activity of PSII (approximated by SIF) and
571 CO₂ exchange (represented by model GPP), have been shown to start to increase at very
572 similar times in Wong and Gamon (2015) in-situ and in e.g. our Fig. 3b at the continental
573 scale which might suggest a similar underlying mechanism. Still, detailed studies are needed
574 to identify the drivers of our observations backed up by investigations across these widely

575 different spatial and temporal scales.

576 The environmental conditions at the time when SIF starts to indicate
577 photosynthetic activity of PSII on the large scale are very similar to results in site-level
578 studies, too. The PAR amounts incident on the canopy are already high (comparable to the
579 conditions in August, 70% of the annual PAR maximum, Fig. 6 and 7, Table 1).
580 Temperatures, despite still being close to the freezing point (Fig. 7, Table 1), have partly
581 released plants from low temperature stress. Thus, our results agree with the general notion in
582 the literature that spring recovery of photosynthetic activity in ENF is temperature driven
583 provided that the canopy is snow free and needles are illuminated. Wind blow, melt and
584 snow sliding off the branches result in a snow free canopy several times during winter and
585 spring. Recovery will not be inhibited in case the ground may still be snow covered as air
586 temperature is the major driver (Tanja et al., 2003; Arneth et al., 2006; Jönsson et al., 2010;
587 Gonsamo et al., 2012, Fig. 6, 7c). As another supporting example at site-level, closer
588 examination of the conditions at the Russian flux tower site Fyodorovskoye reveals that, on
589 average, the photosynthetic recovery commences during snow melt (decreasing snow depth)
590 when there mostly is a uniform snow layer on the ground or the first glades are visible. While
591 the canopy is snow free at SOS_{SIF} and SOS_{GPP} , snow depth on the ground is highly variable
592 and can be as high as 66 cm. The time between the first appearance of snow free spots and
593 complete snow melt ranges between 5 and 15 days at the site. Although snow melt is a
594 gradual process highly dependent on local conditions, this is in accordance with our results
595 on synoptic scales. Despite the fact that a decelerating effect of low soil temperatures on the
596 rate of recovery has been reported (Ensminger et al., 2008), a consistent and significant
597 relationship between the frozen/thawed state of the soil and various indicators of
598 photosynthesis has neither been found at site-level (Tanja et al., 2003; Ensminger et al.,

599 2004) nor at the continental scale in our results. The soil temperature is around the
600 freezing point, in some years slightly above at 3 °C, in other slightly below at -2 °C at SOS_{SIF}
601 (Fig. 6, Table 1). In the uppermost soil layer (0-7 cm depth) temperatures were always at up
602 to 5 °C, except in spring 2009 at 0 °C (not shown). At the same time the annual soil water
603 maximum is reached or has just passed, so that water cannot be assumed to be a limiting
604 factor at the time of the commencement of photosynthesis.

605

606 *Limitations and uncertainties*

607

608 *Confounding effects of data processing*

609 There are several factors affecting the reliability and quality of the remote sensing products
610 as used in this study. Optical remote sensing in high latitudes is particularly influenced by
611 high sun-zenith angles, atmospheric effects, shadows, snow cover and repeated observations
612 in the visible are often complicated by persistent cloud cover (Stow et al., 2004). Also
613 unambiguous interpretation is confounded by canopy structure and density, contributions of
614 background (soil, snow, wetness, understory) and non-active plant materials, or
615 heterogeneity of the land cover (other than the targeted one; Jones and Vaughan, 2010;
616 Klosterman et al., 2014; Damm et al., 2015, and many more). Effects which are particularly
617 relevant for the interpretation of our results are discussed in more detail below.

618

619 The IGBP land cover classification scheme with a frequency threshold was
620 used to isolate regions with the forest type of interest while at the same time trying to make
621 sure that only pixels with high homogeneity are used in the analysis. We checked the
622 composition of the fine scale (0.05°) land cover classification pixels that are the basis for

623 those 0.5° pixels that go into the analysis. Regarding landscape homogeneity, it can be said
624 that 87.7% of the underlying 0.05° pixels are classified as ENF, 0.01% as deciduous and
625 4.7% as mixed forests. All other vegetation types contribute each less than 3% to the total
626 number of ENF pixels. Further, the IGBP classification does not give any information on the
627 density, composition, age or other details of the forest canopy. Thus our results may be
628 affected by changing fractions of visible soil/snow background, by the activity and greenness
629 phenology of understorey vegetation and/or of forest types other than the targeted one. From
630 the results presented in the study by Yuan et al. (2014), we expect that the understorey,
631 particularly if predominantly composed of mosses, has a stronger relative effect on the
632 seasonality of the greenness indices than on the SIF observations and model GPP. Due to the
633 high but still limited homogeneity of the land cover deciduous species with a different leaf
634 phenology and also photosynthetic phenology from the evergreen needleleaf forests will
635 affect the observations. Complete elimination of confounding effects of other vegetation
636 types and varying density cannot be achieved, especially at synoptic scales and the relatively
637 coarse spatial resolution. The numbers above show only marginal mixing of vegetation types
638 which is often limited to the transitional zones between different forest types (not shown).

639

640 It can be argued that the difference in start of increase between SIF and EVI is
641 an artifact of the snow filtering procedure applied to the EVI. Although to a lesser extent than
642 the NDVI, the EVI is unstable in the presence of snow (Huete et al., 2002; Dye and Tucker,
643 2003; Zhang et al., 2004, and Alfredo Huete, pers. comm.). If snow melt and green-up were
644 to overlap in time, both effects could not be distinguished. In this case, it cannot be ruled out
645 that the filtering obscure greenness changes that might occur already before the snow flag
646 indicates that the snow on the ground has completely melted. However, to isolate the

647 greening signal the snow filtering is imperative, and its impact on SOS_{EVI} should be small as
648 a) snow melt cannot unequivocally be distinguished from green-up, b) green-up and snow
649 melt were not found to overlap in time at the local scale (e.g. Böttcher et al., 2014), and c)
650 because less strict filtering thresholds of 10% and 30% surface snow cover were not found to
651 severely affect the identified SOS_{EVI} . This might be due to the fact that a large part of the
652 snow melts before the ground starts to become visible and that the complete snow melt
653 exposing the ground is very fast then (Clark et al., 2006; Böttcher et al., 2014). If this process
654 proceeds faster than the temporal resolution of the data used in this study allow to see, this
655 might explain these observations. Further discussion on this aspect can be found in the
656 supporting information in section S1.2. Also the MODIS snow flag gives no information on
657 whether the snow is on the ground and/or on the canopy and on the timing of initial phases of
658 snow melt when the thickness of the snow layer is reduced but the ground not yet visible. Its
659 application for the snow filtering of the VIs might not be the optimum as the snow flag is
660 known not to be perfect. We refrained from additionally applying a surface temperature
661 threshold (similar to Zhang et al., 2006) to filter out potentially snowy pixel values which
662 are not captured by the MODIS snow flag. This might have affected the results too strongly
663 and we trust in the fitting procedure that it can handle potential snow outliers.

664

665 Although the results of this study are very promising in the use of satellite
666 based SIF measurements to observe vegetation activity, it needs to be acknowledged that the
667 current satellite SIF data are still relatively noisy, especially at times with high sun-zenith
668 angles. This mostly applies to winter times, but might affect also spring SIF values, which is
669 of course critical in a study that aims at identifying the SOS during spring. It has been put
670 some effort on dealing with this issue and the main outcome of this is the extended 'down-

671 weighting' of outliers in the fitting procedure. From all available SIF data sets, in the
672 GOME-2 data set used in this study (Köhler et al., 2015) the noise level was lowest in the
673 investigated areas.

674

675 All data sets but the NDVI3g have been composited in the same way, meaning
676 that averages over valid values of 16 days are assigned to the first day of a 16-day period and
677 sampled every 8 days. Differences exist between MODIS VIs, SIF and model GPP with
678 respect to the number of valid retrievals per 16-day period, the observation conditions (VZA,
679 SZA, time) and the averaging method over the retrievals of 16 days (weighted vs.
680 unweighted). NDVI3g is different from that in that it is a MVC over 15 days with unknown
681 exact acquisition date. We assigned a value to the first day of a 15-day period with the
682 intention to make it comparable to the other data sets. However, biases are still introduced
683 through MVC in contrast to weighted averaging and we expect the effects of different
684 compositing to be strongest for NDVI3g and weaker between SIF, model GPP and MODIS
685 VIs.

686

687 *Knowledge gaps in the mechanistic relationship between SIF and GPP*

688 Earlier in the Discussion section we addressed possible processes and mechanisms on
689 the molecular and leaf scale that might explain our observations on the large scale. However,
690 as suitable measurements bridging the large gap to the satellite scale are not available,
691 verification of the hypotheses is not possible. Also on the small scale there are several open
692 questions arising from the literature regarding the processes that drive and relate SIF (PSII
693 activity) to GPP (CO₂ fixation) and their temporal acclimation and dependence on external
694 factors. In particular, the seasonal variations of chlorophyll fluorescence, and the relationship

695 to NPQ and photochemical quenching of the excitation energy are not yet clear. Specifically,
696 the strength of the positive relationship between SIF and photochemical assimilation might
697 change due to variable NPQ mechanisms and photoinhibition (Porcar-Castell et al., 2014).
698 Also, NPQ can become light-saturated and in that case PSII activity is driven by the
699 processes that consume the energetic products of the linear electron transport (Baker, 2008).
700 The importance of processes downstream of PSII which consume the energetic compounds
701 formed in the light reactions to fix carbon is highlighted by several studies: Monson et al.
702 (2005) report that the factor limiting spring recovery in a coniferous tree the most was the
703 ability to use intercellular CO₂, probably as a result of slow rubisco recovery or synthesis.
704 Soukupová et al. (2008) state that PSII can operate at very low temperatures while CO₂
705 assimilation is rather depressed at temperatures below 5 °C. This leads to seasonally
706 changing relationships between steady-state chlorophyll fluorescence, CO₂ assimilation and
707 the incident photon fluxes on the plant. In line with that, Thum (2009) and Kolari et al.
708 (2014) find different seasonal acclimation of the light reactions (maximum electron transport
709 rate, J_{max}) and the carbon fixation reactions (v_{cmax}). More research is clearly needed to
710 answer the above questions and to be able to fully exploit the information content of SIF
711 complementarily to models and reflectance measurements across the spatial and temporal
712 scales.

713 Studies finding that the commencement of PSII activity and CO₂ assimilation
714 do not necessarily occur at the same time and/or rate were conducted on fine spatial and
715 temporal scales (Ensminger et al., 2004; Soukupová et al., 2008; Ensminger et al., 2008;
716 Wong and Gamon, 2015), so that this time offset can probably not be reproduced with a
717 temporal resolution of 16 days in this work. Despite this, it needs to be mentioned that the
718 start of increase in photosynthesis (if measured visually as start of increase and not midpoint

719 increase) is very similar to the one of electron transport rate and the xanthophyll conversion
720 and very different from the increase in chlorophyll content in the work of Wong and Gamon
721 (2015), which supports the findings of this study.

722

723 *Implications and Outlook*

724 We initially assumed that SIF measurements can be used to track variations in GPP at the
725 large scale. In mid-to-high latitude evergreen forests, we find that SIF contains information
726 on photosynthetic light-use-efficiency Φ_p (Fig. 5) and not only on APAR, which supports our
727 initial premise. Our results confirm a lag between the spring recovery of photosynthesis and
728 green-up that has already been reported at site-level in boreal evergreen forests. This implies
729 that estimates of the SOS purely based on greenness indices will be biased in ENF. This will
730 translate into errors in the spring carbon budget as values of one third to half of the annual
731 maximum of SIF and model GPP are found at SOS_{EVI} both in our results and at site-level
732 (Fig. 3b, Thum et al., 2009).

733

734 Our findings have strong implications for the carbon cycle modelling
735 community, as global SIF measurements from space strongly appear to be apt to constrain
736 parameters in these simulations related to both, leaf phenology and photosynthetic
737 functioning. Especially in the low temperature regime in early spring and late autumn, when
738 carbon models are inaccurate (Schaefer et al., 2012), SIF might bring new insights to
739 improve the simulation results.

740

741 For the definition of GPP out of SIF and hence the usage of SIF in carbon
742 models, it needs to be explained, that SIF is only able to track the light reactions of

743 photosynthesis and therefore cannot directly be translated into GPP (see discussion on
744 knowledge gaps in the mechanistic relationship between SIF and GPP). The scaling
745 between SIF and GPP depends on biome (compare annual maxima of SIF and GPP in Fig. 3
746 and see Guanter et al., 2012) and temporal scale (Damm et al., 2015). It is still uncertain to
747 which extent SIF is sensitive to the maximum carboxylation capacity v_{cmax} across biomes
748 (Zhang et al., 2014; Koffi et al., 2015), which is an important parameter that determines the
749 magnitude of GPP (van der Tol et al., 2009; Koffi et al., 2015). As discussed in Damm et al.
750 (2015) many more aspects related to canopy structure (light environment and absorption,
751 fluorescence escape mostly originates from the upper canopy layers and GPP from the whole
752 canopy) and better process understanding need to be taken into account to translate SIF into
753 GPP. But SIF is strongly dependent on APAR and hence chlorophyll content (at least in the
754 far-red region where SIF is not partly reabsorbed by chlorophyll) and of course on Φ_f (Louis
755 et al., 2005; Porcar-Castell et al., 2014; Koffi et al., 2015), which under NPQ dominance
756 covaries with Φ_p . If Φ_f is largely constant, the fluorescence flux SIF might be used to infer
757 APAR, which is a controlling parameter also for GPP and an important input variable to
758 carbon simulations (Daumard et al., 2012; Koffi et al., 2015). Moreover, the fact that APAR
759 (EVI·PAR) and SIF have different seasonalities over ENF (Fig. 5) suggests that SIF does not
760 only contain information on APAR but also on Φ_p .

761

762 In the study by Wong and Gamon (2015) spring recovery of PRI (which is
763 also related to Φ_p) was timed very close with photosynthesis in conifers. With future research
764 on the confounding effects on PRI mentioned earlier - which partly also apply to SIF and
765 greenness index observations - analysis of PRI combined with SIF and VIs might further our
766 knowledge on vegetation activity (Gamon, 2015; Gamon et al., 2015) and help understand

767 the mechanisms that underlie our observations also at the synoptic scale.

768

769 New SIF data sets from the Orbiting Carbon Observatory-2 (launched in July
770 2014, Frankenberg et al., 2014) and the TROPOMI instrument in the Sentinel-5-Precursor
771 (to be launched early in 2016, Guanter et al., 2015) have a 100 times increase in the number
772 of measurements and a much higher spatial resolution against existing satellite instruments
773 and are expected to bring further new insights into the photosynthetic seasonality, also in
774 boreal evergreen forests.

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1134 **There is additional supporting information available for this manuscript online.**

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	T_{air2m}	T_{air2m}^{min}	T_{air2m}^{max}	PAR [fraction of annual max]	soil water content [mm]	T_{soil} [° C]	snow flag [%]	SOS [DOY]
	[° C]	[° C]	[° C]					
ENF								
SIF	2.7±6.3	-1.6±5.9	7.1±6.5	72±24	6.8±0.6	0.9±4.4	37±42	103±31
EVI	9.2±3.5	4.5±3.2	13.8±3.9	9±13	6.5±0.5	6.1±2.8	4±16	132±19
GPP	1.2±2.8	-2.9±3	5.6±2.8	72±15	7.1±0.5	-1.0±2.5	59±39	98±14
DBF								
SIF	13.8±3.1	10.0±3.1	18.6±3.1	80±8	5.6±0.6	12.6±3.0	0±2	108±16
EVI	14.2±2.7	10.3±2.7	19.0±2.7	81±8	5.5±0.6	12.9±2.6	0±2	108±14
GPP	13.0±2.9	9.1±2.7	17.9±3.0	77±9	5.7±0.6	11.6±2.7	0±1	102±15

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1142 **Table1:** Average environmental conditions and their standard deviation at SOS for SIF, EVI

1143 and model GPP in ENF (north of 50° N) and DBF.

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1159 **List of Figures**

- 1160 1 Comparison of flux tower GPP observations and the satellite SIF measurements
1161 from the GOME-2 instrument (Köhler et al., 2015) within 30 km of the
1162 Russian tower site Fyodorovskoye (56.4615° N, 32.9221° E).
- 1163 2 Example of a real time series of satellite-based SIF data, the fitted
1164 double-logistic function and the start and end of season derived from it.
- 1165 3 Median of the annual cycles (dashed lines) and of the fitted functions (solid
1166 lines) of SIF, model GPP, EVI, NDVI and NDVI3g over (a) deciduous
1167 broadleaf forest and (b) evergreen needleleaf forest (north of 50° N). Sampling
1168 is matched between the fits and the SIF and model GPP time series, but not
1169 with the VI time series because of the many missing values in winter in the
1170 greenness indices.
- 1171 4 (a): Forest areas in 0.5° resolution as delineated by the IGBP scheme for
1172 the year 2009. ENF: evergreen needleleaf forest; DNF: deciduous needleleaf
1173 forest; DBF: deciduous broadleaf forest; MF: mixed forest. (b): Mean
1174 calculated start of season for SIF in day of year (upper colour scale). (c), (d):
1175 Mean differences in the calculated start and end of season dates between SIF
1176 and EVI in days. Colours refer to the left colour bar. Blue colours denote
1177 that the respective date is earlier in SIF than in EVI. The resulting average
1178 differences in the length of the growing season are shown in panel (d) (lower
1179 colour bar, blue colours mean a longer growing season in EVI than in SIF).
- 1180 5 Median of the annual cycles (dashed lines) and of the fitted functions (solid
1181 lines) of SIF, EVI (same as in Fig. 3) and EVI·PAR (as a proxy for APAR)
1182 over evergreen needleleaf forest (north of 50° N). Sampling of the EVI time

1183 series is not transferred to the fits and the SIF time series because of the many
1184 missing values in winter, but sampling is matched between SIF, SIF fits, EVI
1185 fits, and EVI fits·PAR.

1186 6 Evergreen needleleaf forest in the ecoregion of Fenno-Scandinavia and the
1187 western part of Russia (ecoregion number 706 in Olson et al. (2001), 162
1188 pixels in total): (a) Area averaged time series of SIF; dashed vertical lines mark
1189 SOS and EOS (spatial median), shaded areas indicate the interquartile range of
1190 all identified SOS/EOS in the area in the particular year. (b) The same as a) for
1191 MODIS EVI and NDVI. (c, d) Mean 2 m air and soil (7-28 cm) temperature.
1192 The shaded area indicates the range between the mean of daily minimum and
1193 the mean of daily maximum temperatures in a 16-day interval. (e) Average
1194 photosynthetically active radiation reaching the surface (PAR). (f) MODIS
1195 snow flag indicating the average snow cover in percent of the surface; soil
1196 water content in the layer between 7 and 28 cm depth. Sampling of the fits, SIF
1197 and the meteorological variables is aligned with each other. However, sampling
1198 is not matched with EVI and NDVI time series because of the many missing
1199 values in winter. The other way around the sampling of EVI/NDVI time series
1200 is aligned with the one of SIF and and the fits.

1201 7 The maps show the mean temperature conditions of the air and the soil in
1202 7-28 cm depth, the MODIS snow flag and the average photosynthetically active
1203 radiation arriving at the surface at the start of season for SIF and EVI.

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