

1 **Can changes in autumn phenology facilitate earlier green-up date of**
2 **northern vegetation?**

3
4 Running title: Autumn phenology and northern green-up

5
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34 **Abstract**

35 Climate warming has induced substantial advances in the onset of vegetation green-up in the
36 northern hemisphere during recent decades. To date, however, the temporal changes in
37 green-up date have not been adequately explained by the statistical relationships between
38 green-up date and climatic factors, posing challenges in the attribution and prediction of
39 phenological change. In this study, we thus turned to focus on autumn phenology, a critical
40 biotic factor that is likely to affect the subsequent spring phenology of vegetation. Using
41 satellite-retrieved start and end of growing season (SOS and EOS) over the period from 1982
42 to 2015, we examined the association between the EOS and the SOS in the following year in
43 northern middle and high latitudes (north of 25°N). Interannual changes in SOS were
44 significantly ($P < 0.05$) related to changes in EOS in the previous year in 26.4% of the total
45 pixels, mostly in the boreal region, with a 1-day advance of EOS generally resulting in about
46 a 0.5- to 1.0-day advance of the following SOS, suggesting that the advanced SOS may be
47 associated with the advanced EOS. In temperate ecosystems, however, SOS showed a weak
48 negative partial correlation with previous year's EOS (significant for 10.3% of the total
49 pixels), suggesting that the delayed EOS may have limited contribution to the advanced SOS.
50 Our analysis further revealed that changes in the EOS contributed little to the changes in the
51 number of subsequent chilling days in temperate ecosystems and that the sum of forcing
52 temperatures was weakly related with the number of the chilling days in the boreal region,
53 suggesting that EOS may affect SOS through other mechanisms such as changes in the timing
54 when the chilling requirement is met as well as in carbohydrate and nutrient economy. This
55 study suggested that the timing of EOS may explain some of the temporal changes in SOS in
56 the following year in 36.7% of the study region, but further studies are needed to identify the
57 exact mechanisms.

58 **Keywords:** autumn phenology, legacy effect, climate change, northern hemisphere,
59 phenological sequence, spring phenology

60

61 **1 Introduction**

62 Substantial advances in the onset of green-up in temperate and boreal vegetation in the
63 northern hemisphere during recent decades has been widely reported as an easily observable
64 and sensitive indicator of ecosystem responses to climate warming (Badeck et al., 2004;
65 Penuelas and Filella, 2001). The changes in vegetation phenology have had extensive
66 influences on ecosystem structure and functioning, such as species composition, plant
67 distribution, biodiversity, matter cycles, and energy flows, which exert feedbacks to the
68 climate system (Agosta and Klemens, 2008; Chuine, 2010; Keenan et al., 2014; Penuelas et
69 al., 2009; Richardson et al., 2013).

70 An increase in spring temperature is the most influential environmental cue for the
71 advance in vegetation spring phenology (Körner, 2007). Both *in situ* and satellite remote
72 sensing observations have documented significant effects of forcing temperature in late
73 winter and spring on leaf unfolding and the start of the growing season (SOS, in day of year)
74 in temperate, boreal, and alpine vegetation (Garonna et al., 2016; Prevéy et al., 2017).
75 However, the spatial and temporal variations in timing of the vegetation growing season
76 (SOS) could not be fully explained by forcing temperature (Park et al., 2018). For example,
77 Shen et al. (2014a) reported a negative correlation ($P < 0.10$) between SOS and preseason
78 temperature in about 78% of the pixels in the vegetated land between 30°N and 80°N during
79 the period 1982–2008, yet the correlation coefficient varied widely, from -0.94 to -0.32 . The
80 sensitivity of satellite-derived SOS to preseason temperature (changes in SOS per unit
81 temperature) showed substantial spatial variations (Shen et al., 2014a; Wang et al., 2015a)
82 and explained more spatial variation in the temporal trend in SOS than the trend in preseason
83 temperature did (Shen et al., 2015a). Likewise, spatial variations in the sensitivity of leaf
84 unfolding phenology to preseason temperature were also observed in large datasets compiled
85 from *in situ* observations in China and Europe (Menzel et al., 2006; Wang et al., 2015b;
86 Zhang et al., 2015). On the other hand, the sensitivity of SOS to preseason temperature also
87 exhibited large temporal variation. The sensitivity of leaf unfolding date in several temperate
88 European tree species to preseason forcing temperature declined considerably during

89 1982–2013 (Fu et al., 2015b). In China, a recent study based on *in situ* observation also
90 showed large temporal variations in the temperature sensitivity of spring leaf phenology of 40
91 plant species (Dai et al., 2017).

92 Several recent studies have proposed explanations for the variations in temperature
93 sensitivity of individual plant species or vegetation spring leafing phenology. A decrease in
94 the number of chilling days (NCD) induced by winter warming could increase the thermal
95 requirement for spring leafing and green-up onset and thus result in decreasing sensitivity of
96 spring phenology to forcing temperature (Asse et al., 2018; Fu et al., 2015a; Fu et al., 2015b;
97 Shen et al., 2014a; Zhang et al., 2007). Fu et al. (2015b) reported, however, that the decrease
98 in the NCD could not fully explain the variation in the temperature sensitivity. For late
99 successional species, the spring budburst and leaf flushing and their responses to forcing
100 temperature are found to be directly impacted by photoperiod under experimental condition
101 (Basler and Körner, 2012). Long photoperiod might reduce the thermal time requirement for
102 spring budburst and leaf unfolding (Falusi and Calamassi, 1996; Myking and Heide, 1995).
103 Moreover, the leaf flushing could also be impacted by the interaction between chilling and
104 photoperiod (Caffarra and Donnelly, 2011; Caffarra et al., 2011; Gauzere et al., 2017; Zohner
105 and Renner, 2015). However, it remains unclear to what extent these findings for a limited
106 number of species based on experiments in which photoperiod differs greatly from natural
107 condition can explain the variability in temperature sensitivity of spring phenology in the
108 nature. The intraseasonal and interannual variability of pre-season temperature could also
109 result in variation in the temperature sensitivity (Wang et al., 2016; Wang et al., 2014).
110 Changes in water availability may regulate the phenological response to temperature or affect
111 the thermal demand and thus result in variation in the temperature sensitivity (Shen et al.,
112 2015b; Shen et al., 2011; Yun et al., 2018). However, the variations in temperature sensitivity
113 of spring phenology and interannual variations of spring phenology remain to be clarified.

114 In addition to the advance in vegetation spring phenology, climate warming has also
115 resulted in a trend of progressive delay in autumn leaf phenology (or end of the growing
116 season, EOS) during the past few decades in northern temperate and boreal ecosystems

117 (Garonna et al., 2014; Garonna et al., 2016). Changes in EOS may increase or decrease the
118 NCD, depending on the speed of leaf senescence and the meteorological conditions during
119 the endo-dormancy period, which may further induce changes in the thermal requirement of
120 green-up onset and thus spring phenology (Fu et al., 2014b). Moreover, changes in the
121 phenology of leaf senescence involve a variety of programmed age-dependent deterioration
122 processes such as changes in gene expression and metabolism, degradation of
123 macromolecules (e.g., chlorophyll), and recycling and reallocation of resources (Estiarte and
124 Penuelas, 2015; Gan and Amasino, 1997). Therefore, changes in vegetation autumn
125 phenology may change the amount of carbohydrates and nutrients reserves that are to be used
126 for spring budburst and leaf unfolding in the following year. For some species, it has been
127 found that high (low) nutrient level advances (delays) leaf flushing or budburst (Falk et al.,
128 2020; Huang and Li, 2015; Jochner et al., 2013), suggesting a possibility that content of
129 nutrient reserve in dormant season, which could be altered by leaf senescence, may affect the
130 following leaf flushing. For *Quercus robur* L. and *Fagus sylvatica* L., Fu et al. (2014b)
131 observed that the early leaf flushing may be related with higher content of sugar and starch
132 reverse after leaf senescence based on a warming experiment study. Based on those studies,
133 we hypothesize that the shifts in EOS may indirectly cause SOS changes in the following
134 year though modifying the processes during the dormant season.

135 In this study, we first examined the temporal trends in satellite-derived SOS and EOS
136 in northern middle and high latitudes (north of 25°N) over the period 1982–2015. To test this
137 hypothesis, we investigated whether the temporal changes in SOS were related to the changes
138 in the EOS of the previous year by using partial correlation analysis. Complementary to
139 satellite-derived data of SOS and EOS, leaf unfolding and coloring dates (LUD and LCD) in
140 a large dataset based on *in situ* phenological observations were analyzed. A causality
141 detection method based on convergent cross mapping (CCM; Sugihara et al., 2012) was
142 further used to examine whether the changes in autumn senescence (EOS and LCD) caused
143 changes in the following year's spring onset (SOS and LUD). Finally, we explored whether
144 EOS affects SOS by altering the NCD and thermal requirement of SOS.

145 **2 Materials and methods**

146 **2.1 Datasets**

147 The SOS and EOS were detected from the long-term time series of normalized difference
148 vegetation index (NDVI) dataset produced by the Global Inventory Modelling and Mapping
149 Studies (GIMMS) group (Pinzon and Tucker, 2014). The GIMMS NDVI dataset has been
150 widely used as a surrogate of vegetation activity at regional and larger scales as well as for
151 retrieving vegetation phenological metrics in global ecological studies (e.g. Buitenwerf et al.,
152 2015; Garonna et al., 2016; Pan et al., 2018; Xu et al., 2013). The distortion caused by water
153 vapor, aerosols, sensor attenuation, and orbital drift has been eliminated by the GIMMS
154 group (Pinzon and Tucker, 2014). This study used Version 1 of the third generation of the
155 GIMMS NDVI dataset, covering the period 1982–2015, with a temporal resolution of 15
156 days and a spatial resolution of 0.083°. The Version 1 dataset has been improved through
157 cross-validation with SeaWiFS data (Burrell et al., 2018).

158 Monthly mean air temperature and cumulative precipitation data (TS4.0) were
159 provided by the Climate Research Unit (CRU) (Harris et al., 2014). This dataset covers the
160 period 1901–2015. The CRU temperature and precipitation data were used for assessing the
161 pre-season meteorological impact on SOS. The NCD and growing degree days (GDD) were
162 calculated from the daily temperature retrieved from the CRUNCEP Version 7 climate dataset
163 (Wei et al., 2014)
164 (ftp://nacp.ornl.gov/synthesis/2009/frescati/model_driver/cru_ncep/analysis/readme.htm,
165 available at <https://vesg.ipsl.upmc.fr>). The CRUNCEP dataset also includes the shortwave
166 downward solar radiation data that were used in the analysis, with details given in section 2.3.
167 Both the CRU and CRUNCEP datasets have a spatial resolution of $0.5^\circ \times 0.5^\circ$ and were
168 resampled at $1/12^\circ \times 1/12^\circ$ by replication to match the SOS and EOS data.

169 LUD (phase_id = 11, http://www.pep725.eu/pep725_phase.php) and LCD (phase_id =
170 205) data were obtained from the Pan European Phenology network (PEP725; Templ et al.,
171 2018). The PEP725 dataset has been widely used in plant phenological and global climate
172 change studies (Chen et al., 2016; Cook et al., 2012; Piao et al., 2015). To be consistent with

173 the satellite-based analyses, we focused on the records between 1982 and 2015. We excluded
174 the plants that are cultivars (*Malus domestica*, *Prunus amygdalus*, *Prunus avium*, *Prunus*
175 *domestica*, and *Vitis vinifera*). We also removed *Taraxacum officinale* because it only has
176 records at one site. As a result, a total of 5700 site–species combinations were included in the
177 analysis (*Aesculus hippocastanum*, 1491 sites; *Betula pendula*, 1498 sites; *Betula pubescens*,
178 12 sites; *Fagus sylvatica*, 1322 sites; *Quercus robur*, 1355 sites; and *Tilia cordata*, 22 sites).
179 Daily mean air temperature and cumulative precipitation data for *in situ* phenology
180 observations were extracted from the E-OBS dataset (v19.0e, <https://www.ecad.eu/>, assessed
181 on 23 June 2019) provided by the European Climate Assessment & Dataset (ECA&D)
182 (Cornes et al., 2018). The E-OBS dataset covers the area 25°N–71.5°N × 25°W–45°E and the
183 period 1950–2018 with a spatial resolution of 0.1° × 0.1°. The temperature and precipitation
184 data of the grid in which the phenological stations are located were used for analysis.

185 **2.2 Determination of SOS and EOS**

186 The non-vegetation pixels (e.g., bare soils and rocks) were first excluded if annual average
187 NDVI < 0.10 (Jeong et al., 2011). Before retrieving SOS and EOS, the NDVI values
188 contaminated by snow cover were substituted by the mean of 75–95 percentiles of snow-free
189 NDVI values in winter (December–February) of all years. Here, the snow-free winter NDVI
190 values were determined as the winter NDVI value > 0.10. If there was no winter NDVI value >
191 0.10, then the winter NDVI was assigned as 0.10 (Shen et al., 2014b; Zhang et al., 2007).
192 Next, since clouds and poor atmospheric conditions depress NDVI values, a sudden drop of
193 NDVI in the ascending period from winter minimum to summer maximum NDVI was
194 substituted by an NDVI value reconstructed by the Savitzky–Golay filter (Chen et al., 2004;
195 Shen et al., 2014b), and the same procedure was applied symmetrically for the descending
196 period. To focus on the areas where vegetation has an observable phenological pattern (i.e.,
197 with seasonal variations in greenness), we only included pixels for which mean NDVI for
198 July and August was higher than 1.2 times the mean NDVI for winter (Shen et al., 2014b) and
199 the annual maximum NDVI occurred between June and October. Finally, the annual NDVI
200 from March to September was fitted by a 6-order polynomial time-series model to interpolate

201 daily NDVI, and then SOS was defined as the date when NDVI increased by 20% of its
202 annual amplitude (Shen et al., 2014b). Similarly, NDVI from July to December was fitted and
203 EOS was defined as the date when NDVI decreased by 50% of its annual amplitude (White et
204 al., 1997).

205 **2.3 Analyses**

206 Spring temperature is recognized as the main environmental cue of vegetation spring
207 phenology (Körner, 2007), but the duration of the period that precedes the SOS (the
208 “preseason”), during which temperature has the strongest impact on SOS, varies among areas
209 (Fu et al., 2015b; Jeong et al., 2011; Shen et al., 2014a). In addition to temperature, the
210 amount of precipitation and solar radiation before SOS could also potentially affect SOS.
211 Similar to previous studies (Fu et al., 2015b; Jeong et al., 2011; Shen et al., 2014a), the
212 preseason for spring temperature was determined as the period preceding the multiyear
213 average of SOS (with a step of 1 month) in which mean temperature has the largest
214 interannual partial correlation coefficient (absolute value) with SOS, while setting EOS of
215 previous years, NCD, cumulative precipitation, and shortwave downward solar radiation as
216 the control variables. Here, NCD was defined as the number of days with daily mean air
217 temperature lower than 0°C (Fu et al., 2014a) during the period from the previous year’s EOS
218 to the current SOS. Similarly, the preseason lengths for cumulative precipitation and solar
219 radiation were determined using the respective largest interannual partial correlation
220 coefficients (absolute values) with SOS because the preseason lengths for temperature,
221 cumulative precipitation, and solar radiation may be different (Shen et al., 2016).

222 After the preseasons for temperature, precipitation, and solar radiation were
223 determined, the impact of the previous year’s EOS on SOS was assessed as the interannual
224 partial correlation coefficient between SOS and the previous year’s EOS, while setting NCD,
225 preseason temperature, preseason precipitation, and preseason solar radiation as control
226 variables. Similarly, the impact of preseason temperature on SOS was assessed using the
227 interannual partial correlation between them while selecting the other variables as the control
228 variables. The sensitivity of SOS to the previous year’s EOS and preseason temperature was

229 quantified by the coefficients in the multiple linear regression model between the dependent
230 variable SOS and five explanatory variables (previous year's EOS, NCD, mean pre-season
231 temperature, cumulative pre-season precipitation, and cumulative pre-season solar radiation).
232 In addition, the impact of EOS on NCD was assessed using the interannual partial correlation
233 between EOS and NCD while controlling SOS. The impact of NCD on GDD was assessed as
234 the interannual partial correlation between NCD and GDD, while controlling precipitation
235 and solar radiation between EOS and SOS because those two factors may affect GDD (Fu et
236 al., 2014a). GDD is the sum of daily mean air temperatures $> 0^{\circ}\text{C}$ between the EOS and SOS.
237 For boreal ecosystems where there are no daily mean air temperatures $> 0^{\circ}\text{C}$, we used a base
238 temperature of -5°C to calculate GDD (Botta et al., 2000). The interannual partial correlation
239 between LUD and the previous year's LCD was analyzed in the same way.

240 Complementary to the partial correlation analysis, the causal influence of EOS (LCD) on
241 SOS (LUD) was examined using CCM based on dynamical systems theory (Sugihara et al.,
242 2012). CCM evaluates the causal relationship between two time series by quantifying the
243 extent to which the past record of one time series can reliably estimate the other. Taking SOS
244 and EOS, for example, EOS could be reliably reconstructed by SOS based on CCM only if
245 EOS causally influences SOS. Unlike correlation and other causal analysis methods, CCM
246 requires the convergence between the time series length (L) and the reconstruction skill,
247 which is usually quantified using the correlation coefficient (ρ) between reconstructed and
248 observed time series. In other words, CCM assumes that reconstruction skill increasing with
249 data length is necessary for the causal linkage. In our case, the correlation coefficient (ρ)
250 between the EOS reconstructed by SOS in CCM and the observed EOS increases with the
251 length of the time series (L) used for EOS and SOS and converges to a large positive value.
252 Spearman's rank correlation coefficient between ρ and L was used to quantify the
253 convergence of ρ with regard to L .

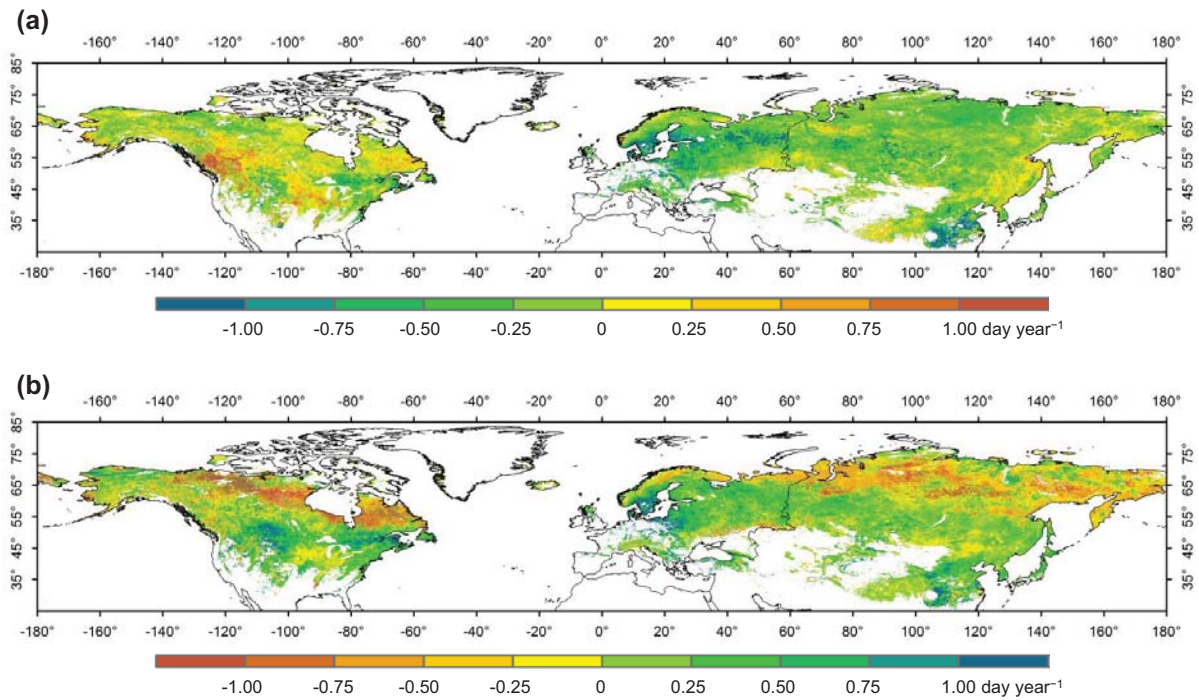
254 **3 Results**

255 **3.1 Temporal changes in SOS and EOS**

256 We first re-examined the temporal trends in the SOS over 1983–2015 and EOS over

257 1982–2014. In general, the northern hemisphere showed advancing SOS, but with differences
258 between Eurasia and North America (Fig. 1a). Eurasia experienced a substantial advance in
259 SOS in most areas, particularly in central and eastern Europe and eastern China, where the
260 temporal trend of SOS was larger than 0.75 day/year. A slight delay in SOS was observed in
261 northeastern Asia, the southwestern Tibetan Plateau, and southeastern Europe. In contrast, a
262 smaller advance in SOS was observed in North America. In southwestern Canada, the
263 north-central U.S., and eastern Canada, there were substantial delays in SOS by more than
264 0.25 day/year. SOS showed a significant ($P < 0.05$) advancing trend in 28.1% of the pixels,
265 mostly in Eurasia, and a significant delaying trend in 8.6% of the pixels, mostly in North
266 America (Fig. A1a).

267 Unlike SOS, the temporal trends in EOS showed a strong latitudinal pattern. In most
268 of the regions north of 55°N in Asia and North America, EOS advanced by more than 0.50
269 day/year. In contrast, in most of the regions south of 55°N in Asia and North America and
270 most areas of Europe, EOS tended to be delayed by more than 0.25 day/year; in central North
271 America, central Europe, and eastern China, the EOS was mostly delayed by more than 0.50
272 day/year. A similar latitudinal pattern of EOS trends was also reflected in those pixels with
273 significant advancing and delaying trends, which accounted for 23.8% and 26.0% of the
274 pixels, respectively (Fig. A1b).



275

276 **Figure 1.** Temporal trends in the start of the growing season (SOS) over the period 1983–2015 (a) and in the end of the growing season (EOS)

277 over the period 1982–2014 (b). The areas are blank if there was low vegetation coverage or lack of seasonal variations in greenness, or annual

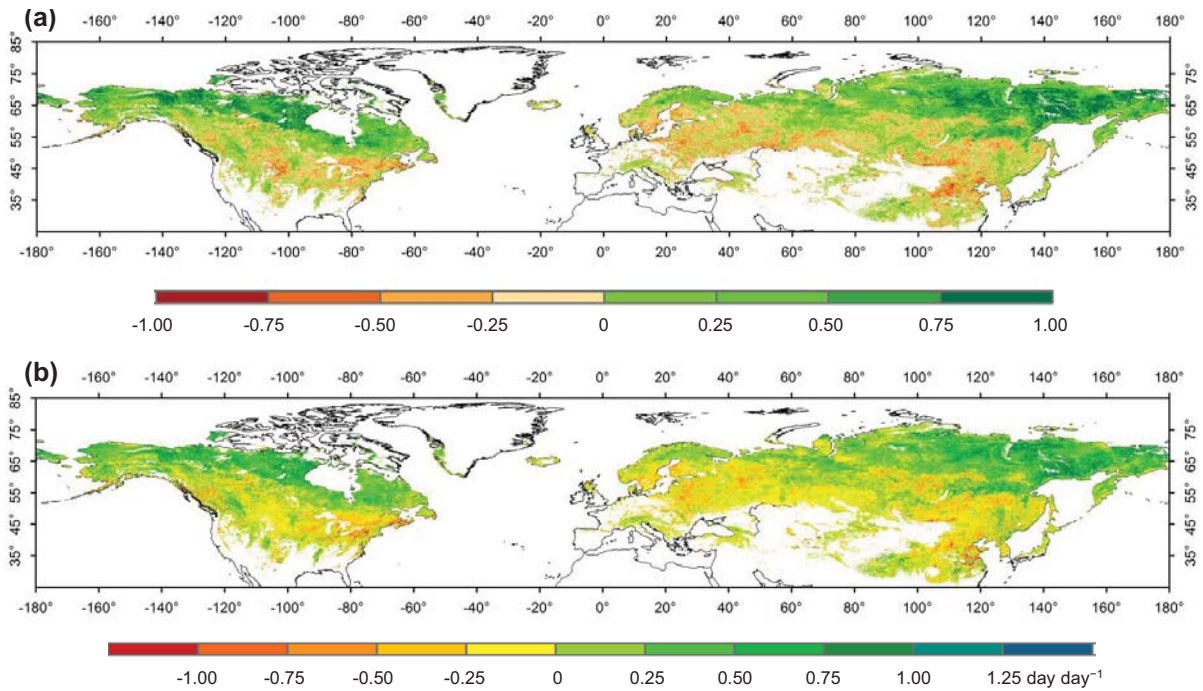
278 maximum greenness occurred between November and May (see section 2.2 for details).

279 3.2 Relationship between SOS and the previous year's EOS

280 We first examined the interannual partial correlation between EOS over 1982–2014 and SOS
281 over 1983–2015. In most of the areas in boreal ecosystems in North America and Asia, SOS
282 was strongly related to the previous year's EOS after accounting for confounding factors with
283 a partial coefficient higher than 0.50 (Fig. 2a). In northern Europe and alpine regions such as
284 the Tibetan Plateau and Rocky Mountains, there was a weaker positive partial correlation
285 between EOS and SOS. The positive partial correlation was significant ($P < 0.05$) in 26.4%
286 of the pixels (Fig. A2). In contrast, the SOS–EOS partial correlation was mainly negative in
287 temperate ecosystems and was significantly negative in 10.3% of the pixels. In accordance
288 with this result, analysis based on the PEP725 dataset showed a weak interannual partial
289 correlation between LUD and the previous year's LCD for the temperate tree species (Fig. 3).

290 We further examined the sensitivity of SOS to the previous year's EOS. According to
291 multiple regression, when a 1-day change in EOS occurred in most areas in boreal
292 ecosystems in Asia and northern Canada, SOS changed by 0.50–1.00 day in the same
293 direction (Fig. 2b). The sensitivity was mostly between 0 and 0.50 day day⁻¹ in Alaska, the
294 Rocky Mountains, eastern Canada, northern Europe, western Russia, and the Tibetan Plateau.
295 In most areas in temperate ecosystems, the sensitivity ranged from 0 to 1.00 day day⁻¹.

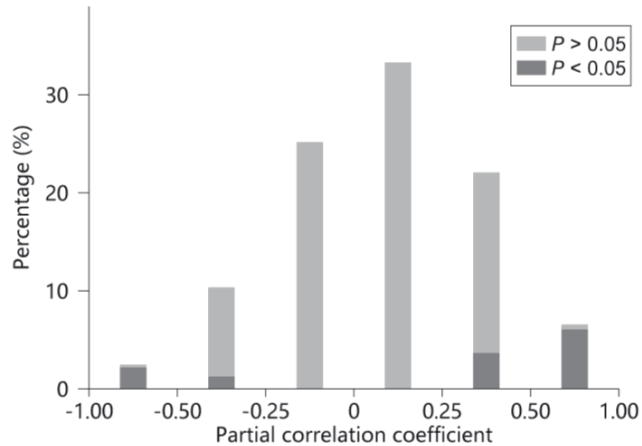
296 Finally, we compared the contribution of EOS to SOS with the contribution of preseason
297 temperature to SOS by using the ratio of standardized regression coefficient for EOS to that
298 of preseason temperature in the multiple regression between SOS and previous year's EOS,
299 NCD, and preseason temperature, precipitation, and solar radiation. As shown in Figure 4, in
300 most temperate ecosystems, EOS had less of an effect on interannual changes in SOS than
301 preseason temperature did (ratio < 1), which is associated with strong impact of preseason
302 temperature on SOS (Fig. A3a). However, EOS had a much greater effect on SOS than
303 preseason temperature did in northern and northeastern Canada, Alaska, and north of 55°N in
304 Asia, with absolute ratios higher than 2 in most of those areas, mainly due to the strong
305 impact of EOS on SOS (Fig. A3b).



306

307 **Figure 2.** (a) Partial interannual correlation coefficient between end of the growing season (EOS) of 1982–2014 and start of the growing season
 308 (SOS) of 1983–2015, setting number of chilling days (NCD) and pre-season temperature, precipitation, and solar radiation as control variables.

309 (b) Sensitivity of SOS to EOS of the preceding autumn.



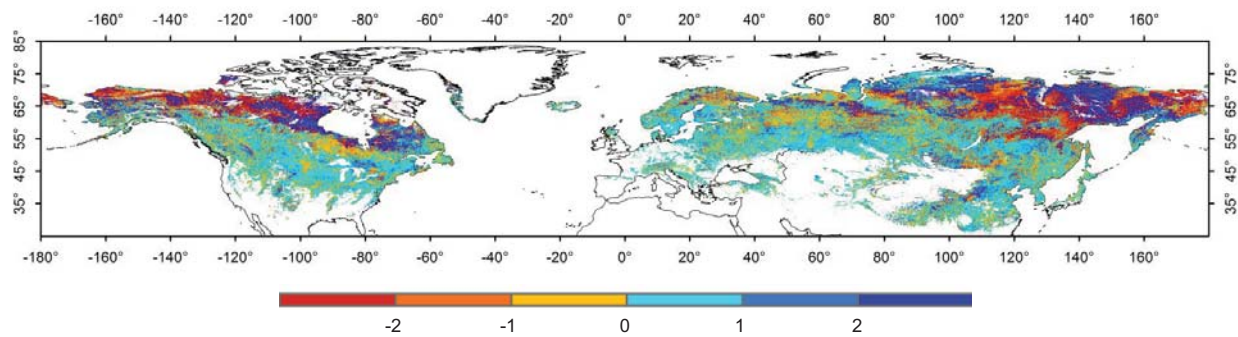
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311 **Figure 3.** Partial interannual correlation coefficient between leaf coloring date of 1982–2014
 312 and leaf unfolding date of 1983–2015, with number of chilling days, preseason temperature,
 313 precipitation, and solar radiation set as control variables. The y-axis shows the percentage of
 314 site–species combinations with a certain interval of partial correlation coefficient to total
 315 number of site–species combinations.

316 **4 Discussion**

317 **4.1 Legacy effect of EOS on SOS**

318 Our results showed a significant ($P < 0.05$) interannual partial correlation between SOS and
 319 the previous year’s EOS in 36.7% of the pixels, indicating that the interannual variations in
 320 SOS were likely driven in part by the previous year’s EOS in those areas, particularly in
 321 boreal ecosystems. Because correlation is not necessarily causation, we also used the CCM
 322 method to detect causation from EOS (LCD) to SOS (LUD) in the following year. The results
 323 show causation from EOS to SOS in 44.3% of the pixels across the northern hemisphere and
 324 causation from LCD to LUD in 39.4% of the site–species combinations analyzed (Figs. A4,
 325 A5). These statistical and CCM results provide evidence that supports the hypothesis in those
 326 regions and site–species combinations. Note that the spatial distribution of pixels in which
 327 causality was detected by the CCM method is not identical to that from partial correlation
 328 analysis. The spatial mismatch is likely due to some environmental factors being unaccounted
 329 for in the partial correlation analysis. The uncertainty of meteorological data from high
 330 latitudes and alpine landscapes may also have contributed to the mismatch (Rao et al., 2018).



331

332 **Figure 4.** Ratio of standardized coefficient for the end of the growing season (EOS) to that of pre-season temperature in the multiple regression
333 between the start of the growing season (SOS) and previous year's EOS, number of chilling days (NCD), and pre-season temperature,
334 precipitation, and solar radiation.

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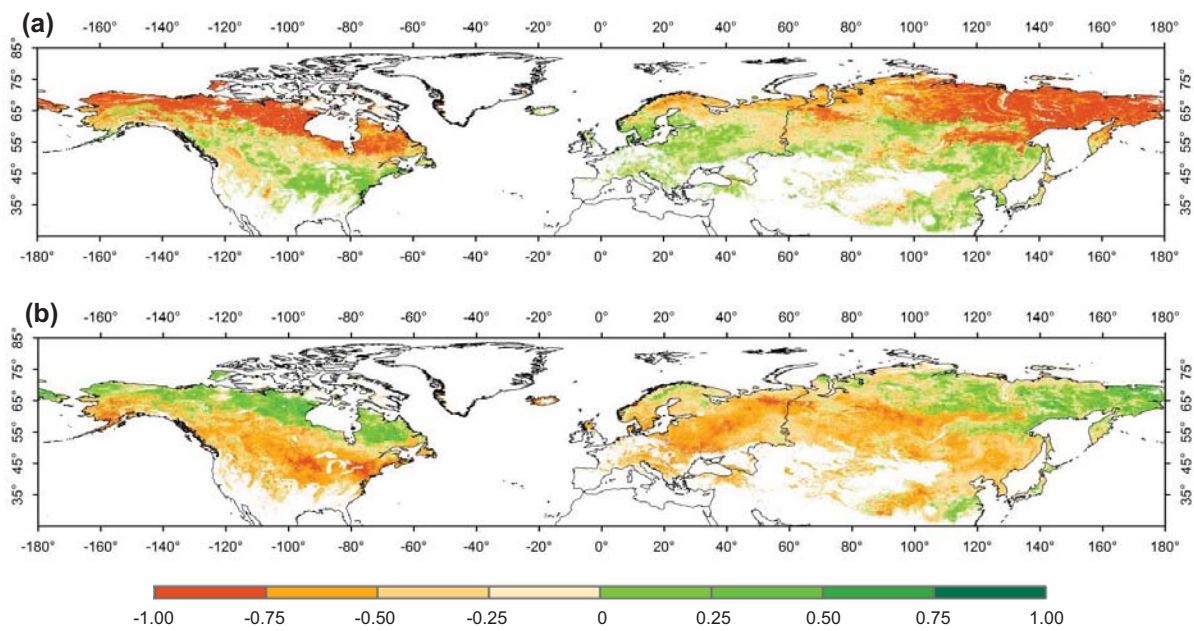
337 Previous studies have revealed various environmental cues that trigger spring leafing
338 phenology, such as pre-season temperature, winter chilling, precipitation, solar radiation, and
339 photoperiod (Basler and Körner, 2012; Chapman, 2013; Clark et al., 2014; Laube et al., 2014;
340 Leblans et al., 2017; Shen et al., 2015b; Yun et al., 2018). Among those factors, forcing
341 temperature and winter chilling were recognized as the two most influential drivers of
342 interannual changes in SOS under natural condition, particularly in the context of climate
343 warming (Asse et al., 2018; Körner and Basler, 2010; Richardson et al., 2018; Vitasse et al.,
344 2017). Insufficient chilling will increase the thermal requirement for spring budburst and leaf
345 unfolding, resulting in a delay in spring onset (Fu et al., 2015a; Kramer et al., 2017; Yu et al.,
346 2010). Therefore, we examined whether changes in EOS will alter the subsequent NCD,
347 which is a factor potentially affecting GDD and thus SOS. The results reveal strong negative
348 partial correlations between EOS and NCD and a weak partial correlation between GDD and
349 NCD in most boreal ecosystems (Figs. 5 and A6). In temperate ecosystems, GDD mainly
350 showed a moderate to strong negative partial correlation with NCD, but NCD was weakly
351 related with EOS in the partial correlation. Therefore, the effect of EOS on the following SOS
352 was not likely propagated by the impact of EOS on the NCD or by the impact of NCD on the
353 thermal requirement of SOS.

354 However, it should be noted that the total NCD during the dormant season does not
355 necessarily equal the NCD required by plants. If the latter is less than the former, the advance
356 of EOS may allow earlier entrance into the endodormant period in which chilling units
357 accumulate, which provides a condition for earlier fulfillment of the chilling requirement and
358 thus earlier break of endodormancy. This may result in an earlier start of ecodormancy,
359 providing the conditions needed for earlier leaf flushing if warm temperatures in spring allow
360 (Fu et al., 2014b; Körner and Basler, 2010). Extended exposure to chilling could advance the
361 time to budburst for some species (Nanninga et al., 2017). For example, a warming
362 experiment indicates that earlier leaf flushing for *Quercus robur* and *Fagus sylvatica* is
363 related to an advancement in fulfillment of chilling requirement as a result of earlier autumnal

364 senescence in the preceding year (Fu et al., 2014b). This could help explain the positive
365 partial correlation between SOS and previous year's EOS in the boreal region where both
366 SOS and EOS advanced. Alternatively, later EOS may result in later entrance into the
367 endodormancy period, which may shorten the period for accumulation of chilling units and
368 thus postpone fulfillment of the chilling requirement for breaking endodormancy or even
369 deficiency in chilling and thus increase the thermal demand for green-up onset, resulting in a
370 potentially later SOS (Asse et al., 2018; Chen et al., 2019; Fu et al., 2015a; Fu et al., 2015b).
371 This suggests that EOS may affect SOS of the next year by modifying the timing of when the
372 chilling requirement is met. Thus, there could be a positive partial correlation between SOS
373 and previous year's EOS in some areas where both EOS and SOS are delayed. Nevertheless,
374 at this stage we were unable to quantify the contribution of the timing and amount of chilling
375 accumulation altered by shifts in EOS to the impact of EOS on SOS, because we could not
376 exactly quantify the chilling requirement by vegetation green-up at the pixel level, which
377 includes multiple species for most of which the chilling requirements have not been
378 quantified (Chuine et al., 2016).

379 Quantification of such contribution is further complicated by the impacts of
380 interactions between chilling and photoperiod on leaf flushing. For some photosensitive
381 species (e.g. *Fagus sylvatica*), long photoperiod could partially compensate for the unmet
382 chilling requirements (Caffarra and Donnelly, 2011; Gauzere et al., 2017; Zohner and Renner,
383 2015) and short photoperiod performs as an environmental cue to prevent early release from
384 the endodormancy when the chilling requirements had been met (Caffarra and Donnelly,
385 2011). In contrast, for some opportunistic species (e.g. *Betula pubescens*), chilling could also
386 regulate the photoperiod threshold required for budburst, with a decreasing photoperiod
387 threshold upon increasing chilling durations (Caffarra et al., 2011). However, these studies
388 only included a few species under extreme photoperiod conditions and only parts of the
389 species in nature use photoperiod as a budburst signal (Basler and Körner, 2012; Tang et al.,
390 2016; Zohner et al., 2016). Photoperiod (daylength) only depends on the location and day of
391 year. With the limited range of inter-annual variations in SOS, the fluctuation of photoperiod

392 was very small, thus could not be as large as the difference in photoperiod in the indoor
393 experiments (e.g. 8 h for short-day and 16 h for long-day). Actually, the controlled warming
394 experiments by Richardson et al. (2018) and Fu et al. (2019) both showed that, with a 4 °C
395 -5 °C increase in temperature, the effect of photoperiod constraint on the response of
396 green-up dates to forcing temperature was not observed. A recent meta-analysis also found
397 that the leaf-out times of species from northern high latitude are independent on photoperiod
398 (Zohner et al., 2016). Those studies indicate that, photoperiod, either direct or through
399 regulating chilling or heat requirements, may influence spring leaf flushing or SOS, but the
400 effect should be limited in nature.



401

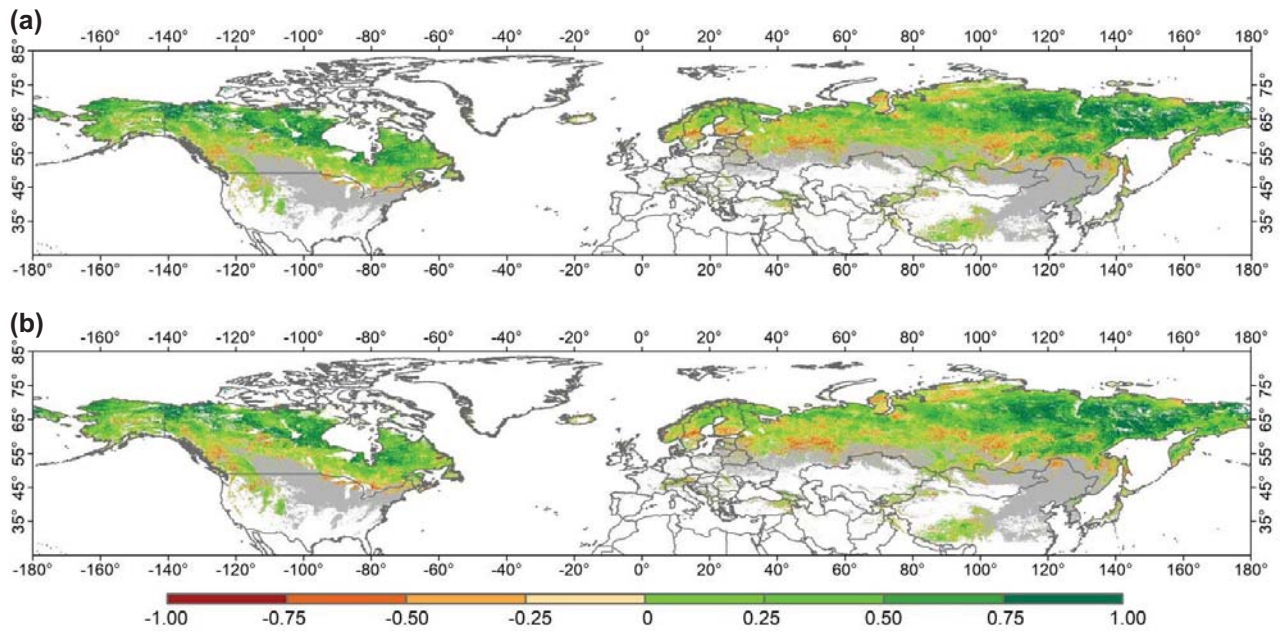
402 **Figure 5.** (a) Partial interannual correlation coefficient between end of the growing season (EOS) and number of chilling days (NCD), while
 403 setting start of the growing season (SOS) as a control variable. (b) Partial interannual correlation coefficient between NCD and growing degree
 404 days, while setting precipitation and solar radiation during dormant period as control variables.

405

406 The physiological processes for spring bud and leaf development require
407 carbohydrates and nutrients stored in reserve organs (Bazot et al., 2016; Cooke and Weih,
408 2005; El Zein et al., 2011; Han and Kabeya, 2017; Millard and Grelet, 2010). Those
409 carbohydrate and nutrient contents were associated with by the advance or delay in leaf
410 senescence in the previous autumn, since carbon assimilation, metabolism, and reallocation
411 and nutrient resorption and reallocation vary with the progression of leaf senescence (Aerts,
412 1996; Charrier and Améglio, 2011; Estiarte and Penuelas, 2015; Fu et al., 2014b; Lawrence
413 and Melgar, 2018; Shi et al., 2015). This implies that the timing of leaf senescence could
414 impact the SOS by changing the carbohydrate and nutrient contents. Delayed leaf senescence
415 associated with autumn warming could result in more efficient nutrient resorption and higher
416 contents of nitrogen or other nutrients in reserve organs (Estiarte and Penuelas, 2015;
417 Lawrence and Melgar, 2018). Leaf senescence affects nutrient resorption and nutrient content
418 in reserve organs that can be used for budburst and new leaf growth in the next spring. Indeed,
419 there are evidences, although few, that high (low) nutrient level advances (delays) leaf
420 flushing or budburst (Andresen et al., 2018; Falk et al., 2020; Huang and Li, 2015; Jochner et
421 al., 2013). Therefore, we speculate that a delay in leaf senescence may have affected budburst
422 and leaf unfolding in the following spring through nutrient economics, although little direct
423 evidence is available at either the species or community-ecosystem level. This speculation
424 may help explain the negative partial correlation between SOS and previous year's EOS in
425 the temperate region, where EOS was delayed and SOS advanced. In addition to nutrient
426 economics, higher content of sugar and starch are related with earlier leaf flushing and
427 budburst (Fu et al., 2014b; Perez-de-Lis et al., 2016). Changes in sugar and starch content and
428 metabolism also could have played a role in the relationship between SOS and previous
429 year's EOS, although the exact role of nonstructural carbohydrates in leaf spring phenology
430 and the impact of leaf senescence on carbohydrates reserve are poorly understood (Fu et al.,
431 2014b; Perez-de-Lis et al., 2016). Of course, these explanations are not mutually exclusive.
432 The timing and amount of chilling accumulation and carbon and nutrient economics may all

433 have contributed to the EOS–SOS relationship, although their exact contributions are difficult
434 to clarify, particularly in empirical analysis at such a large scale based on remote sensing
435 retrieval of phenology.

436 In addition to the above mentioned environmental factors that may influence SOS, it
437 was suggested that variations in SOS may be associated with snow cover (Chen et al., 2015).
438 We thus examined whether the inter-annual partial correlation between EOS and SOS of the
439 following year was caused by the co-founding effect of snow cover. To do this, we added the
440 snow cover fraction temporally closest to the SOS as an extra controlling variable when
441 calculating the partial correlation coefficient between EOS and SOS of the following year.
442 The snow cover fraction was derived from MODIS/Terra snow cover products (MOD10C2
443 Collection 6, available at <https://nsidc.org/data/MOD10C2>, accessed on 20 February, 2020),
444 which provides the maximum percentage of snow-covered land during an eight-day period at
445 a spatial resolution of $0.05^\circ \times 0.05^\circ$. The data were resampled to $1/12^\circ \times 1/12^\circ$ by a
446 nearest-neighbor method to match the SOS data. To determine snow cover fraction closest to
447 SOS, we need the observation day for each eight-day composite period, which, however, is
448 not provided in MOD10C2. Therefore, the observation day of each period was assigned as
449 the mean of the middle two days of the eight-day period. The result shows that, the partial
450 correlation coefficient between EOS and SOS of the following year with snow cover fraction
451 as an extra controlling variable (Fig 6a) exhibits a very similar pattern to that without snow
452 cover fraction (Fig. 6b). This similarity suggests that the correlation between EOS and SOS
453 of the following year was not caused by the snow cover.



454

455 Figure 6. Partial inter-annual correlation coefficient between end of the growing season (EOS) of 1999-2014 and start of the growing season
 456 (SOS) of 2000–2015. In (a), the snow cover fraction temporally closest to the SOS, number of chilling days (NCD), and preseason temperature,
 457 precipitation, and solar radiation were set as control variables. In (b), NCD and preseason temperature, precipitation, and solar radiation were set
 458 as control variables. Gray pixels indicate that snow cover fraction closest to the SOS was zero for more half of the years.

459

460 **4.2 Caveats and limitation of the study**

461 In this study, SOS and EOS were retrieved from the NDVI data calculated from observations
462 by the Advanced Very High Resolution Radiometer (AVHRR), which is the longest NDVI
463 time series available. The data quality issue in the previous generation of AVHRR GIMMS
464 NDVI data is serious in some regions (Zhang et al., 2013). The third generation of AVHRR
465 GIMMS NDVI was improved by the GIMMS group (Pinzon and Tucker, 2014). In more
466 recent studies (Piao et al., 2015; Xu et al., 2019), the relationships between climatic factors
467 and phenological metrics determined from the third generation of AVHRR GIMMS NDVI
468 appeared to be similar to those for MODIS NDVI during the overlapping period. Although
469 considerable efforts have been made to improve data quality of the GIMMS NDVI time
470 series from AVHRR, residual noise and uncertainties remain. Such noise and uncertainties
471 may have prevented us from accurately retrieving SOS, even at the pixel scale. In addition,
472 NDVI is calculated from reflectance at the red band, an indicator of chlorophyll absorption of
473 radiation, and from reflectance at the near infrared band, an indicator of mesophyll scattering
474 of radiation, which is an indirect measure of canopy greenness. Therefore, the noise and
475 uncertainties and indirectness of the satellite retrieval of SOS and EOS may explain the low
476 correlation between climatic factors and SOS and between EOS and SOS. On the other hand,
477 uncertainty of meteorological data and the scale mismatch between different data used in the
478 analyses may also have contributed to the low correlation.

479 Many previous studies analyzed the relationship between satellite retrieval or ground
480 observation of vegetation/plant phenology or greenness and climatic factors by using
481 empirical approaches (Badeck et al., 2004; Fu et al., 2014a; Menzel et al., 2006; Park et al.,
482 2018; Shen et al., 2015b; Vitasse et al., 2017). Similar to those studies, in our study the SOS
483 and EOS were mostly retrieved from NDVI measured by a satellite-onboard sensor, and the
484 relationship between EOS and SOS was analyzed by using partial correlation analysis,
485 although the leaf unfolding and coloring dates were included in the CCM analysis. In most
486 cases, satellite-derived data of vegetation phenology cannot be directly compared to field

487 phenology observations due to differences in spatial coverage and definitions of phenology
488 events, except when there are few species exhibiting synchronous phenology in a pixel (e.g.,
489 cropland). For a pixel that covers dozens of kilometers and includes multiple species
490 exhibiting various phenological stages driven by various environmental factors, it is difficult
491 to directly and comprehensively explain the empirical results based on satellite retrieval of
492 vegetation phenology by up-scaling the findings for a single species and to realistically
493 simulate phenology at the pixel level by using a model developed for a single species (Tang
494 et al., 2016). The coexistence of multiple species even prevented us from identifying the
495 temperature metric that is fully representative of the forcing that the plants are actually
496 sensitive to (e.g., time window, base temperature) at the pixel scale. Therefore, in most of the
497 studies based on satellite-derived data of vegetation phenology, the ecological processes
498 could only be discussed based on the physiological and ecological mechanisms at the species
499 level (or the community-ecosystem level in a few cases) and could not be elucidated as in
500 studies based on manipulative experiments with clear physiological and ecological
501 mechanisms.

502 **4.3 Implications**

503 Full attribution of the temporal phenological change and accurate quantification of the impact
504 of climate change (particularly climate warming) on vegetation spring phenology is essential
505 for the assessment and prediction of ecosystem responses and feedback to climate change
506 (Penuelas et al., 2009; Richardson et al., 2013; Tang et al., 2016). However, interannual
507 changes in pre-season meteorological conditions could not fully explain the temporal trends in
508 SOS during the past few decades (Cook et al., 2012; Fu et al., 2015b; Shen et al., 2015a;
509 Wolkovich et al., 2012). Our results imply that the advance in SOS in the northern
510 hemisphere may have been partly driven by changes in previous year's EOS. In boreal
511 ecosystems, the positive partial regression coefficient between EOS and SOS suggests that
512 the advance in SOS might have been partly caused by the advancing trend in EOS of previous
513 years. In temperate ecosystems, the advance in SOS could be partly associated with the
514 delaying of EOS, as indicated by the negative partial regression between SOS and EOS.

515 Moreover, previous studies reported that sensitivity of vegetation SOS to pre-season
516 temperature was lower in boreal ecosystems than in temperate ones (Shen et al., 2015a; Wang
517 et al., 2015a). The contribution of EOS to the advance in SOS and stronger impact of EOS on
518 SOS in boreal ecosystems indicate that the difference in temperature sensitivity of SOS
519 between boreal and temperate ecosystems could be larger than previously reported. Although
520 similar temporal trends in SOS and EOS over a period (1982–2012) similar to our study was
521 reported previously (Garonna et al., 2016), the impact of EOS on the following SOS has not
522 been revealed before. Our study provided a new potential explanation for vegetation spring
523 phenological changes in about 36.7% of the pixels of the northern hemisphere.

524 Recent studies have revealed a nonlinear response of plant leafing phenology in
525 spring to pre-season temperature (Fu et al., 2015b; Güsewell et al., 2017; Jochner et al., 2016;
526 Rutishauser et al., 2008), which predicts a decline in temperature sensitivity of leafing
527 phenology if temperature continuously increases over the long term. For example, Fu et al.
528 (2015b) found that temperature sensitivity of the spring leaf unfolding date of several
529 temperate trees declined with continuous warming over the past few decades. The
530 contribution of delayed EOS to the advance in SOS presented in our study suggests that the
531 decline in temperature sensitivity of spring leaf phenology could be underestimated if the
532 impact of EOS on SOS was not excluded. Moreover, Fu et al. (2015b) also found that current
533 phenology theory could not fully explain such a decline, with the modeled decline being less
534 than the observed one. This should perhaps be expected, because our current phenology
535 model could not effectively capture interannual variation in spring phenology (Chuine and
536 Régnière, 2017; Tang et al., 2016). Our findings suggest that current phenology models could
537 be improved by including the impact of leaf senescence in the previous autumn on spring
538 leafing phenology, such that the decline of temperature sensitivity could be better simulated.

539 **5 Conclusion**

540 This study provides an exploratory assessment of how the end of the vegetation growing
541 season in autumn affects the start of the growing season in the following year for the middle
542 and high latitudes in the northern hemisphere. The significant interannual partial correlation

543 between SOS and previous year's EOS in 36.7% of the pixels indicates an impact of
544 vegetation autumn phenology on the spring phenology of the subsequent year in those areas,
545 particularly in boreal ecosystems. The statistical results based on satellite-derived data
546 suggest that the advance in SOS over 1983–2015 was associated with changes in EOS of the
547 previous year in those areas. The relationships between EOS and SOS may be associated with
548 the mutually non-exclusive mechanisms, carbohydrate and nutrient economy and winter
549 chilling. Advanced EOS may result in earlier entrance into endodormancy period, providing
550 condition for earlier fulfillment of the chilling requirement and earlier entrance into
551 ecodormancy period and SOS, which helps explain the EOS-SOS relationship in boreal
552 ecosystems. Delayed EOS may increase the carbohydrate contents and nutrition in reserve
553 organs that could be used for budburst and leaf growth in the following spring; this helps
554 explain the EOS-SOS relationship in temperate region. These speculative explanations,
555 however, need further evidence from experiment based studies.

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563 **Data Accessibility Statement**

564 All the data used in this research are publicly available through internet.

565

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